Testing the hypothesis of modularity on head capsule in millipede *Megaphyllum bosniense* (Verhoeff, 1897) (Diplopoda: Julida)

Vukica Vujić*, Zvezdana Jovanović, Bojan Ilić, Luka Lučić, Boris Dudić, Sofija Pavković-Lučić, Slobodan Makarov

University of Belgrade, Faculty of Biology, Studentski Trg 16, 11000 Belgrade, Serbia

*Correspondence: vukica.vujic@bio.bg.ac.rs

Introduction and the aim of the study

- The presence of subunites (modules) and level of integration both within and between themselves have been frequently studied in the field of developmental evolutionary biology.
- Separate modules may have different developmental and evolutionary pathways.
- Adaptive value of the organism is directly correlated with the presence of modularity.
- **Tested hypothesis:** Is the distal region of the head capsule a modul in millipede *Megaphyllum bosniense* (Verhoeff, 1897) (Figure 1)?

Figure 1. Individual of *Megaphyllum bosniense.*

Material and Methods

- Sample site: Čarapićev Brest, village of Beli Potok, Mt. Avala (near Belgrade, Serbia).
- For this study, the following programs were used:

- MakeFan program (to position semi-landmarks) (Figure 2),
- TpsDig program (to position landmarks) (Figure 2),
- CoordGen program (to calculate centroid size),
- MorphoJ program (to perform regression analyses, to test modularity hypothesis) (Figure 3),
- R program (for conducting other statistical analyses).

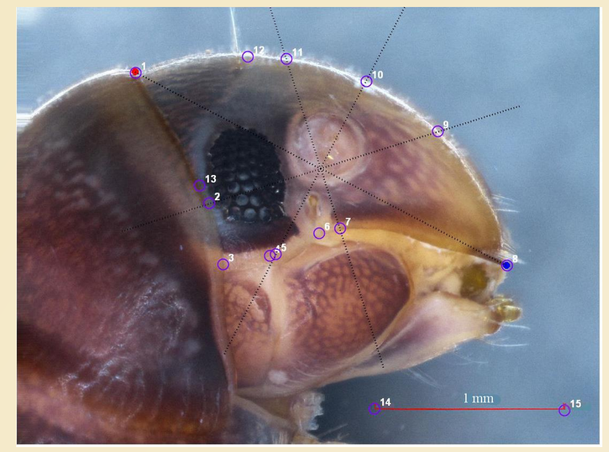

Figure 2. Position of semi-landmarks and landmarks on the lateral part of the head capsule in *M. bosniense.*

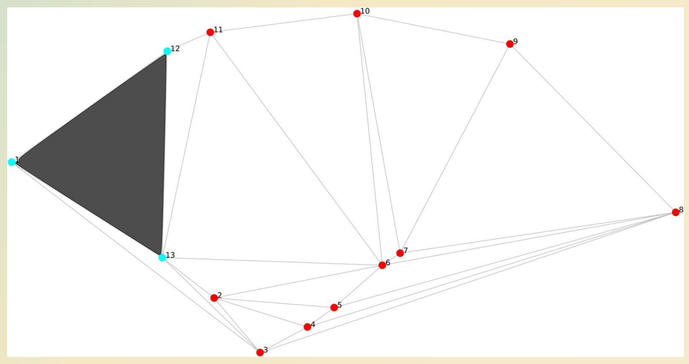

Figure 3. *A priori* defined modules on the lateral part of the head capsule in *M. bosniense*

Results and Discussion

- Allometry was significant for the asymmetric component (FA) (3.27% explained, $p <$ **0.0001**).
- Modularity hypothesis is accepted, because covariance coefficients (RV) for FA had lower values than 92.86% of other RV coefficients obtained by a random contiguous partition of the head capsule lateral part (Table 1, Figure 4).
- A high level of similarities between the covariance matrices based on residual shape variables of the asymmetric, and those based on shape variables of the asymmetric component, is obtained by Matrix correlation analysis (MC= 0.936, p< **0.0001**) .

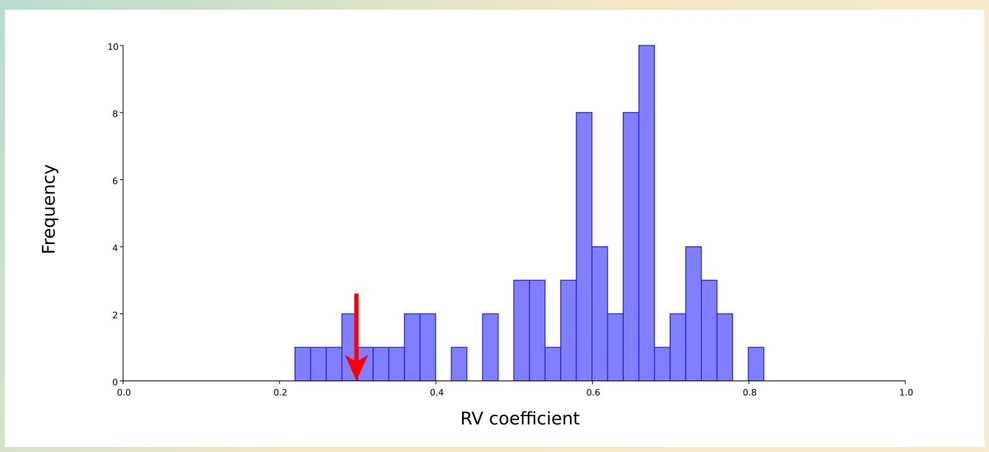

Figure 4. The squared trace correlations between all possible partitions of the millipede head capsule. The arrow depicts the values of the squared trace correlation between the subsets of landmarks in the proximal and distal head parts.

Table 1. Testing modularity hypothesis for the lateral part of the head capsule.

	Asymmetric component		
	RV	Ncon/Nless	P
Dorsal head capsule shape	0.298	70/5	0.0714

- Scaled values of eigenvalues variance from covariance matrices of the original data set of the asymmetric component, and those based on residual shape variables of the asymmetric component, were significantly different (T = 8.4054, $p <$ **0.0001**).
- The scaled variance of the eigenvalues of the FA (EV) was significantly lower after than before allometry removal (Figure 5).

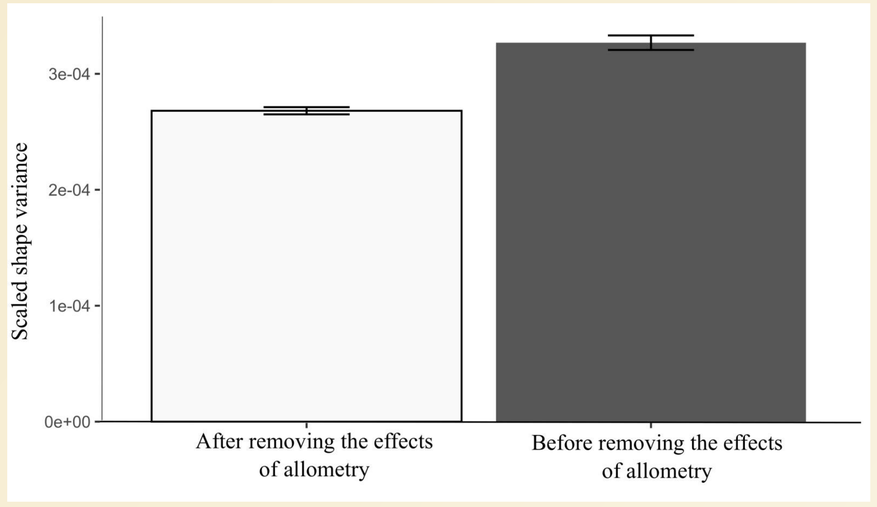

Figure 5. Mean and standard error of the scaled shape variance of the head capsule lateral part, calculated after the bootstrap resampling procedure on original data sets with 1000 resampling iterations.

- Based on presented results, distal and proximal regions of the head capsule develop and evolve as separate modules in analyzed millipede species.

Acknowledgement: This work was supported by the Serbian Ministry of Education, Science and Technological Development (Grant No. 451-03-9/2021-14/ 200178).