

Biometric analysis of the Eocene Lucinidae shells from Croatia

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Abstract

Numerous marine bivalves of the family Lucinidae were collected from the Eocene localities at the Promina Mt. and Imotski area (Lažete) in Croatia. The specimens are today housed in the Croatian Natural History Museum in Zagreb. The Lucinidae shells were measured and the biometric analysis was performed to compare morphometric characteristics of the height, length and width of the shells between the localities in Croatia, and the comparative specimens from the Paris Basin housed in the Museum. Morphometric analyses showed differences between the lucinid samples in Croatia, also between the samples from Croatia and specimens from the Paris Basin. Lucinidae samples from Croatia have higher morphometric values and indicate the possible favourable paleoecological conditions for the growth of the bigger shells. This study is the first step in the further biometric research on the Eocene malacofauna from Croatia and its comparison with the neighbouring contemporaneous localities.

Keywords: Biometry, Lucinidae, Eocene, Croatia

1. Introduction

Lucinidae are a family of marine bivalves known in the fossil record from Paleozoic to today, especially from the Paleogene and Neogene periods. In Croatia, numerous specimens of lucinids are recorded in the Eocene sediments in Dalmatia (for references see next chapter). Part of the Eocene lucinids from Croatia are housed in the Croatian Natural History Museum (abbr. CNHM) in Zagreb. Here presented specimens are part of the five collections which are result of the long year's field- and cabinet work of the museum curators, as well as international cooperation with other Museums. The lucinids were mostly collected and determined during the second half of the 20th century by the curators Ante Milan and Krešimir Sakač, who were investigating Eocene localities with lucinids in Lika (Bunić-Kozijan), Dalmatia (Ostrovica-Benkovac, Otres-Ostrovica, Dubravica-Skradin, Kosavin-Bribir, Promina and Imotski – Lažete, Borak, Mamutovo brdo, Podgradina, Suvaja and Čosići localities) and Herzegovina (Vir). Professor Gjuro Pilar, who was also a curator in the CNHM, enriched the Museum fundus with the comparative collection “Tertiary fauna of the Paris basin”, containing lucinids among other fauna.

In this paper authors presented the biometric analysis on part of the lucinids from the Museum collections. Biometrical analysis included comparison of measured parameters of the lucinid shells (height, length and width) (e.g., **Malvić et al., 2020 and references therein**) to study differences between the morphometry of the lucinid shells from the two localities in Croatia (Promina and Imotski area), and to compare samples from Croatia with the lucinids from the Paris Basin present in the Museum comparative collection (**Figure 1**). This paper is part of the research started on Eocene localities in Imotski area and Herzegovina (**Sremac et al., 2014, 2015**), and represents a baseline study on the morphometry of the Lucinidae, as a first step in the biometrical analysis of the Eocene macrofauna from the Museum collections and specimens collected during the field work in Imotski area.



Figure 1: Geographical location of the localities with Eocene Lucinidae presented in this paper (**Google Earth Pro**, <https://earth.google.com/web/>)

2. Historical background on the Eocene lucinids from the Museum collections

Milan (1956) described various Eocene fossil fauna, including Lucinidae, collected from the yellowish marls and sandstones in Dalmatia, in the area between Otres and Ostrovica. According to **Dainelli (1905)**, **Schubert (1905)** and **Kochansky (1947)** the deposits with lucinids are of the Middle Eocene, Upper Lutetian age.

Dainelli (1905) compared Eocene fauna from the several localities in Dalmatia with the other known Eocene fossil fauna, concluding that the fauna from Croatia corresponds to the fauna from the localities San Giovanni and Ronca in Italy.

Part of the lucinids in the Museum collections is collected at the Promina Mt. **Kühn (1946)** gave historical review of geological research on Promina Mt. He determined the Upper Eocene age of the sediments, and the deposits with fossils as the lowest part of the Upper Eocene.

Sakač (1965) described Cretaceous and Lower Paleogene sediments from the Imotski area. According to him the lower Paleogene deposits of Imotski area are rich with fossil molluscs, and cosmopolitan species recorded in the Middle- and Upper Eocene deposits, also mentioning the species *Lucina dalmatina* characteristic for the Upper Eocene. Sakač concluded that the Eocene molluscs correspond to the other fauna in the Dinarides, especially to the fauna of the Promina Mt.

Sakač et al. (1984) continued the research of the Imotski area and collected fossil macrofauna with numerous lucinids from different localities of the Imotski area and Herzegovina. Among the collected lucinids there are gigantic specimens, what was later confirmed by **Sremac et al. (2014, 2015)**.

Lucinid specimens from the comparative Museum collection from the Paris Basin are very well preserved, diversified and collected at various localities in the Paris Basin. The Paris Basin is an area of a typical development of Paleocene and Eocene deposits, with a clear boundary between Paleogene and Neogene marked by a marine regression.

First description of the Eocene deposits comes from the Paris and London basins by C. Lyell. From the fossil record of the Paris Basin, the main contributions in paleontology are made on the molluscan fauna from Eocene and Oligocene deposits described by Jean-Baptiste Pierre Antoine de Monet, chevalier de Lamarck, and Gérard-Paul Deshayes (e.g., **Lozouet, 2014 and references therein**). Geology of this basin has been intensively analysed, and the synthesis of the results is presented in **Mégnién and Mégnién (1980)**. The Paris Basin is considered as one of the best researched Eocene sites in the stratigraphic and paleontological sense (e.g., **Čvorović, 2000**).

3. Methods

We analyzed 204 Lucinidae shell from the following CNHM collections: “Fauna of the Eocene deposits of Croatia and Dalmatia” (in Croatian, “*Fauna eocenskih naslaga Hrvatske i Dalmacije*”; 5 specimens, inventory numbers: 1996, 1998₁₋₂, 1999₁₋₂), “Molluscan fauna of the Middle Eocene of the northern Dalmatia” (in Croatian, “*Fauna molusaka srednjeg eocena sjeverne Dalmacije*”, 4 specimens, inventory numbers: 20, 21₁₋₂, 22₃), two Professor Sakač’s

collections (77 specimens, temporary inventory numbers: 1L-5L, 8L-14L, 17L-19L, 21L, 24L-27L, 29L, 32L-41L, 43L, 45L-47L, 50L-54L, 1KS-29KS, 32KS-39KS), and “Tertiary fauna of the Paris Basin” (in Croatian, “Zbirka tercijarne faune Pariške kotline”, 118 specimens, inventory numbers: 113, 113bb, 114₁₋₄, 115₁₋₃, 116₁₋₅, 117₁₋₂, 118₁₋₁₀, 119₁₋₅, 119bb, 120, 121₁₋₃, 122₁₋₃, 123₁₋₄, 124₁₋₆, 128_{1,3,4}, 129₁₋₆, 130₁₋₃, 131₁₋₃, 132₁₋₆, 133₁₋₇, 134_{2,3}, 135, 136₁₋₇, 139, 142₁₋₄, 143₁₋₁₀, 144₁₋₂, 145₁₋₃, 146_{1,2,4-8,10-13}).

There are various sizes of lucinid specimens present in the Museum collections, therefore we analysed the specimens by biometrical analyses. Using the digital caliper, we measured the height (H), length (L) and width or thickness (W) of the shell (**Figure 2**). Height (H) is the largest measurement perpendicular to the length. Length (L) is the largest measurement in the antero-posterior axis. The width or thickness of the shell (W) is the maximum thickness of two joined valves. Measurements are presented in **Tables 1, 2, 3** and **4**. We also calculated morphometric indices of the shell showing elongation (H/L ratio), compactness or roundness (E/L ratio) and convexity (E/H ratio) of the shell (e.g., **Modestin 2017 and references therein**).

The measured lucinid shells had a complete valve and we did not include the specimens representing the lucinid fragmented shells. As mentioned above, the width or thickness of the shell is measured as a thickness of two valves. This was not possible to perform in here presented analysis on all the specimens, due to the fossil preservation of lucinids having mostly only one valve preserved. Thickness is therefore here presented as the width of only one valve for part of the measured specimens.

Descriptive analysis of the morphometric relations between measured lucinid shells was carried out using the XY graphs and histograms in the PAST (PAleontological STatistics) Program (**Hammer et al., 2001**).

Authors also revised the determinations of Lucinidae species names according to the fossil databases „Paleobiology Database. Fossilworks.“ (**fossilworks.org**) and „World Register of Marine Species (WORMS, **www.marinespecies.org**) to compare similarities of the findings from Croatia with the ones from the Paris Basin collection. The revised names are shown in **Table 5**.

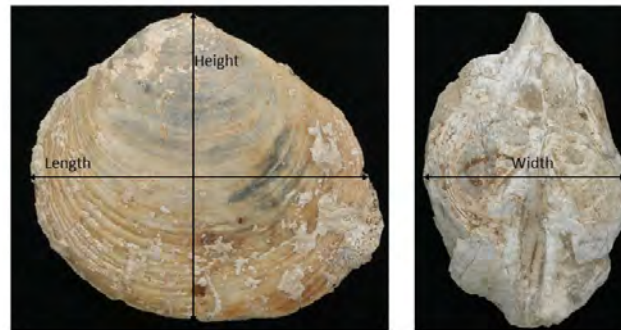


Figure 2: Measured elements height, length and width of the Lucinidae shells

Table 1: Measured Lucinidae shells from the CNHM collection “Fauna of the Eocene deposits of Croatia and Dalmatia”. Revised names are presented in **Table 5**.

Inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
1996.	<i>Lucina gigantea</i> Deshayes	79.9	88.5	30.7
1998. ₁	<i>Lucina zignoi</i> Oppenheim	49.9	56.2	28
1998. ₂	<i>Lucina zignoi</i> Oppenheim	32.8	33	19.2
1999. ₁	<i>Lucina</i> sp.	32.9	25.9	15.6
1999. ₂	<i>Lucina</i> sp.	33.1	31.5	20.4

Table 2: Measured Lucinidae shells from the CNHM collection “Molluscan fauna of the Middle Eocene of the northern Dalmatia”. Revised names are presented in **Table 5**.

Inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
20.	<i>Lucina escheri</i> Mayer	37.2	42.1	10
21. ₁	<i>Lucina dalmatina</i> Oppenheim	18.1	22.3	11.4
21. ₂	<i>Lucina dalmatina</i> Oppenheim	14.4	18.7	7.8
22. ₃	<i>Lucina saxorum</i> Lamarck	44.6	50	27.3

Table 3: Measured Lucinidae shells from the Professor Sakač's collections. a) Lucinidae from Lažete locality near Imotski. b) Lucinidae from Promina Mt. Revised names are presented in **Table 5**.

a) Lucinidae from Lažete locality near Imotski.

b) Lucinidae from Promina Mt.

Temporary inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
1 L	<i>Lucina</i> sp.	138.7	170.2	80.5
2 L	<i>Lucina</i> sp.	162.3	170.2	75.8
3 L	<i>Lucina</i> sp.	157.9	172.9	75.5
4 L	<i>Lucina</i> sp.	171	188.5	44.3
5 L	<i>Lucina</i> sp.	144.2	145.3	66.2
8 L	<i>Lucina</i> sp.	137.1	164.6	45.7
9 L	<i>Lucina</i> sp.	126.8	148.5	64.4
10 L	<i>Lucina</i> sp.	138.6	141.1	46.5
11 L	<i>Lucina</i> sp.	106.6	115	61.9
12 L	<i>Lucina</i> sp.	94.1	129	51.5
13 L	<i>Lucina</i> sp.	132.1	129.9	46.2
14 L	<i>Lucina</i> sp.	106.5	125.8	57.5
17 L	<i>Lucina</i> sp.	126.7	87.8	70.9
18 L	<i>Lucina</i> sp.	106.3	114.5	57.9
19 L	<i>Lucina</i> sp.	120.1	116.9	51.9
21 L	<i>Lucina</i> sp.	104.9	83.2	75
24 L	<i>Lucina</i> sp.	77.2	74.6	40.4
25 L	<i>Lucina</i> sp.	89.6	91.2	47.6
26 L	<i>Lucina</i> sp.	100.5	93.5	31.7
27 L	<i>Lucina</i> sp.	88.5	91.9	27.1
29 L	<i>Lucina</i> sp.	72	87.8	24.4
32 L	<i>Lucina illyrica</i> Oppenheim	103.6	118.2	52.3
33 L	<i>Lucina</i> sp.	89.9	91.4	43.2
34 L	<i>Lucina</i> sp.	47	58.7	8.3
35 L	<i>Lucina</i> sp.	95.7	107.4	19.4
36 L	<i>Lucina</i> sp.	45.5	64.8	23.3
37 L	<i>Lucina</i> sp.	52.1	53.3	13.6
38 L	<i>Lucina prominensis</i> Oppenheim	69.7	65	32.1
39 L	<i>Phacoides (Lucinoma) dinarii</i> Kühn	27.6	26	13.8
40 L	<i>Lucina</i> sp.	73.1	68.3	25.2
41 L	<i>Lucina</i> sp.	64.4	75.6	30.5
43 L	<i>Lucina</i> sp.	83	68.4	14.9
45 L	<i>Lucina</i> sp.	66.2	70.1	44.2
46 L	<i>Lucina</i> sp.	45.7	72.4	22.4
47 L	<i>Lucina</i> sp.	48	35.5	27.3
50 L	<i>Lucina</i> cf. <i>escheri</i> Mayer 1870	50.2	68	13.4
51 L	<i>Lucina saxorum</i> Lamarck	24.5	26.6	14.1
52 L	<i>Lucina saxorum</i> Lamarck	22.2	20.1	12.7
53 L	<i>Lucina</i> sp.	42.3	44.6	18.2
54 L	<i>Lucina</i> sp.	40.1	44.4	8.6

Temporary inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
1 KS	<i>Lucina prominensis</i> Oppenheim	54.1	61.6	25.2
2 KS	<i>Lucina prominensis</i> Oppenheim	57.3	62.9	25.6
3 KS	<i>Lucina prominensis</i> Oppenheim	19.7	23.2	5.4
4 KS	<i>Lucina prominensis</i> Oppenheim	64.6	66.6	25.3
5 KS	<i>Lucina prominensis</i> Oppenheim	48.2	69.6	20.2
6 KS	<i>Lucina dalmatina</i> Oppenheim	18.9	24.8	11.2
7 KS	<i>Lucina dalmatina</i> Oppenheim	18.4	22.3	11.9
8 KS	<i>Lucina saxorum</i> Lamarck	40.4	37.4	19.1
9 KS	<i>Lucina saxorum</i> Lamarck	40	44.1	19.2
10 KS	<i>Lucina saxorum</i> Lamarck	38.3	47.9	21.7
11 KS	<i>Lucina saxorum</i> Lamarck	45.6	49.9	27.4
12 KS	<i>Lucina saxorum</i> Lamarck	48.6	44.2	25.8
13 KS	<i>Lucina saxorum</i> Lamarck	51.2	55.8	28.3
14 KS	<i>Lucina saxorum</i> Lamarck	46.1	49	24.4
15 KS	<i>Lucina saxorum</i> Lamarck	59.2	58.4	31
16 KS	<i>Lucina saxorum</i> Lamarck	51.9	55.2	27.3
17 KS	<i>Lucina saxorum</i> Lamarck	22.1	19.2	12.8
18 KS	<i>Lucina saxorum</i> Lamarck	21.2	18.5	7.7
19 KS	<i>Lucina saxorum</i> Lamarck	16.2	14.4	8.4
20 KS	<i>Lucina saxorum</i> Lamarck	18.3	18.1	12.6
21 KS	<i>Phacoides (Lucinoma) dinarii</i> Kühn	35.7	34.2	21.1
22 KS	<i>Phacoides (Lucinoma) dinarii</i> Kühn	38.6	41.3	24.4
23 KS	<i>Phacoides (Lucinoma) dinarii</i> Kühn	22.2	19.2	7.9
24 KS	<i>Lucina dalmatina</i> Oppenheim	20.3	25	13.3
25 KS	<i>Lucina dalmatina</i> Oppenheim	21.6	24.9	12.8
26 KS	<i>Lucina dalmatina</i> Oppenheim	16.9	22.6	12.6
27 KS	<i>Lucina</i> cf. <i>dalmatina</i> Oppenheim	16.8	20.1	11.6
28 KS	<i>Lucina</i> cf. <i>dalmatina</i> Oppenheim	18.5	21	14.1
29 KS	<i>Lucina</i> cf. <i>dalmatina</i> Oppenheim	16.1	20.6	10.4
32 KS	<i>Lucina</i> cf. <i>dalmatina</i> Oppenheim	38.5	36.9	17.4
33 KS	<i>Lucina dalmatina</i> Oppenheim	17.9	20.4	13.6
34 KS	<i>Lucina dalmatina</i> Oppenheim	18.6	24.2	8.7
35 KS	<i>Lucina prominensis</i> Oppenheim	27.6	18.4	16
36 KS	<i>Lucina prominensis</i> Oppenheim	23.5	20.1	12.1
37 KS	<i>Lucina prominensis</i> Oppenheim	18	21.4	12.1
38 KS	<i>Lucina prominensis</i> Oppenheim	18.3	21.6	13.3
39 KS	<i>Lucina prominensis</i> Oppenheim	17	17.9	7.3

Table 4: Measured Lucinidae shells from the CNHM collection “Tertiary fauna of the Paris Basin”. Revised names are presented in **Table 5**.

Inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
113	<i>Lucina columbella</i> Lamarck	16.9	16.4	6.9
113 bb	<i>Lucina columbella</i> Lamarck	15.4	15.6	6.9
114. ₁	<i>Lucina heberti</i> Deshayes	15.7	16.1	4.3
114. ₂	<i>Lucina heberti</i> Deshayes	14	15.4	3.9
114. ₃	<i>Lucina heberti</i> Deshayes	14.2	15.1	3.4
114. ₄	<i>Lucina heberti</i> Deshayes	14.6	15.8	3.3
115. ₁	<i>Lucina elegans</i> Deshayes	22.2	24.4	4.4
115. ₂	<i>Lucina elegans</i> Deshayes	14.8	16	3.5
115. ₃	<i>Lucina elegans</i> Deshayes	10.9	11.2	2.6
116. ₁	<i>Lucina elegans</i> Deshayes	14.7	15.9	3.6
116. ₂	<i>Lucina elegans</i> Deshayes	14.4	15.7	2.4
116. ₃	<i>Lucina elegans</i> Deshayes	12.8	13.4	2.5
116. ₄	<i>Lucina elegans</i> Deshayes	11.9	13	3.5
116. ₅	<i>Lucina elegans</i> Deshayes	8.4	10.5	1.9
117. ₁	<i>Lucina pulchella</i> Lamarck	13.2	15.3	4
117. ₂	<i>Lucina pulchella</i> Lamarck	12.8	13.9	3.6
118. ₁	<i>Lucina saxorum</i> Deshayes	21.3	20.3	4.5
118. ₂	<i>Lucina saxorum</i> Deshayes	17.9	18.4	4.3
118. ₃	<i>Lucina saxorum</i> Deshayes	17.7	17.9	4.3
118. ₄	<i>Lucina saxorum</i> Deshayes	15.7	16.3	3.6
118. ₅	<i>Lucina saxorum</i> Deshayes	16	16.8	2.9
118. ₆	<i>Lucina saxorum</i> Deshayes	15.8	16.4	3.8
118. ₇	<i>Lucina saxorum</i> Deshayes	14.8	15.6	2.9
118. ₈	<i>Lucina saxorum</i> Deshayes	14.1	14.5	2.5
118. ₉	<i>Lucina saxorum</i> Deshayes	16.3	16.5	2.9
118. ₁₀	<i>Lucina saxorum</i> Deshayes	13.8	13.7	2.8
119. ₁	<i>Lucina scalaris</i> Deshayes	17.8	17.4	4.9
119. ₂	<i>Lucina scalaris</i> Deshayes	13.1	13.2	3.1
119. ₃	<i>Lucina scalaris</i> Deshayes	13.5	12.8	3.7
119. ₄	<i>Lucina scalaris</i> Deshayes	10.4	11.1	2.2
119. ₅	<i>Lucina scalaris</i> Deshayes	9.6	10.5	2.2
119.bb	<i>Lucina scalaris</i> Deshayes	8.5	8.4	2.3
120.	<i>Lucina unicata</i> Defrance	19.5	20.3	2.1
121. ₁	<i>Lucina sulcata</i> Lamarck	12.5	12.9	3.7
121. ₂	<i>Lucina sulcata</i> Lamarck	10.9	11.4	2.9
121. ₃	<i>Lucina sulcata</i> Lamarck	4.5	5.1	1.5
122. ₁	<i>Lucina sulcata</i> Lamarck	12.2	12.5	3.6
122. ₂	<i>Lucina sulcata</i> Lamarck	11.8	11.5	3.1
122. ₃	<i>Lucina sulcata</i> Lamarck	5.9	6.8	1.3
123. ₁	<i>Lucina squammula</i> Deshayes	12.5	13.1	2.9
123. ₂	<i>Lucina squammula</i> Deshayes	10.1	10.2	2.6
123. ₃	<i>Lucina squammula</i> Deshayes	11	10.1	3.1
123. ₄	<i>Lucina squammula</i> Deshayes	8.6	8.8	2.1
124. ₁	<i>Lucina saxorum</i> Lamarck	19	19.3	4.9
124. ₂	<i>Lucina saxorum</i> Lamarck	14.2	14.6	5.9
124. ₃	<i>Lucina saxorum</i> Lamarck	12.6	12.8	5.4
124. ₄	<i>Lucina saxorum</i> Lamarck	17.7	19.2	4.2
124. ₅	<i>Lucina saxorum</i> Lamarck	16.3	16.5	3.6
124. ₆	<i>Lucina saxorum</i> Lamarck	13.9	14.1	3.4
128. ₁	<i>Lucina contorta</i> Defrance	20.5	34.8	3.6
128. ₃	<i>Lucina contorta</i> Defrance	20.7	21.8	3.9
128. ₄	<i>Lucina contorta</i> Defrance	17.6	21.5	4
129. ₁	<i>Lucina gibbosula</i> Lamarck	19.1	19.7	4.8
129. ₂	<i>Lucina gibbosula</i> Lamarck	17.8	20.1	4.6
129. ₃	<i>Lucina gibbosula</i> Lamarck	16.1	19.5	4.1
129. ₄	<i>Lucina gibbosula</i> Lamarck	14.5	15.6	6.2
129. ₅	<i>Lucina gibbosula</i> Lamarck	14	15.5	4
129. ₆	<i>Lucina gibbosula</i> Lamarck	14.5	15.9	4.1

Inventory number	Species name	Height, H (mm)	Length, L (mm)	Width, W (mm)
130. ₁	<i>Lucina connubrica</i> Lamarck	33.7	34.9	8.9
130. ₂	<i>Lucina connubrica</i> Lamarck	30.1	31.8	6.9
130. ₃	<i>Lucina connubrica</i> Lamarck	22.9	25.3	4.3
131. ₁	<i>Lucina callosa</i> Deshayes	11.1	11.6	3.1
131. ₂	<i>Lucina callosa</i> Deshayes	10.9	11.9	2.8
131. ₃	<i>Lucina callosa</i> Deshayes	9.7	10.3	3.4
132. ₁	<i>Lucina rigaulti</i> Deshayes	13.4	15.1	3.7
132. ₂	<i>Lucina rigaulti</i> Deshayes	10.4	10.7	3.6
132. ₃	<i>Lucina rigaulti</i> Deshayes	10.3	10.6	3.4
132. ₄	<i>Lucina rigaulti</i> Deshayes	10.1	10.4	3.4
132. ₅	<i>Lucina rigaulti</i> Deshayes	9.2	9.4	3.3
132. ₆	<i>Lucina rigaulti</i> Deshayes	8.6	8.8	3.2
133. ₁	<i>Lucina concentrica</i> Lamarck	33.2	34.7	7.5
133. ₂	<i>Lucina concentrica</i> Lamarck	28.3	32.6	6.2
133. ₃	<i>Lucina concentrica</i> Lamarck	30.5	33.6	6.3
133. ₄	<i>Lucina concentrica</i> Lamarck	29.8	30.5	6.9
133. ₅	<i>Lucina concentrica</i> Lamarck	31.9	32.9	6.7
133. ₆	<i>Lucina concentrica</i> Lamarck	29.3	31.2	5.8
133. ₇	<i>Lucina concentrica</i> Lamarck	20.9	24.6	4
134. ₂	<i>Lucina gigantea</i> Deshayes	44.4	51.5	7.2
134. ₃	<i>Lucina gigantea</i> Deshayes	37.2	43.5	8.8
135.	<i>Lucina gigantea</i> Deshayes	71.1	76.8	9.3
136. ₁	<i>Lucina gibbosula</i> Lamarck	16.9	18.6	5.1
136. ₂	<i>Lucina gibbosula</i> Lamarck	16	18.3	4.7
136. ₃	<i>Lucina gibbosula</i> Lamarck	16.6	18.2	4.8
136. ₄	<i>Lucina gibbosula</i> Lamarck	16.7	17.3	4.1
136. ₅	<i>Lucina gibbosula</i> Lamarck	15.8	16.9	3.9
136. ₆	<i>Lucina gibbosula</i> Lamarck	13.5	14.5	3.7
136. ₇	<i>Lucina gibbosula</i> Lamarck	7.2	8.3	2.4
139.	<i>Lucina albella</i> Lamarck	12.2	12.1	5.5
142. ₁	<i>Lucina saxorum</i> Lamarck	13.2	14.3	3.2
142. ₂	<i>Lucina saxorum</i> Lamarck	13.7	14.2	3.3
142. ₃	<i>Lucina saxorum</i> Lamarck	11.2	11.5	2.8
142. ₄	<i>Lucina saxorum</i> Lamarck	7.7	8.3	2.4
143. ₁	<i>Lucina circinaria</i> Lamarck	18.2	16.8	4.3
143. ₂	<i>Lucina circinaria</i> Lamarck	17.2	18.1	3.7
143. ₃	<i>Lucina circinaria</i> Lamarck	16.7	17.8	4.1
143. ₄	<i>Lucina circinaria</i> Lamarck	14.8	15.3	3.3
143. ₅	<i>Lucina circinaria</i> Lamarck	15.7	16.7	3.3
143. ₆	<i>Lucina circinaria</i> Lamarck	15.1	16.5	3.3
143. ₇	<i>Lucina circinaria</i> Lamarck	14.8	15.9	3.5
143. ₈	<i>Lucina circinaria</i> Lamarck	13.7	14.7	2.7
143. ₉	<i>Lucina circinaria</i> Lamarck	11.4	11.8	2.8
143. ₁₀	<i>Lucina circinaria</i> Lamarck	9.1	10.3	2.2
144. ₁	<i>Lucina concentrica</i> Lamarck	24.3	26.3	5.5
144. ₂	<i>Lucina concentrica</i> Lamarck	23.2	25.4	6.4
145. ₁	<i>Lucina lapidum</i> Lamarck	18.4	19.5	4
145. ₂	<i>Lucina lapidum</i> Lamarck	18.8	18	4.8
145. ₃	<i>Lucina lapidum</i> Lamarck	18.9	19.6	4.1
146. ₁	<i>Lucina proxima</i> Deshayes	17.5	18	3.9
146. ₂	<i>Lucina proxima</i> Deshayes	16.1	15.7	4.3
146. ₄	<i>Lucina proxima</i> Deshayes	14.5	14.7	3.7
146. ₅	<i>Lucina proxima</i> Deshayes	13.7	13.5	3.2
146. ₆	<i>Lucina proxima</i> Deshayes	13.8	12.6	2.3
146. ₇	<i>Lucina proxima</i> Deshayes	11.8	11.6	3.1
146. ₈	<i>Lucina proxima</i> Deshayes	11.7	11.6	2.5
146. ₁₀	<i>Lucina proxima</i> Deshayes	11.3	12.1	2.5
146. ₁₁	<i>Lucina proxima</i> Deshayes	10.1	10.5	2
146. ₁₂	<i>Lucina proxima</i> Deshayes	11.7	11.9	3.6
146. ₁₃	<i>Lucina proxima</i> Deshayes	10.4	10.7	2.6

Table 5: Revision of the Lucinidae species names and comparison between the findings from Croatia and Paris Basin. Light orange rows represent the specimens present in Croatia and in the Paris Basin. ¹ „Paleobiology Database. Fossilworks.“ (fossilworks.org), ² „World Register of Marine Species (WORMS, www.marinespecies.org).

CNHM inventory book	Species name Revised name	Number of specimens	Croatia (Dalmatia)	Paris Basin
<i>Lucina gigantea</i> Deshayes	<i>Pseudomiltha gigantea</i> (Deshayes, 1825) ¹	4	1	3
<i>Lucina zignoi</i> Oppenheim	<i>Saxolucina saxorum</i> Lamarck 1806 ¹	2	2	/
<i>Lucina escheri</i> Mayer	no available data ^{1,2}	2	2	/
<i>Lucina dalmatina</i> Oppenheim	no available data ^{1,2}	11	11	/
<i>Lucina saxorum</i> Lamarck	<i>Saxolucina saxorum</i> Lamarck 1806 ¹	36	16	20
<i>Lucina prominensis</i> Oppenheim	no available data ^{1,2}	10	10	/
<i>Lucina illyrica</i> Oppenheim	no available data ^{1,2}	1	1	/
<i>Phacoides (Lucinoma) dinaril</i> Kühn	no available data ^{1,2}	3	3	/
<i>Lucina columbella</i> Lamarck	<i>Lucina (Linga) columbella</i> Lamarck 1818 ¹	2	/	2
<i>Lucina heberti</i> Deshayes	no available data ^{1,2}	4	/	4
<i>Lucina elegans</i> Deshayes	<i>Monitilora (Monitilora) elegans</i> DeFrance 1823 ¹	8	/	8
<i>Lucina pulchella</i> Lamarck	<i>Boeuvia pulchella</i> Agassiz 1845 ¹ ; <i>Liralucina lyngei</i> M. Huber, 2015 ²	2	/	2
<i>Lucina scalaris</i> Deshayes	no available data ^{1,2}	6	/	6
<i>Lucina unicata</i> DeFrance	no available data ^{1,2}	1	/	1
<i>Lucina sulcata</i> Lamarck	<i>Cavilucina (Cavilucina) sulcata</i> Lamarck 1806 ¹	6	/	6
<i>Lucina squammula</i> Deshayes	no available data ^{1,2}	4	/	4
<i>Lucina contorta</i> DeFrance	<i>Miltha (Eomiltha) contorta</i> DeFrance 1823 ¹	3	/	3
<i>Lucina gibbosula</i> Lamarck	<i>Gibbolucina (Gibbolucina) gibbosula</i> Lamarck 1806 ¹	13	/	13
<i>Lucina connubrica</i> Lamarck	no available data ^{1,2}	3	/	3
<i>Lucina callosa</i> Deshayes	no available data ^{1,2}	3	/	3
<i>Lucina rigaulti</i> Deshayes	no available data ^{1,2}	6	/	6
<i>Lucina concentrica</i> Deshayes	<i>Codakia (Epilucina) concentrica</i> Lamarck 1806 ¹	9	/	9
<i>Lucina albella</i> Lamarck	<i>Parvilucina (Callucinella) albella</i> Lamarck 1806 ¹	1	/	1
<i>Lucina circinaria</i> Lamarck	no available data ^{1,2}	10	/	10
<i>Lucina lapidum</i> Lamarck	no available data ^{1,2}	3	/	3
<i>Lucina proxima</i> Deshayes	no available data ^{1,2}	11	/	11

4. Results

The descriptive biometric analysis of the measured elements of the height, length and width of the lucinid shells and their morphometric indices can be seen on **Figure 3**.

As presented on **Figure 3**, three groupings can be distinguished: first group make the specimens from the Paris Basin (black dots), second group the specimens from the Imotski-Lažete area (violet rectangulars), and to the third group belong the Lucinidae from Promina Mt. (blue diamonds and red rectangular). Lucinidae from the Paris Basin are smaller in size than the specimens from Croatia, and in size they are similar to the specimens from the Promina Mt. than Imotski area. Lucinidae from Imotski-Lažete are more scattered, bigger in size and less comparable with the samples from the Promina Mt. and the Paris Basin. Specimens from Paris Basin are in all graphs more or less homogenous, and the most scattered are the samples from Imotski-Lažete. As the elongation grows, roundness and convexity have lower values in Lucinidae from Paris Basin, and the samples from Croatia are dispersed. Convexity and roundness are proportional in all specimens, showing higher values in specimens from Croatia (**Figure 3**).

Differences between samples from Croatia (Promina Mt. area and Imotski-Lažete) are visible on **Figure 3** by grouping of those samples, and Imotski-Lažete specimens being more scattered and of bigger dimensions. On **Figure 4** we show the relations between height, length and width of the lucinid shells from Promina Mt. and Imotski-Lažete.

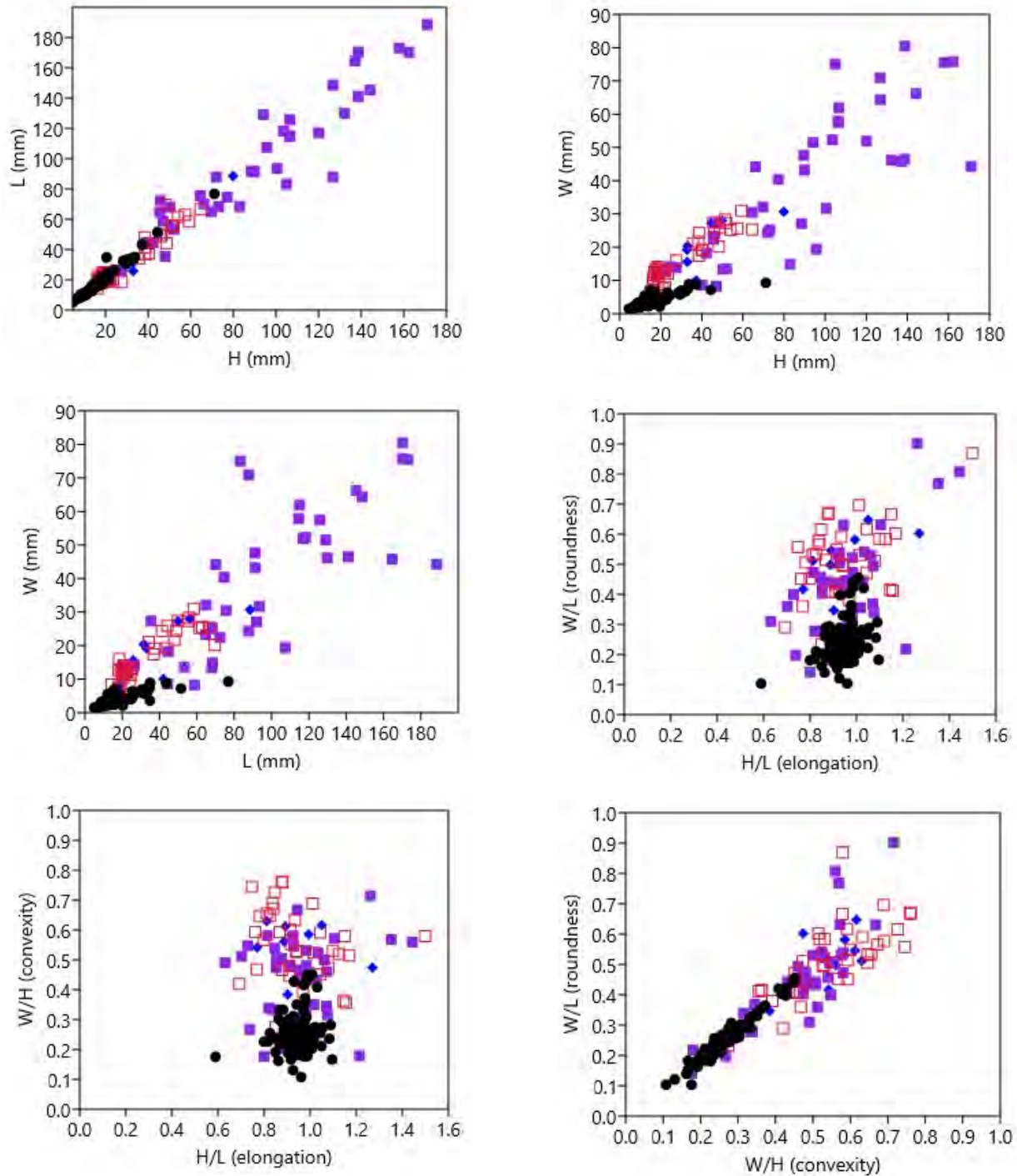


Figure 3: Relations of the measured elements of height (H), length (L) and width (L) of the Lucinidae shells from Promina Mt. (blue diamond, red rectangular; each sign representing one Museum collections), Imotski-Lažete (violet rectangular) and Paris Basin (black dots)

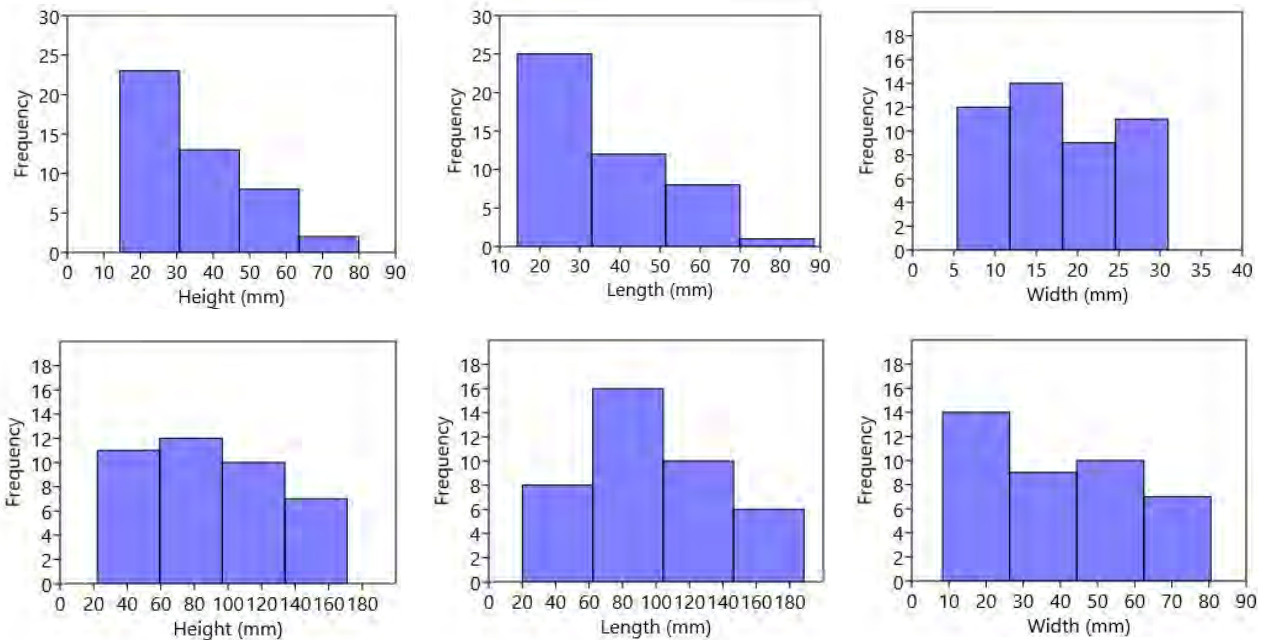


Figure 4: Histograms of height, length and width of the shells of Lucinidae from Promina Mt. (upper row) and Imotski-Lažete (bottom row)

Figure 4 shows differences between the specimens from Croatia. Smaller height range values of Lucinidae show the specimens from Promina Mt., and Lucinidae from Imotski-Lažete have wider range value and they are more or less evenly distributed. The length values of Promina Mt. specimens are similar as the one regarding the height of the shell. Lucinidae from Imotski-Lažete again have wider length value range, but they are not so evenly distributed as in height histogram, here we see more middle values. Value range of the shell width is again narrower for the samples from Promina Mt., but here samples from both localities are more or less evenly distributed, with prevailing smaller values of shell thickness.

The comparison between Lucinidae species present in the Paris Basin and Croatia based on the revision of the names from the Museum inventory book and the fossil databases is shown in **Table 5**. Only two species are mutual to the localities, *Pseudomiltha gigantea* and *Saxolucina saxorum*, two extinct species of the family Lucinidae. To see differences in the sizes of the mutual species, we present the histograms of the *Saxolucina saxorum* shell specimens from Croatia and Paris Basin on **Figure 5**. Since there is only one specimen of *P. gigantea* present in Croatia, the sample size is not sufficient for the histogram plotting.

As presented on **Figure 5**, *S. saxorum* shells from Croatia have a smaller range of height and length values than the specimens from Paris Basin. Looking at the height, they are more or less equally distributed in those ranges, and comparing to the shell length, the specimens are either smaller or bigger. Lucinidae from the Paris Basin have a bigger range of shell height and length values, and they are more homogeneously distributed in the smaller specimens, with a few of them larger. Range of shell width values is higher in lucinids from Croatia, but again the specimens from Paris Basin are more homogenous and show lower values.

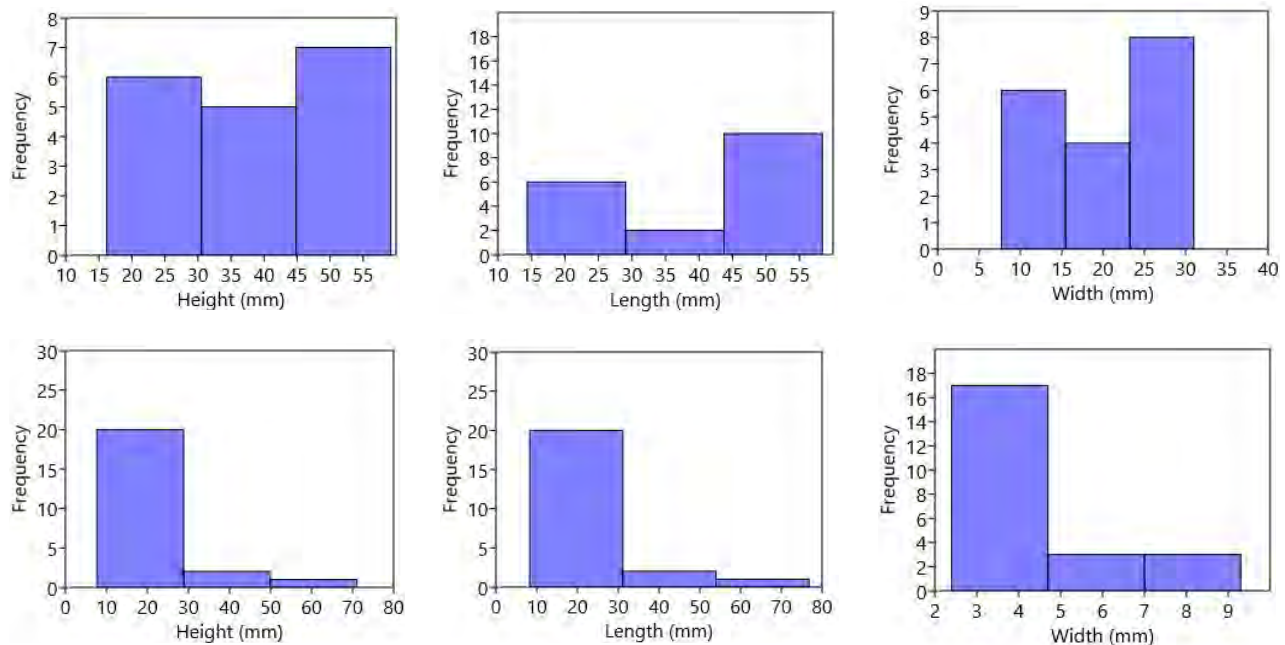


Figure 5: Histograms of height, length and width of the shells of the *Saxolucina saxorum* specimens from Croatia (upper row) and Paris Basin (bottom row)

5. Discussion and Conclusions

Bivalves Lucinidae are today widely distributed in various marine habitats, from the intertidal zone to bathyal depths of over 2100 m, over a broad geographical range (60°N–55°S). As **Taylor and Glover (2006, and references therein)** describe, Lucinidae occur in mangrove muds, intertidal and offshore muds, offshore locations where sunken vegetation accumulates, cold seeps and mud oxygen minimum zones (some species) and a single species from a hydrothermal vent. Lucinidae are very diversified group of bivalves with more than 400 living species, and usually are considered as a shallow water group with recent greatest species richness in the coral reef and seagrass environments of the tropical Atlantic and Indo-West Pacific (**Taylor et al., 2014**). In several families of bivalves, including Lucinidae, the nutritional strategy of chemosymbiosis with sulphide-oxidizing and less commonly methane-oxidizing bacteria is recognized, and the widespread sulphide-rich habitats with chemosymbiotic organisms are the suboxic zones of the marine sediments, where most of the lucinids live (e.g., **Taylor and Glover, 2006; Taylor et al., 2014**).

As presented in chapter Results, there are differences in shell morphology regarding its size between Eocene Lucinidae from Croatia (Promina Mt. and Imotski-Lažete), and from the comparative specimens of the Paris Basin. Samples from Croatian localities have higher height, length and width values, and the samples from Paris Basin showed better grouping in the descriptive analyses being more homogenous in size. Higher values of the measured shell parameters (height, length, width) seen on the samples from Croatia could indicate the more favourable paleoecological conditions that result in the bigger size of the Lucinidae shell. However, more samples are required to get a more precise conclusion. Generally, morphology of a species shell depends on various abiotic and biotic factors, for example latitude, depth, shore level, tidal level, currents, water turbulences, wave exposure, type of bottom, type of sediment, characteristics of the seagrass bed, the density of the population, predation, trophic conditions, burrowing behaviour etc. (e.g., **Derbali et al., 2018 and references therein; Modestin, 2017 and references therein**).

Localities of Promina Mt. and Lažete near Imotski are rich in Lucinidae findings, which are also the most numerous bivalves here recorded. At Lažete locality, near Imotski, „gigantic“ dimensions of Lucinidae shells are recognized, as well as at the nearby Eocene localities (**Sremac et al., 2015**). This big shell sizes are indicative for the period of the Paleocene/Eocene thermal maximum, and Eocene climatic events (**Figure 6**). Eocene malacofauna represented in this paper and previous research by **Sremac et al. (2014, 2015)** is of the Middle and Upper Eocene age (see references in chapter 2). The numerous molluscs recorded in the Eocene deposits of the Promina Mt. and Imotski-

Lažete, including the localities in Sremac et al. (2014, 2015), correspond to the global biodiversity of molluscs during the Eocene (Figure 6).

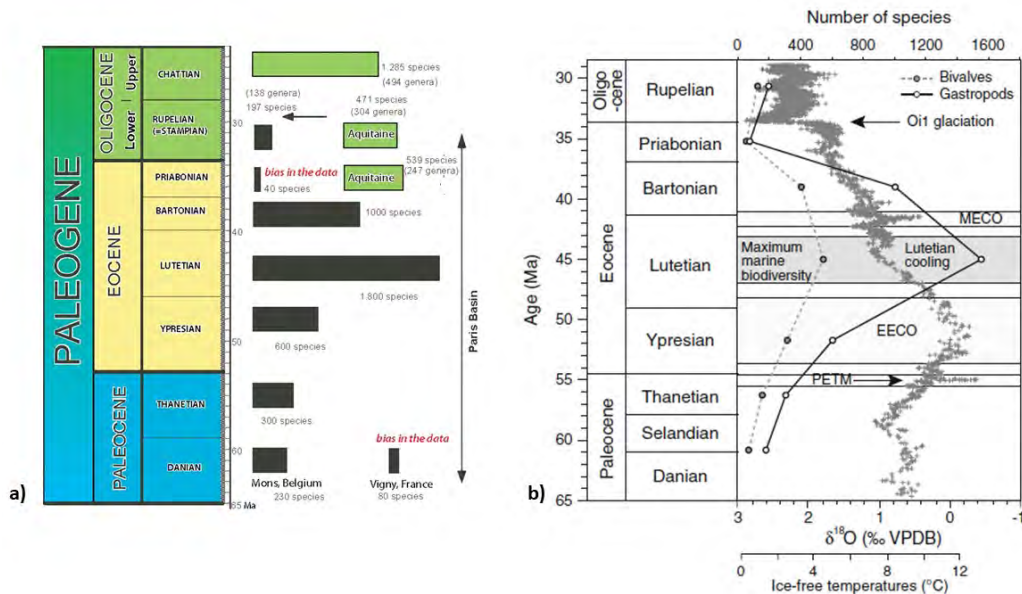


Figure 6: Richness of molluscan fauna during the Eocene compared to the climatic conditions on the example of Paris Basin. a) Gastropods biodiversity after Lozouet (2014); b) Climate events and molluscs species richness during the Eocene after Huyghe et al. (2012).

According to the published papers (e.g., Sakač, 1965; Sakač et al., 1984; Sremac et al., 2014, 2015) we can see that the rich lucinids of the Western Tethys bioprovince findings possibly correspond to the age of the Eocene „bloom“ during the Lutetian, Middle Eocene climatic optimum, and gradual decrease of the molluscs biodiversity after the Lutetian (Figure 6). Lutetian molluscan fauna of the Paris Basin is one of the finest in the world and records the greatest Cenozoic shallow-water marine biodiversity, with around 2700 marine species, of which 1500 species belong to gastropods and 540 to bivalve species (e.g., Lozouet, 2014; Huyghe et al., 2012) (Figure 6). After Huyghe et al. (2012) Lutetian was a warm period in the Paris Basin, with mean annual temperatures around 20°C, maximum summer temperatures close to 30°C and mild winters, and the southern part of the Mediterranean Sea could be considered as a modern model of the Lutetian climate of the Paris Basin. To get more insight into the Eocene malacofauna and paleoecology, comparisons with other localities are necessary. For example, Huyghe et al. (2012) considered the island arcs of the western Tethys as the centres of a large hotspot, analogue to the today's Indo-Pacific biota, and the Lutetian malacofauna of the northern Italy as a comparison with the Paris Basin.

As we presented in this paper, Lucinidae findings in the Eocene of Croatia are rich, and the biometrical analyses showed differences in shell morphology not only among the localities in Croatia, but also among the specimens from the comparative locality of the Paris Basin. The differences can be a product of numerous factors, and for the further research of the Eocene malacofauna from Croatia the first step is the revision of the Lucinidae specimens to see the distribution of the species and the mutual records with other representative localities in Europe. The concluding step to our further work is the comparison with the molluscs from the other contemporaneous nearby Eocene localities, as it is started by Sremac et al. (2014), to fulfil the current knowledge on the paleoenvironments of Croatia and paleoecological conditions during the Eocene.

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SAŽETAK

Biometrijska analiza eocenskih školjkaša Lucinidae iz Hrvatske

Na eocenskim lokalitetima na području Promine i Imotskog (Lažete) u Hrvatskoj prikupljeni su brojni primjerci morskih školjkaša iz familije Lucinidae. Primjerci se danas čuvaju u Hrvatskom prirodoslovnom muzeju u Zagrebu. Na temelju mjera ljuštura lucinida napravljena je biometrijska analiza kako bi se usporedile morfometrijske karakteristike visine, širine i debljine ljuštura primjeraka na lokalitetima u Hrvatskoj, kao i komparativnih primjeraka iz Pariškog bazena koji se čuvaju u Muzeju. Morfometrijske analize pokazale su razlike između primjeraka iz Hrvatske, koji se također razlikuju i od primjeraka iz Pariškog bazena. Lucinide iz Hrvatske imaju veće morfometrijske vrijednosti i ukazuju na moguće povoljnije paleoekološke uvjete za veći rast ljuštura školjkaša. Ovaj rad predstavlja prvi korak u daljnjoj biometrijskoj analizi eocenske malakofaune prikupljene na području Hrvatske i njezine usporedbe sa susjednim istovremenim lokalitetima.

Ključne riječi: biometrija, Lucinidae, eocen, Hrvatska

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Author's contribution

Marija Bošnjak (1) (Dr, senior curator, paleontology, geomathematics) provided the biometry analysis, preparation of computer graphs and the graphics, comparison, interpretation and presentation of the results. **Nediljka Prlj Šimić (2)** (Mr.sc., senior curator, paleontology, geomathematics) provided the measuring of 204 Lucinidae shells, revision of 26 Lucinidae species names, methodological data, comparison and presentation of the results. **Jasenka Sremac (3)** (Dr, Full Professor, geology, paleontology, paleoenvironment) provided the comparison of data, interpretation and presentation of the results.