Predictors of shell size in long-lived lake gastropods

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ABSTRACT

Aim To investigate shell size variation among gastropod faunas of fossil and recent long-lived European lakes and discuss potential underlying processes.

Location Twenty-three long-lived lakes of the Miocene to Recent of Europe.

Methods Based on a dataset of 1412 species of both fossil and extant lacustrine gastropods, we assessed differences in shell size in terms of characteristics of the faunas (species richness, degree of endemism, differences in family composition) and the lakes (surface area, latitude and longitude of lake centroid, distance to closest neighbouring lake) using multiple and linear regression models. Because of a strong species–area relationship, we used resampling to determine whether any observed correlation is driven by that relationship.

Results The regression models indicated size range expansion rather than unidirectional increase or decrease as the dominant pattern of size evolution. The multiple regression models for size range and maximum and minimum size were statistically significant, while the model with mean size was not. Individual contributions and linear regressions indicated species richness and lake surface area as best predictors for size changes. Resampling analysis revealed no significant effects of species richness on the observed patterns. The correlations are comparable across families of different size classes, suggesting a general pattern.

Main conclusions Among the chosen variables, species richness and lake surface area are the most robust predictors of shell size in long-lived lake gastropods. Although the most outstanding and attractive examples for size evolution in lacustrine gastropods come from lakes with extensive durations, shell size appears to be independent of the duration of the lake as well as longevity of a species. The analogue of long-lived lakes as ‘evolutionary islands’ does not hold for developments of shell size because different sets of parameters predict size changes.

Keywords Ancient lakes, freshwater gastropods, lake surface area, shell size, species richness, species–area relationship

INTRODUCTION

Body size is an important functional and evolutionary trait, closely interrelated with individual fitness (Maurer et al., 1992; Hone & Benton, 2005; Clauset & Erwin, 2008) and metacommunity structure (Woodward et al., 2005; Loeuille & Loreau, 2006; Damuth, 2007; Jennings et al., 2007; De Bie et al., 2012). Size changes harbour advantages and disadvantages in terms of individual survival, fecundity, mating success, development time, nutrient requirement, dispersal and prey–predation interactions (Osenberg & Mittelbach, 1989; Hone & Benton, 2005; Jenkins et al., 2007; De Bie et al., 2012). Among populations or faunas, size distribution is coupled with species richness and abundance (McClain, 2004; Jennings et al., 2007; White et al., 2007). On a larger scale, size changes affect vulnerability to ecological crises and
extinction (Payne, 2005; Twitchett, 2007; He et al., 2010; Metcalfe et al., 2011).

Notable tendencies of size increase have been documented for fossil freshwater and brackish-water gastropods. Particularly among the families Lymnaeidae and Melanopsidae, several species lineages are famous for their outstandingly large shells (e.g. Moos, 1944; Geary et al., 2012; Neubauer et al., 2013). Members of the Valencienniinae, comprising large, low patelliform lymnaeids, attain maximum shell lengths of 125 mm (Moos, 1944). Comparable examples for extraordinary large shell sizes have been reported for brackish-water bivalves as well (Harzhauser & Mandic, 2004; Geary et al., 2010).

Among non-marine systems, such an extraordinary size evolution seems to be entirely restricted to long-lived lakes. These environments are commonly referred to as ‘evolutionary islands’ for their exceptional biogeographical and evolutionary relationships (Browne, 1981; Arnott et al., 2006; Wesselingh, 2007). The analogy between lakes and islands seems to encompass also developments of size. Outstanding patterns of size evolution have been recorded for island faunas. As a general rule, large species typically tend towards dwarfisms, while small species become larger, a trend termed ‘island rule’ (Lomolino, 2005; Whittaker & Fernández-Palacios, 2007; Lomolino et al., 2012, 2013; but see also Meiri et al., 2008 for an opposing view).

The present work investigates variation in shell size among gastropod faunas of fossil and recent long-lived (‘ancient’) lakes across Europe. Based on a dataset of over 1400 species of lacustrine gastropods from 23 lakes, we assess differences in shell size in relation to species richness, endemism and family composition of the lake fauna, as well as a lake’s physiographical parameters. Since lakes are often referred to as ‘evolutionary islands’, we compare our results with size evolution in island faunas. Moreover, we test whether the observed overall pattern of size change is a phenomenon established by certain families or constitutes a general rule valid across families of different size classes. This work is the first large-scale evaluation of shell size evolution of lacustrine animals.

MATERIALS AND METHODS

Dataset

The fossil record is commonly biased towards larger species (Cooper et al., 2006), so we included only well-studied faunas to ensure that small species are also covered. For the present paper, we acquired size information for faunas of 23 long-lived European lakes (Fig. 1), comprising 1412 gastropod species deriving from 1250 localities. The dataset includes 1243 species from 19 Neogene lakes (23.03–2.588 Ma) and 185 species from four recent ones (Table 1). Only lakes with four species or more and with guaranteed continuous temporal persistence and reliable age constraints were included. For details on taxonomic and stratigraphic treatment see Neubauer et al. (2015a,b). Palaeo-lake outlines for area calculation follow the reconstructions by Neubauer et al. (2015a) using ESRI® ArcGIS™.

Size measures

Where possible, size was taken from the species’ original descriptions to avoid biases from misidentifications. These papers are the source for most of the size data because the majority of the species is endemic to single lakes and has not been described again in detail. Where the original description was unavailable to us or does not contain the required information, size was gathered from other sources that are considered taxonomically reliable. We had to exclude 22 species,
for which no size information was available to us, corresponding to 1.6% of the total number of species, from the analyses.

Shell size was captured as height and width. In general, the maximum value per measure found in the literature was always recorded to exclude immature specimens. Only in rare cases is more than a single measurement available for a species, which is why we could not provide mean sizes or size ranges. In addition, the accuracy of the measurements varies considerably, usually declining with increasing size. However, no strong bias is expected from this as we used log_{10}-transformed data. To obtain a single value for the statistical analyses, we applied the estimator $S$ as used by Huang et al. (2015) and calculated as follows:

$$S = \sqrt{h \cdot w}$$

This value reflects the length of a square that has the same area as the rectangle formed by height $h$ and width $w$.

| Lake      | Countries covered | Max. temporal range of environment (Ma) | Latitude | Longitude | Area (km²) | Duration (Ma) | % Endemism | Distance (km) | Number of species across entire duration | Avg. beta diversity |
|-----------|-------------------|----------------------------------------|----------|-----------|------------|---------------|-------------|----------------|-----------------------------------------|---------------------|
| Bresse   | FR                | 4.5–1.5*                               | 46.641   | 5.243     | 9651.04    | 1.80          | 17.19       | 28             | 64                                      | 0.540               |
| Caspian Sea | AZ, IR, KZ,         | 0.88–0                                 | 41.808   | 50.513    | 378666.31  | 0.88          | 92.39       | 207            | 92                                      | 0.528               |
| Dacia     | BG, MD, RO, UA     | 8.6–2.6                                 | 45.132   | 26.295    | 98730.88   | 6.00          | 56.44       | 30             | 303                                     | 0.551               |
| Drniš     | HR                | 15.7–15.0                               | 43.836   | 16.263    | 24.89      | 0.70          | 16.28       | 12             | 43                                      | 0.638               |
| Gacko     | BA                | 15.8–15.2                               | 43.140   | 18.544    | 39.57      | 0.60          | 0.00        | 60             | 12                                      | 0.502               |
| Granada   | ES                | 7.5–5.33*                               | 37.110   | −3.832    | 931.43     | 1.70          | 0.00        | 50             | 21                                      | 0.500               |
| Groizenbach | AT                      | 16.0–13.8*                             | 47.543   | 15.270    | 22.63      | 0.20          | 91.67       | 40             | 12                                      | 0.728               |
| Kosovo    | KV                | 6.0–4.7                                 | 42.590   | 21.066    | 920.44     | 1.30          | 27.27       | 12             | 22                                      | 0.584               |
| Kupres    | BA                | 15.7–15.3                               | 43.986   | 17.215    | 65.40      | 0.40          | 0.30        | 30             | 23                                      | 0.445               |
| Le Locle  | CH                | 13.5–14.0                               | 47.074   | 6.779     | 11.38      | 0.50          | 5.56        | 13             | 18                                      | 0.413               |
| Metohia   | KV                | 6.04–2.588                              | 42.501   | 20.544    | 1805.05    | 3.45          | 70.93       | 12             | 86                                      | 0.565               |
| Nördlinger Ries | DE                      | 15.0–13.8                             | 48.885   | 10.564    | 438.24     | 1.20          | 16.67       | 5              | 6                                       | 0.490               |
| Ohrid     | AL, MK            | 1.5–0                                  | 41.037   | 20.716    | 356.37     | 1.50          | 64.71       | 9              | 68                                      | 0.409               |
| Pamvotis  | GR                | 0.4–0                                  | 39.663   | 20.884    | 22.70      | 0.40          | 12.00       | 95             | 25                                      | 0.481               |
| Pannon    | AT, BA, CZ, HR, RU, RO, RS, SI, SK | 11.6–4.5                             | 46.491   | 20.340    | 233485.79  | 7.10          | 74.61       | 55             | 579                                     | 0.435               |
| Randeck Maar | DE                      | 17.0–15.0*                             | 48.576   | 9.526     | 1.08       | 0.30          | 0.00        | 13             | 4                                       | 0.607               |
| Sinj      | HR                | 18.0–15.0                               | 43.695   | 16.682    | 131.80     | 3.00          | 39.66       | 12             | 58                                      | 0.556               |
| Slavonia  | BA, HR, HU, RS    | 4.5–2.0                                | 43.404   | 18.765    | 24243.25   | 2.50          | 44.24       | 125            | 165                                     | 0.545               |
| Sofia     | BG                | 5.8–4.3                                | 42.732   | 23.385    | 908.40     | 1.50          | 16.67       | 96             | 6                                       | 0.493               |
| Soitanj   | SI                | 5.3–2.6*                               | 46.382   | 15.071    | 13.87      | 0.50          | 66.67       | 67             | 9                                       | 0.503               |
| Steinheim | DE                | 15.0–13.8                               | 48.886   | 10.070    | 7.32       | 1.20          | 47.62       | 10             | 42                                      | 0.474               |
| Transylvania | RO                      | 3.8–0.8                               | 45.840   | 25.751    | 2221.12    | 3.00          | 53.85       | 30             | 78                                      | 0.579               |
| Trichonis | GR                | 2.6–0                                  | 38.559   | 21.552    | 94.83      | 2.60          | 13.04       | 3              | 23                                      | 0.549               |

*Precise age ranges missing (in those cases, duration is mainly estimated by available sedimentation rates).

Thereby, it contains the information of both height and width, facilitating the comparison between dissimilar morphologies such as planorbids (planispiral) and hydrobiids (turriform).

**Predictor variables, resampling and statistical analyses**

Four size measures were used for the regression models (all log_{10}-transformed), that is, mean size ($S_{mean}$), to investigate differences in the average size of the studied faunas; maximum ($S_{max}$) and minimum size ($S_{min}$), to assess extreme values; and size range ($S_{range}$), as a measure of the covered size spectrum. We investigated potential relationships between these measures and eight lake- and fauna-specific parameters, that is, latitude and longitude of lake centroid, lake surface area, closest distance to neighbouring lake, species richness of the lake’s gastropod fauna, its degree of endemism (i.e. 2064 Journal of Biogeography 43, 2062–2074 © 2016 The Authors. Journal of Biogeography Published by John Wiley & Sons Ltd. T. A. Neubauer et al. 2064
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The investigated lakes show a strong species–area relationship, which is not unexpected but reflects their character as continental islands (Wesselingh, 2007; Neubauer ship, which is not unexpected but reflects their character as in Supporting Information). Differences in family composition among the lakes, which might affect the size distribution of a fauna, were evaluated using the Beta-Jaccard ($\beta_{bc}$) dissimilarity measure for pairwise comparisons (Base

![Figure 2](image-url) Species–area relationship for the 23 Miocene to recent European lake faunas. The correlation is based on the number of measured species, which largely coincides with the total species richness.

RESULTS

The frequency distribution of shell sizes exhibits a non-normal, weakly right-skewed pattern (Shapiro–Wilk test: $W = 0.977, P < 0.001$; Skewness: $G_1 = 0.355$; Fig. 3). Right-
tailed distributions are typical for many other taxa as well (Maurer et al., 1992; Knouft & Page, 2003; Clauset & Erwin, 2008), whereas communities on small landmasses are expected to show less positively skewed body size distributions (Maurer et al., 1992; Marquet & Taper, 1998).

The mean family-level differences as evaluated with the Beta-Jaccard ($b_{\text{jac}}$) dissimilarity analysis are summarized in Table 1 (for full matrix see Table S2.14 in Appendix S2). The Shapiro–Wilk tests indicate normal distribution for all variables used in the multiple regressions except maximum size ($P = 0.035$), size range ($P = 0.031$) and longitude ($P = 0.010$) (see Table S1.1 in Appendix S1). We still chose to include them in the regression models because the Q-Q plots indicate that most cases match the expected distribution (see Fig. S1.1 in Appendix S1).

Size ranges and mean, maximum and minimum sizes of lacustrine faunas vary considerably across the studied lakes (Fig. 4). The broadest size ranges, as well as the largest and smallest species, occur in the two big, long-lived lakes Pannon and Dacia. Even among faunas of similar size ranges, mean size may diverge strongly, reflecting the various faunal compositions.

Given the lack of multicollinearity (VIF values < 3), all explanatory parameters were included in the models (see Table S1.2 in Appendix S1). The models for size range, maximum size and minimum size are all significant, with the combination of variables explaining between 35.4% and 72.5% of the variation (Table 2). In all three models, species richness proves to be the most important contributor, followed by surface area. The relationships of both variables with size measures indicate that with increasing values, expanding size ranges can be expected, variably related to increasing maximum size or decreasing minimum size. The model with mean size is not significant ($P = 0.379$).

The linear regressions between all variables and size measures yield similar results as the multiple regressions (Fig. 5), confirming species richness and area as the most important predictors for size range, maximum and minimum size. However, the regressions between lake surface area and maximum size and size range, respectively, are hardly significant ($P = 0.088$ and $P = 0.083$), which reflects the exceptionally small-sized fauna of the Caspian Sea (Fig. 5). Excluding the Caspian fauna, both regressions are highly significant (maximum size: $R^2 = 0.426$, $P < 0.001$; size range: $R^2 = 0.424$, $P = 0.001$). The strong correlation between minimum and maximum size and size range with species richness also persists when using the temporally subdivided faunas (as used for the regression with lake age; see Tables S1.10 and S1.12 in Appendix S1). Additionally, the degree of endemism yields a low relationship with minimum size. Resampling analyses reveal no significant effects of species richness on the observed correlations with area and endemism (all $P > 0.05$; see Table S1.13 in Appendix S1).
The linear regressions between size measures and species richness on the family level reveal similar results across different groups (see Table S1.3 and Fig. S1.2 in Appendix S1) irrespective of the overall size of the clade. Although $R^2$ values vary across different families and size measures, comparable results are obtained for clades of generally small size (Bithyniidae, Hydrobiidae, Neritidae and Valvatidae) and those comprising large species and wide size ranges (Lymnaeidae and Melanopsidae). The Planorbidae, comprising equally small and large species, show rather low correlations between size measures and richness. Similar as for species richness, the regressions between size measures and lake surface area exhibit moderate to high values across the Hydrobiidae, Neritidae, Valvatidae, Lymnaeidae and Bithyniidae (see Table S1.4 and Fig. S1.3 in Appendix S1).

The variables for the regression of size onto species longevity are not normally distributed, but the Q-Q plots indicate that most of the cases fit the expected distribution (see Table S1.5 and Fig. S1.4 in Appendix S1). The linear regression yields a significant but minor association ($R^2_{adj} = 0.033$, $P < 0.001$; see Table S1.6 and Fig. S1.5 in Appendix S1). None of the regressions between size measures and lake age is significant (see Tables S1.8 and S1.9 in Appendix S1).

The phylogenetic lineages of Valencienniinae and Melanopsidae all exhibit significant size increases over evolutionary time, while showing considerable variation on smaller scales (Fig. 6).

**DISCUSSION**

Lakes are commonly considered as islands in terms of faunal evolution and biogeographical relationships (Browne, 1981; Arnott et al., 2006; Wesselingh, 2007). This comparison is particularly often applied to long-lived lakes, which accommodate highly diverse faunas (e.g. Martens, 1997; Schön & Martens, 2004; Wesselingh, 2007; Harzhauser & Mandic, 2008; Hauffe et al., 2011; Wagner et al., 2012; Neubauer et al., 2013). Both in recent and fossil representatives, intralacustrine radiations produced diversities far above the common average and high levels of endemism (e.g. Schön & Martens, 2004; Wesselingh, 2007; Harzhauser & Mandic, 2008; Neubauer et al., 2015a,c). Islands are well known for their unique endemic developments related to body size. As a general rule, small species tend to increase in size (island gigantism) and larger species become smaller (island dwarfism); but see also Meiri et al. (2008). Both are frequent
phenomena, demonstrated for numerous animal groups (Lomolino, 2005; Whittaker & Fernández-Palacios, 2007; Lomolino et al., 2013 and references therein). Size evolution in island species is considered to converge on a size optimal for ecological strategies in dependence on characteristics of the island such as time in isolation, latitude, island area, and species interactions, that is, competition and predation (Lomolino, 2005; Lomolino et al., 2012, 2013). Regarding lakes as islands, we assessed the developments of shell size in lacustrine gastropods in a comparable manner. Our results indicate that a different combination of parameters is related to shell size trends. Species richness and lake area are significant predictors for gastropod body size in long-lived lakes, while geographical isolation, latitude and temporal existence of a lake apparently play minor roles. With rising diversity and lake surface area, maximum size increases and minimum size decreases (Fig. 5, Table 2). The Caspian Sea seems to be an exception to the rule as it is characterized by an exceptionally small-sized fauna in relation to its large surface area. Possibly, large gastropods were out-competed there by the highly diverse bivalve fauna comprising numerous large Dreissenidae and Lymnocardiidae (Logvinenko & Starobogatov, 1968). The individual linear model of minimum size with

Figure 5 Plots of all significant linear regression models between size measures and predictor variables (all log10-transformed) across all Miocene to recent European lacustrine gastropod taxa. $S_{\text{min}}$ = minimum shell size per fauna; $S_{\text{max}}$ = maximum shell size per fauna; $S_{\text{range}}$ = shell size range per fauna; $S_{\text{mean}}$ = mean shell size per fauna. Dashed lines indicate 95% confidence intervals.
degree of endemism is marginally significant and indicates a weak relationship.

What drives shell size evolution?

The selective forces underlying the trend towards expanding size range are difficult to infer from the mostly fossil data. The theoretical optimal size depends highly on characteristics of the environment and ecological interactions, such as competition and predation (Lomolino et al., 2012). Size changes variably impact individual survival, fecundity, mating success, development time, requirement of nutrients and prey–predation interactions (e.g. Osenberg & Mittelbach, 1989; Kingsolver & Pfennig, 2004; Hone & Benton, 2005; Metcalfe et al., 2011). On the larger scale, Heim et al. (2015) suggest basic body plan and ecological life mode as driving factors favouring overall increasing size in marine animals rather than competitive advantages. Size decrease in the fossil record is, in turn, commonly related to lowered vulnerability to ecological crises and extinction (Payne, 2005; Twitchett, 2007; He et al., 2010; Metcalfe et al., 2011). The only detailed study on size variation in a fossil brackish-water gastropod lineage is provided by Geary et al. (2012). They demonstrated successive size increase in a melanopsid species lineage from Lake Pannon, interpreted as greater individual longevity. Escape from predators, avoidance of resource competition, and especially increased fecundity are discussed as potential selective agents. Similarly, Lomolino et al. (2012, 2013) indicated for island populations that body size variation in both large and small species is influenced by ecological interactions, whereas pure size decrease is mainly a response to climatic, geographical and physiographical variables.

The positive relationship between shell size and lake surface area compares with developments on islands. Studies on insular species have yielded diverse results with respect to island area, variably demonstrating decreasing body size range (Marquet & Taper, 1998) and increasing maximum body size (Maurer et al., 1992) for islands of decreasing area. All studies, however, indicate that mean size tends to converge on a hypothetical optimum (Lomolino, 2005; Lomolino et al., 2012, 2013). Area is positively coupled with resource availability and diversity of habitats, predators and competitors (Lomolino, 2005; Lomolino et al., 2012). That relationship is strongly linked to the scaling of individual space requirements and its impact on population survival in environments of different area (Marquet & Taper, 1998).

Figure 6 Shell size evolution in three species lineages endemic to Lake Pannon. Phylogenetic relationships for Valencienniinae lineages follow Moos (1944); size data for the melanopsid lineage derive from Neubauer et al. (2013). Note that in all lineages the final stage involves a size decrease. Schematic drawings of phylogenetic starting and end point as well as the largest representative are provided for each lineage (specimens to scale within each plot). M. = Melanopsis; P. = Provalenciennesia; R. = Radix; V. = Valenciennius.
Size variation as a response to predation is weakly supported by previous studies (Geary et al., 2012). Predation pressure has been considered a main trigger for the morphological evolution in a hydrobiid clade in extant Lake Ohrid (Schreiber et al., 2012), whereas its effect on shell size evolution has not been explored so far. Similarly, predation pressure by crabs apparently promotes morphological evolution in a Theodoxus species lineage in the latest Miocene of the Thessaloniki area, while shell size remained unaffected (Rust, 1997).

The response to selective agents certainly varies among different faunas and lakes, depending on ecological setting and community structure (Lomolino et al., 2012, 2013). Unfortunately, these considerations cannot be tested individually since most of the studied environments no longer exist.

Other factors related with size

Because of varied evolutionary processes, one might also expect differing developments of shell size between species that evolved within a lake by intralacustrine speciation and those transported into the lake. While the degree of endemism does not seem crucial for the evolution of particularly large sizes, it does affect the minimum size of a fauna (Fig. 5). The negative relationship between minimum size and degree of endemism indicates that increasing endemism yields an averagely smaller fauna. This correlation is strongly influenced by the Caspian Sea and Lake Groisenbach, which have highly endemic faunas (92.3% and 91.7% respectively) that comprise mostly small species. On the one hand, this result may imply that those species evolved through intralacustrine speciation are tendentially smaller. Another, more likely option is that a higher number of small species evolved within the lakes than large ones, shifting minimum size towards lower values. Despite this correlation for the overall gastropod fauna, no significant relation between endemism and minimum shell size on the family level was detected (see Fig. 3.6 in Appendix S3).

The absence of a relationship between size measures and latitude is not surprising because only a narrow latitudinal range is covered by the studied lakes. Across a variety of organisms, size has been shown to increase with higher latitudes, reflecting better heat retention because of a lowered surface-volume ratio, a pattern generally referred to as Bergmann’s Rule (Meiri, 2011; Berke et al., 2013). Inclusion of more data to test for a possible dependence is unfortunately hampered by the limited availability of outcrops. Because of erosion by advancing and retreating ice shields during the Ice Ages, no surface outcrop with Neogene sediments is preserved north of c. 52° N. Likewise, information on southernmost European gastropod faunas is limited (Neubauer et al., 2015a,b). In addition, a clear latitudinal pattern cannot be expected because the lakes come from different time slices with different climatic regimes.

The absence of an association of shell size with isolation, being a measure of immigration selection on islands (Whittaker et al., 2001, 2014; Lomolino, 2005), may root in the limited dispersal possibilities for many groups of continental aquatic gastropods. While many freshwater caenogastropods and viviparids require good hydrological connectivity of surface waters for their dispersal (see Van Bocxlaer et al., 2011 and references therein), truncatelloid and pulmonate snails largely rely on passive dispersal, commonly via waterfowl or post-larval drift (Kappes & Haase, 2012; van Leeuwen et al., 2012, 2013). Inferences about dispersal mechanisms for fossil freshwater gastropods are rare, but indicate the presence of similar modes at that time already (Harzhauser et al., 2016). The successful introduction or active immigration into other continental aquatic systems depends on abiotic and biotic preferences and limitations, so the effective faunal exchange is probably limited and not necessarily dependent on geographical distance. Moreover, there is a crucial difference between lakes and islands in terms of isolation. Patterns of body size evolution as well as diversification events in island species are commonly discussed with reference to their mainland relatives (Lomolino, 2005; Whittaker & Fernández-Palacios, 2007; Stuart et al., 2012). Lake faunas, in contrast, represent mixed entities that cannot be assigned to a common origin, but rather comprise an accumulation of species variably deriving from intralacustrine speciation and introduction from different origins.

Generality of the pattern at different levels

The relationship between size and species richness and area, respectively, varies across different families, but seems independent of size class. It applies equally to the small-sized Hydrobiidae (mean $S = 2.9$ mm) and the moderate- to large-sized Lymnaeidae (mean $S = 26.9$ mm). This fact also explains why differences in the lakes’ family compositions scarcely affect changes of shell size. No significant association was detected for the family Viviparidae, which nonetheless constitutes important parts of the studied faunas. Viviparidae seem relatively size-stable through time. Conspicuous morphological radiations have been reported for viviparids across several long-lived Neogene lakes, all of which involve changes of shape and sculpture rather than size (e.g. Willmann, 1981; Lubenescu & Zazuleac, 1985; Mandic et al., 2015).

Within-lake patterns

Size evolution through time is commonly discussed with reference to Cope’s Rule, that is, the tendency for organisms in evolving lineages to increase in size over time (Hone & Benton, 2005). While numerous theoretical and empirical studies support this hypothesis (Alroy, 1998; Kingsolver & Pfennig, 2004; Hone et al., 2005; Novack-Gottshall & Lanier, 2008; Heim et al., 2015), a considerable amount of works argues against it (e.g. Jablonski, 1997; Knouft & Page, 2003; Harries & Knorr, 2009). Gastropod lineages in long-lived lakes differ considerably from marine and terrestrial groups because of their relatively limited temporal existence. With the
disappearance of the environment, the often highly specialized species and thus the lineages become extinct too (see, for example, Harzhauser & Mandic, 2004). Only few cases of successful immigration to other lakes are known (Wesselingh, 2007).

Unfortunately, little is known about the phylogenetic relationships among the studied gastropods, which is why an inference about the validity of Cope’s Rule in lacustrine snails cannot be made from our data. Figure 6 shows size changes in the few species lineages derived from the literature where the phylogenetic relationships are known. While the trend towards an overall increasing size is significant for all three lineages (corresponding to Cope’s Rule), each of them involves notable size variation, particularly in the case of the Valencienniinae. Similarly, the faunas of the lakes Pannon and Metoitia reach their maximum and minimum size as well as their widest size ranges in their early phases (see Table S1.7 in Appendix S1). Hence, shell size evolution involves a considerable degree of variation over time, explaining the absence of a relationship of size measures with lake age.

CONCLUSION

Species richness and lake surface area are the best predictors of shell size of gastropods from long-lived lakes. With both variables increasing, shell size range expands, maximum size increases and minimum size decreases. Moreover, minimum shell size is weakly related to the degree of endemism of a lake’s entire gastropod fauna, suggesting that a higher number of small species originate from intralacustrine speciation. Size is independent of the longevity of a species or lake age. This is an important conclusion as the most outstanding and attractive examples for size evolution in lacustrine gastropods (the Valencienniinae) derive from lakes Pannon and Dacia, and have therefore often been related to the extensive durations of these environments. We provide selected examples that indicate that size evolution is not necessarily linear but involves variation on smaller temporal scales, explaining the lacking correlation with time. Resampling analyses substantiated that the detected correlations are not driven by differences in diversity among the lakes. Moreover, the strong relationships between shell size and species richness and area, respectively, are consistent across gastropod families. This suggests a general rule unaffected by differences in ontogenetic development.

Given the unavailability of ecological data, we could only hypothesize about the underlying processes driving the patterns observed. Long-lived lake environments are famous for their unique internal evolutionary processes and ecological interactions, which differ conspicuously from marine and terrestrial settings and thus may have a distinctive impact on size evolution. Broader future investigations should aim at inferring causal processes and should reveal whether the pattern is restricted to lacustrine gastropods or a phenomenon typical for inhabitants of long-lived lakes.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Basic statistics, linear regressions and resampling.

**Appendix S2** Beta-Jaccard dissimilarity measure for pairwise comparisons.

**Appendix S3** Minimum size versus endemism for gastropod families.

**DATA ACCESSIBILITY**

All data used for this study are available from the Pangaea database: http://doi.pangaea.de/10.1594/PANGAEA.858575.

**BIOSKETCH**

Thomas A. Neubauer is a palaeobiologist and PostDoc at the Natural History Museum Vienna. He and the whole FreshGEN team are interested in reconstructing large-scale patterns of biodiversity and biogeography of Miocene to Recent European freshwater gastropod faunas.

Author contributions: M.H. and O.M. developed the initial design for the study; A.K. and T.A.N. developed the database; T.A.N., E.G., M.H. and O.M. compiled the data; T.A.N., E.G. and A.K. analysed the data; all authors contributed to the interpretations; T.A.N. wrote the manuscript.

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