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Sexual dimorphism and left-right asymmetry of carapace ornamentation in *Hemicytheria setosa* RUNDIĆ, 2002

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Abstract

In biostratigraphic research of the Upper Miocene of the Pannonian Basin System, one of the frequently detected and important ostracod genera is *Hemicytheria*. Among more than 20 species of this genus, *Hemicytheria setosa* is present in sandy facies of the Lake Pannon sediments in Serbia and Bosnia and Herzegovina. The aims of this study were to describe sexual dimorphism and differences between left and right valve morphology in *Hemicytheria setosa*. Landmark based geometric morphometrics is applied on the grounds of existence of the homologue pattern of the fossae and pore conuli on the valve surface of this group of ostracods. Significant differences between the sexes and between the left and right valves are detected in the present study. The obtained results indicate that applied methods and chosen landmarks could be useful in the studies of valve ornamentation-variation in fossil and recent Ostracoda.

1. INTRODUCTION

The genus *Hemicytheria* POKORNÝ (1955) is one of the very abundant ostracod genera, important for the biostratigraphy of the Late Miocene of Serbia and the Pannonian Basin System (SOKAČ, 1963; SOKAČ, 1972; KRSTIĆ, 1973, 1985; RUNDIĆ, 1997, 2006). For this reason, RUNDIĆ (1991, 1997) gave more attention to the genus *Hemicytheria* from the Late Miocene of Lake Pannon sediments of the Belgrade vicinity and Kolubara coal basin (50 km SW of Belgrade). Based on the distribution of this genus, a few ostracod biozones were established within the Late Miocene Lake Pannon (KRSTIĆ, 1985; RUNDIĆ, 1997; RUNDIĆ et al., 2011). This exclusively fossil ostracod tolerated a salinity range between 3-18‰ (PIPÍK, 2007). Herein, we present one of the species of *Hemicytheria* which has an interesting carapace pattern and has been the subject of a geometric morphometric study.

Morphological differences between the genera *Hemicytheria* (POKORNÝ, 1955) and *Tyrrhenocythere* (RUGGIERI, 1955) were the focus of some studies. A few authors state that the genus *Tyrrhenocythere* represents a descendant form and it occurs in the stratigraphic record after *Hemicytheria* disappeared (OLTEANU & VEKUA, 1989; RUNDIĆ, 2006; PIPÍK, 2007). In fact, according to OLTEANU & VEKUA (1989), *Tyrrhenocythere* is a "*Hemicytheria* with radial pore canals concentrated in fascicles". The authors considered the arrangement of the radial canals as a qualitative leap, a specific adaptation, necessary in a particular ecological context.

The studied species, *Hemicytheria setosa* was first discovered more than 30 years ago. The first determination concerning this species, mentioned as *Aurila* (*Hemicytheria*) sp. (*setosa*) (KRSTIĆ, 1985) contained the first photo but without a description. Later, Rundić (2002) highlighted some important features of some new *Hemicytheria* species from the Late Miocene of Serbia from the area of Mali Požarevac, including a full description of this species as a new one. This species was discovered together with other "caspibrackish" Upper Pannonian (Late Miocene) ostracods and Rundić (2002) also mentioned that it has a relatively small and thick-shelled carapace. However, in *H. setosa* the size and shape of the reticula is different, sometimes with poorly developed second-order reticulation. This feature is not common for the genus *Hemicytheria* that comprises more than 20 species from the Middle – Late Miocene (SOKAČ, 1972; JIŘÍČEK, 1985; OLTEANU & VEKUA, 1989; OLTEANU, 2011). This form represents a very abundant ostracod species within the sandy facies of the long-lived Lake Pannon (Late Miocene) (RUNDIĆ, 2006; KOVÁCS et al., 2016). Additionally, some other ostracodologists from the area of the Pannonian (POKORNÝ, 1952, 1955; SOKAČ, 1972; JIŘÍČEK, 1985; PIPÍK, 2007), and Transylvanian and Dacian basins (OLTEANU & VEKUA, 1989; OLTEANU & JIPA, 2006; OLTEANU, 2011; KOVÁCS et al., 2016) discovered large differences in the sculpture of the carapace between the *Hemicytheria* species during the period from the Middle Miocene (Sarmatian) to the end of the Late Miocene (Pannonian s. lato).

Most studies come from the sediments of the ancient Lake Pannon which was a remnant of the Central Paratethyan Sea and existed during the Late Miocene (ca. 11.6 – 5.3 Ma). Apart from the studies of SOKAČ (1972), RUNDIĆ (1997, 2002), PIPÍK (2007) and OLTEANU (2011), there are no publications that have focused on the genus *Hemicytheria*. Also, to our best knowledge there is no geometric morphometric study applied to this genus, although geometric morphometrics is used in study of the Ostracoda (ABE et al., 1988; BALTANÁS & GEIGER, 1998; BALTANÁS & DANIELOPOL, 2011; MAZZINI et al., 2014; AIELLO et al., 2016; KARANOVIC et al., 2017).

The aims of this research were to describe sexual dimorphism and differences between left and right valves in carapace ornamentation of *Hemicytheria setosa*, using the landmark based geometric morphometrics.

2. GEOLOGICAL BACKGROUND

Belgrade city area and its surroundings belongs to the southern part of the Pannonian basin (PB) that has a dynamic geological evolution through the Neogene (HARZHAUSER & PILLER, 2007; MAROVIĆ et al., 2007). Miocene sediments were deposited discordantly over Mesozoic rocks and represent the infill of the Paratethys Sea or its successor – Lake Pannon (HARZHAUSER & PILLER, 2007; HARZHAUSER & MANDIC, 2008; RUNDIĆ et al., 2011).

Early to Middle Miocene sediments of the PB and its southern part (e.g. Serbia) show a transition from continental alluvial-lacustrine to fully marine environments (MAROVIĆ et al., 2007; PAVELIĆ & KOVAČIĆ, 2018). Extensional tectonics reached their maximum during the Middle Miocene rifting phase (ca. 16–11.6 Ma) when marine water flooded the whole region (e.g. MATENCO & RADIVOJEVIĆ, 2012; RADIVOJEVIĆ & RUNDIĆ, 2016). At the Middle/Late Miocene boundary (11.6 Ma) as a result of the tectonic uplift of the Carpathians, the PB was isolated from marine influences and the long-lived Lake Pannon formed (MAGYAR et al., 1999; TER BORGH et al., 2013; SZTANÓ et al., 2015). Seven million years later, Lake Pannon was infilled by lacustrine and fluvial-deltaic sediments derived from the surrounding orogenic belts (MAGYAR et al., 2013; RADIVOJEVIĆ & RUNDIĆ, 2016) (Fig. 1).

The Late Miocene sediments contain numerous fossils (molluscs, ostracods, etc.) widely distributed in the Belgrade city area and its vicinity (RUNDIĆ, 1993; RUNDIĆ et al., 2011). Most of them have an endemic character and settled the littoral and sublittoral environs of the ancient Lake Pannon (MAGYAR et al., 1999; RUNDIĆ et al., 2011). Among the ostracods, large numbers of originally freshwater taxa were recognized, candonids predominantly (KRSTIĆ, 1973; RUNDIĆ, 2006). However a lot of genera show brackish and so-called the "caspibrackish" character (similar to the modern Caspian Sea). Among them, the genus *Hemicytheria* and its species is very important for biostratigraphic zonation of the Pannonian Stage (KRSTIĆ, 1973, 1985; RUNDIĆ, 2006; KOVÁCS et al., 2016). Generally, older low diversity ostracods from the early Pannonian expanded to the abundant taxa during the late Pannonian age. This interval is designated as the "bloom time" for many ostracods, both qualitatively and quantitatively (RUNDIĆ, 2006).

Based on the stratigraphic division of the Late Miocene Lake Pannon province as well as the biostratigraphic zonation, the *Hemicytheria setosa* interval corresponds to the early Pannonian age (Fig. 2). According to KRSTIĆ (1973, 1985) and RUNDIĆ (1997, 2006) this species is found in the fifth and sixth ostracod biozones (*Amplocypris abscissa* and *Hemicytheria croatica*). Its discovery suggests the sublittoral/littoral environs of Lake Pannon. Besides the studied area, *Hemicytheria setosa* is found in the Upper Pannonian s.str. (Late Miocene) of Serbia (e.g. Kolubara basin, Vrčin) and Bosnia and Herzegovina (north-eastern part of the Mt. Majevica) (RUNDIĆ, 1993, 2002).

Figure 1. The Pannonian basin and its southern and eastern margins (SCILANDS, 2015). White rectangle indicates the studied area.

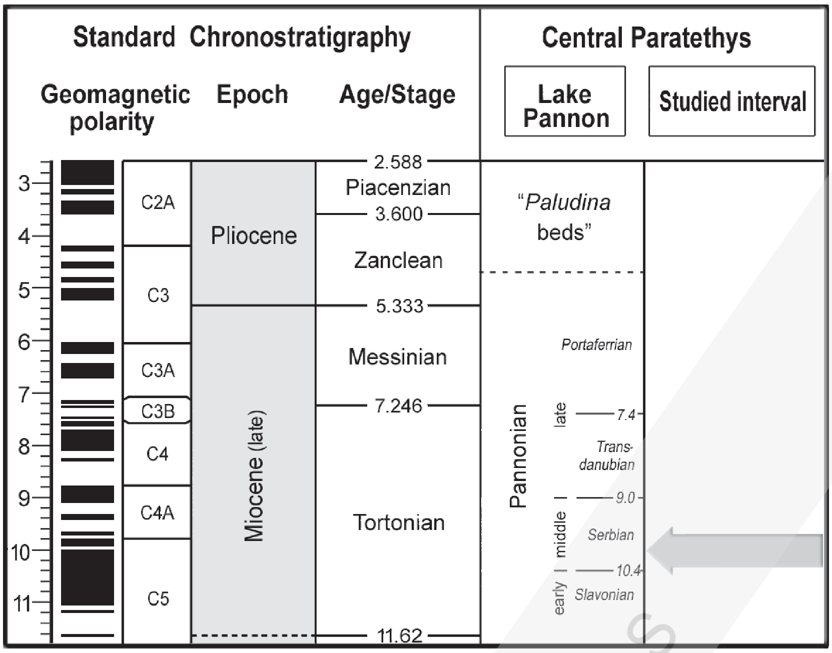

Figure 2. A chronostratigraphic chart of the Late Miocene Lake Pannon (modified after NEUBAUER et al., 2015). Gray arrow marks the position of the studied interval.

3. MATERIALS AND METHODS

3.1. Locality and the studied species

The sample for this study is taken from the sandy facies of the Lake Pannon sediments, from the left tributary of the Kokorin stream, Djurinci near Mali Požarevac, central Serbia, 44°31'51.70"N, 20°38'49.21"E at an altitude of 187 m a.s.l. (see Fig. 1).

This species has a small, thick-shelled trapezoidal carapace. Convexity is considerable, highest in the anterior part. The straight or slightly arched dorsal margin descends obliquely toward the posterior part. The ventral margin is straight or slightly concave in the first third, while the anterior margin is rounded, semicircular. Posterior end perpendicular, in males posterio-ventrally extended. Margins are without denticulation. Surface reticulated. Normal pore canals arranged in the suboval fossae separated with slightly faveolate muri. In the middle of the valves, fossae are tiny and shallow. There is a clearly arched ridge in the eye part, which is continuous with the anterior rib. Ventral rib poorly developed. Marginal zone broad. Hinge holoamphidont, in the juvenile forms poorly developed. Other features are the same as the genus *Hemicytheria* (RUNDIĆ, 2002).

Class Ostracoda LATREILLE, 1802
Order Podocopida SARS, 1866
Superfamily Cytheroidea BAIRD, 1850
Family Hemicytheridae PURI, 1953
Subfamily Hemicytherinae PURI, 1953
Genus *Hemicytheria* POKORNÝ, 1955
Species *Hemicytheria setosa* RUNDIĆ, 2002

Synonymy:

1985 Aurila (*Hemicytheria*) sp. (*setosa*) – KRSTIĆ, Pl.14, fig.1

1991 *Hemicytheria setosa* KRSTIĆ – RUNDIĆ, Pl.1, Figs.1-4

1997 *Hemicytheria setosa* n. sp. RUNDIĆ & KRSTIĆ – RUNDIĆ, p.66-67, Pl.10 Figs.1-4

2002 *Hemicytheria setosa* n. sp. – RUNDIĆ, p.138-139, Pl. 1, Figs.1-6

3.2. Material preparation and applied analyses

The field campaign and sampling were performed during the autumn of 1992. Eight bulk sandy samples (ca. 400 g) have been taken from the Kokorin stream. After the standard procedure of washing and sieving (meshes from 0.6-0.125mm) and H_2S_2 treatment, ostracods were picked and analysed under an Olympus BH2 stereomicroscope (Faculty of Mining and Geology, University of Belgrade). Some of the samples are very rich in ostracod content (more than 350 specimens including both carapaces and valves). Those samples marked as 1/92OS and 1A/92OS contain more than 300 adult *H. setosa* specimens of both sexes. The ostracod collection is stored at Faculty of Mining and Geology, University of Belgrade.

In this study, the female and male valves were photographed on the stereomicroscope Discovery V.8 with a Zeiss camera Icc1 in AxioVision 4.6.3 software (Carl Zeiss, Jena, Germany). To compare left-right asymmetry, all photographs are flipped to the left orientation prior to the landmark placement.

To determine shape differences between the sexes, as well as differences in left (LV) and right valve (RV) morphology, ge-

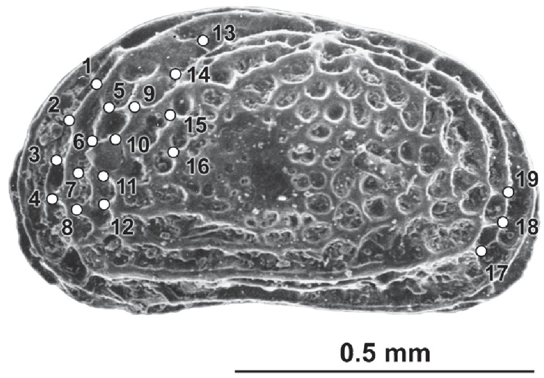

Figure 3. Position of landmarks on the carapace of *H. setosa* (female left valve SEM image modified from RUNDIĆ, 1991).

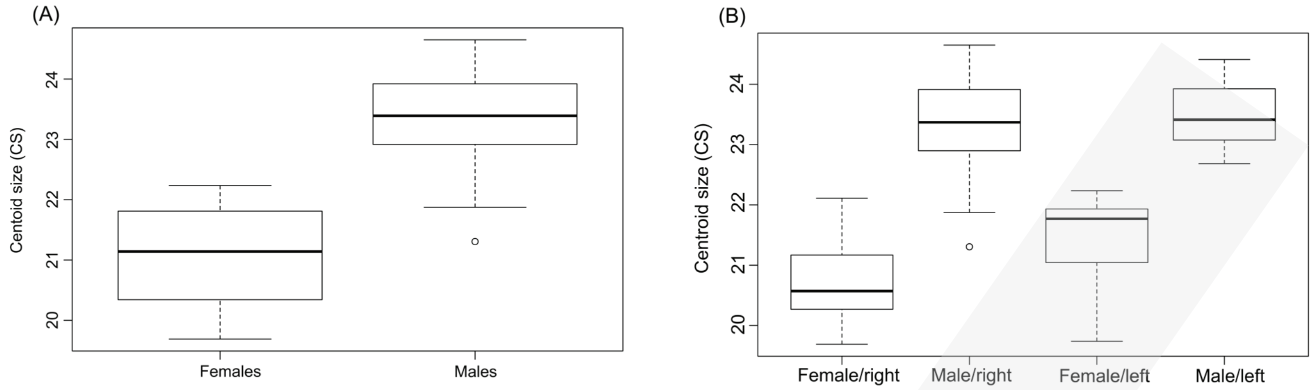

Figure 4. Differences in carapace CS between the sexes (A) and the sides of both sexes (B). The median with the first and the third quartiles is shown (in boxes), together with the range of variation and outliers.

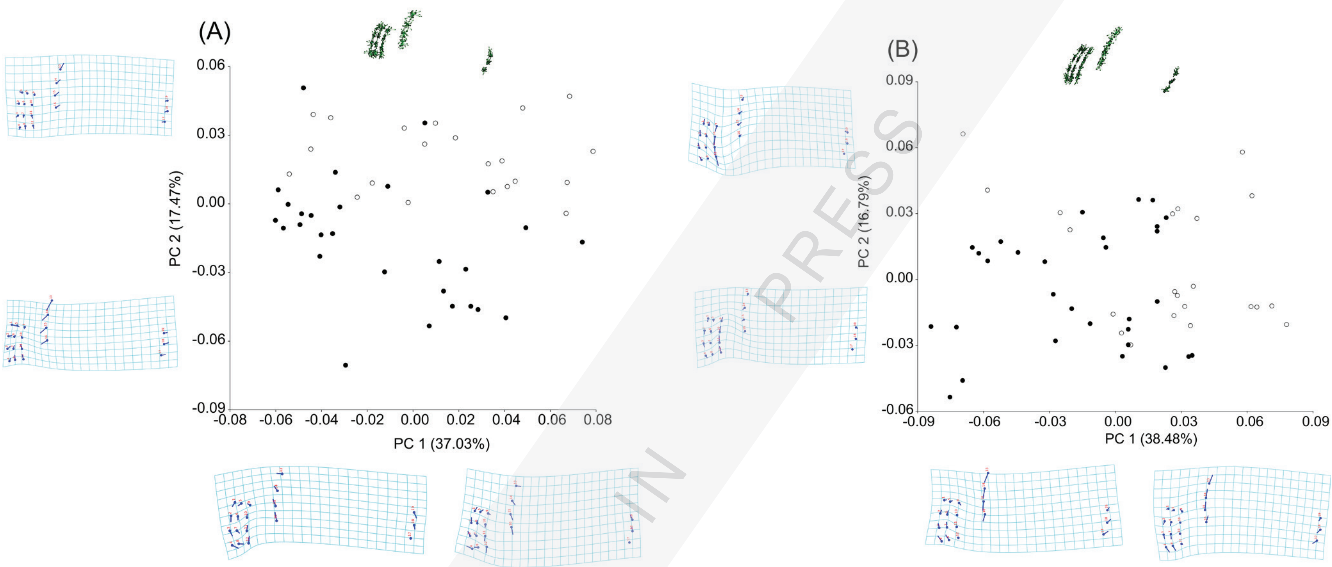

Figure 5 Principal component analyses and warp analyses in: (A) right and (B) left valves in both sexes (F - white circle, M - black circle). The pattern of morphological variation is illustrated using the position and size of vectors which influence on a thin plate spline deformation grid.

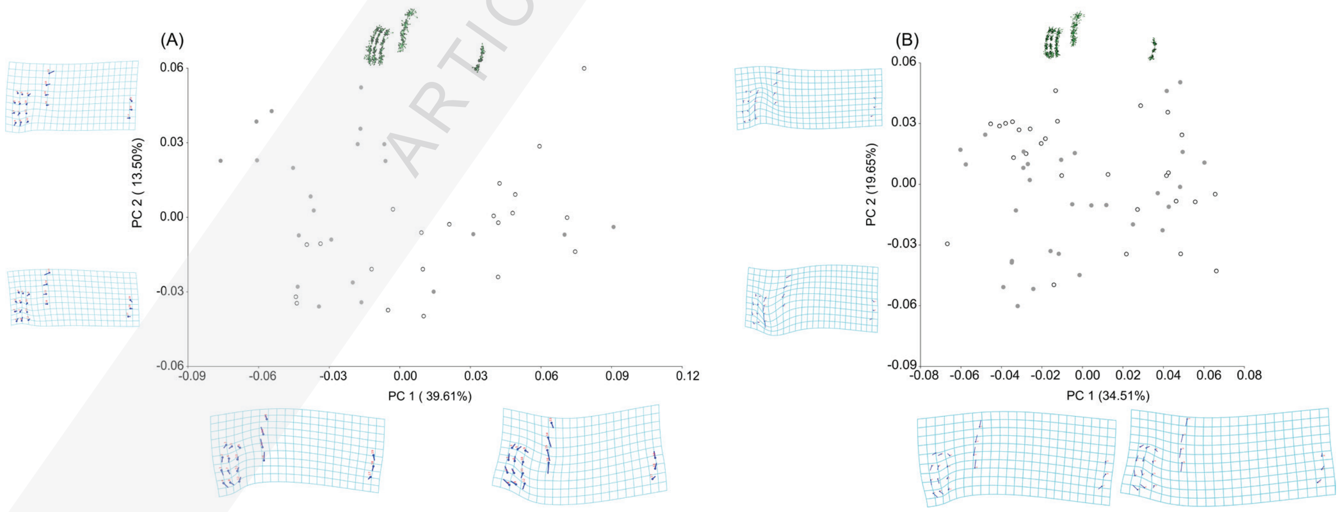

Figure 6 Principal component analyses and warp analyses in: (A) females and (B) males (left valves - grey circles, right valves - white circles). The pattern of morphological variation is illustrated using the position and size of vectors which influence on a thin plate spline deformation grid.

ometric morphometric analyses were used. In total, 19 landmarks are chosen based on the homology of the fossae in the Hemicytheridae (AL FURAIH, 1977; LIEBAU, 1977; AIELLO et al., 2016). We placed landmarks on some of the fossal groups proposed by AIELLO et al. (2016). They are positioned on the pore conuli, recognizable as prominent ridges on the valve surface

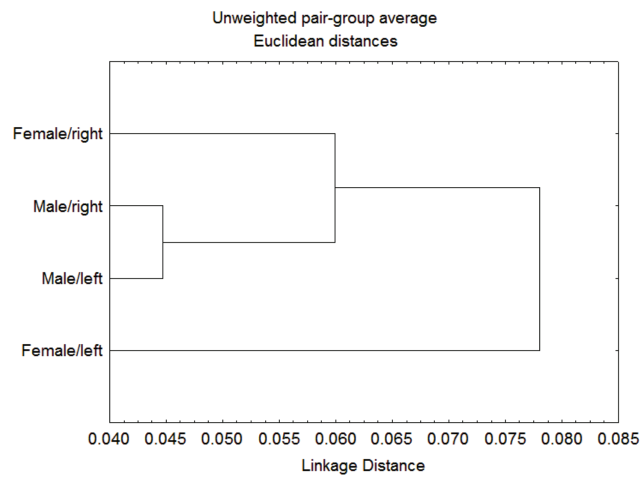

Figure 7. Valve shape similarities among left and right valves in both sexes are shown by the unweighted pair-group method using arithmetic averages (UPGMA).

(Fig. 3). Four landmarks on each of the first three series of fossae, that are parallel to the anterior margin, are placed between the fossae (1 – 12). Also, four landmarks are set starting from the ocular riblet, running in a row that surrounds the subcentral tubercle of the valve (13 – 16). The last three landmarks are placed between the fossae on the valve rear ridge (17 – 19). All landmarks are locally defined and classified as Type I according to Bookstein (BOOKSTEIN, 1991; ZELDITCH et al., 2004).

The program TpsDig2 (ROHLF, 2008a) was used to place the landmarks on photographs of 21 LV and 22 RV of females and 28 LV and 30 RV of males (in total, 101 valves).

To calculate the centroid size (CS) the CoordGen6 program (SHEETS, 2003) was used. Size in geometric morphometrics is noted as the centroid size that quantifies the spread of landmarks around their centroid (KLINGENBERG, 2013). In this study, the centroid size of each specimen was determined based on the reference length on each picture. Principal component analysis (PCA) and Canonical Variate Analysis (CVA) were performed in the MorphoJ program (KLINGENBERG, 2011). Also, morphological variation of the valves shape and size was analysed by Warp analysis in TpsRelw programme (ROHLF, 2008b). The warp analyses show dispersal of each landmark and its distance from the centroid in the sample, while PCA analysis exhibits total morphological variability in the sample. The shape analyses were done by Canonical Variate Analysis which was performed based on values of Procrustes coordinates and values of centroid size that is treated as the covariate in the analyses. Additionally, cluster analysis based on Procrustes distances from CVA and the unweighted pair-group method using arithmetic averages (UPGMA) was performed. All statistical analyses were done in STATISTICA 5.1 (StatSoft, 1997) and R statistical software (R Development Core Team, 2008).

4. RESULTS

The results of the analyses indicated that the centroid size of the valves is statistically different between the sexes ($p < 0.0001$; Fig. 4A). Differences in the CS between the left and right valve of females and males separately are significant only in females (females: $p < 0.0005$; males: $p < 0.334$) (Fig. 4B). Intersexual morphological variability in valve shape and CS are shown on Fig. 5. Additionally, variability of valve shape and CS of left and right valves into the same sex are exhibited in Fig. 6.

Results of cluster analysis show that the shape of the right and left valves in males is more morphologically similar in comparison with the shape of left and right of valves in females (Fig. 7).

The spatial relationship of the fossae and pore conuli on the valve surface is different between the sexes (Fig. 8). The differences in shape are more prominent in the central and posterior part of the valves. The lateral protrusion of the valves in females is positioned further backward than in males, relative to the anterior part that does not show statistical differences in position between the sexes (Fig. 8). The posterior part shows the opposite tendency, as the posterior ridge is moved forward in the females, and backward in the males (Fig. 8).

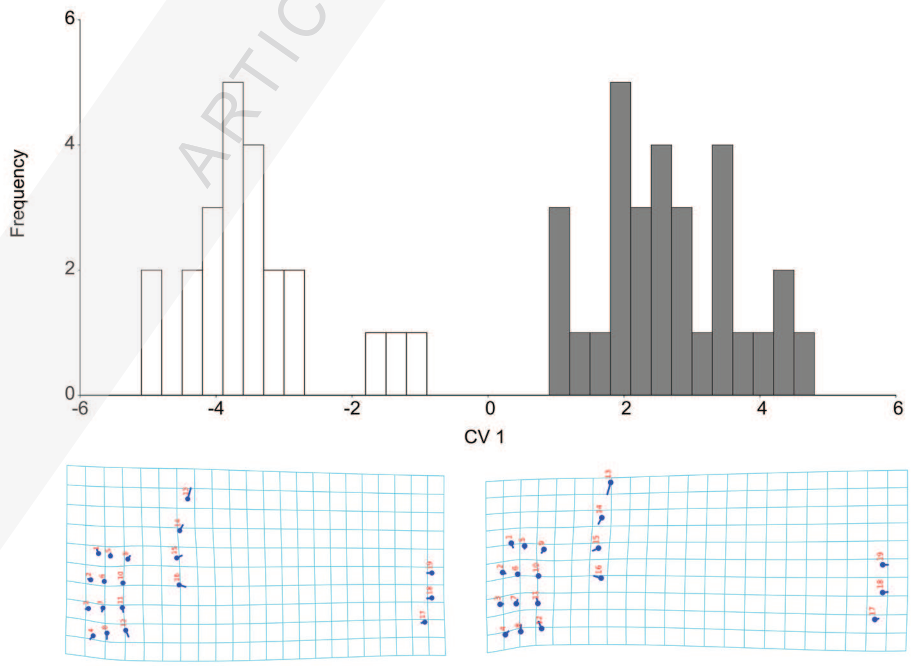

Figure 8. Intersexual carapace shape differences (white bars - females, grey bars - males). The pattern of the mentioned differences is illustrated using the position and size of vectors which influence on a thin plate spline deformation grid.

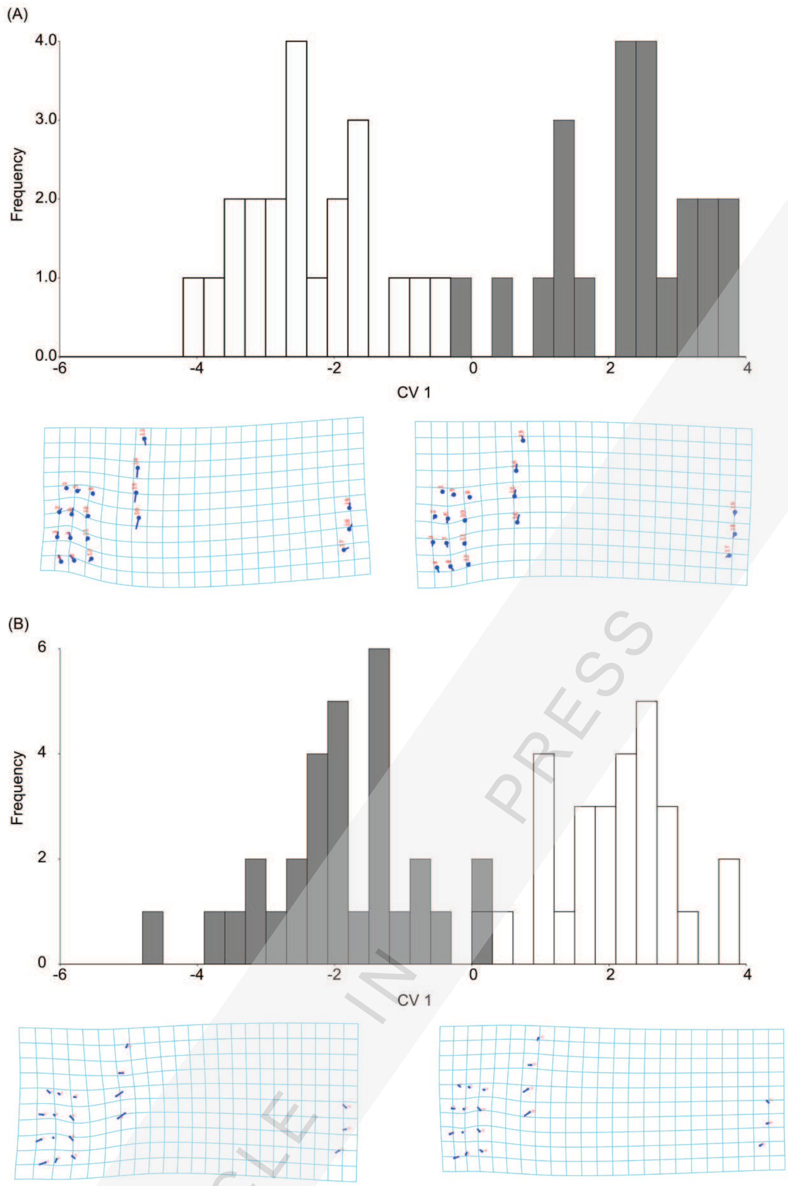

Figure 9. Carapace shape differences between left (grey bars) and right (white bars) valves in: (A) females and (B) males. The pattern of the aforementioned differences is illustrated using the position and size of vectors which influence on a thin plate spline deformation grid.

The differences in shape based on superficial ornamentation between left and right valves are detected in both sexes separately (Fig. 9 A and B). In females, the variation is less prominent in the anterior part. The central and posterior part of the left and right valve differ in the ornamentation pattern, as the fossae on the lateral protrusion of the left valve are placed more downward, whereas the fossae on the posterior part are more upward. The opposite tendency is noted on the right valve of females (Fig. 9 A). In males, the most conspicuous is the variation of the first anterior ridge, which is moved forward in comparison to the same ridge on the right valve. Also, the fossae on the lateral protrusion of the left valve are placed more backward, whereas the posterior ridge of the left valve is more forward in comparison with the right valve (Fig. 9 B).

5. DISCUSSION AND CONCLUSIONS

The valve morphology is the most crucial for palaeontological identification. Morphological variability of this trait is analyzed here in detail on an intersexual level and between left and right valves in *Hemicytheria setosa*, bearing in mind that there is a lot of carapace morphological variation among species within the genus *Hemicytheria* (e.g. SOKAČ, 1972). The results of landmark based geometric morphometric analysis that is applied, suggest significant differences are present in the carapace shape between the sexes and between the left and right valves in *Hemicytheria setosa*.

In relation to other forms of the genus *Hemicytheria*, this species shows variation in carapace sculpture. The polygonal to suboval fossae in combination with large semi-circular pits are the main characteristics that differentiate this form from others. Namely, SOKAČ (1972), RUNDIĆ (1997, 2002, 2006) and PIPÍK (2007) already mentioned there are *Hemicytheria* species which have three types of valve ornamentation: pitted, reticulated and smooth.

Valve shape intersexual differences are already described in cytheroids (MARTINS et al., 2017) and *Hemicytheridae*, as "high-doomed and oval" in females and "more rectangular" in males (BATE et al., 1981). The results of the present study show that the shape of the valve surface is in line with the findings of the aforementioned authors. The greatest differences between the sexes are noted in the posterior part of the valves, which are more elongated in males. That is in accordance with the findings of MARTINS et al. (2017), who concluded that males have larger posterior parts and because of a large copulatory apparatus that is located beneath this part of the carapace.

Apart from intersexual differences in carapace ornamentation, results of this study represent the first assessment of differences in carapace ornamentation between left and right sides in some cyteroid species. It is interesting to note that left-right asymmetry in size between valves was present in females, but not in males. This notion needs to be more deeply investigated in further research. Left-right asymmetry in females of *H. setosa* shows a different ornamentation pattern than in males, which adds one more characteristic to conspicuous intersexual differences. In females, the differences between sides are absent in the anterior region of the valves, whereas in the central and posterior part, placement of the fossae and pore conuli show movements in the vertical line. In males, the most differences between valves are in the anterior part, while the central and posterior valve surfaces, show differences in ornamentation along the horizontal line, that is the opposite in comparison with females.

This research is the first attempt to explore a suitable method to assess valve ornamentation-variation and to suggest the choice of landmarks which could be useful in future, more extensive investigations, on a larger interspecific sample.

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