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Penile Morphology in Six Populations of *Branchipus schaefferi* Fischer, 1834 (Crustacea: Branchiopoda) from Serbia

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Abstract: Male genital morphology of six populations of *Branchipus schaefferi* from different locations in Serbia is described. Both qualitative and quantitative morphological traits were taken into consideration. The majority of males from lowland parts of the country (Pannonian Plane) had a long sickle-curved or arched spine situated on the basal part of the penis. Males sampled in the south-eastern part of the country (the region of Stara Planina Mountains) possessed short, straight or slightly bowed basal spine. A distal penile part appeared as a more stable character than the proximal one. Males from one of the examined populations possessed roundish and spineless penile tip, a feature heretofore not described in *B. schaefferi*.

Key words: penis; morphology; variability; *Branchipus schaefferi*

Introduction

The first information about male genitalia in large branchiopods (Branchiopoda) appeared in 18th century, in the description of "*Apus pisciformis*" by Schaeffer (1752), a species described later as *Branchipus schaefferi* Fischer, 1834. Schaeffer (1752) was the first to found paired and partially retractile genital organs in male specimens. Later, Thompson (1834) published drawings of penile organs in the genus *Branchipus* Schaffer, 1766 that were very similar to those published by Schaeffer (1752, 1754). It is interesting that those quite correct morphological descriptions made more than 200 years ago and still are used. Despite the extensive development of microscopic techniques, several of the early published illustrations can be compared even with some of the 20th century descriptions (see Fryer 2008).

A two-part penile morphology in members of the family Branchipodidae has been an integral component of descriptions in several taxonomic studies (Daday 1910, 1913; Linder 1941; Flössner 1972). Authors mainly discussed taxonomical importance of the male genital structures and antennal appendages in Branchipodidae (Brendonck 1995; Brendonck & Belk 1997; Gandolfi *et al*. 2015), or proposed using a multidisciplinary approach (Mura *et al*. 2005; Scalone & Rabet 2013). However, penile morphology is still insufficiently described, mainly due to the limited accessibility of the distal part (when not projected, its distal part lies retracted within the abdominal cavity). Cottarreli & Mura (1983) emphasised the importance of the distal retractile part, especially the shape and appearance of the penile tip. Belk (1991) also emphasised the morphology of retractile part and suggested its use as a valuable character in defining different genera. On the other hand, Brendonck (1995) stressed that the morphology of the basal part was more conservative (at least among members of the family Branchipodidae), and suggested this character to be adopted as a criterion for distinguishing of certain genera. Later, the use of both basal and distal penile morphology was recommended by both authors (Brendonck & Belk 1997).

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Many authors considered the male copulatory structures as a rather conservative character and discussed them in the light of their role in recognising individuals of the same species during mating (Paterson 1985; Brendonck & Belk, 1997; Rogers 2002). However, literature data on penile morphology of the genus *Branchipus* have so far been scarce and not substantiated with new data. In order to update the information about morphology of the male copulatory apparatus, we aimed to screen whether the variation in male copulatory structures is driven by geographical and local environmental factors. With this goal, we studied the patterns of variation in the penile morphology of *B. schaefferi* originating from six localities in Serbia.

Materials and Methods

Site descriptions

We analysed the penile morphology of specimens from six populations of *Branchipus schaefferi* in Serbia. The majority of the analysed localities belong to the northern, lowland parts of Serbia (the area of Pannonian Plain). Brtek & Thiéry (1995) marked this region as a distinct area of endemism in Central Europe, and as an important zone where some large branchiopods originated, such as *B. schaefferi*. On the other hand, the mountainous area of the Balkans was also pointed as a potential centre of diversification of some branchiopod families (Branchipodidae, Chirocephalidae, Limnadiidae) in Europe (Brtek & Thiéry 1995). The only known locality of *B. schaefferi*, situated in the hilly area in Serbia, lies in the south-eastern part of the country, in the foothills of Stara Planina Mountains (Cvetković-Miličić *et al*. 2005).

Morphological analysis of male copulatory organs included the samples from six localities presented in Fig. 1. Populations 1-5 occurred in ponds situated in the northern parts of the Republic of Serbia (Pannonian Plain), while population 6 was found in the south-eastern part of the country, near the Serbian-Bulgarian border (Table 1). All populations

Fig. 1. Graphical presentation of the six localities in Serbia

Table 1. Data on the studied localities of *Branchipus schaefferi* in Serbia

	Locality name	Region	Coordinates	Altitude (m a.s.l.)	Site description
	B. Arandjelovo	Northern Serbia (Banat Province)	46°04’00” 20°15’00”	83 m	Rain puddles to the side of a local village road, with scarce vegetation
2.	**Sutjeska**	Northern Serbia (Banat Province)	45°23’00” 20°22’54”	56 m	Small shallow puddles with turbid water
3.	**Titel**	Northern Serbia (Bačka Province)	45°12’21” 20°17’39”	111 m	Small ponds with turbid water
4.	**Progar**	Northern Serbia (Srem Province)	44°71’00” 20°16’00”	60 m	Turbid ponds in the crops fields (without vegetation) in the shallow tracks made by agricultural machinery
5.	**Ogar**	Northern Serbia (Srem Province)	44°39’14” 20°12’00”	76 m	Turbid water surfaces on the left bank of the Sava River, with a scarce grassy bottom
6.	**Trnjana**	Eastern Serbia	43°09’11” 22°35’09”	387 m	Small, turbid ponds several centimetres in depth, with a muddy bottom, along the left bank of the Nišava River

were found in small shallow temporary puddles, and were fixed immediately in the field in 70% alcohol. The material is deposited in the Institute of Zoology, Faculty of Biology, University of Belgrade.

The body measures (mean, min. and max. lengths) in males from different localities were as follows: Banatsko Arandjelovo (B. Arandjelovo) - collection group number BA04/07/95, mean 11.5 mm (min 10 mm, max 14 mm); Sutjeska - collection group number ST19/08/97 mean 13 mm (min 9.1 mm, max 15.8 mm); Titel - collection group number TM08/05/88 mean 11.7 mm (min 8.1 mm, max 17.4 mm); Progar - collection group number PR31/05/84 mean 13.1 mm (min 9.3 mm, max 15.8 mm); Ogar - collection group number OG10/05/97 mean 10.7 mm (min 9.8 mm, max 11.4 mm) and Trnjana - collection group number TR30/04/00 mean 11.9 mm (min 9.3 mm, max 13.4 mm).

Morphological analysis

Ten adults per each locality were used. We analysed both qualitative and quantitative traits of basal and distal parts of the penis. The basal parts are non-eversible and bear one chitinised sickle-like spine. In the qualitative analysis, we considered the position of the spine along the basal part, and the shape of this spine (Fig. 2). With respect to the position of the spine (PS), three variations could be distinguished. As spine appearance (AS), we described the growth and shape of the spine in the basal part of the penis. It was possible to clearly distinguish four types of AS.

The distal eversible part possesses one long lateral row of flat spines and a shorter dorso-medial row of irregularly positioned conical spines. The lateral row is composed of relatively blunt spines with a broad base. They are more or less evenly spaced and arranged in longitudinal series. Spines in the medial row are unevenly distributed over the distal penile surface. They are conical and somewhat rounded in the base.

Observations of the proximal parts were carried out on the right penis of each examined specimen. Drawings were made with a Carl Zeiss binocular microscope equipped with a camera lucida. To study retractile penile morphology, animals were dissected under a ZEISS Discovery V8 stereomicroscope. The permanent mounts of dissected retractile parts were made by immersing in pure liquid glycerol. The sides of the cover slip were sealed with nail polish to prevent evaporation and leakage of the fixative medium. Photos of the microscope slides were taken with a Moticam 2000 Camera connected to a Nikon SMZ800 Stereozoom microscope (magnification ×11.25) and were further processed using Adobe Photoshop 7.0 software.

Statistical analysis

Statistical analyses were performed for two types of data: qualitative analysis for the features of the basal part of penis and quantitative analysis on the number of medial and lateral spines on the retractile part of penis. The locality Titel was omitted from the quantitative analysis because the sample size was too small due to limited accessibility of the erectile part of penis in this population.

Correspondence analysis (CA) was performed to detect similarities or differences between populations in the number of males with a particular position and appearance of the spine on the proximal part of the penis. The normal distribution of data

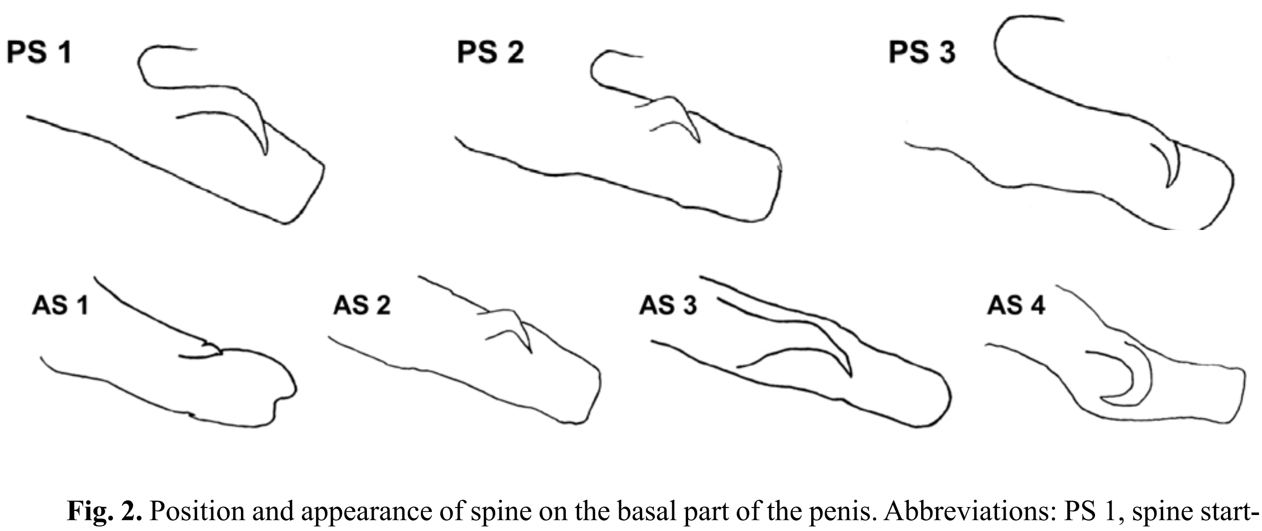

Fig. 2. Position and appearance of spine on the basal part of the penis. Abbreviations: PS 1, spine starting from the first third; PS 2, spine starting from the middle part; PS 3, spine starting from the last third of the penis; AS 1, short, straight spine; AS 2, short, bowed spine; AS 3, long, arched spine; AS 4, long, sickle-curved spine

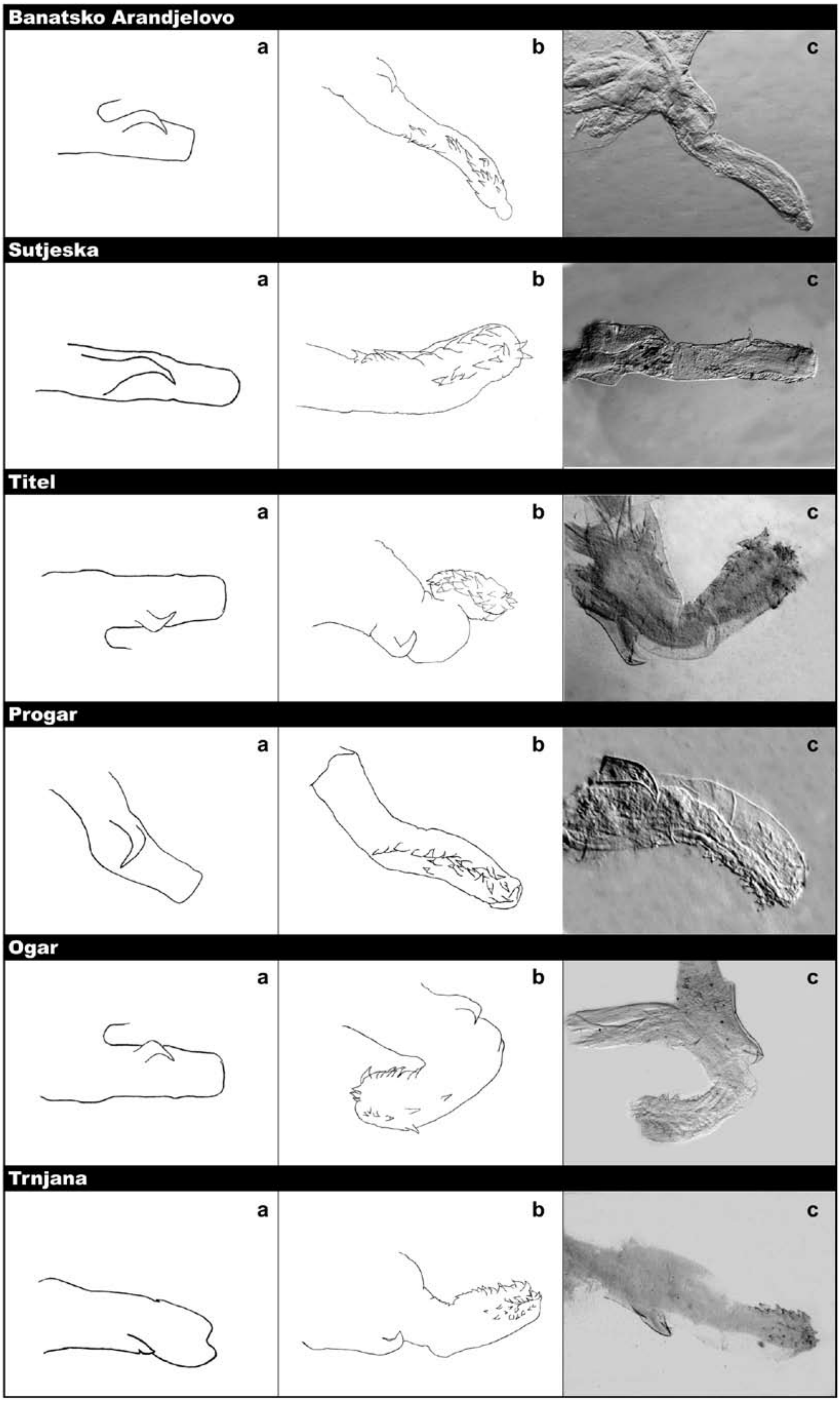

Fig. 3. Representative pictures of penile morphology in males of each examined population: a) basal parts; b), distal parts; c) original photos of penises. Magnification ×11.25, orig

was assessed using the Kolmogorov-Smirnov test. The observed values were normally distributed and homogeneity of variances was confirmed by Leven's tests. One-way ANOVA was used in order to test if the mean number of medial and lateral spines was the same at each location. Spearman's rank correlation coefficient was used to test the association between medial and lateral spines. All statistical analyses were performed using Statistica 5.0 software (Copyright StatSoft, Inc., 1995).

Results

Representative pictures of all the morphological variants for each locality are presented in Fig. 3.

Basal part of the penis

Based on the pooled data from all populations, the most common position of the spine was on the first third of the penis (PS 1). This position was recorded in 46% of the individuals. A spine in the middle position (PS 2) was observed in 38%, while spine on the last third part (PS 3) was found in 16% of the individuals.

A spine starting from the first third of the penis was found in 80% (B. Arandjelovo) and 60% (Titel) of the individuals. In other individuals, the spine started from the middle part of the penis. Males from Ogar, Sutjeska, Progar and Trnjana populations had all three possible spine positions (Fig. 4). Correspondence analysis showed that males only from the northern populations (B. Arandjelovo and Titel) could be clearly separated on the basis of spine position (Fig. 5). The first dimension extracts 41.77% of total inertia, while the second dimension extracts 27.82% of total inertia, representing together 69.59% of total inertia.

A long and sickle-curved spine (AS 4) was observed in 38% of all examined males. A short and bowed spine (AS 2) was found in 30% of individuals. Short and straight (AS 1) spines and long and arched ones (AS 3) were recorded in about 16% of individuals each.

A short and straight spine (AS 1) was the predominant morphological variant found in the population from Trnjana (55.56% of individuals). Males from Ogar and Titel predominantly showed a short and bowed spine appearance (AS 2 comprising 62.5% and 60%, respectively). All males from B. Arandjelovo and the majority of males from Progar (75%) had long and sickle-curved spine (AS 4), whereas the majority of males from Sutjeska (70%) had long and arched spines (AS 3; Fig. 6).

According to CA, males from B. Arandjelovo and Sutjeska were clearly separated with respect to spine appearance, followed by males from Progar and Trnjana (Fig. 7). The first dimension extracts 41.77% of total inertia, and the second dimension extracts 27.82% of total inertia, representing together 69.59% of total inertia.

Distal part of the penis

There were 10-20 spines in each row (marginal and lateral), with the exception of some individuals from the Trnjana population whose retractile part possessed a somewhat larger number of spines (up to 30) in each row, and individuals from the Progar population with more than 30 spines in the medial row.

Average values for medial and lateral spines on the eversible part of the penis are presented in Fig. 8. One-way ANOVA did not indicate significant differences in the average number of either medial ($F = 1.91$, $p > 0.05$) or lateral ($F = 2.60$, $p > 0.05$) spines between the analysed populations. A signifi-

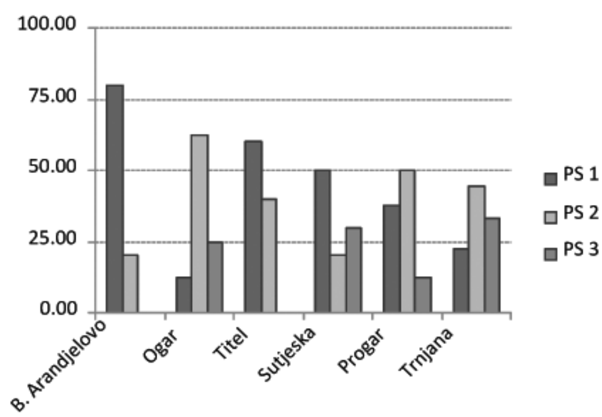

Fig. 4. Number of males (%) from the six populations with different spine positions on the basal part of the penis. Abbreviations as given in Fig. 2

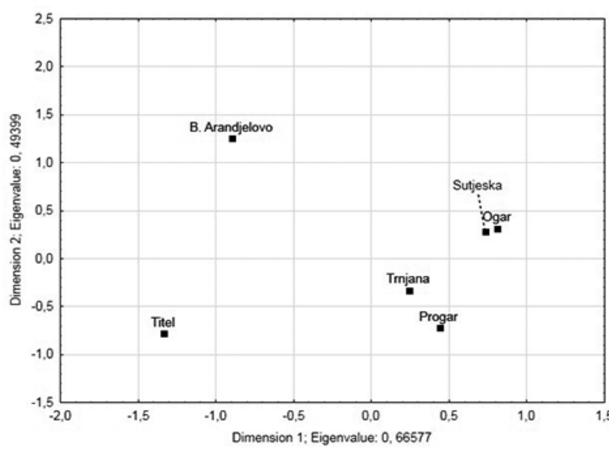

Fig. 5. Correspondence analysis of spine position on the basal part of the penis in males from the six populations

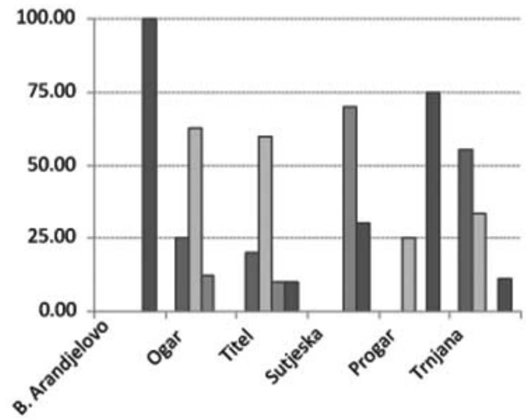

Fig. 6. Number of males (%) from the six populations with different spine appearances. Abbreviations as given in Fig. 2

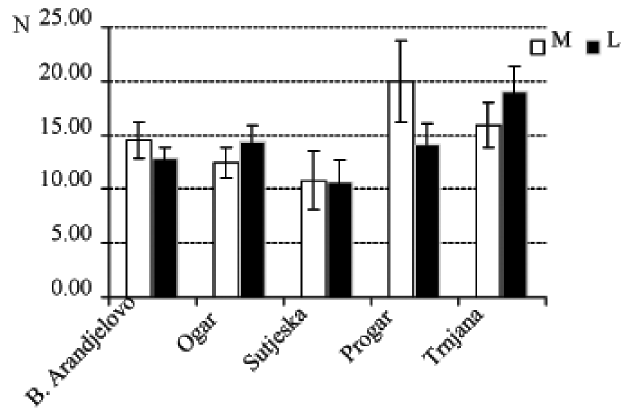

Fig. 8. Average numbers of medial and lateral spines on the eversible part of the penis, presented as mean ± S.E. Abbreviations: M - medial spines; L - lateral spines

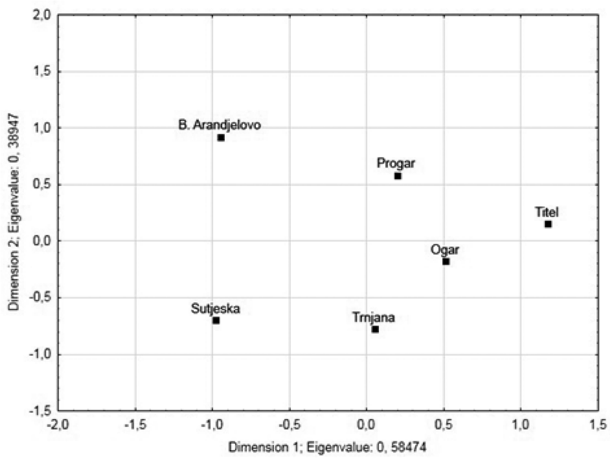

Fig. 7. Correspondence analysis of spine appearance on the basal part of the penis in males from six populations

cant positive coefficient of correlation ($r = 0.764$; $p < 0.05$) was recorded only for the number of medial and lateral spines in males from the Progar population. Although the spines usually extended over the entire length of the eversible part, in males from B. Arandjelovo and Progar they have never reached the tip (apical part) of the penis. In addition, males from B. Arandjelovo had a thin and elongated distal part with a rounded apex lacking spines. In other populations, spines covered the tip of the penis.

Discussion

Description of genital organs has been an integral part of many taxonomic studies on the genus *Branchipus*, as is discussed hereinafter. The basal outgrowth (spine) on the proximal part of the penis is usually shortly described as a "curved spine-like", i.e. in *B. blanchardi* Daday, 1908 and *B. cortesi* Alonso & Jaume, 1991 (as described by Alonso 1989 and Alonso & Jaume 1991, respectively); or as an "outwardly curved chitinised spur present on its median border", which is characteristic for *B. intermedius* Orghidan, 1947 (see Petkovski 1997). The basal part has also been described as "robusted and curved" in *B. pasai* Cottarelli, 1969 (see Cottareli & Mura 1983), or "hooked, situated on the inner distal corner" in *B. schaefferi* as described by Cottareli & Mura (1983). For some species, information is available only from illustrations, as is the case of the *B. laevicornis* Daday, 1912 (see Cottarelli & Mura 1974).

In this study we aimed to describe in more detail the morphology and variability of the external male genitalia in *B. schaefferi* in Serbian populations of different geographical origin. Despite still having some obstacles in interpreting and quantifying differences in penile morphology, we found that the variability of proximal part accounts for most of the differences between different populations. Males from B. Arandjelovo and Titel populations could be clearly separated with respect to the position of the spine on the proximal part of the penis (with a spine starting mostly from the first third). However, according to the spine appearance, males from B. Arandjelovo, Progar and Sutjeska populations were clearly separated, having a long sickle-curved or arched spine. Males from the south-eastern population Trnjana exhibit somewhat unusual spine morphology (short and straight). Also, two northern populations (Ogar and Titel) had a short, but slightly-bowed basal spine.

In the majority of the samples the ornamentation of the distal part was characterised by rows of spines placed over its surface and by a field of spines covering the tip of the penis, which is typical for *B. schaefferi* (see Cottarreli & Mura 1983). However, we found that spines did not reach the tip of the penis in some populations. This observation may indicate that the naked tip of the penis without spines is also typical for *B. schaefferi*. We could then speculate that the apical spines observed in several of our samples or being described for *B. schaefferi* in the literature, could represent an artefact due to incomplete evagination of the hardly accessible retractile part. However, markedly rounded, spineless penile tip in males from the far north population of B. Arandjelovo is still interesting, since a similar shape of the apical part of penis has not been described neither in other samples from Serbia, nor for the genus *Branchipus*.

The variability in penile structures observed in our study could be owing to inter-population hybridisation due to the occurrence of a largely overlapping "mate recognition system", which is common for large branchiopods (Wiman 1979a,b; Paterson 1985; Dubois 1988; Fugate 1992; Maeda-Martinez *et al*. 1992; Brendonck & Belk 1997).

Moreover, it is worth noting that the penile structures (at least their proximal, always visible spine-bearing part) could represent a visual signal that influences the female choice prior and during the courtship. Differences in spine shape, or their position, could cause males to vary in their attractiveness to females, thus representing traits under pre-copulatory sexual selection. This intra-specific variation in male genital morphology may further influence fertilisation success and affects the post-copulatory sexual selection. A distal, retractile part appears as a more conservative than the proximal one, probably due to its essential role in attaching individuals during mating (Belk 1991). It is also acting as a behavioural stimulus, since its physical pressure induces movements of mature oocytes from the ovary into the female egg pouch during copulation (Brendonck 1995). A relative uniformity of retractile part can also be considered as a direct or indirect consequence of uniformity of the female reproductive organs (Wiman 1981; Rogers 2002).

McLain (1993) indicated that if the balance between natural and sexual selection is caused by environmental factors, then they may trigger some differences in the structure of reproductive organs. The phenotypic plasticity of *B. schaefferi* (reflected in the great intra- and inter-population diversity) could appear as a response to the highly variable and unpredictable environments, typical for large branchiopods (Cohen 2012). Recent studies on *B. schaefferi* revealed variability in the degree of sexual dimorphism among populations of different geographical origin in Serbia (Miličić *et al*., 2013). The present work demonstrates that *B. schaefferi* can be considered a species with remarkable intraspecific diversity, and indicates that environmental factors (or geographical origin) may affect variability of different body traits, including the morphology of male genital organs.

Combining traditional taxonomy with molecular phylogeny is an approach that is increasingly used for understanding the causes of evolutionary processes in anostracans (Zofkova & Timms 2009; Naceur *et al*. 2011; Gandolfi *et al*. 2015; Atashbar *et al*. 2016). In further studies, it would be interesting to combine morphological analysis with molecular genetic approach in order to identify variability between geographically isolated populations of *B. schaefferi*.

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