Conference proceedings

RGNF

"Mathematical methods and terminology in geology 2022"

4th Croatian scientific congress about geomathematics and

terminology in geology

Matematičke metode i nazivlje u geologiji 2022

IV. hrvatski znanstveni skup iz geomatematike i nazivlja u geologiji

održan na Rudarsko-geološko-naftnom fakultetu
Sveučilišta u Zagrebu

listopad 2022. godine

Skup su priredili:

Rudarsko-geološko-naftni fakultet
Sveučilišta u Zagrebu

Geomatematički odsjek
Hrvatskoga geološkog društva

Mathematical methods and terminology in geology 2022

4th Croatian scientific congress from geomathematics and terminology in geology
held on Faculty of Mining, Geology and Petroleum Engineering, University of Zagreb

October 2022

Organised by:

RGNF

Facuty of Mining, Geology and Petroleum Engineering of the University of Zagreb

Geomathematical Section of the Croatian Geological Society

Matematičke metode i nazivlje u geologiji 2022

ZBORNIK RECENZIRANIH RADOVA

IZDAVAČ:

Sveučilište u Zagrebu

RGNF

Rudarsko-geološko-naftni fakultet

Zagreb, 2022.

Mathematical methods and terminology in geology 2022

PROCEEDINGS OF REVIEWED PAPERS

PUBLISHER:

University of Zagreb

RGNF

Faculty of Mining, Geology and Petroleum Engineering

Zagreb, 2022

Urednici

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Rudarsko-geološko-naftni fakultet

Za nakladnika
dr. sc. Vladislav Brkić, izv. prof. (dekan RGNF-a)

Naklada u
obliku e-knjige

ISBN 978-953-6923-48-9

Zbornik će biti indeksiran u bazama Petroleum Abstracts (Sveučilište u Tulsi),te u Google Schoolar (preko Hrvatske znanstvene bibliografije). Bit će predložen i za indeksaciju u bazi Conference Proceedings Citation Index (Clarivate). Autori su odgovorni za sadržaj i jezičnu lekturu priloga.

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ISBN 978-953-6923-48-9

The proceedings will be indexed in Petroleum Abstracts (University of Tulsa) and Google Scholar (via Croatian scientific bibliography). It will be also proposed for indexation in Conference Proceedings Citation Index (Clarivate). Authors are solely responsible for content and Croatian/English proofreading.

Mathematical methods and terminology in geology 2022
UDC: 56:591.2/.9

Original scientific paper

Numerical analysis of the Middle Miocene *Panopea* bivalves (geoducks) from the southwestern margin of the Central Paratethys, Croatia

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Abstract

Here presented numerical analysis shows a variety of shell morphologies of the genus *Panopea*, based on the geoduck samples from the Middle Miocene (Badenian) deposits of Northern Croatia (southwestern margin of the Central Paratethys), previously considered as different species/subspecies. Specimens were measured, analyzed using PAST software, and data were compared with the available measurements from earlier studies. Results showed morphological variability of the geoducks shell shape from all localities, with Lower Badenian geoducks showing the lower median shell values than the Upper Badenian geoducks. Consistency with the comparative material is also concluded. Despite the shape varieties, which are also present in the modern geoducks, they are all considered as ecotypes of the morphologically variable species *Panopea* (*Panopea*) *menardi* (Deshayes, 1828). Middle Miocene climate shifts were probably the main cause of the shell size variability.

Keywords: numerical analysis; *Panopea*; Middle Miocene; Central Paratethys; Croatia

1. Introduction

Fossil bivalves from the genus *Panopea* Ménard de la Groye, 1807 have been recorded in Northern Croatia in the Middle Miocene – Badenian (Langhian) deposits. Species *Panopea* (*Panopea*) *menardi* (Deshayes, 1828) was described from Medvednica Mt. (Gornje Vrapče and Gornji Stenjevec localities) in **Kochansky (1944)**, **Budak (1974)**, **Butković (1979)**, **Vrsaljko et al. (2006)**, **Šoić (2011)** and **Fio et al. (2014)**, Pokupsko area in **Bigunac (1990)** and **Dželalija (2007)**, and Zrinska Gora Mt. in **Pikija (1987a,b)**. Several findings from Medvednica Mt. have been described as *Panopea* sp. considering slightly different shell morphology of the panopean casts and molds (**Šoić, 2011**; **Fio et al., 2014**).

Genus *Panopea* has medium-sized to large, elongated and thick shells, rounded anterior region and truncate posterior region that is widely gaping; subcentral beaks; a weak hinge plate, equal in both valves; a deeply impressed pallial line and a triangular pallial sinus (**Moore, 1969**; **Bosio et al., 2021**). The shape and depth of the pallial sinus vary among species (**Leyva-Valencia et al., 2015** after Yonge, 1971). Genus *Panopea* is recorded since the Cretaceous (maybe even Triassic) to recent (**Moore, 1969**).

Today clams of the genus *Panopea*, known as geoducks, represent one of the largest burrowing bivalves in the world, which can be found in the Pacific Ocean, the Mediterranean Sea, Australia and New Zealand, and in the Atlantic Ocean where one species is endemic to its southwestern part (**Leyva-Valencia et al., 2012 and references therein**; **Aragón-Noriega et al., 2015 and references therein**). Modern representatives of *Panopea* species live in sandy and muddy substrate, and are found from the intertidal zone to depths greater than 110 m, with most live individuals recorded from above 60 m. They live buried in the sediment up to a depth of 1 m, with large incurrent and excurrent siphons extending upward with the tip above the sea bed (**Bureau et al., 2002**; **Thomsen et al., 2009**; **Wood et al., 2018**; **Bosio et al., 2021**). Species of the genus *Panopea* can reach shell length over 200 mm (e.g., **Aragón-Noriega et al., 2019 and references therein**). Within five years they reach their mean size, and rapid growth is present during the

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first ten years and slower in the later years (e.g., **Thomsen et al., 2009**; **Zaidman & Morsan, 2015**). Recent geoducks are long-living bivalves, with life span up to 168 years (**Bureau et al., 2002**).

This paper presents numerical analysis of the panopean casts and molds shape morphology. Analyzed panopeans were found in the Upper Badenian deposits of the Medvednica Mt. (Gornje Vrapče and Gornji Stenjevec localities; e.g., **Kochansky, 1944**; **Šikić et al., 1977, 1979**; **Vrsaljko et al., 2006**; **Pezelj et al., 2016** and references therein) and determined as *Panopea* (*Panopea*) *menardi* (Deshayes, 1828) species, and in the Lower Badenian deposits of Pokupsko area which were determined as *Panope menardi rudolphii* Eichwald, 1934 subspecies after **Bigunac (1990)** (**Figures 1 and 2**). Results of the numerical analysis were compared with the measurements of **Šoić (2011)**, who described *in situ* panopean findings from the Upper Badenian deposits from Gornje Vrapče locality, Medvednica Mt. (**Figure 1**). Goal of this research was to check whether two panopean species can be distinguished based on the numerical analysis of the shell shape morphology, or the differences in the shell shape are the consequence of the morphological variability within a single geoduck species.

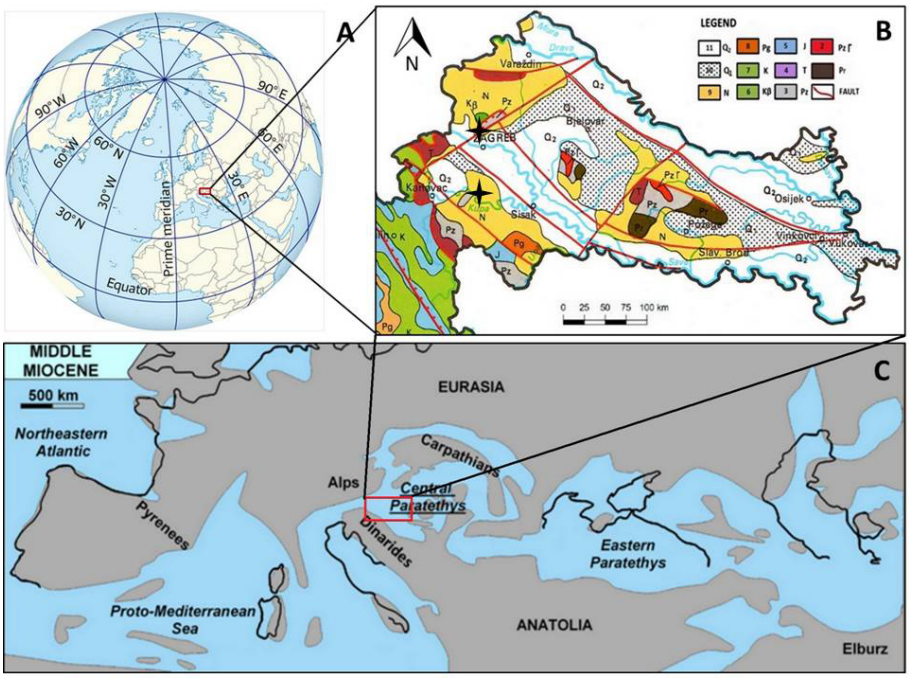

Figure 1: Geographical and paleogeographical location of the Badenian localities in Northern Croatia: (**A**) Geographic position of Croatia marked by red rectangle (modified after https://www.sailingissues.com/navcourse1.html). (**B**) Geographical location of the Badenian localities **(from Sremac et al., 2022, map after Velić & Velić, 1995)** where the panopean findings analyzed in this paper have been recorded (Medvednica Mt. near Zagreb, with Gornje Vrapče and Gornji Stenjevec localities, and Pokupsko area near the River Kupa). Four-Point stars in Figure B mark Medvednica Mt. near Zagreb (Gornje Vrapče and Gornji Stenjevec localities) and Pokupsko area localities; (**C**)Paleogeographical location of the Badenian localities in Northern Croatia (modified after **Harzhauser & Landau, 2019 and Sremac et al., 2022 and references therein**). Red rectangle in Figure C marks the area of North Croatian Basin in the Central Paratethys during Badenian. Legend (after **Sremac et al., 2022 and references therein**): 1. Precambrian metamorphic rocks; 2. Paleozoic granites; 3. Paleozoic sedimentary rocks; 4. Triassic carbonates, sporadically clastites; 5. Jurassic carbonates with scarce volcanoclastites; 6. Cretaceous dominantly carbonate rocks; 7. Cretaceous basalts; 8. Paleogene limestones; 9. Neogene clastic and carbonate rocks; 10. Pleistocene, dominantly unconsolidated clastites; 11. Holocene unconsolidated clastites.

Figure 2: Part of the analyzed *Panopea* (*Panopea*) *menardi* specimens. Scale bar: 10 mm.

2. Material and methods

In total 24 fossil panopeans were included in this numerical analysis. Specimens are preserved as casts and molds, and collected at three Badenian sites in Croatia; two Upper Badenian sites are located in the southwestern part of the Medvednica Mt. (Gornji Stenjevec and Gornje Vrapče localities, e.g., **Kochansky, 1944**; **Šikić et al., 1977, 1979**; **Vrsaljko et al., 2006**; **Pezelj et al., 2016** and references therein), and the third site of the Lower Badenian age (after **Bigunac, 1990**) is in the Pokupsko area (**Figure 1**). From the Medvednica Mt. (**Figure 1**) 12 specimens were measured; 6 of them are part of the Academician Vanda Kochansky-Devidé collection, housed at the Croatian Natural History Museum (CNHM) in Zagreb, and other 6 specimens were collected by Professor Jasenka Sremac and donated to the CNHM. Specimens from the V. Kochansky-Devidé collection (specimens VKD 1 – VKD 6) were determined as *Glycymeris menardii* Deshayes in **Kochansky (1944)**, today classified as *Panopea* (*Panopea*) *menardi* (Deshayes, 1828) (e.g., **Studencka, 1986 and references therein**; **fossilworks.org**). Specimens collected by Professor J. Sremac (specimens JS 1 – JS 6) are determined as *Panopea* (*Panopea*) *menardi* (Deshayes, 1828). From the Pokupsko area (**Figure 1**) 12 specimens collected by Dijana Bigunac (specimens DB 1 – DB 12) were measured. These geoducks were determined as *Panopea menardi rudolphii* Eichwald, 1934 and described in D. Bigunac Master Thesis (**Bigunac, 1990**). On these 24 specimens length, height and width of the *Panopea* casts and molds was measured as shown in **Figure 3**. Data on the analyzed *Panopea* specimens are presented in **Table 1**. Part of the specimens show more elongated shape comparing to the other specimens in the sample (e.g., see **Figure 2**, specimen DB 4, and **Šoić, 2011**), and the elongate specimens were initially classified as well as *Panopea* sp.? (see **Table 1, Figure 2**). Three specimens (VKD 2, VKD 6 and DB 12) were discarded from the analysis because they represent fragmented *Panopea* molds.

In order to fulfill the numerical analysis, the directly obtained measurements from this study (**Table 1**) were compared with those from the Gornje Vrapče locality (SW Medvednica Mt.) which are described and measured in **Šoić (2011)** as a part of his Master Thesis, and later in **Fio et al. (2014)**. Comparative material is shown in **Table 2**. As described in **Šoić (2011)**, the author also noticed differences in *Panopea* shape and marked those specimens as *Panopea* sp.

Numerical analysis of the here presented *Panopea* shells is done in the PAST software (**Hammer et al., 2001**) using the XY graphs, boxplots and cluster analysis, showing the values and the relations between the measured shell elements, as well as the morphological variability of the *Panopea* (*Panopea*) *menardi* species.

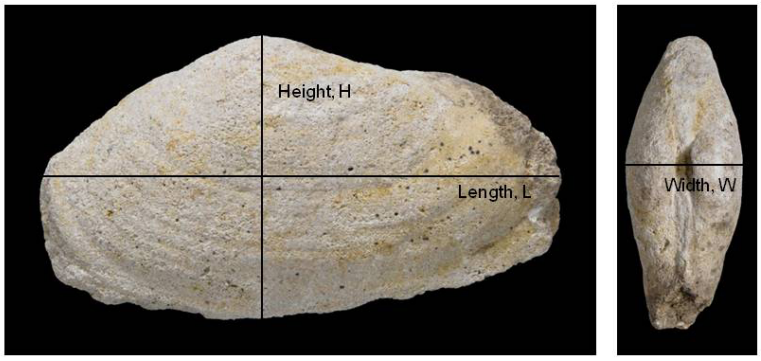

Figure 3: Measured elements of the *Panopea* shell: length (L), height (H) and width (W)

SPECIMEN	Name	Length, L (mm)	Height, H (mm)	Width, W (mm)	Locality
VKD 1	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	74.1	39.47	28.57	Gornji Stenjevec, Medvednica Mt.
VKD 2*	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	45	44.82	15.71	Gornji Stenjevec, Medvednica Mt.
VKD 3**	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	138.46	67.25	32.25	Gornji Stenjevec, Medvednica Mt.
VKD 4	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	130.57	76.58	45.59	Gornji Stenjevec, Medvednica Mt.
VKD 5	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	95.33	65.97	49.82	Gornji Stenjevec, Medvednica Mt.
VKD 6*	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	60.84	60.46	45.85	Gornje Vrapče, Medvednica Mt.
JS 1	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	122.36	72.82	52.25	Gornje Vrapče, Medvednica Mt.
JS 2**	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	130	73.77	52.94	Gornje Vrapče, Medvednica Mt.
JS 3	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	122.08	71.21	49.64	Gornje Vrapče, Medvednica Mt.
JS 4	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	124.83	65.13	44.69	Gornje Vrapče, Medvednica Mt.
JS 5	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	114.95	72.83	51.26	Gornje Vrapče, Medvednica Mt.
JS 6**	*Panopea* (*Panoepa*) *menardi* (Deshayes, 1828)	108.59	64.61	47.44	Gornje Vrapče, Medvednica Mt.
DB 1	*Panope menardi rudolphii* Eichwald, 1934	125.23	79.06	57.08	Pokupsko area
DB 2	*Panope menardi rudolphii* Eichwald, 1934	105.31	67.51	51.08	Pokupsko area
DB 3**	*Panope menardi rudolphii* Eichwald, 1934	141.1	64.16	44.33	Pokupsko area
DB 4**	*Panope menardi rudolphii* Eichwald, 1934	147.76	75.45	59.95	Pokupsko area
DB 5	*Panope menardi rudolphii* Eichwald, 1934	149.29	76.64	48.97	Pokupsko area
DB 6	*Panope menardi rudolphii* Eichwald, 1934	103.76	57.94	38.35	Pokupsko area
DB 7	*Panope menardi rudolphii* Eichwald, 1934	85.62	58.09	40.37	Pokupsko area
DB 8	*Panope menardi rudolphii* Eichwald, 1934	90.72	60.48	38.43	Pokupsko area
DB 9	*Panope menardi rudolphii* Eichwald, 1934	83.67	56.41	30.71	Pokupsko area
DB 10	*Panope menardi rudolphii* Eichwald, 1934	86.77	55.86	35.79	Pokupsko area
DB 11	*Panope menardi rudolphii* Eichwald, 1934	93.59	52.81	33.02	Pokupsko area
DB 12*	*Panope menardi rudolphii* Eichwald, 1934	58.32	40.43	22.76	Pokupsko area

Table 1: Determinations and measurements of the analyzed *Panopea* (*Panopea*) *menardi* specimens. Localities shown in **Figure 1**. Legend: VKD 1 – VKD 6: specimens from the Academician Vanda Kochansky-Devidé collection (**Kochansky, 1944**); JS 1 – JS 6: specimens collected by Professor Jasenka Sremac; DB 1 – DB 12 specimens from D. Bigunac Master Thesis (**Bigunac, 1990**). All specimens are today housed at the CNHM. * marks fragmented specimens which are excluded from the numerical anaylsis. ** marks *Panopea* (*P.*) *menardi* specimens which are also observed as *Panopea* sp. ?

SPECIMEN	Name	Length, L (mm)	Height, H (mm)	Locality
V-1	*Panopea menardi* Deshayes, 1828	112	72	Gornje Vrapče, Medvednica Mt.
V-2	*Panopea menardi* Deshayes, 1828	122	75	Gornje Vrapče, Medvednica Mt.
V-3	*Panopea menardi* Deshayes, 1828	104	74	Gornje Vrapče, Medvednica Mt.
V-4	*Panopea menardi* Deshayes, 1828	112	60	Gornje Vrapče, Medvednica Mt.
V-5	*Panopea menardi* Deshayes, 1828	123	70	Gornje Vrapče, Medvednica Mt.
V-7	*Panopea menardi* Deshayes, 1828	110	74	Gornje Vrapče, Medvednica Mt.
V-6	*Panopea* sp. A	80	65	Gornje Vrapče, Medvednica Mt.
V-8	*Panopea* sp. B	110	57	Gornje Vrapče, Medvednica Mt.
V-9	*Panopea* sp. B	129	71	Gornje Vrapče, Medvednica Mt.

Table 2. Comparative *Panopea* specimens after **Šoić (2011)** and **Fio et al. (2014)**. Locality is shown in **Figure 1.**

Abbreviations used in text (in alphabetical order):
CNHM: Croatian Natural History Museum
DB 1 – DB 12: specimens from D. Bigunac Master Thesis (Bigunac, 1990)
H: shell height
JS 1 – JS 6: specimens collected by J. Sremac
L: shell length
V-1 – V-9: comparative specimens from N. Šoić (2011)
VKD 1 - VKD 6: specimens collected by Academician V. Kochansky-Devidé
W: shell width

3. Results

In order to analyze morphological variability of the panopean shells (**Figure 3**), the measured elements (length and height, after **Figure 3** and **Table 1**) were plotted in XY graph and compared with the measurements of *Panopea* shells from Medvednica Mt. (Gornje Vrapče locality) by **Šoić (2011) (Table 2)**, as shown in **Figure 4**.

Plotted shell measurements show dispersity of data (**Figure 4)**, although two possible trends could be recognized (**Figure 4A**). Specimens from the Upper Badenian Gornje Vrapče locality on Medvednica Mt. are showing the best correlation, and geoducks from the Lower Badenian deposits of Pokupsko area are the most dispersed (**Figures 1 and 4**). As seen in **Figure 4**, Lower Badenian geoducks show smaller values of shell dimensions, than the Upper Badenian specimens from Medvednica Mt. (**Figure 4B, C** and **D**). The assumed *Panopea* sp. specimens are grouping well with the *Panopea* (*P.*) *menardi* specimens. As seen in **Figure 4**, this species shows the lowest and the highest values of shell length and height (from both, Medvednica Mt. and Pokupsko area), while the assumed *Panopea* sp. specimens fit between those minimum and maximum values.

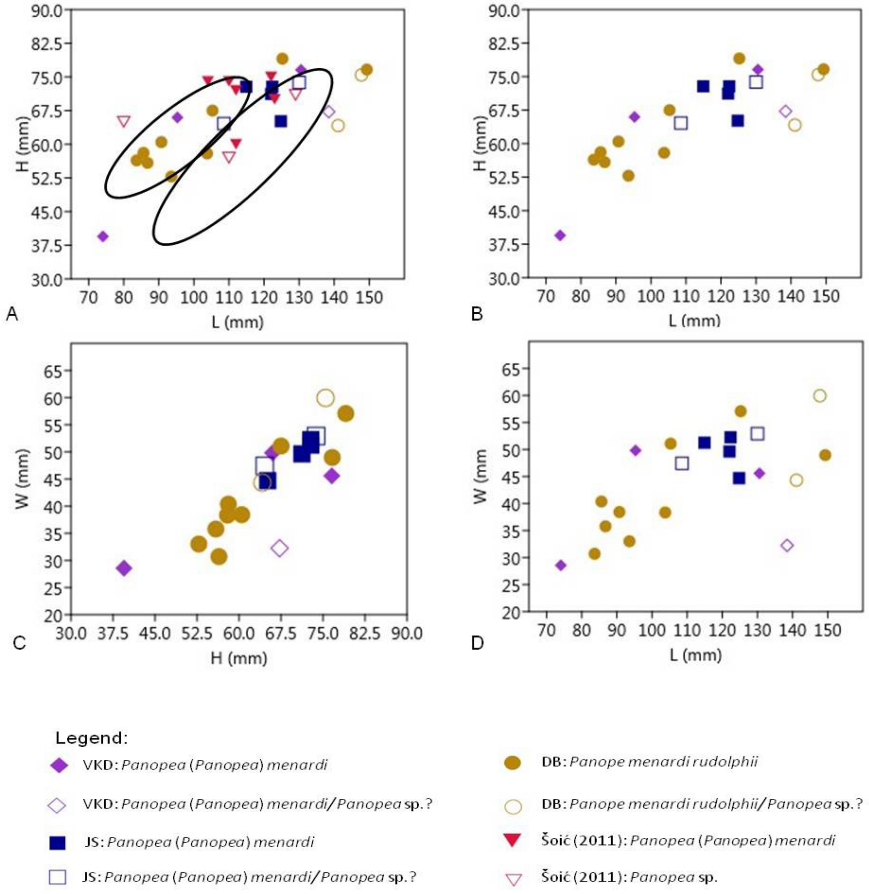

Figure 4: Correlation of the measured shell elements of the analyzed *Panopea* specimens. (**A**)Length and height of the analyzed geoducks compared to the measurements of **Šoić (2011)**; black ellipses: possible trends of the specimens. (**B**) Length and height of the analyzed specimens housed at the CNHM (**C**) Height and width of the analyzed specimens housed at the CNHM (**D**) Length and width of the analyzed specimens housed at the CNHM. For measurements and determinations of specimens see **Tables 1 and 2**. Legend: L – length (mm); H – height (mm); W – width (mm). Samples DB are collected in the Lower Badenian deposits of the Pokupsko area and determined as *Panope menardi rudolphii* Eichwald, 1834. Samples VKD, JS and V are collected from the Upper Badenian deposits on Medvednica Mt. and determined as *Panopea* (*P.*) *menardi* and *Panopea* sp. (see **Figure 1, Tables 1 and 2**).

Further comparison of the analyzed specimens is shown in **Figure 5**. All specimens were compared, and, afterwards specimens from Medvednica Mt. were separated from the ones from the Pokupsko area. As it can be seen in **Figure 5** and **Table 3**, median length value of the specimens is 114.95, and looking at the separated localities, specimens from Medvednica Mt. have higher median length value which is 122.22, and Pokupsko area specimens have lower median value of 103.76. Median height value of all specimens is 65.97; however, geoducks from the Pokupsko area have lower median height value (60.48) than the ones from Medvednica Mt (69.23), as shown in **Figure 5** and **Table 3**. Median width value of all specimens is 45.59 (**Figure 5**, **Table 3**), except again for Medvednica Mt, where it is higher (48.54), and Pokupsko area specimens where it is lower (40.37).

The comparative measurements of *Panopea* specimens from Gornje Vrapče locality, Medvednica Mt. after **Šoić (2011)** are shown in **Figure 6** and **Table 3**. As it can be seen, the median length value of all those specimens is 112, and the median height value is 71. The separated *Panopea* (*P.*) *menardi* samples after **Šoić (2011)** are shown in **Figure 6B**, and they show the same median length value, and slightly higher median height value of 73.

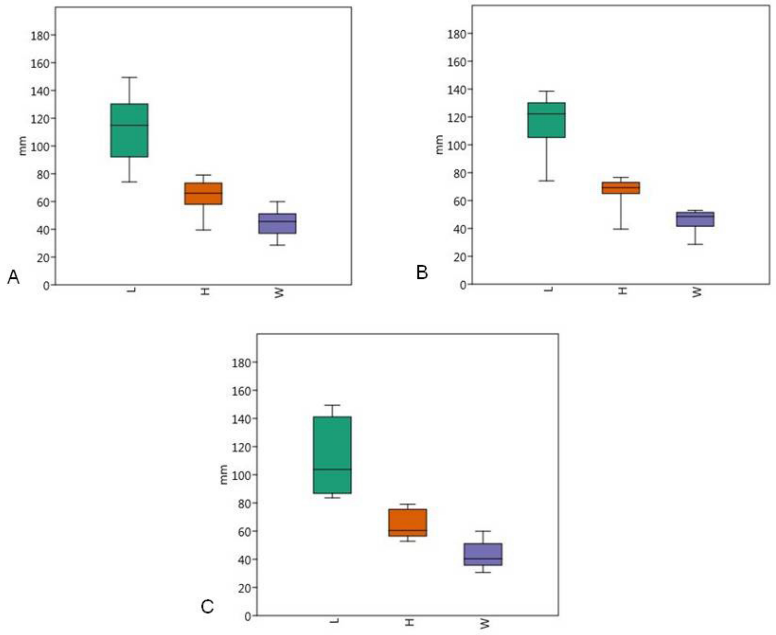

Figure 5: Boxplot of the analyzed *Panopea* specimens. **(A)** Localities Medvednica Mt. and Pokupsko area (all measured specimens). **(B)** Medvednica Mt. locality (all measured specimens). **(C)** Pokupsko area (all measured specimens). For each sample, the 25-75 percent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines ("whiskers") (**Hammer et al., 2001**). Legend: L – length, H – height, W – width.

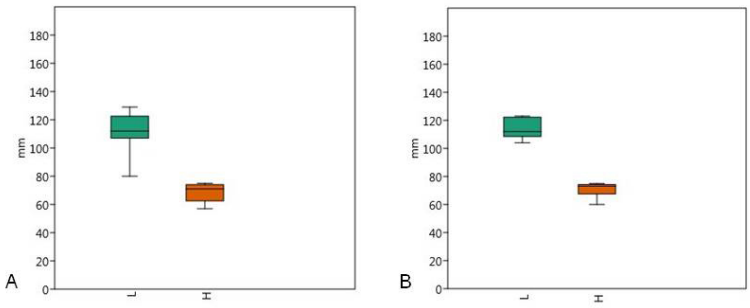

Figure 6: Boxplot of the compared measurements of *Panopea* specimens from **Šoić (2011)**. **(A)** All specimens from Gornje Vrapče locality, Medvednica Mt. **(B)** Specimens determined as *Panopea* (*P.*) *menardi* from Gornje Vrapče locality, Medvednica Mt. For each sample, the 25-75 percent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines ("whiskers") (**Hammer et al., 2001**). Legend: L – length, H – height, W – width.

In order to compare the measured samples determined as *Panopea* (*P.*) *menardi* with those from **Šoić (2011)**, they are plotted separately (**Figure 7**). Specimens marked as VKD and JS (Table 1) from the Gornje Vrapče locality show median length values of 122.08, median height value 71.21, and median width value of 49.64 (**Figure 7A** and **Table 3**). Specimens from the Pokupsko area are showing lower values, with the median length value of 93.59, median height value of 58.09, and the median width value of 38.43 (**Figure 7B** and **Table 3**).

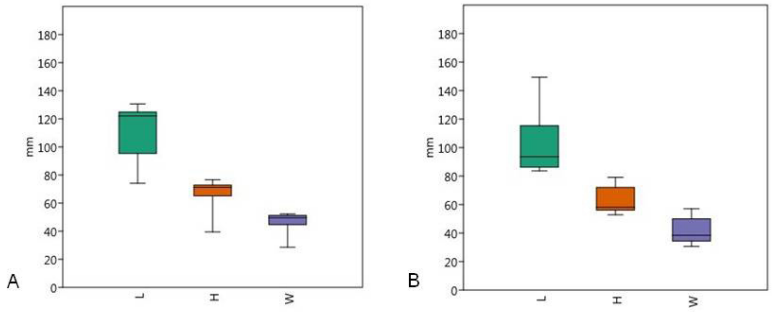

Figure 7: Boxplot of the measured *Panopea* (*P.*) *menardi* specimens. **(A)** Gornje Vrapče and Gornji Stenjevec localities, Medvednica Mt. **(B)** Pokupsko area. For each sample, the 25-75 percent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines ("whiskers") (**Hammer et al., 2001**). Legend: L – length, H – height, W – width.

The measured specimens from Medvednica Mt. and Pokupsko area were also analyzed by cluster analysis, which confirmed the dispersion of the measured data.

SPECIMENS	MEDIAN LENGTH	MEDIAN HEIGHT	MEDIAN WIDTH
VKD, JS, DB	114.95	65.97	45.59
VKD, JS	122.22	69.23	48.54
VKD, JS (except **)	122.08	71.21.	49.64
DB	103.76	60.48	40.37
DB (except **)	93.59	58.09	38.43
V	112	71	/
V (except **)	112	73	/

Table 3. Median values of the measured shell parameters. For specimens determinations see **Tables 1 and 2.**

4. Discussion

The analyzed and measured Middle Miocene *Panopea* specimens from the southwestern margin of the Central Paratethys (**Figure 1**) show slight differences between the two analyzed localities: Medvednica Mt. and Pokupsko area. Specimens from Pokupsko area show lower median length, height and width values than the specimens from Medvednica Mt. (**Figure 5**, **Table 3**). Here presented specimens from Medvednica Mt. and Pokupsko area (**Tables 1 and 3**) have slightly higher median length value and lower median height value compared to the *Panopea* specimens from Medvednica Mt. by **Šoić (2011)** (**Tables 2 and 3**, **Figures 5A and 6A**).

Specimens determined as *Panopea* (*Panopea*) *menardi* (**Table 1**) from Medvednica Mt. show higher median length value than the comparative samples of the same species and locality by **Šoić (2011)** (**Tables 2 and 3**), while the median height value is lower (**Figures 6 and 7**). Specimens of *Panopea* (*Panopea*) *menardi* from Pokupsko area have lower median length and height values than the samples from Medvednica Mt., both here presented samples and the comparative ones (**Figures 6 and 7**, **Table 3**).

Considering the above mentioned and as shown in **Figure 4**, the highest dispersity of data is visible in the specimens from Pokupsko area, and better grouping of the data in the specimens from Medvednica Mt., which also have higher length and height values. That grouping of higher shell elements values could also indicate a second trend in height/length ratio (**Figure 4**).

Specimens which were questioned to belong to *Panopea* (*Panopea*) *menardi* species and marked as *Panopea* sp.? (**Table 1**) show good fitting between the minimum and maximum length and height values of *Panopea* (*Panopea*) *menardi* specimens (**Figure 4**), so this could point to the differences in the shell morphology of the single, *Panopea* (*P.*) *menardi* species.

In the studies on the recent species of the genus *Panopea*, intraspecific variability of the shell size and shape has been recorded among the different regions (e.g., **Bureau et al., 2002**; **Aragón-Noriega et al., 2015, 2019 and references therein**; **Zaidman & Morsan, 2015**; **Wood et al., 2018 and references therein**). **Bureau et al. (2002)** mention earlier results by **Goodwin & Pease (1991)** who found a link between the sediment type and panopean length, with larger specimens found in the sand and sand/mud than in the mud or pea gravel. **Wood et al. (2018)** show significant differences in *Panopea generosa* valve length, with specimens reaching larger sizes in areas with colder water and higher primary productivity, what is also mentioned in earlier papers (e.g., **Goodwin & Pease, 1987 in Bureau et al., 2002 and references therein**). Authors also show spatial variability in shell morphology of the species *P. generosa*; specimens from subtidal and intertidal differed based on the shell compression in the dorsoventral region. Similar results to **Wood et al. (2018)**, considering the different growth parameters of modern *Panopea generosa* between the different regions and among sites have been recorded also in other studies, e.g., **Leyva-Valencia et al. (2012 and references therein)**, **Aragón-Noriega et al. (2015, and differences therein)**. **Leyva-Valencia et al. (2012)** discuss problems regarding identification of modern *Panopea* species considering the morphometric plasticity that occurs in the genus, differences in shell morphology influenced by environmental factors (temperature, tidal excursion, wave exposure, water currents, sediment type) and genetic difference, and the unknown relationship between the local environmental conditions and shell morphology (**Leyva-Valencia et al., 2012 and references therein**). **Zaidman & Morson (2015 and references therein)** mention results of studies that show connection of size and growth of modern geoducks to environmental factors, and conclude that their work on the recent *Panopea abbreviata* species growth variability suggests that growth is mainly governed by local environmental conditions.

The two *Panopea* sites mentioned in this study are of different stratigraphic age; Gornji Stenjevec and Gornje Vrapče localities on Medvednica Mt. belong to the Upper Badenian (e.g., **Kochansky, 1944**; **Šikić et al., 1977, 1979**; **Vrsaljko et al., 2006**; **Pezelj et al., 2016 and references therein**), while the Pokupsko area belongs to the Lower Badenian age (after **Bigunac, 1990**), as shown in **Figure 8**. According to **Bigunac (1990)**, the Pokupsko area deposits can be asserted to the Lower Badenian Upper Lagenidae Zone, with the most common foraminifer *Borelis melo* (Fichtel & Moll, 1798). This means that these sediments were deposited during the Miocene Climatic Optimum (**Figure 8**). Geoduck specimens from Medvednica Mt. were collected in younger, Upper Badenian deposits (**Figure 8**). These specimens have generally higher median shell height, length and width values than those from the Pokupsko area specimens, as presented in the chapter Results and described above. Modern geoduck shell growth studies showed that the panopeans reach larger sizes in the cooler waters (e.g., **Wood et al., 2018 and references therein**). This could also be a factor in the panopean shell growth during the Badenian; the older Badenian panopeans corresponding to the time of the Miocene Climatic Optimum have smaller values of the measured shell parameters (**Figure 3**), than the panopeans of the younger Badenian age, living in cooler climate, after the Miocene Climatic Optimum. The authors consider this

as a hypothesis, where more results are needed to make more conclusions on the variability of the geoduck shell variability.

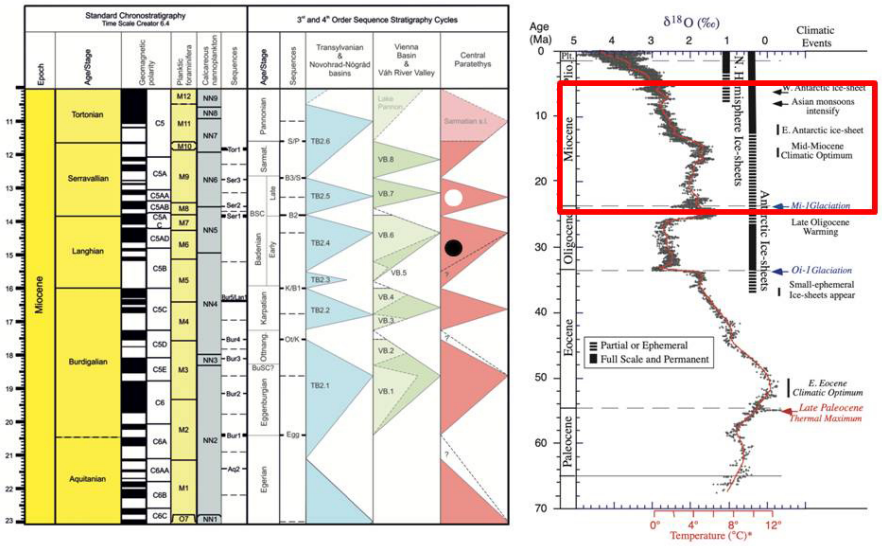

Figure 8: Stratigraphic age of the localities where analyzed panopean specimens were collected (after **Kováč et al., 2018**), and Neogene temperature curve with mentioned major climatic events (after **Zachos et al., 2001**). Black circle marks Pokupsko area locality (after **Bigunac, 1990**), and white circle marks the Medvednica Mt. localities (**Kochansky, 1944**; **Šikić et al., 1977, 1979**; **Vrsaljko et al., 2006**; **Pezelj et al., 2016 and references therein**).

The length and height deviations of the specimens assumed as another *Panopea* species or subspecies as seen in **Figure 4**, are most probably the consequence of the intraspecific morphological variability of the species *Panopea* (*P.*) *menardi*. These morphological varieties previously resulted with the recognition of different *Panopea* species (e.g., **Studencka, 1986 and references therein**). **Studencka (1986)** describes *Panopea* (*P.*) *menardi* specimens from the Badenian sediments of southern Poland, and discusses their morphology and their assignment to one or more panopean species. Taking into account all the above mentioned, the authors agree with the opinion of **Studencka (1986 and references therein)** that variable Middle Miocene (Badenian) panopeans, despite their variability of the shell shape, represent the ecotypes of a single *P.* (*P.*) *menardi* species.

5. Conclusions

Performed numerical analysis on the Middle Miocene (Lower and Upper Badenian) geoducks from the two areas (three localities) situated at the southwestern margin of the Central Paratethys in Croatia showed the following results:

(1) Measured parameters of the panopean casts and molds (height, length and width) show morphological variability of the shell shape seen through the dispersity of data on the presented graphics;

(2) Geoducks initially determined on the genus level (*Panopea* sp.?) group well into the plotted graphs with the measured elements of *Panopea* (*Panopea*) *menardi*, supporting the hypothesis that they are also the ecotypes of *Panopea* (*P.*) *menardi*;

(3) The numerical results can be grouped according to the geoduck stratigraphic age: Lower Badenian geoducks show lower median length, height and width values than the Upper Badenian geoducks;

(4) Hypothesis is made that the smaller size of the Lower Badenian geoducks is the consequence of higher water temperature during the Miocene Climatic Optimum. On the contrary, Upper Badenian geoducks, living in cooler seas, are larger, a pattern also recognized in studies of the modern geoducks;

(5) Further analysis of Badenian geoducks is needed to record more ecotypes of the *Panopea* (*Panopea*) *menardi* species and to test the validity of suggested hypothesis based on the climatic effects on the geoducks shell shape and its connection in the fossil record.

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Sažetak

Numerička analiza srednjomiocenskih školjkaša iz roda *Panopea* („geoducks“) iz jugozapadnog dijela Centralnog Paratethysa, Hrvatska

U radu je prikazana numerička analiza koja pokazuje raznolikost morfologije ljušture školjkaša iz roda *Panopea*, poznatih u engleskom jeziku kao „geoducks“. Primjerci su prikupljeni u srednjomiocenskim (badenskim) naslagama Sjeverne Hrvatske (jugozapadni rub Centralnog Paratethysa). U starijoj literaturi se za primjerke ove jedne vrste panopeja smatralo da je riječ o više vrsta/podvrsta ovih školjkaša. Analizirani primjerci su izmjereni i obrađeni u software-u PAST. Dobiveni podatci su uspoređeni s dostupnim mjerenjima ovih školjkaša u ranijim istraživanjima. Rezultati su pokazali morfološku varijabilnost oblika ljušture panopeja iz donjobadenskih i gornjobadenskih naslaga, pri čemu donjobadenske panopeje pokazuju niže vrijednosti medijana mjerenih parametara ljušture od gornjobadenskih panopeja. Također je zaključeno slaganje s komparativnim materijalom. Usprkos raznolikosti oblika, koje su prikazane u analiziranim primjercima, svi se obrađeni primjerci smatraju ekotipovima morfološki varijabilne vrste *Panopea* (*Panopea*) *menardi* (Deshayes, 1828). Mogući glavni uzrok varijabilnosti oblika ljušture panopeja bile su srednjomiocenske klimatske promjene.

Ključne riječi: numerička analiza; *Panopea*; srednji miocen; Centralni Paratethys; Hrvatska

Acknowledgment

Results for this research were obtained through the projects “Mathematical methods in geology VII” (2022), led by Professor T. Malvić at the University of Zagreb, Faculty of Mining, Geology and Petroleum Engineering, and The Croatian Science Foundation Project IP-2019-04-7042 (Sedimentary paleobasins, water corridors and biota migrations, PI: Professor M. Kovačić, University of Zagreb, Faculty of Science). We wish to thank Nives Borčić, senior museum technician, Croatian Natural History Museum, for the photographs of the *Panopea* specimens.

Author's contribution

Marija Bošnjak (Dr.sc., senior curator, geology, paleontology, geomathematics) measured the analyzed material, provided the numerical analysis, data analysis, data and paleoenvironmental interpretations, and presentation of the results. **Jasenka Sremac** (Dr.sc., Full Professor, retired, geology, paleontology, paleoenvironment) provided the field work, collected and determined part of the analyzed fossil bivalves, provided the paleontological analysis, paleoenvironmental interpretation and presentation of the results. **Dijana Bigunac** (Dr.sc., senior expert geophysicist, sedimentology, geophysics) provided the field work, collected and determined part of the analyzed fossil bivalves, and contributed in the taxonomic discussion. **Davor Vrsaljko** (Dr.sc., geology, paleontology, biostratigraphy, malacology) provided the paleoenvironmental interpretations, and discussion on the taxonomy and broader regional geological context.