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Comparison of regional intraspecific differences in shell size in the Jordanian desert snails *Sphincterochila fimbriata*, *S. zonata* and *S. prophetarum* (Gastropoda: Pulmonata).

verfasst von / submitted by

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1 Abstract

The land snail species *Sphincterochila fimbriata, S. zonata* and *S. prophetarum* found in the Jordanian desert each show intraspecific differences in shell volume at different collection sites. This study tries to find out whether these differences are significant and, if so, to find the ecological reasons behind these differences. Significant differences in intraspecific shell volume were found. Abiotic factors like precipitation, temperature, latitude and altitude at the collecting sites were analysed to see whether they have an influence on shell growth.

2 Zusammenfassung

Die in der jordanischen Wüste vorkommenden Schneckenarten *Sphincterochila fimbriata, S. zonata* und *S. prophetarum* zeigen an verschiedenen Fundorten einen innerartlichen Unterschied der Gehäusevolumina. Diese Arbeit versucht herauszufinden, ob diese Unterschiede signifikant sind, und wenn dem so ist, die ökologischen Faktoren, die zu diesen Unterschieden führen, zu eruieren. Signifikante Unterschiede der Gehäusevolumina konnten nachgewiesen werden. Abiotische Faktoren wie Niederschlag, Temperatur, geographische Breite und Höhe der Fundorte wurden verwendet, um einen möglichen Zusammenhang mit den Gehäusevolumina herzustellen.

3 Introduction

The desert, as an extreme habitat, demands a variety of adaptations from animals to successfully live in it.

For hydrophilic animals, such as terrestrial gastropods, with their permeable skin and their locomotion on moist mucus trails (Moreno-Rueda, 2007), arid environments are demanding habitats as the rate of water loss for these animals is equal to that of a free water surface (Heller, 1988). Adaptations for water and heat management are crucial (Goikas et al., 2014).

Facing problems like high solar radiation, high ground temperatures, high evaporation and low relative humidity (Nevo et al., 1981) as well as a scarce vegetation (Moreno-Rueda, 2007), terrestrial gastropods living in the desert have to come up with a number of behavioural, morphological, physiological and biochemical adaptations and can be designated as one of the most adapted invertebrates (Mizrahi, 2012; Alon, 2007).

The genus *Sphincterochila* (Gastropoda, Pulmonata, Stylommatophora, Helicoidea, Sphincterochilidae) is found from northern Africa to Greece, the south of France and Italy, including Malta, southern Turkey and the Iberian Peninsula (Abbes et al., 2011). The distribution of species genus *Sphincterochila* suggests a connection with annual rainfall (Nevo et al., 1983; Heller, 1988). The populations are sedentary, and gene flow within populations is restricted. As individuals of *S. fimbriata* and *S. zonata* only move up to 20m per year, an intense micro-geographical differentiation can be expected (Nevo et al., 1983).

In addition, the snails' habitats are isolated as the snails lack the ability to close distances over sandy substrate and live mostly on peak plateaus of rock towers.

However, on wet sand during the rainfalls in winter it seems to be certainly possible for snails to cover longer distances (Waitzbauer 2019, verbal statement).

To overcome extreme heat and the absence of water for most of the year and, therefore, limited food resources, snails of the genus *Sphincterochila* show cycles of activity and aestivation throughout the year (Arad et al., 2010; Mizrahi, 2012).

During aestivation, the snails are retracted into their shells. The metabolism is slowed down to minimize water loss (Nopp, 1974). In addition, a thick epiphragm is produced to seal the aperture to reduce water loss even more (Arad et al., 1989). Water loss through the snails' shell is relatively low (Nopp, 1974).

During aestivation, the oxygen consumption of *S. zonata* is discontinuous (Fig. 01) and at times even too low to be registered. This is followed by periods of increased respiratory activity. Under these conditions, snails can aestivate for up to four years. Water and weight loss during aestivation

are reduced to a minimum. *S. zonata* loses 0.1 to 0.2‰ of their total bodyweight per day.
Aestivation in snails is not only an avoidance of unfavourable conditions.
This adaption in xerophile snail species in the form of changes in activity and inactivity (aestivation) is needed, and these snails would not thrive under too moist conditions (Nopp, 1974).

The snails are active from November to April while aestivating the rest of the year. Reproduction also takes place during these active months. However, activity can also be observed with the appearance of night dew in the time from August to October (Yom-Tov & Galun, 1971).
Apart from their pattern of activity, they show adaptations to desiccation in the form of a favourable volume to surface ratio as well as the shell's properties regarding heat flow and temperature distribution, which creates a beneficial microclimate (Fig. 02) (Nopp, 1974; Arad et al., 1989). In addition, the white shell and its reflective properties, often observed in xerophile snails, lead to a reflection of up to 95% of the sun's radiation. This is the reason for the difference in temperature of the snail in comparison to its surroundings of up to 15°C (Nopp, 1974).

Out of the three species collected, *S. zonata* seems to be the best adapted to desiccation. It shows a high lethal body temperature; specimen of *S. zonata* can survive 50°C for up to eight hours (Nopp, 1974). Together with *S. fimbriata*, whose adaptation to desiccation is in the middle between *S. zonata* and *S. prophetarum*, it has the smallest aperture to shell size ratio of the three species. Apart from the narrowing of the aperture, which reduces water loss (Heller, 1988), also a thickening of the shell as an additional protection against water loss is noticeable in *S. zonata* compared to *S. fimbriata* (Waitzbauer & Petutschnig 2004). The water economy of *S. prophetarum* is more suited for Mediterranean climates. Being an understone dweller, it overcomes its disadvantage of physiological adaptation to desiccation by selecting stony habitats where, beneath the stones, microclimates are beneficial (Arad et al., 1989).

Sphincterochila zonata (Bourguignat, 1853) is a simultaneous hermaphrodite (Alon, 2007) that reaches sexual maturity with approximately three years (Shachak et al., 1981). Individuals can reach an age of up to eleven years (Shachak & Steinberger, 1980). The snails aestivate buried in the sand in a depth of about 1cm to 5cm (Yom-Tov & Galun, 1971) up to even 20cm (Waitzbauer 2019, verbal statement). Their weight is about 4g to 5g, half of which is the soft body, which consists of 80 to 90% water (Yom-Tov, 1970). Activity is shown at temperatures ranging from 5°C to 29°C and a relative humidity of 30% to 100%.

The snails lay their eggs whenever it rains more than 3mm during their period of activity until the last rains in the end of March. They dig holes approximately 3,5cm deep in the wet soil that widen to form a “laying room”. *S. zonata* produces a mucid saccule, which is hung in this “laying room” without touching the walls. The incubation time for *S. zonata* is 21 to 28 days. Juvenile snails stay in the hole until the following winter.

The food sources of *Sphincterochila* found in literature differ.
According to Shachak and Steinberger (1980), *Sphincterochila* feeds on algae exclusively. It is a soil eater feeding on soil crust algae that grow on the ground surface after the winter rainfalls and is, thereby, also helping the algae’s dispersal. Not all algae are digested. Transported by the snails and excreted, the still alive algae can colonise new patches (Shachak & Steinberger, 1980). Yom-Tov (1970) and Schmidt-Nielson, Taylor and Shkolnik (1971) state that the snails also feed on lichens. According to Yom-Tov (1971), *Sphincterochila zonata* feeds mainly on lichens and soil algae. Slotow and Ward (1992, 1997) state that the snails change from feeding on vascular plants to algae as soon as rainfalls provide enough moisture for algae growth as algae are the snails’ preferred food source.

S. prophetarum starts its activity when the soil moisture reaches a level of 3%, which also is the threshold at which algae growth can start (Steinberger et al., 1981).
According to Slotow and Ward (1997), algae are the snails’ main food source and, therefore, the main resource of $CaCO_3$, which is needed for shell growth (Slotow & Ward, 1997). Experiments have shown that snails living under moister conditions grow more in comparison to snails living under dryer conditions (Slotow & Ward, 1992), and, therefore, moisture seems to have a strong effect on the body size (Stiven, 1989). But terrestrial snails cover their calcium needs not only through the ingestion of calcium through food. In addition, they use their radula to take in calcium from limestone or empty snail shells or eat soil directly (Nopp, 1974).

The shell size is both influenced by the genetic background and abiotic variables (Kappes, 2009). Abiotic factors like mean annual temperature, mean annual precipitation and altitude could explain intraspecific differences in size.
When young specimens of *Cepaea nemoralis* collected from sites with different adult shell sizes are reared under laboratory conditions, they lose the inter-site difference in shell size. This suggests a strong correlation between environmental factors and snail shell size (Stiven & Foster, 1996).
In deserts, the primary production is depending on precipitation, and one can expect a positive correlation between body size and precipitation values (Yom-Tov & Geffen, 2006).

This thesis wants to give a closer insight regarding possible reasons for intraspecific differences in shell volume of *S. zonata, S. fimbriata* and *S. prophetarum* collected in the Jordanian desert at different locations. A strong correlation between differences in intraspecific shell sizes and variances in the species' environment can be expected (Proćków et al., 2017). The hypothesis is that shell volumes increase depending on the amount of mean annual precipitation, due to a greater availability of food and, therefore, a greater availability of $CaCO_3$.

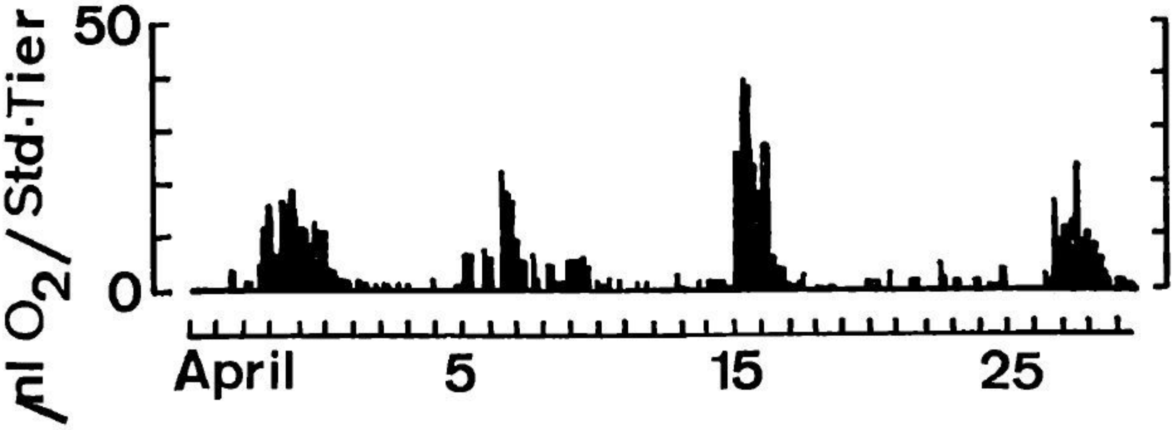

Fig. 01: Oxygen consumption of *S. zonata* over a four-week period (Temp. 15°C, constant light) (Nopp, 1974).

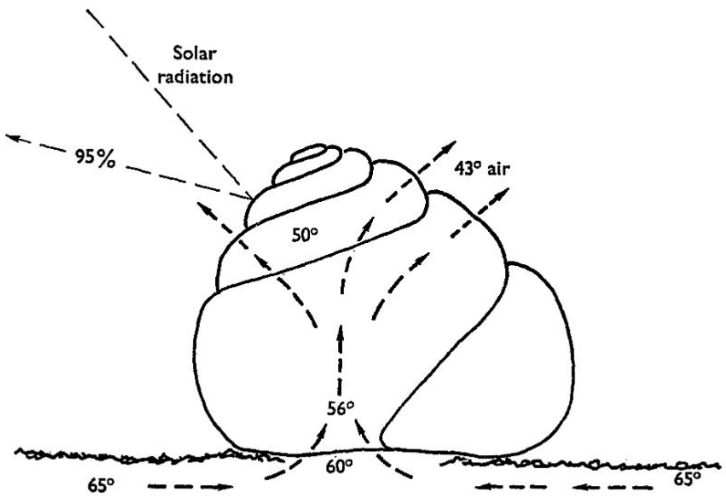

Fig. 02: Shell heat flow and temperature distribution of *S. zonata* (Schmidt-Nielsen et al., 1971).

4 Material and Methods

4.1 Material Collection

In total, 652 snail shells were measured. 323 shells of *S. prophetarum* were collected during an excursion to the Jordanian desert in 2014. They were brought back to Vienna and determined to species level. In addition, 329 shells of *S. zonata* (111), *S. fimbriata* (116) and *S. prophetarum* (102), collected and determined by Univ.-Prof. Dr. Wolfgang Waitzbauer in the years from 1996 to 2010 (stored in the Natural History Museum Vienna), were included in the study.

Location	Coordinates Collection Points	Found species	Number of collected shells
A	31°52`48`` N 36°49`52`` E	*S. zonata*	54
B	32°10`00`` N 36°28`00`` E	*S. zonata*	43
C	31°28`00`` N 35°35`00`` E	*S. fimbriata*	20
D	29°29`11`` N 35°11`55`` E	*S. prophetarum*	168
E	29°28`48`` N 35°17`00`` E	*S. prophetarum*	148
F	31°48`00`` N 36°35`00`` E	*S. fimbriata*	23
G	29°28`00`` N 35°19`00`` E	*S. prophetarum*	109
H	31°00`00`` N 35°30`00`` E	*S. fimbriata*	29
I	32°11`35`` N 37°07`36`` E	*S. fimbriata / S. zonata*	44 / 14

Tab. 01: Number of shells found at the collection points.

Collected data included: height and width of the shells, mean annual temperature, mean annual precipitation as well as altitude and latitude of the collection sites.
Values for mean annual precipitation and mean annual temperature have been taken from literature (Tarawneh & Kadioglu, 2003; Waitzbauer & Petutschnig, 2004).
Values for latitude and altitude have been collected via GPS at the collection sites.
Distances between measuring stations and collection points have been calculated with http://www.movable-type.co.uk/scripts/latlong.html.

Location	Coordinates Collection Points	Coordinates Measuring station	Distance between Collection point and Measuring station	Found species	Mean annual Precipitation (mm/y)	Mean annual Temperature (°C)	Altitude (m.a.s.l.)
A	31°52`48`` N 36°49`52`` E	31°49`N 36°49`E	6 km	*S. zonata*	60	20	630
B	32°10`00`` N 36°28`00`` E	32°21`N 36°15`E	29 km	*S. zonata*	155	18	676
C	31°28`00`` N 35°35`00`` E	31°02`N 35°28`E	49 km	*S. fimbriata*	75	24	350
D	29°29`11`` N 35°11`55`` E	29°33`N 35°00`E	19 km	*S. prophetarum*	31	22	722
E	29°28`48`` N 35°17`00`` E	29°33`N 35°00`E	29 km	*S. prophetarum*	31	22	860
F	31°48`00`` N 36°35`00`` E	31°49`N 36°49`E	22 km	*S. fimbriata*	60	20	600
G	29°28`00`` N 35°19`00`` E	29°33`N 35°00`E	32 km	*S. prophetarum*	31	22	878
H	31°00`00`` N 35°30`00`` E	31°02`N 35°28`E	5 km	*S. fimbriata*	75	22	430
I	32°11`35`` N 37°07`36`` E	32°12`N 37°07`E	2 km	*S. fimbriata / S. zonata*	72	20	680

Tab. 02: Details regarding the position and abiotic factors of the collection sites.

Description of the collection sites:

A NE Jordan, 10km east of Azraq, flat, rocky basalt desert (Harra) with hardened sandy ground, grazed vegetation, stones covered by rock lichens, wind-exposed, very dry, winter rain between November and January

B NE Jordan, As Safawi, flat, rocky basalt desert (Harra) with hardened sandy ground, large sandy areas between the basalt rocks, grazed vegetation, stones covered by rock lichens, wind-exposed, very dry, winter rain between November and January

C S Jordan, Mujib Nat. Res. near the Dead Sea, semi-desert, loamy hills on top of lime, free of vegetation, very dry

D S Jordan, Wadi Emran, dry, stony riverbed with extended coarse sandy alluvial fans adjacent to hilly landscape, loam over granite, scarce vegetation (grazing)

E S Jordan, Wadi Rum, Rab Anta, sand dunes, small Wadid valleys between high rock faces, shells have been collected at the foot of these rock faces (washed/blown down)

F NE Jordan, Wadi Butm, near Qasr Amra, Wadi with puddles of water, partially Hamada or loamy/sandy ground, *Retama raetam* and scattered *Pistazia atlantica*

G S Jordan, Wadi Rum (Rska area), sand dunes, small Wadi valleys between high rock faces, sandy areas between high rocks and flat shelfs (sandstone), little vegetation, shells have been collected at the foot of these rock faces (washed/blown down)

H Wadi al Hasa, loamy, stony Hamada, degraded vegetation

I NE Jordan, Tulu al Ashagif, rugged, basalt, rocky landscape, covered by lichens, sand dunes

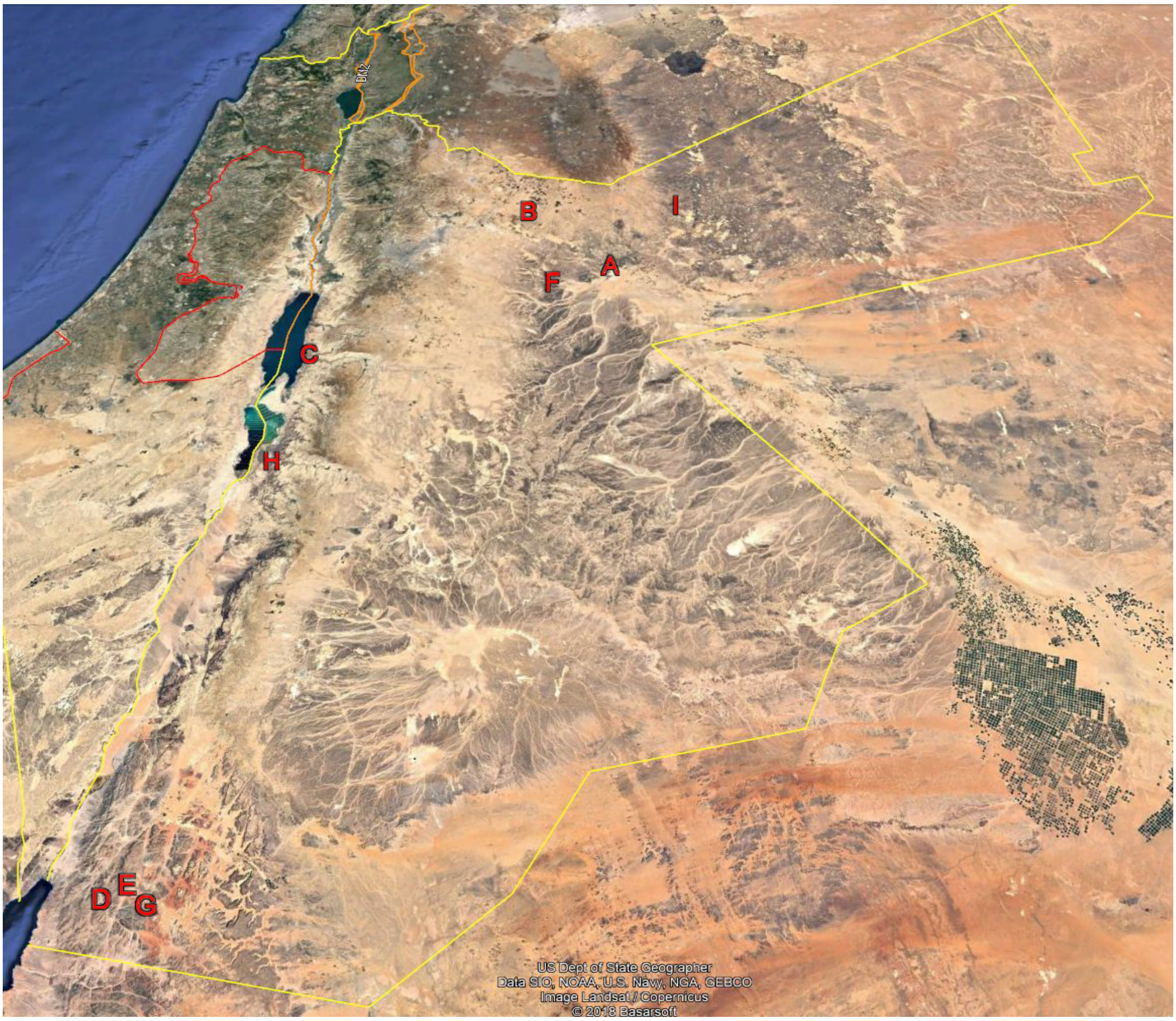

Fig. 03: Map of Jordan showing the collection sites (Google Earth Pro, v 7.3.2.5776).

Sphincterochila prophetarum (Fig. 04)

4–5 whorls; white, glossy, medium-sized shell

Diameter: 16–20mm

(Neubert et al., 2015)

Fig. 04: *Sphincterochila prophetarum* (Neubert et al., 2015)

Sphincterochila fimbriata (Fig. 05)

5–6 whorls; cream-whitish, medium-sized shell

Diameter: 13.4–26.6mm

(Neubert et al., 2015)

Fig. 05: *Sphincterochila fimbriata* (Neubert et al., 2015)

A giant form of this species can be found in Wadi Butm, Jordan (Neubert et al., 2015). *S. fimbriata* collected at location F (Wadi Butm) seems to be this giant form (highest measured diameter at location F: 27.12mm). The mean shell volume is twice as high compared to other locations where this species was collected (location H: average shell volume of 4420.44mm³, location F: 9181.06mm³).

Sphincterochila zonata (Fig. 06)

5–6 whorls; thick, white, glossy, large-sized shell

Diameter: 20–26mm

(Neubert et al., 2015)

Fig. 06: *Sphincterochila zonata* (Neubert et al., 2015)

4.2 Measurement and Species Determination

The determination of the species was carried out by Eike Neubert (Natural History Museum Basel, Switzerland), Zuhair Amr (Jordan University of Science & Technology, Irbid, Jordan) and Anita Eschner (Museum of Natural History, Vienna, Austria).

Height and width were measured (Fig. 07) with a digital calliper (Model M47, Steiner-Feinmechanik, Salzburg). Volumes were calculated (H*W*W).

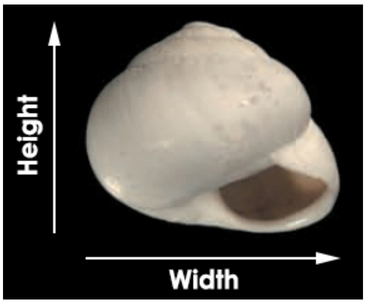

Fig. 07: Height and width taken from a shell (following Neubert et al., 2015).

4.3 Statistics

Statgraphics Centurion XVII Version 17.2.05 (Statpoint Technologies, Inc.) was used to analyse the collected data. Volumes were calculated. Volumes higher than 30,000mm³ (one data point) were considered to be measurement errors and have, thus, been excluded from the statistical analysis.
At location F, only *Sphincterochila fimbriata* was found. This location was not included in all of the comparative statistical analyses and will be discussed separately.
Intraspecific shell volume differences were evaluated by means of the One-Way ANOVA level of significance 95% (multiple range test, LSD). The graphs feature individual confidence intervals (level of significance: 95%).

5 Results

5.1 *Sphincterochila prophetarum*

S. prophetarum was found at three different locations (D, E, G). The difference in shell volumes at the three locations is significant: location H with a mean volume of 2735.36 mm³, location F with a mean volume of 2562.16 mm³, location E with a mean volume of 2414.81mm³ (Fig. 08).
All of the three locations show both the same mean annual precipitation (31mm) and the same mean annual temperature (22°C). So instead of comparing locations regarding these two factors, only the distribution of volumes at these conditions could be shown. The average shell volume of *S. prophetarum* under these conditions is 2547.89mm³ (Fig. 09).
All three locations differ in altitude: location D, 722m a.s.l.; location E, 860m a.s.l.; location G, 878m a.s.l. (Fig. 10).
Although the difference in latitude is fairly small, it was still taken under consideration to include all possible abiotic factors in the analysis: location G, 29°28′N; location E, 29°28′N, location D, 29°29′N (Fig. 11).

5.2 *Sphincterochila zonata*

S. zonata was found at three locations (A, B, I). At these locations, the difference in shell volume is significant: location A with a mean volume of 3307.6mm³; location B with a mean volume of 2486.33mm³; location I with a mean volume of 4989.72mm³ (Fig 12).
S. zonata was only found in two different ranges of mean annual temperature: location A and I, 20°C mean annual temperature; location B, 18°C mean annual temperature. Within these two ranges, the difference in average shell volume of *S. zonata* is significant. The average shell volume at a mean annual temperature of 18°C is 2486.33mm³. The average shell volume at a mean annual temperature of 20°C is 3653.92mm³ (Fig. 13).
All three locations where *S. zonata* was found differ in mean annual precipitation: location A, 60 mm/y; location I, 72mm/year; location B, 155mm/year (Fig. 14).
There is a small difference in altitude at all three locations: location A, 630 m a.s.l.; location I, 680 m a.s.l.; location B, 676 m a.s.l. (Fig 15).
The three locations also differ in latitude: location A, 36°49′N; location I, 32°11′N; location B, 32°10′N (Fig 16).

5.3 *Sphincterochila fimbriata*

S. fimbriata was found at four locations. Only some show a significant difference in shell volume. Location C and I as well as location H form homogeneous groups. Location F shows a significant difference in shell volumes compared to all the other locations (giant form).

Location H, average shell volume of 4420.44mm³; location I, 2184.67mm³; location C, 2137.02mm³; location F, 9181.06mm³ (Fig. 17).

As location F shows very different volumes in comparison to the other locations (giant form), it was not integrated in the statistical analyses and will be discussed separately.

S. fimbriata was found in three different ranges of mean annual temperature: location I with a mean annual temperature of 20°C; location H with a mean annual temperature of 22°C; location C with a mean annual temperature of 24°C. Within those ranges, the shell volumes form two significantly different homogeneous groups. The average shell volume in the range of a mean annual temperature of 22°C (4603.94mm³) is significantly different compared to the shells found in the mean annual temperature ranges of 20°C (2184.67mm³) and 24°C (2137.02mm³) (Fig. 18).

If location F with a mean annual temperature of 20°C is included in the statistical analysis the volumes still form two homogeneous groups but now in different temperature ranges, one at a mean annual temperature of 24°C (average shell volume of 2137.02mm³) and the other at a mean annual temperature of 20°C (average shell volume of 4586.42mm³) and 22°C (average shell volume of 4603.94mm³) (Fig. 19).

S. fimbriata was found in two different ranges of mean annual precipitation: location I, 72mm/y; locations C and J, 75mm/y. The shell volumes form two homogeneous groups. Location I forms the first group. The second group is formed by location C and H, which share the same mean annual precipitation values (Fig. 20).

If location F with a mean annual precipitation of 60mm/y is included in the statistical analysis, another homogeneous group, location F, is formed (Fig. 21).

S. fimbriata was found in three different altitudes (excluding location F). The shell volumes form two homogeneous groups. The average shell volumes at 350m a.s.l. (2137.02mm³) and 680m a.s.l. (2184.67mm³) form the first homogeneous group. The average shell volume at 430m a.s.l. (4420.44mm³) forms the second homogeneous group (Fig. 22).

If location F is included in the statistical analysis, the average shell volumes at different sea levels now form three homogeneous groups, adding another homogeneous group at an altitude of 600m a.s.l. with an average shell volume of 9181.06mm³ (Fig. 23).

The three locations where *S. fimbriata* was found differ in latitude (excluding location F). Location C (31°28′N) and I (32°11′N) form the first homogeneous group. Location H (31°00′N) forms a second homogeneous group (Fig. 24).

If location F (31°48′N) is included in the statistical analysis, a third homogeneous group is formed (Fig. 25).

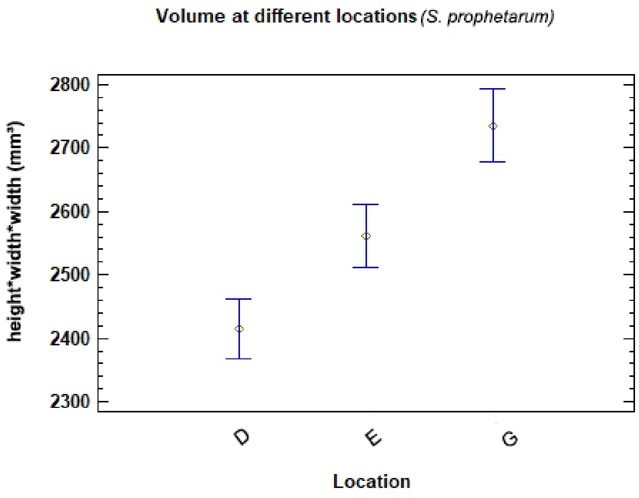

Fig. 08: Shell volume of *S. prophetarum* at three collection sites.

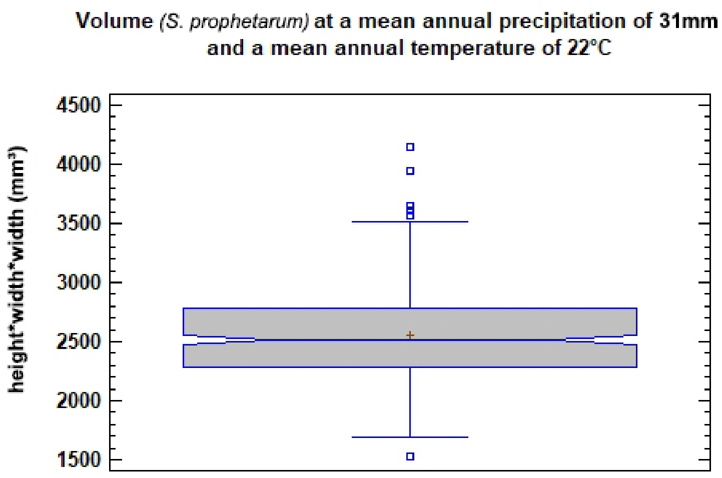

Fig. 09: Distribution of shell volume of *S. prophetarum* under the given condition of mean annual precipitation and mean annual temperature.

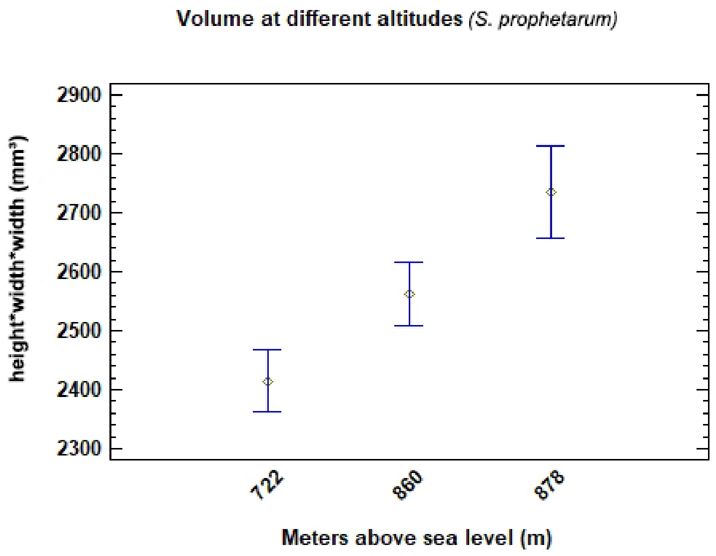

Fig. 10: Shell volume of *S. prophetarum* at different altitudes.

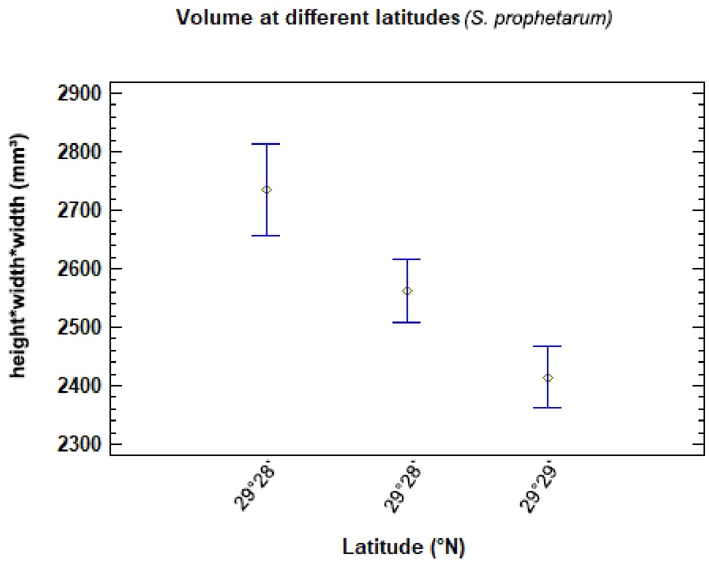

Fig. 11: Shell volume of *S. prophetarum* at different latitudes.

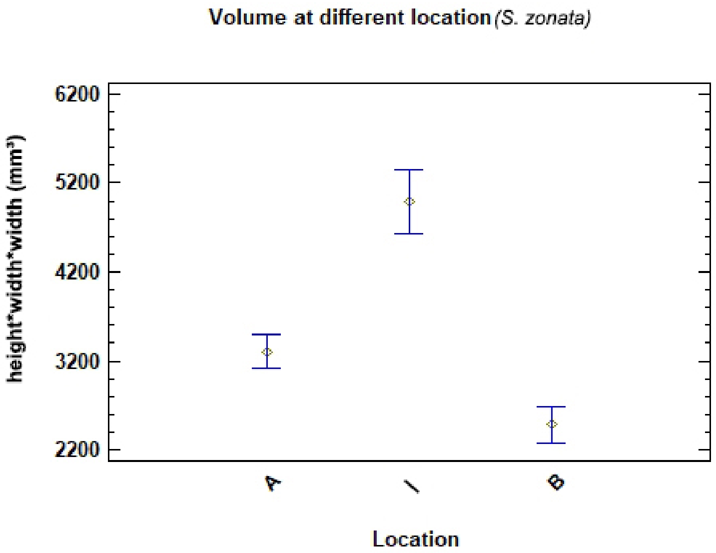

Fig. 12: Shell volumes of *S. zonata* at three collection sites.

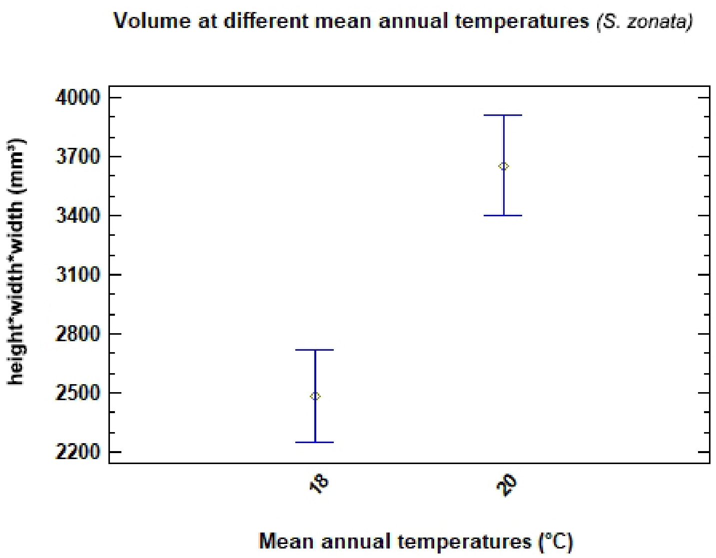

Fig. 13: Shell volume of *S. zonata* at different mean annual temperatures.

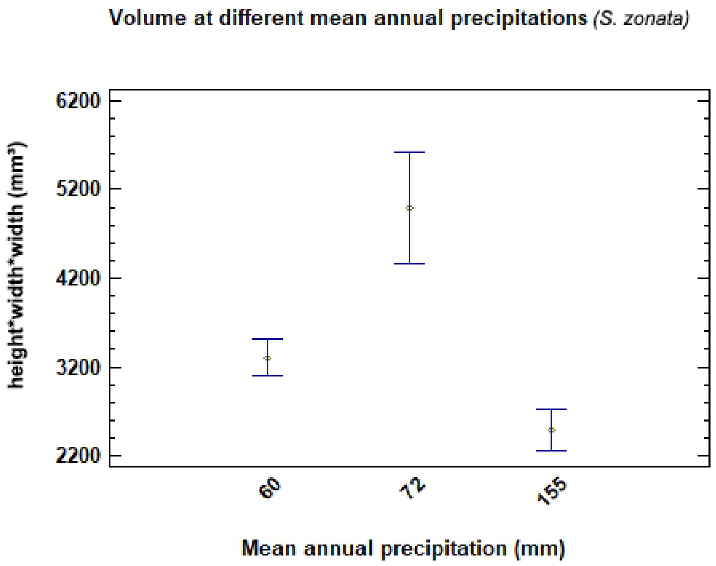

Fig. 14: Shell volume of *S. zonata* at different mean annual precipitations.

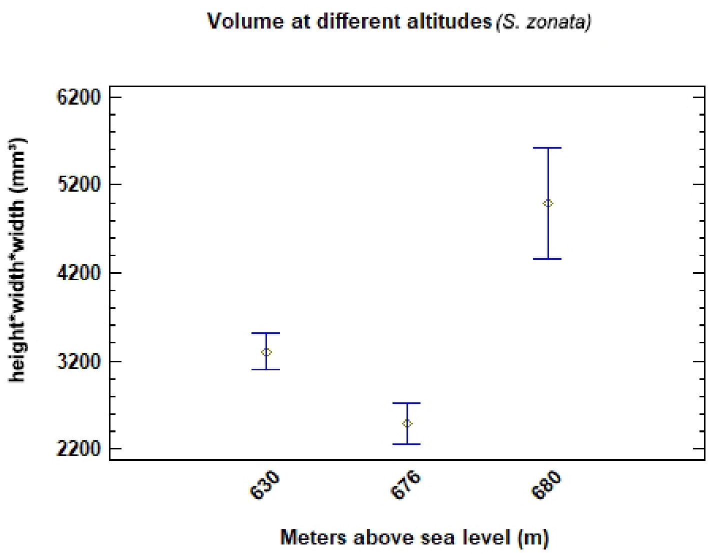

Fig. 15: Shell volume of *S. zonata* at different altitudes.

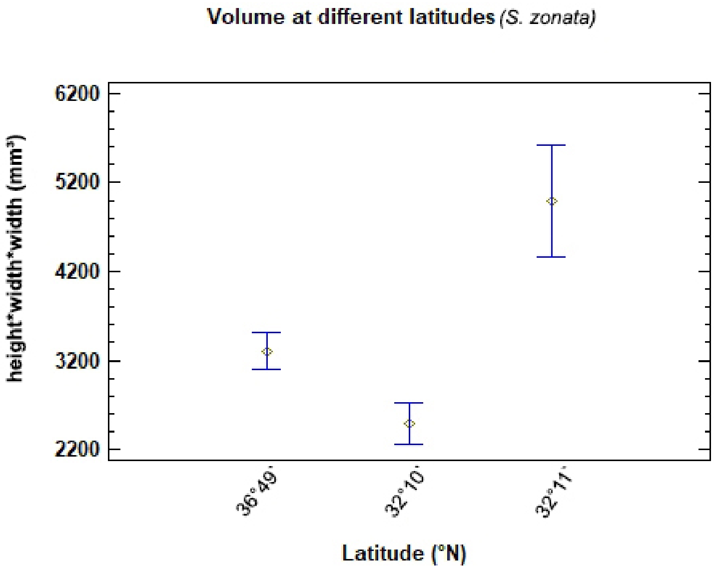

Fig. 16: Shell volume of *S. zonata* at different latitudes.

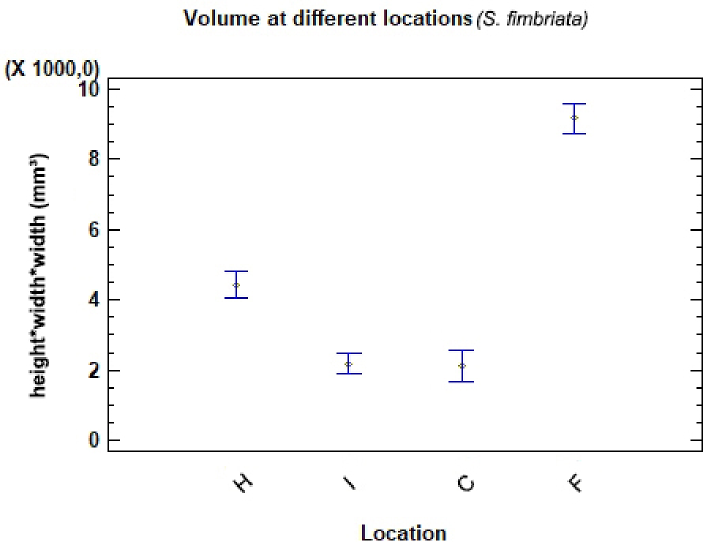

Fig. 17: Shell volume of *S. fimbriata* at four collection sites.

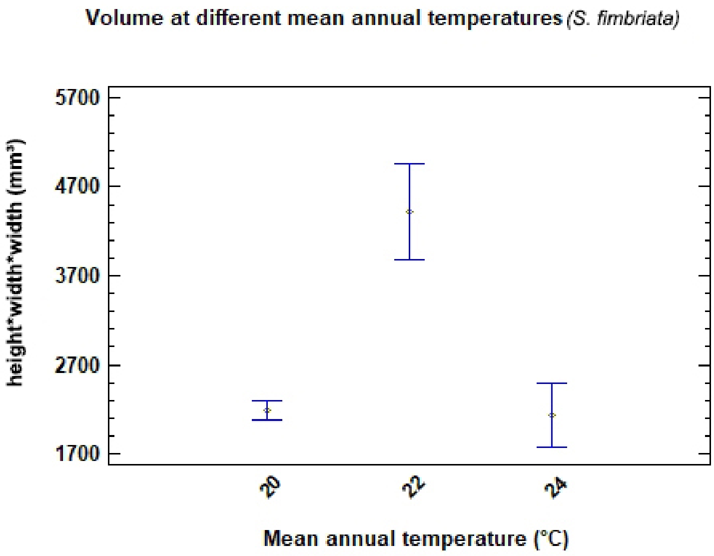

Fig. 18: Shell volume of *S. fimbriata* at different mean annual temperatures.

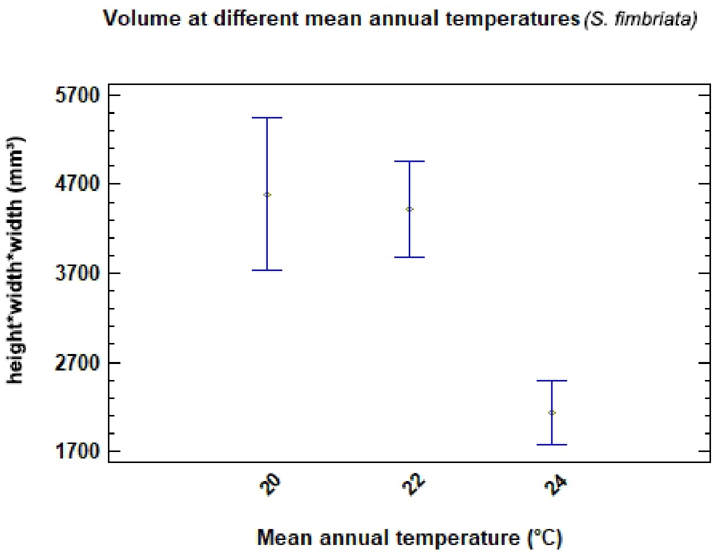

Fig. 19: Shell volume of *S. fimbriata* at different mean annual temperatures, including location F.

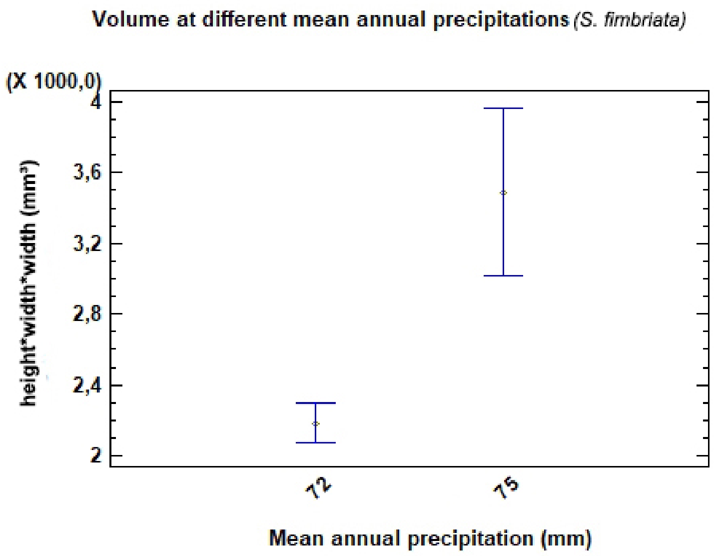

Fig 20: Shell volume of *S. fimbriata* at different mean annual precipitations.

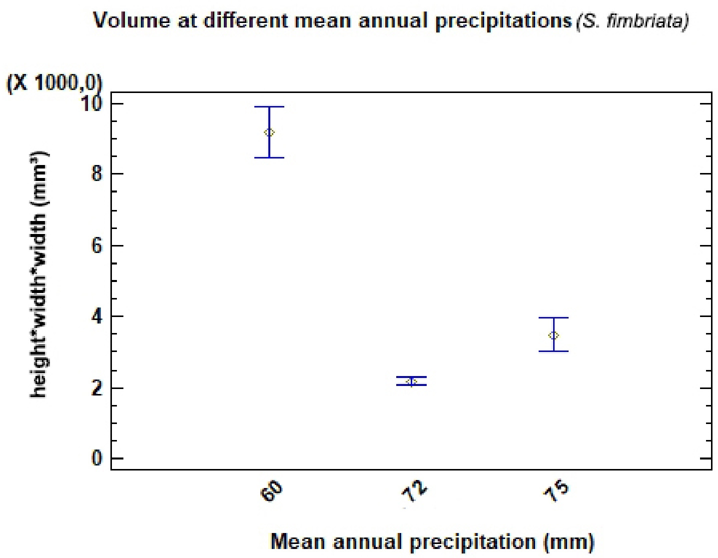

Fig. 21: Shell volume of *S. fimbriata* at different mean annual precipitations, including location F.

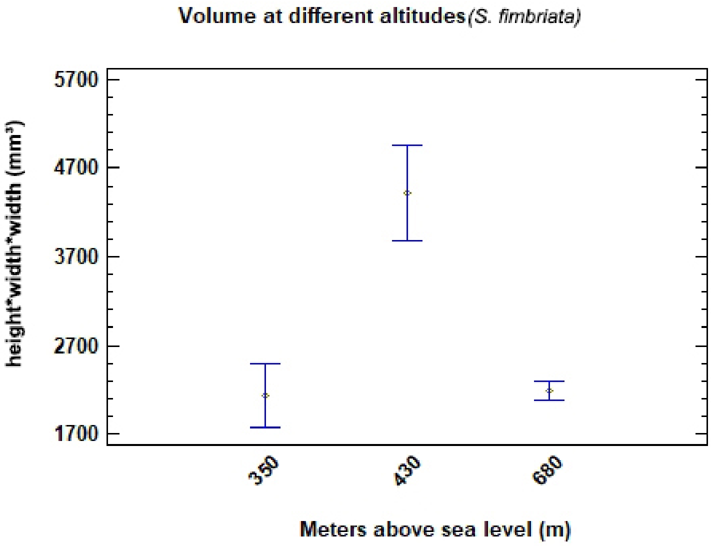

Fig. 22: Shell volume of *S. fimbriata* at different altitudes.

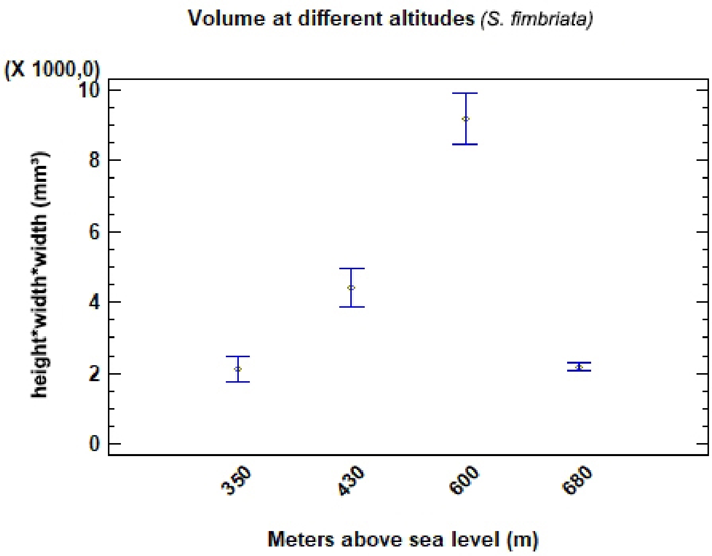

Fig. 23: Shell volume of *S. fimbriata* at different altitudes, including location F.

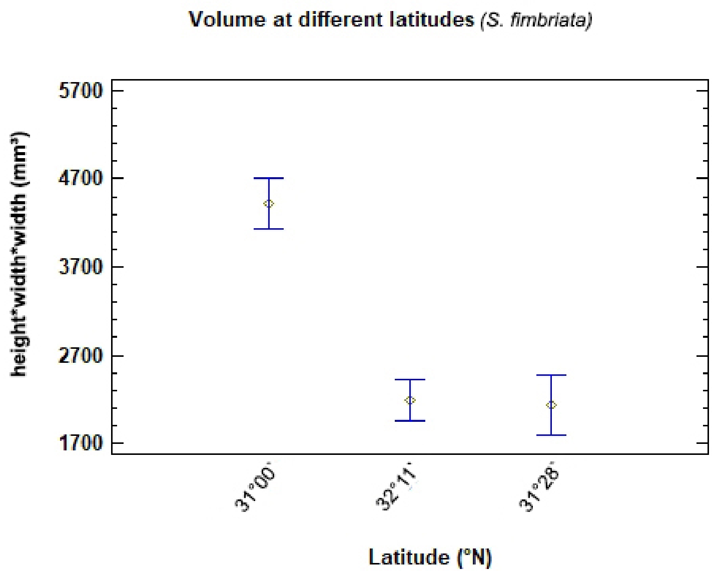

Fig. 24: Shell volume of *S. fimbriata* at different latitudes.

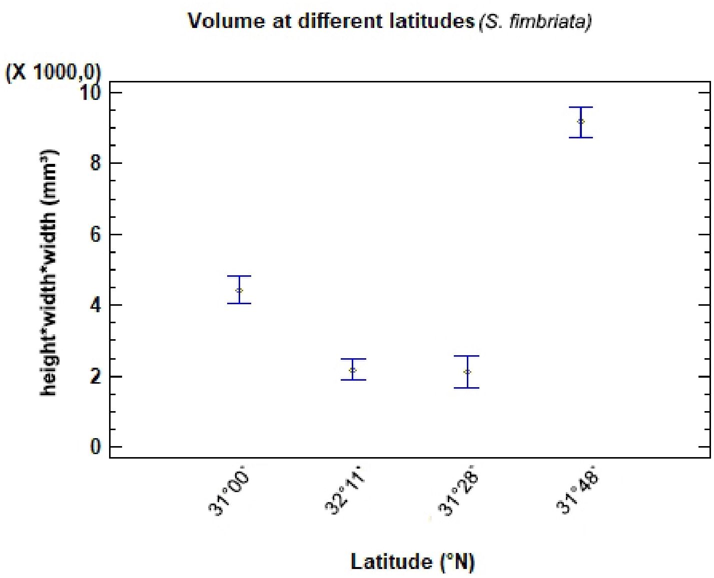

Fig. 25: Shell volume of S. *fimbriata* at different latitudes, including location F.

6 Discussion

Although there are significant differences in shell volume within the species *S. prophetarum*, *S. zonata* and *S. fimbriata* at different locations, the hypothesis that higher mean annual precipitation means higher shell volumes cannot be verified.

Shell volumes of *S. zonata* are notably higher in areas with lower mean annual precipitation and higher mean annual temperature. These snails seem to be adapted to dryer conditions.

The shell volume of *S. fimbriata* is significantly higher in areas with a higher mean annual precipitation (excluding location F because of the giant form of *S. fimbriata,* which shows much bigger shell volumes, found here).

S. prophetarum was only found at locations with the same values in mean annual precipitation and mean annual temperature. Still, the results show significant intraspecific differences in shell volume throughout all locations.

The correlation between the factors body size and precipitation (humidity) is not linear. Above and below a certain value of mean annual precipitation, the shell size of species decreases. This optimum differs for different species (Hausdorf, 2006). For *S. zonata* and *S. fimbriata,* this optimum seems to be close to a mean annual precipitation of approximately 75mm/y.

As suggested by Slotow and Ward (1997), the snails meet their $CaCO_3$ needs by ingesting $CaCO_3$ from rasped soil particles as well as from the algae directly. $CaCO_3$ is needed for the snails' shell growth. The availability of algae is dependent on humidity and, therefore, rainfall (Shachak & Steinberger, 1980). Ward and Slotow (1992) reported a higher growth increment in desert snails as well as a longer period of activity on watered plots. But no significant difference in shell diameter between dry and wet plots was found (Ward & Slotow, 1992). Ali et al. (2016) state that the average shell diameter in *Eremina d. desertorum* increased with decreasing temperature and increasing precipitation. On the other hand, a study from 2006 came to the conclusion that body size in land snails in Palestine and Israel is not directly correlated to mean annual rainfall (Hausdorf, 2006), and Proćków et al. (2017) state that intraspecific shell size in *Trochulus striolatus* is decreasing with higher precipitation and lower temperatures. Welter-Schultes (2000) also found no correlation between precipitation and shell size in the snail *Albinaria idaea*.

Anderson et al. (2007) found a strong correlation between shell size, temperature and population density. Decreasing population density and increasing mean annual temperature lead to bigger shells in *Oreohelix cooperi*.

The results of this study support these findings. The mean annual precipitation values of the collection sites are very similar, but most of them still show significant intraspecific differences in the snails' shell volume.

Many studies show a negative correlation between shell size and population density (Oosterhoff,

1976; Cameron & Carter, 1979; Baur, 1988).
Williamson et al. (1976) and Carter and Ashdown (1984) come to the conclusion that the differences in shell size depending on the population density in *Cepea nemoralis* under laboratory conditions as well as in field observations are not a result of limited food availability.

For snails living in arid habitats, being bigger and, therefore, having higher shell volumes can be an advantage. The loss of water due to evaporation changes with volume to surface ratio. Larger animals lose less water (Nevo et al., 1983). This could explain why *S. zonata* is much bigger in areas with a lower mean annual precipitation.
However, this is not true for *S. fimbriata*.

Smaller specimens, on the other hand, could have an advantage due to avoiding great water loss by hiding in crevices which would be too small for snails with bigger shells (Heller, 1988; Hausdorf, 2006). *S. prophetarum*, although more suited for Mediterranean climates, can survive in the desert because of its microhabitat selection. It prefers rocky habitats, so it can retreat under stones where moisture is preserved longer (Arad et al., 1989). For *S. prophetarum,* being smaller would be an advantage in dryer habitats. Unfortunately, *S. prophetarum* was only found at locations with both the same annual precipitation and temperature, so no correlation between precipitation and shell volume can be shown.

The correlation between body size and latitude is a known concept (Bergmann's rule). An intraspecific extension of this rule was made by F. C. James in 1970. The intraspecific variation in body size changing with latitude could allow animals to adapt to different environmental conditions (Blackburn et al., 1999).
The differences in latitude and altitude of the locations where snails were collected are overall not that big. The shell volumes of *S. prophetarum* are decreasing with increasing latitude.
Nekola et al. (2014) state that within species of land snails there seems to be no relation between body size and latitude and that Bergmann's rule does not apply. In invertebrates, the converse Bergmann's rule, decreasing body size with increasing altitude/latitude, can be observed as growth periods shorten with increasing altitude/latitude (Baur & Reboud, 1988; Proćków et al., 2017).
Baur and Raboud (1988) and Baur and Baur (1998) found the shell volume of *Arianta arbustorum* to decrease with increasing altitude along an altitude gradient of 1,380m or rather 1,970m.
No clear assertion can be made regarding the relation of altitude/latitude and shell size as both negative and positive correlations were found (Welter-Schultes, 2000) and the differences in altitude of the collection sites are not substantial.

No clear trend for all collected species can be recognised. Hausdorf even states that there seems to be no dependence between latitude/altitude and shell size (Hausdorf, 2003).

The patchy distribution of populations and the inability to close distances over sandy substrate can lead to snails showing evolutionary patterns and geographic structuring in relatively small spatial scales (Schilthuizen, 1999). Due to the quality of the snails' habitats, micro geographical differentiation as an explanation for the intraspecific differences is very likely as genetic variation, among other things, is highly affected by the founder effect, low gene flow and random drift (Stiven, 1989). Habitat fragmentation is expected to have an influence on the shell shape (Kappes, 2009) as the lack of genetic exchange between populations favours the formation of genetic differences which could, inter alia, lead to population subdivisions and subsequently be expressed in different shell sizes (Schilthuizen, 1994; Goikas & Mylonas, 2003; Kappes, 2009). Among others, one consequence of spatial subdivisions is random genetic drift (Greve et al., 2017).

Mäkinen et al. (2008) suggest that, in the case of the marine snail *Littorina saxatilis*, the main factor for genetic variation via populations is genetic drift. The lack of pelagic larvae limits the dispersal capability of *L. saxatilis*, and its situation is, therefore, comparable to the isolated habitats of *Sphincterochila* in the Jordanian desert.

In species with low mobility and limited dispersal capability, habitat fragmentation may influence the genetic structure of populations and makes them susceptible to the effects of this fragmentation, such as restricted gene flow (Kappes, 2009).

Intraspecific differences in shell types are commonly known in snails. These area effects are often the result of selection by features of the microclimate, bottleneck events or genetic drift (Davison, 2002) and can take place even in geographically close and ecologically uniform habitats (Baur, 1994; Schilthuizen et al., 2006). The phenotypic differences often lack a consistent relation to environmental correlates (Goikas et al., 2014).

7 Conclusion

As no clear trend is detectable, the differences in shell volume seem not to be dependent on climatic factors such as temperature, precipitation, altitude or latitude. Influences on shell volume, in general, could include moisture, temperature, interactions between related species, predation and population density because of growth inhibiting pheromones in the snails' mucus (Goodfriend, 1986; Perry & Arthur, 1991).
As shown in Oosterhoff (1976), Cameron and Carter (1979), Tattersfield (1981), Dan and Bailey (1982), Baur (1988, 1988) and Stiven and Foster (1996), the growth rate and adult shell size of land snails is negatively correlated with population density.
Dan and Bailey (1982) show that under laboratory conditions the snails' mucus even affects individuals from other snail species.
Tattersfield (1981) states that the snails' assessment of specimen density and, therefore, the availability of food via mucus can help to avoid an unnecessary waste of energy reserves.

Yom-Tov (1972) studied population densities of snails in the Negev desert. For *S. zonata*, these densities differ depending on the slope direction. On a south-facing slope 0.3 ± 0.13 specimens/m² and on a north-facing slope 0.25 ± 0.06 specimens/m² were observed. In the same study, the fecundity of *Trochoidea seetzeni* on these slopes was evaluated. The number of eggs as well as the number of snails laying eggs decreases with growing population density. Yom-Tov and Heller suggest a connection with the pheromones in the excreted mucus (Yom-Tov, 1972; Heller, 1988). However, specimens per m² are much higher in *T. seetzeni* (1.08 specimens/m² on the south-facing slope and 4.95 specimens/m² on the north-facing slope), and it is not clear how dense a population has to be for these mechanisms to take effect. But even for low-density snail populations, a highly significant negative correlation between shell diameter and population density, ranging from 3.4 to 18.3 individuals/100m², in *Mesodon normalis* was found by Stiven and Foster (1996).
Further investigations on population densities of *Sphincterochila* are suggested as this could explain the differences in shell volume at the different collection sites.

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