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# Global Diversification Dynamics Since the Jurassic: Low Dispersal and Habitat-Dependent Evolution Explain Hotspots of Diversity and Shell Disparity in River Snails (Viviparidae)

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9

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11

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45 ABSTRACT

46 The Viviparidae, commonly known as River Snails, is a dominant group of freshwater snails  
47 with a nearly worldwide distribution that reaches its highest taxonomic and morphological  
48 diversity in Southeast Asia. The rich fossil record is indicative of a probable Middle Jurassic  
49 origin on the Laurasian supercontinent where the group started to diversify during the  
50 Cretaceous. However, it remains uncertain when and how the biodiversity hotspot in  
51 Southeast Asia was formed. Here, we used a comprehensive genetic dataset containing both  
52 mitochondrial and nuclear markers and comprising species representing 24 out of 28 genera  
53 from throughout the range of the family. To reconstruct the spatiotemporal evolution of  
54 viviparids on a global scale, we reconstructed a fossil-calibrated phylogeny. We further  
55 assessed the roles of cladogenetic and anagenetic events in range evolution. Finally, we  
56 reconstructed the evolution of shell features by estimating ancestral character states to assess  
57 whether the appearance of sculptured shell morphologies was driven by major habitat shifts.  
58 The molecular phylogeny supports the monophyly of the three subfamilies, the Bellamyinae,  
59 Lioplacinae, and Viviparinae, but challenges the currently accepted genus-level classification  
60 in several cases. The almost global distribution of River Snails has been influenced both by  
61 comparatively ancient vicariance and more recent founder events. In Southeast Asia, Miocene  
62 dispersal was a main factor in shaping the modern species distributions. A recurrent theme  
63 across different viviparid taxa is that many species living in lentic waters exhibit sculptured  
64 shells, whereas only one strongly sculptured species is known from lotic environments. We  
65 show that such shell sculpture is habitat-dependent and indeed evolved several times  
66 independently in lentic River Snails. Considerably high transition rates between shell types in  
67 lentic habitats probably caused the co-occurrence of morphologically distinct shell types in  
68 several lakes. In contrast, directional evolution towards smooth shells in lotic habitats, as  
69 identified in the present analyses, explains why sculptured shells are rarely found in these

70 habitats. However, the specific factors that promoted changes in shell morphology require  
71 further work.

72

73 **KEYWORDS:** Southeast Asia, fossil-calibrated phylogeny, biogeographical analyses, fossil-  
74 constrained analyses, stochastic character mapping

75 INTRODUCTION

76 Integrating molecular phylogenetic methods and biogeographical theory promises to improve  
77 our understanding of the distribution of life on Earth by providing new insights into the  
78 timing and spatial extent of distributional shifts on a global scale (e.g., Ree and Smith 2008;  
79 Ronquist and Sanmartín 2011; Matzke 2013a, 2014; Ho et al. 2015; Yu et al. 2015). Such  
80 insights are crucial to discern the factors and processes that have shaped current patterns of  
81 biodiversity. The importance of geological events as drivers of vicariance was recognized  
82 early (e.g., Wegener 1912a, 1912b, 1912c; Arldt 1917; du Toit 1937), which led to the rise of  
83 cladistic biogeography in the 1980s (see e.g., Hallam 1981; Wiley 1988; Upchurch 2008;  
84 Briggs 2009; Crisp et al. 2011; McIntyre et al. 2017). However, this focus on vicariance has  
85 increasingly been challenged with the recognition that additional factors, both intrinsic (e.g.,  
86 dispersal ability) and extrinsic (e.g., wind and vectors), also play influential roles in  
87 determining species distributions (e.g., de Queiroz 2005; Cowie and Holland 2008; Gillespie  
88 et al. 2012; Shaw and Gillespie 2016). Many freshwater taxa are particularly suitable for the  
89 study of biogeographical patterns and processes and how they affect diversification dynamics  
90 as they inhabit an environment that is delimited by well-defined boundaries that act as  
91 effective dispersal barriers (i.e., both terrestrial and marine environments). Those taxa with a  
92 long evolutionary history, a rich fossil record, and a nearly global distribution, such as various  
93 freshwater gastropods (see e.g., Strong et al. 2008), are particularly suited to examine the  
94 biogeographical context of diversification across large spatial and temporal scales.

95         One such gastropod family is the Viviparidae, or River Snails (and also sometimes  
96 referred to as Mystery or Pond Snails), which currently occur on almost all continents from  
97 sea level to about 2,700 m a.s.l., where they frequently dominate the mollusk fauna (e.g.,  
98 Strong et al. 2008; Van Bocxlaer and Strong 2019). Viviparidae is a well-supported family  
99 within the Caenogastropoda based on morpho-anatomical and molecular evidence (see e.g.,

100 Colgan et al. 2007; Ponder et al. 2008; Strong et al. 2011). It has a rich fossil record, with the  
101 oldest taxa known from the Mesozoic, including several Jurassic and Cretaceous  
102 representatives (see Van Bocxlaer and Strong 2019 and references therein). River Snails are  
103 commonly subdivided into three subfamilies, the Bellamyinae, Lioplacinae, and Viviparinae  
104 (= Campelomatinae, *fide* Bouchet et al. 2017). This classification is mainly based on  
105 anatomical features (see Rohrbach 1937; Vail 1977), which suggest a close relationship  
106 between Lioplacinae and Viviparinae (see Vail 1977). Whereas Lioplacinae are indigenous to  
107 eastern North America, the Viviparinae occur in North America, the western Palearctic and  
108 eastern Asia. The most diverse and widespread subfamily is Bellamyinae comprising  
109 numerous species from Africa, Asia, and Australia (Fig. 1). River Snails mainly inhabit lentic  
110 waters, such as (ancient) lakes, rice paddies, wetlands, and ponds, but are also common in  
111 large rivers and streams (i.e., lotic habitats), such as the Nile and Zambezi in Africa (genus  
112 *Bellamya*), the Mekong in Asia (genus *Mekongia*), or the North American Alabama-Coosa  
113 river system (genus *Tulotoma*).

114 Viviparidae are represented by roughly 125-150 extant species worldwide and reach  
115 their highest taxonomic diversity (c. 40-60 species) in Southeast Asia (Strong et al. 2008).  
116 This region also harbours most currently accepted genera (Fig. 1). Encompassing several  
117 global biodiversity hotspots, Southeast Asia is of great interest to biogeographers and  
118 evolutionary biologists because it has experienced a dynamic and complex tectonic and  
119 climatic history, particularly since the Early Miocene (Woodruff 2010; Lohman et al. 2011;  
120 Metcalfe 2011; de Bruyn et al. 2014; Klaus et al. 2016). The interplay of tectonic and climatic  
121 processes has triggered extensive *in situ* diversification in several taxonomic groups, but it has  
122 also facilitated widespread biotic exchange via dispersal and vicariance across prominent  
123 biogeographical barriers in numerous taxonomic groups (see e.g., Stelbrink et al. 2012; de

124 Bruyn et al. 2014; Crayn et al. 2015 for meta-analyses), including freshwater mollusks (e.g.,  
125 Köhler and Glaubrecht 2010; von Rintelen et al. 2014; Zielske et al. 2017).

126 Owing to their evolutionary age and widespread distribution, biogeographical patterns  
127 in River Snails across Southeast Asia should reflect the past environmental history well.  
128 Consequently, the study of diversification dynamics in this group would allow a better  
129 understanding of the mechanisms that have structured freshwater biodiversity throughout the  
130 region. Despite the ubiquity of viviparids, and their potential for biogeographical studies,  
131 surprisingly few modern studies have sought to unravel global diversification dynamics.  
132 Several recent studies have investigated the phylogeography and population genetic structure  
133 (e.g., Johnson and Bragg 1999; Johnson and Leefe 1999; Chiu et al. 2002; Carini and Hughes  
134 2006; Carini et al. 2006; Schultheiß et al. 2014; Gu et al. 2015b, 2015a) or addressed the  
135 systematic relationships among species in a regional context (Sengupta et al. 2009; Schultheiß  
136 et al. 2011; Du et al. 2013; Hirano et al. 2015, 2019a, 2019b; Zhang et al. 2015; Gu et al.  
137 2019; Rysiewska et al. 2019; Sil et al. 2019). These studies identified high levels of local and  
138 regional endemism and the importance of intralacustrine radiation in generating this diversity.  
139 They further indicated that past geological and climatic events and palaeohydrological  
140 connections have shaped the present-day distribution of viviparids. However, because of the  
141 lack of comprehensive taxonomic and genetic datasets, phylogenetic relationships, and global  
142 diversification dynamics of River Snails have remained poorly understood.

143 Irrespective of their considerable taxonomic diversity, Viviparidae are also renowned  
144 for their remarkable conservatism in shell morphology. Most taxa exhibit conical to  
145 subglobose shells that lack sculpture, and the observed variation in shell characters is  
146 comparatively small in comparison to the taxonomic diversity and evolutionary age of the  
147 family. However, there are notable exceptions of taxa, among both extant and fossil lineages,  
148 of taxa primarily from lacustrine (lentic) environments exhibiting highly divergent shell



149 morphotypes that include whorls covered in spiral lines, keels, or even noded spirals and  
150 spines. Such examples are found in the extant viviparid faunas of Lake Lanao, Philippines  
151 (*Torotaia* spp.; Bartsch 1907; Stelbrink et al. 2019) and Lake Inlé, Myanmar (*Taia* spp.; e.g.,  
152 Annandale 1924), but also the fossil assemblages of *Neothauma* from the palaeo-Lake  
153 Obweruka in the East African Rift (see e.g., Van Damme and Pickford 1999; Salzburger et al.  
154 2014) and *Margarya/Macromargarya* from the Chinese palaeo-Lake Nanning (Tian et al.  
155 2013, 2018). Whereas shell sculpture has been emphasized in taxonomy, little is known about  
156 how often and when such sculptured shells have evolved, for how long they persisted, and  
157 whether their occurrence is dependent on the habitat type in which these forms are found.

158         Here, we present the first molecular phylogeny of viviparid snails based on a  
159 comprehensive genetic dataset with a global coverage that comprises most of the extant  
160 genera (24 out of 28). We calibrated the phylogeny using five fossil calibration points and  
161 considered distributional and shell shape information of both extant and extinct species to  
162 inform various analyses. The aims of this study are: (1) to identify the evolutionary centre of  
163 origin of River Snails and to shed light on the relative importance of cladogenetic range  
164 evolution (e.g., vicariance or founder events) and anagenetic dispersal in shaping modern  
165 distribution patterns, and (2) to assess whether shell sculpture evolved several times  
166 independently in River Snails, and if so, whether it was linked to major habitat shifts. On the  
167 basis of modern species distributions and life-history traits, we expect a considerable role of  
168 palaeogeographical processes and vicariance, whereas dispersal in River Snails may have  
169 been of less importance. Moreover, morphological disparity across the family suggests that  
170 shell evolution was closely linked to the differential ecology of major viviparid habitats.

171

## 172 MATERIALS AND METHODS

### 173 *Materials*

174 The bulk of material used in this study was collected throughout Southeast Asia and Australia  
175 between 2001-2010 and is deposited in the Malacological Collection of the Museum für  
176 Naturkunde Berlin (ZMB), the Bogor Zoological Museum (Cibinong, Indonesia), and the  
177 National Museum of the Philippines (Manila). Additional ethanol-fixed samples have been  
178 obtained from the Florida Museum of Natural History, Gainesville (FLMNH), the North  
179 Carolina State Museum of Natural Sciences, Raleigh (NCSM), the National Museum of  
180 Natural History, Smithsonian Institution, Washington (USNM), and the Systematics and  
181 Biodiversity Collection, University of Giessen (UGSB).

182 While most of the genetic data analysed herein was newly generated, complementary  
183 sequences have been obtained from GenBank (Supplementary Table S1 available on Dryad).  
184 For the African species (*Bellamyia* spp. and *Neothauma tanganyicense*), we subsampled all  
185 major taxonomic groups and biogeographical clades that were published by Schultheiß et al.  
186 (2014). Our final dataset contained 61 nominal species from 24 out of 28 viviparid genera  
187 (sampling sites shown in Fig. 1 and Supplementary Fig. S1 available on Dryad). Two  
188 caenogastropod representatives belonging to the families Ampullariidae (*Pomacea*  
189 *canaliculata*) and Bithyniidae (*Bithynia* sp.) were used as outgroups to root the trees (see e.g.,  
190 Ponder et al. 2008).

191

#### 192 *DNA Isolation, PCR Amplification and DNA Sequencing*

193 Genomic DNA was isolated from c. 1 mm<sup>3</sup> of muscle tissue from the foot using a mollusk-  
194 specific protocol by Winnepeninckx et al. (1993). A single mitochondrial (COI, 660 base  
195 pairs, bp) and two nuclear markers (28S rRNA, c. 1,078 bp; H3, 328 bp) were amplified by  
196 using primers and PCR cycling conditions described by Van Bocxlaer et al. (2018) to resolve  
197 relationships from within species to between subfamilies and genera.

198 In some individuals (N = 24; Supplementary Table S1-S2 available on Dryad), the  
199 COI sequences contained apparently heterozygous sites, possibly indicating the presence of  
200 nuclear copies of mitochondrial DNA (NUMTs; e.g., Bensasson et al. 2001). In these cases,  
201 the PCR amplifications were repeated and the PCR products were subsequently purified using  
202 magnetic beads (SPRI beads, Agencourt AMPure XP). Amplicon sequencing was then  
203 performed on a Roche 454 GS FLX Titanium platform at the Berlin Center for Genomics in  
204 Biodiversity Research (BeGenDiv) using the direct multiplex sequencing (DMPS) protocol of  
205 Stiller et al. (2009). Multiple fragments were aligned against a reference sequence obtained by  
206 Sanger sequencing, translated into amino acids to check for stop codons or non-coding  
207 positions and were subjected to a phylogenetic analysis by maximum likelihood (ML) to  
208 allow unambiguous identification of the mitochondrial fragment.

209

#### 210 *Alignment and Identification of Best-Fit Partition Models*

211 The ribosomal sequences were aligned using the MAFFT WEB SERVICE (Kato and Toh  
212 2008; Kato and Standley 2013) with default settings. Ambiguous alignment sites were  
213 removed using the GBLOCKS SERVER 0.91b (Castresana 2000) with all three options enabled  
214 for a less-stringent selection (i.e., smaller final blocks, gap positions within the final block and  
215 less strict flanking positions). The resulting 28S rRNA alignment included 1,078 bp, or 93%  
216 of the original 1,150 positions.

217 The final three-gene dataset was investigated for the best-fit partition models in  
218 PARTITIONFINDER 2 (Guindon et al. 2010; Lanfear et al. 2012, 2016) by using a greedy  
219 algorithm with codon-position data blocks (for COI and H3) and linked branch lengths. The  
220 best-fit scheme revealed by PARTITIONFINDER 2 using the corrected Akaike information  
221 criterion (AICc) suggested seven partitions for both criteria: 28S rRNA = GTR+I+ $\Gamma$ , COI<sup>1st</sup> =  
222 GTR+I+ $\Gamma$ , COI<sup>2nd</sup> = GTR+I+ $\Gamma$ , COI<sup>3rd</sup> = HKY+I+ $\Gamma$ , H3<sup>1st</sup> = GTR+ $\Gamma$ , H3<sup>2nd</sup> = GTR+I, and

223 H3<sup>3rd</sup> JC+I, whereas the Bayesian information criterion (BIC) favoured a similar but slightly  
224 less complex partitioning scheme: 28S rRNA+ H3<sup>2nd</sup> = GTR+I+ $\Gamma$ , COI<sup>1st</sup> = GTR+ $\Gamma$ , COI<sup>2nd</sup> =  
225 GTR+I+ $\Gamma$ , COI<sup>3rd</sup> = HKY+I+ $\Gamma$ , H3<sup>1st</sup> = K80+ $\Gamma$ , and H3<sup>3rd</sup> JC+I. Phylogenetic reconstructions  
226 were highly similar under both partitioning schemes and we applied the AICc partitioning  
227 scheme in the following analyses.

228

### 229 *Phylogenetic Analyses*

230 Phylogenetic analyses were conducted on the CIPRES Science Gateway (Miller et al. 2010)  
231 using ML as implemented in RAXML-HPC BLACKBOX (8.2.10; Stamatakis 2014), and  
232 Bayesian inference (BI) using MRBAYES 3.2.6 (Ronquist et al. 2012) with the above-  
233 mentioned partitioning scheme. However, for ML we used the only available substitution  
234 model GTR+ $\Gamma$  for all partitions (Supplementary Fig. S2 available on Dryad). ML  
235 bootstrapping was performed by employing a stop rule (the analysis was automatically  
236 stopped after 456 bootstrap replicates). The settings for BI were: ngen = 10,000,000,  
237 samplefreq = 500, nchains = 4, burn-in = 10,001; Supplementary Fig. S3 available on Dryad).  
238 Convergence of the BI analysis was assessed using TRACER 1.5 (Rambaut and Drummond  
239 2007).

240

### 241 *Fossil-Calibrated Molecular-Clock Analyses*

242 For the molecular-clock analyses, we reduced the dataset and retained the most basal lineage  
243 of each species according to the ML and BI analyses, resulting in a total of 74 operational  
244 taxonomic units (OTUs; see Fig. 2). The discrepancy between the number of nominal species  
245 vs. OTUs (i.e., 61 vs. 74) is related to the non-monophyly of various *Bellamyia* species (see  
246 also Schultheiß et al. 2014) and the presence of undetermined species in the dataset. Because  
247 *Filopaludina javanica* was consistently recovered to be non-monophyletic, we predefined two

248 OTUs for this taxon: whereas ‘*F. javanica 1*’ included individuals from Sumatra, Java, and  
249 Sulawesi, ‘*F. javanica 2*’ comprises specimens from Bali, Borneo, and Sulawesi plus *F.*  
250 *decipiens* from New Guinea. We re-ran PARTITIONFINDER and used the best-fit substitution  
251 models and partitioning scheme as suggested by the AICc, which was very similar compared  
252 to the full dataset: 28S rRNA = GTR+I+ $\Gamma$ , COI<sup>1st</sup>+COI<sup>2nd</sup>+COI<sup>3rd</sup> = GTR+I+ $\Gamma$ , H3<sup>1st</sup> =  
253 K80+I+ $\Gamma$ , H3<sup>2nd</sup>+H3<sup>3rd</sup> = GTR+I.

254 The rich fossil record of Viviparidae provides excellent opportunities for time  
255 calibration, but also a risk, as several fossils have a questionable taxonomic status, are  
256 difficult to place within the phylogeny, or are derived from strata with poor age constraints.  
257 Here, we only used well-preserved taxa from non-marine facies, which could be confidently  
258 allocated based on synapomorphic shell features and are stratigraphically well constrained  
259 (following Parham et al. 2012; Supplementary Tables S3-S4 available on Dryad).

260 Divergence times were estimated using BEAST 1.8.4 (Drummond et al. 2012) by  
261 employing the ages of five fossils from the Jurassic, Cretaceous, Oligocene, and Miocene to  
262 calibrate the phylogeny (Fig. 2, Supplementary Fig. S4 and Supplementary Table S3 available  
263 on Dryad). The oldest known and reliably classified fossil viviparid is †*Viviparus langtonensis*  
264 from England, UK (Middle Jurassic; Hudleston 1896; Tracey et al. 1993). It was used to  
265 constrain the age of the most recent common ancestor (MRCA) of all extant viviparids (crown  
266 node; calibration point, CP1). The remaining fossils were used to calibrate internal nodes:  
267 †*Campeloma harlowtonense* from Montana, USA (Early Cretaceous; Stanton 1903; Yen  
268 1950) was used to calibrate the split between *Campeloma* and *Lioplax* (CP2); †*Margarya*  
269 *nanningensis* from Guangxi, China (Early Oligocene; Tian et al. 2013, 2018; Quan et al.  
270 2016) for the MRCA of *Margarya melanioides*, *M. oxytropoides*, and *Cipangopaludina* spp.  
271 from East Asia and New Guinea based on similar embryonic shell features (CP3); *Bellamya*  
272 cf. *unicolor* from Napak, Uganda (Early Miocene; Pickford 2004) for the MRCA of *Bellamya*

273 spp., *Neothauma tanganyicense*, and *Idiopoma* sp. (CP4; see also Schultheiß et al. 2014); and  
274 †*Neothauma hattinghi* from the Albertine Rift Valley in Uganda (Middle/Late Miocene; Van  
275 Damme and Pickford 1999) for the stem age of the two *Neothauma tanganyicense* lineages,  
276 which represents the MRCA of *Neothauma tanganyicense*, *Bellamyia* cf. *capillata*  
277 (‘Northern’, ‘Southern’, and ‘Zambezi’), *B. cf. monardi* ‘Northern’, *B. crawshayi*, and *B.*  
278 *pagodiformis* based on the topology inferred from the ML and BI analyses (CP5; see also  
279 Schultheiß et al. 2014).

280         A gamma prior was chosen for all fossil calibrations with a hard minimum age and a  
281 soft maximum age corresponding to the fossil’s stratigraphic age (Supplementary Table S3  
282 available on Dryad). Accordingly, scale values were selected that ensure that the median of  
283 the prior represented the maximum age of the respective fossil, whereas shape values were  
284 always set to 1.0. By doing so, a broad confidence interval was selected that accounts for the  
285 incompleteness of the fossil record (see e.g., Marshall 1990): CP 1: offset = 166.0, scale =  
286 11.5 → 95% quantile of the prior = 200.5; CP 2: offset = 112.0, scale = 13.0 → 95% = 150.9;  
287 CP 3: offset = 25.0, scale = 7.3 → 95% = 46.9; CP 4: offset = 18.5, scale = 2.2 → 95% =  
288 25.1; and CP 5: offset = 10.0, scale = 1.5 → 95% = 14.5. Analyses were run on the CIPRES  
289 server in two replicates with an uncorrelated lognormal relaxed-clock (UCLN) model, with  
290 codon partitions, unlinked clock models (but linked among codon positions), and a birth–  
291 death tree prior (settings: ngen = 200,000,000, samplefreq = 10,000). Separate log and tree  
292 files were combined using LOGCOMBINER 1.8.4 and a 50% burn-in (resulting in a total of  
293 20,000 trees). The maximum clade credibility (MCC) tree was identified using  
294 TREEANNOTATOR 1.8.4. Because convergence was not reached using the best-fit substitution  
295 models from PARTITIONFINDER for each of the seven data partitions, less complex substitution  
296 models (i.e., HKY instead of GTR) were used for the relevant partitions (see above), which  
297 resulted in considerably higher effective sample size (ESS) values (>200) for all parameters.

298 Branch-specific rates for 28S rRNA, COI, and H3 derived from the BEAST MCC tree are  
299 shown in Supplementary Fig. S5 available on Dryad.

300 To assess how the different fossil calibration priors interact with each other and how  
301 they influence divergence times, we performed additional BEAST analyses, in which: (1) we  
302 sampled from the prior only, (2) only CP1 was enforced, or (3) only CP3-CP5 were enforced  
303 (Supplementary Fig. S6 and Supplementary Table S5 available on Dryad).

304

### 305 *Biogeographical Analyses*

306 Ancestral areas were estimated using BIOGEOBEARS 1.1 (Matzke 2013b, 2013a) for the R  
307 statistical environment 3.5.1 (R Core Team, 2018). We delimited thirteen geographical areas;  
308 Southeast Asia was subdivided into eight geographical areas following the study by de Bruyn  
309 et al. (2014), whereas some large areas with sparse representation such as North America and  
310 Africa were not further subdivided for the purpose of this study: (A) = North America, (B) =  
311 Africa, (C) = Europe, (D) = East Asia (China, Far East Russia, Japan, and South Korea), (E) =  
312 India, (F) = Indochina (incl. the Thai-Malay Peninsula and Singapore), (G) = Sumatra, (H) =  
313 Philippines, (J) Palawan, (K) = Borneo, (L) = Java (incl. Bali), (M) = Sulawesi, and (N) =  
314 ‘East of Wallacea’ (Australia and New Guinea).

315 In a second, fossil-constrained biogeographical analysis, we assessed the impact of the  
316 geographical occurrence of fossils on the estimation of ancestral areas. Thus, the  
317 BIOGEOBEARS arguments ‘fixnode’ and ‘fixlikes’ were used to apply hard geographical  
318 constraints to the five nodes used to time-calibrate the molecular phylogeny: CP1 = Europe  
319 (C), CP2 = North America (B), CP3 = East Asia (D), and CP4 and CP5 = Africa (B).

320 Three different biogeographical models were tested (i.e., BayAreaLIKE, DEC, and  
321 DIVALIKE) plus their +J version, which implements jump dispersal at cladogenetic events  
322 and represents founder-event speciation (see Matzke 2013a, 2014). Lineages were allowed to

323 occur in a maximum of four combined areas. The best-fit biogeographical model for each  
324 approach was identified using the AIC (Supplementary Table S6 available on Dryad).  
325 Because estimated ancestral areas alone do not necessarily reflect the history of  
326 biogeographical events, an additional analysis using biogeographical stochastic mapping  
327 (BSM; see Dupin et al. 2017) was performed in BIOGEOBEARS (settings: nsim = 1,000).  
328 Parameters estimated for the best-fit model for both the unconstrained and fossil-constrained  
329 analyses were used as priors, and the frequency of cladogenetic and anagenetic events was  
330 counted.

331

### 332 *Analysis of Shell Characters and Habitat Types*

333 Representative specimens of all 74 OTUs included in the biogeographical analyses were  
334 photographed in a standardized view (Supplementary Fig. S7 available on Dryad). Standard  
335 shell parameters (height, width, width/height ratio; Supplementary Table S7 available on  
336 Dryad) were plotted against each other per genus and clade (Supplementary Fig. S8 available  
337 on Dryad). Phylogenetic ANOVAs (Garland et al. 1993) were performed using the R package  
338 PHYTOOLS 0.6-44 (Revell 2012) to test for clade-specific shell differences.

339 We also constructed a matrix, in which three discrete states representing gradations of  
340 spiral sculpture (i.e., ‘absent’, ‘fine’, ‘coarse’ incl. noduled spirals) and two discrete habitat  
341 categories (i.e., lentic = rice paddies, wetlands, ponds, lakes; lotic = creeks, rivers) were  
342 assigned to the 74 OTUs (Supplementary Table S7 available on Dryad). Shell and habitat  
343 information were coded based on sequenced specimens and general information from the  
344 literature. Accordingly, a total of six possible categories were obtained: ‘LeA’ = lentic with  
345 shell type A (‘absent’), ‘LeB’ = lentic with shell type B (‘fine’), ‘LeC’ = lentic with shell type  
346 C (‘coarse’), ‘LoA’ = lotic with shell type A, ‘LoB’ = lotic with shell type B, and ‘LoC’ =  
347 lotic with shell type C.



348 To estimate transition rates among these categories, three different models for discrete  
349 character evolution (i.e., ‘ER’ = equal rates, ‘SYM’ = symmetric rates, and ‘ARD’ = all rates  
350 different) were fitted in PHYTOOLS and compared using the AIC; Supplementary Table S8  
351 available on Dryad). To account for these different models and to differentiate between  
352 habitat-independent and habitat-dependent transition rates, a total of twelve Q (transition)  
353 matrices were created that constrain particular transition rates (Supplementary Fig. S9  
354 available on Dryad). Whereas models with habitat-independent transitions assume equal rates  
355 for shell type transitions in both lentic and lotic habitats (e.g., ‘LeA’→‘LeB’ =  
356 ‘LoA’→‘LoB’), habitat-dependent models suppose different shell transition rates  
357 (‘LeA’→‘LeB’ ≠ ‘LoA’→‘LoB’). Simultaneous transitions in habitat and shell sculpture  
358 (e.g., ‘LeA’→‘LoB’) were not allowed *a priori*. This is a multistate extension of the model of  
359 correlated evolution of binary traits (Pagel 1994). Ancestral state estimation was performed  
360 using stochastic character mapping (Huelsenbeck et al. 2003) as implemented in PHYTOOLS,  
361 which samples character histories from the posterior probability distribution (settings: nsim =  
362 1,000).

363 As for the biogeographical analysis, a fossil-constrained analysis of habitat-shell  
364 evolution was performed by constraining the ancestral states for the five nodes used as fossil  
365 calibration points: CP1 = ‘LeA’/‘LoA’, CP2 and CP4 = ‘LoA’, CP3 = ‘LeC’, and CP5 =  
366 ‘LeB’/‘LoB’ (see Supplementary Material available on Dryad). Accordingly, five additional  
367 tips with the mentioned character states were incorporated into the phylogeny at the nodes of  
368 interest using the PHYTOOLS function ‘bind.tip’. After re-running the above-mentioned  
369 analyses (settings: nsim = 1,000), the five additional tips were removed and the fossil-  
370 constrained ancestral states were mapped onto the original phylogeny. Because of the general  
371 difficulty to infer habitat types of fossil species, we evaluated the impact of our fossil states  
372 on the analysis by an additional analysis, in which the habitat type remained uncertain for all

373 five fossil species (i.e., ‘LeA’/LoA’, ‘LeB’/LoB’, and ‘LeC’/LoC’). In the fossil-constrained  
374 analyses, we estimated considerably high transition rates (e.g., ‘LeA’→‘LeB’) for few of the  
375 models of character evolution. These corresponded to an instantaneous state change and  
376 prevented the subsequent stochastic mapping of ancestral states. Because transition rates  
377 higher than 10 did not substantially improve model likelihoods, we fixed their upper bound  
378 during the maximum likelihood search to 10.

379 In contrast to the biogeographical models that only contained 3 parameters, up to 14  
380 free parameters needed to be estimated by the models of habitat-shell evolution. Together  
381 with our incomplete taxon sampling, this increases the chance of selecting the wrong model.  
382 We therefore used a bootstrapping approach in which we performed the following steps: 1)  
383 we estimated speciation and extinction rates under consideration of the incomplete taxon  
384 sampling with the R package DIVERSITREE 0.9-13 (FitzJohn 2012); although c. 125-150 extant  
385 species are currently recognized (Strong et al. 2008), we applied a very conservative sampling  
386 fraction of c. 0.40 based on the number of extant taxa found at MolluscaBase (2019; N =  
387 186); 2) speciation and extinction rates were used to simulate 250 taxonomically complete  
388 phylogenies (i.e., number of taxa = 186) with PHYTOOLS; 3) habitat and shell states were  
389 simulated for all taxa using the parameters from the best-fit habitat-shell evolution model; 4)  
390 phylogenies and states were pruned to the number of observed taxa (N = 74); and 5) all  
391 abovementioned models of habitat-shell evolution were fitted and ranked.

392

## 393 RESULTS

### 394 *Phylogenetic Relationships and Divergence Time Estimates*

395 Our dataset included 193 sequences from 74 OTUs representing 61 nominal species (see  
396 explanation above) in 24 genera and is the most comprehensive dataset for River Snails  
397 analysed thus far. The topologies of the unconstrained (ML and BI; Supplementary Figs. S2-

398 S3 available on Dryad) and fossil-calibrated trees (BEAST) were almost identical and were  
399 consistent with the anatomy-based taxonomic subdivision of the family into three subfamilies.  
400 Whereas prior and posterior distributions were very similar for CP1 and CP3, the comparison  
401 for the remaining calibration points indicated that divergence times were mainly informed by  
402 the sequence information and not only by the priors (Supplementary Fig. S6 available on  
403 Dryad). Mean ages for CP2-CP5 only differed by c. 2-17% (except for CP3, which was  
404 considerably younger) when only the oldest fossil calibration point (CP1) was used. Similarly,  
405 a reduced set of fossil calibration points (CP3-CP5) resulted in only c. 11-18% younger mean  
406 ages for the nodes corresponding to CP1 and CP2, respectively (Supplementary Table S5  
407 available on Dryad). Both suggesting that the placement of the fossils in the tree was  
408 generally reasonable and that age estimates are robust.

409         The monophyly of Lioplacinae and Viviparinae, respectively, was highly supported  
410 (Fig. 2 and Supplementary Figs. S2-S3 available on Dryad). However, branch support for  
411 their sister group relationship was low (ML bootstrap value: <0.50; BI posterior probability:  
412 0.76; BEAST posterior probability: 0.68; see also Fig. 2 and Supplementary Figs. S2-S3  
413 available on Dryad). The estimated age of the Lioplacinae–Viviparinae split (mean = 155.2  
414 million years ago, Ma; 95% highest posterior density, 95% HPD = 129.4-178.7 Ma) and the  
415 initial diversification within each of these clades dated back to the Mesozoic (Fig. 2). Within  
416 the Lioplacinae, *Campeloma* and *Lioplax* were recovered reciprocally monophyletic, whereas  
417 the three genera within the Viviparinae fall into two distinctive and highly supported sister  
418 groups: the European *Viviparus* species are sister to the Chinese *Rivularia*, whereas the North  
419 American *Viviparus* and *Tulotoma* are sister within a separate clade. The split between the  
420 European/East Asian and North American Viviparinae was estimated at c. 106.1 Ma (95%  
421 HPD = 67.8-148.3).

422 The sister clade of Lioplacinae + Viviparinae is the highly supported Bellamyinae  
423 (Fig. 2 and Supplementary Figs. S2-S3 available on Dryad). The initial diversification of  
424 Bellamyinae probably began during the Late Cretaceous, c. 87.2 Ma (95% HPD = 63.3-  
425 113.9), i.e., considerably later than the initial diversification of the other two subfamilies.  
426 Within the Bellamyinae, two distinct clades were recovered: Bellamyinae-clade A includes  
427 only Asian genera (*Angulyagra*, *Anularya*, *Celetaia*, *Cipangopaludina*, *Margarya*, *Sinotaia*,  
428 and *Torotaia*), whereas Bellamyinae-clade B is geographically more widespread comprising  
429 African (*Bellamyia*, *Neothauma*), Asian (*Angulyagra*, *Anulotaia*, *Filopaludina*, *Idiopoma*,  
430 *Mekongia*, *Taia*, *Tchangmargarya*, and *Trochotaia*), and Australian genera (*Larina* and  
431 *Notopala*). However, the support for Bellamyinae-clade B is comparatively low given the  
432 uncertain phylogenetic positions of *Mekongia* and *Tchangmargarya* (Fig. 2). Moreover, the  
433 monophyly of the Australian clade remains uncertain because of low node support. The  
434 MRCA of each of Bellamyinae clades A and B is estimated to have originated in the Eocene,  
435 c. 46.9 Ma (95% HPD = 31.4-63.7), and in the Late Cretaceous c. 78.7 Ma (95% HPD = 55.9-  
436 103.7), respectively.

437 Most of the genera studied here are reciprocally monophyletic and highly supported  
438 (Fig. 2 and Supplementary Figs. S2-S3 available on Dryad). However, several paraphyletic  
439 and polyphyletic groups were recovered, including e.g., *Viviparus* (Viviparinae),  
440 *Cipangopaludina* (Bellamyinae-clade A), *Angulyagra* (Bellamyinae-clades A and B), and  
441 perhaps *Filopaludina* (Bellamyinae-clade B), although low support values do not allow to  
442 draw final conclusions on this latter taxon.

443

#### 444 *Major Biogeographical Patterns*

445 In both analyses (unconstrained vs. fossil-constrained), DEC+J was identified as the best-fit  
446 biogeographical model (Supplementary Table S6 available on Dryad). The biogeographical

447 models BayAreaLIKE, DEC, and DIVALIKE consistently revealed a lower fit to the data  
448 than their +J versions. However, the jump-dispersal weight was generally low in all analyses  
449 (Supplementary Table S6 available on Dryad). According to the BSM analyses, the largest  
450 share of cladogenetic events (unconstrained: c. 74% vs. fossil-constrained: c. 73%) was  
451 attributed to sympatry ('y', *sensu* (Matzke 2014). In contrast, range-changing jump-dispersal  
452 ('j'), subset sympatry ('s'), and vicariance ('v') were only rarely identified in the  
453 unconstrained and fossil-constrained analyses ('j': c. 10% vs. 16%, 's': c. 7% vs. 5%, and 'v':  
454 10% vs. 3%, corresponding 19-20 out of 73 cladogenetic events; see colour-codes nodes in  
455 Fig. 3). In contrast, only few anagenetic events were recovered (unconstrained vs. fossil-  
456 constrained: 5 vs. 7 dispersal events out of a total of 146 branches; no extinction events, i.e.,  
457 range contraction; see colour-coded branches in Fig. 3).

458         The unconstrained analysis suggested that the MRCA of all viviparids inhabited North  
459 America + East Asia + Indochina (Fig. 3; see Supplementary Material available on Dryad).  
460 The first diversification event that gave rise to the MRCA of Lioplacinae and Viviparinae  
461 (North America) and the MRCA of the Bellamyinae (East Asia + Indochina) was likely  
462 caused by a vicariant event (BSM: c. 82%). A combination of cladogenetic events (sympatry  
463 and vicariance/jump-dispersal) resulted in the colonization of Europe via East Asia by  
464 Viviparinae. The split between the Lioplacinae and Viviparinae (sympatry, BSM: c. 68%) and  
465 within the Viviparinae occurred in North America, followed by either a vicariant (BSM: c.  
466 57%) or jump-dispersal event (BSM: c. 43%) that gave rise to the North American and  
467 European/East Asian clades in the Viviparinae (Fig. 3). Similarly, the split between the  
468 European *Viviparus* and the Chinese *Rivularia* was either caused by vicariance or jump  
469 dispersal (BSM: c. 53 and c. 47%, respectively). Within the Bellamyinae, clade A probably  
470 originated in East Asia, whereas clade B probably emerged in East Asia + Indochina. In clade  
471 A, different SE Asian islands or archipelagos, such as the Philippines, Sulawesi, and New

472 Guinea, were colonized mainly by jump dispersal events during the Middle and Late  
473 Miocene. In clade B, ancestral lineages from Indochina colonized Africa via vicariance  
474 (BSM: c. 58%) or jump dispersal (BSM: c. 42%) and Australia + New Guinea (sympatry and  
475 subset sympatry) during the Late Oligocene to Early Miocene, the latter of which gave rise to  
476 the geographically widespread genus *Filopaludina*. This genus may have originated in  
477 Indochina during the Early Miocene where it still occurs today (*F. doliaris*, *F. filosa*, *F.*  
478 *martensi*, *F. polygramma*, and *F. sumatrensis*). *Filopaludina* also colonized several islands  
479 within the Indo-Australian Archipelago (IAA) from Indochina during the Late Miocene (*F.*  
480 *javanica* 1, *F. javanica* 2, and *F. luzonica*). These colonization events were mainly associated  
481 with anagenetic dispersal (Fig. 3).

482         The fossil-constrained analysis revealed similar results to the unconstrained analysis  
483 described above, however, the reconstruction of the centre of origin of River Snails changed.  
484 Accordingly, the MRCA of all viviparids originated in Europe, whereas both the Lioplacinae  
485 and Viviparinae originated in North America + Europe and the split within the North  
486 American and European/East Asian Viviparinae was caused by vicariance (BSM: c. 81%).  
487 For the Bellamyinae, a jump dispersal-event from Europe into Indochina (BSM: 100%),  
488 followed by dispersal into Indochina + East Asia is suggested. Other, more recent, nodes  
489 indicated similar cladogenetic events regardless of whether or not fossil constraints were  
490 used, except for nodes related to *Mekongia* and *Tchangmargarya*. In summary, adding fossil  
491 constraints reduced the number of possible ancestral areas estimated for the MRCA of  
492 Viviparidae and several descendent nodes in comparison to the unconstrained analyses (Fig.  
493 3).

494

495 *Shell Character Evolution across Habitat Types*

496 General shell measurements (height, width, and width/height ratio) did not allow separation of  
497 viviparid species into taxonomic groups at the genus or subfamily level (Supplementary Fig.  
498 S8 available on Dryad). Similarly, despite the fact that clade A may be characterized by larger  
499 and potentially more slender species on average in comparison to clade B (Supplementary  
500 Fig. S8 available on Dryad), no significant differences were identified between the two clades  
501 by the phylogenetic ANOVAs ( $F_{\text{height}} = 79.8$ ,  $p = 0.19$ ;  $F_{\text{width}} = 72.9$ ,  $p = 0.21$ ;  $F_{\text{width/height ratio}} =$   
502  $7.9$ ,  $p = 0.68$ ).

503         Forty-eight of the 74 OTUs (c. 65%) represented in the phylogeny possess a smooth  
504 shell, 17 OTUs (c. 23%) exhibit a fine spiral sculpture, and 9 OTUs (c. 12%) a coarse spiral  
505 sculpture that may include noded spirals (Fig. 4 and Supplementary Fig. S7 available on  
506 Dryad). With the exception of *Tulotoma magnifica*, all extant members of the Lioplacinae and  
507 Viviparinae lack significant sculpture. This is also true for many species belonging to  
508 Bellamyinae–clade B. In contrast, the extant representatives of Bellamyinae–clade A display  
509 considerably greater disparity in shell sculpture compared to the three above-mentioned  
510 clades (Fig. 4). Species with a smooth shell or a fine spiral sculpture mainly inhabit lotic but  
511 also lentic habitats. In comparison, taxa with a coarse spiral shell sculpture are almost  
512 exclusively found in lacustrine environments (except *Tulotoma magnifica*; Fig. 4). Within the  
513 Bellamyinae, most species within clade A inhabit lentic habitats. In contrast, clade B mainly  
514 consists of lotic species except for *Neothauma* and some *Bellamyia* and *Filopaludina* species.

515         According to the AIC comparisons, the habitat-dependent HabDep-Hab<sub>ER</sub>-Shell<sub>ARD</sub>  
516 model featuring equal rates for habitat transitions and different rates for shell transitions  
517 (Supplementary Fig. S9 available on Dryad) was identified as the best-fit model for both the  
518 unconstrained and fossil-constrained analyses (Supplementary Table S8 available on Dryad).  
519 Both the unconstrained and fossil-constrained analyses identified smooth shells and a  
520 predominantly lotic habitat for the root of the tree (Fig. 4). The shell of the MRCA of all three

521 subfamilies was also estimated to be smooth, but the ancestral habitat remains largely  
522 inconclusive. A smooth shell in combination with a lotic habitat was estimated for the MRCA  
523 of Bellamyinae–clade B and most of its descendent nodes. In contrast, species belonging to  
524 clade A may have been derived from an ancestor with fine or coarse spiral shell sculpture.  
525 This pattern is even more pronounced in the fossil-constrained analysis (Fig. 4). Remarkably,  
526 the occurrence of sculptured shells in clade A coincided with a major shift from lotic to lentic  
527 habitats as indicated by the colour gradient across the branches. However, such habitat shifts  
528 did not coincide with a change in shell sculpture, for example, in *Bellamyia* species (clade B)  
529 inhabiting ancient lakes such as Lake Malawi (Fig. 4; see also Schultheiß et al. 2011).

530         Estimated transition rates were generally very similar between the unconstrained and  
531 fossil-constrained analyses, but were highly asymmetric (Supplementary Table S9 available  
532 on Dryad). Habitat transition and shell transition rates were estimated to be comparatively  
533 low. However, elevated rates were identified for bidirectional transitions between smooth and  
534 finely sculptured shells in lentic ('LeA'↔'LeB') habitats. In lotic habitats, transition rates  
535 towards more weakly sculptured shells ('LoC'→'LoB' and 'LoB'→'LoA') were substantially  
536 higher than transitions towards sculptured shells. Finally, the magnitude of the above-  
537 mentioned transition rates in lentic habitats were considerably higher than in lotic habitats.  
538 Interestingly, direct transitions between 'LeA'↔'LeC' and 'LoA'↔'LoC' were not observed  
539 (Fig. 4, inset).

540         Our bootstrapping approach showed that, independent of our incomplete taxon  
541 sampling and the high number of transition rates, a scenario of habitat-dependent asymmetric  
542 shell transitions remained the best-fit model and we obtained a reasonable precision of rate  
543 estimation (Supplementary Fig. S10 available on Dryad).

544

545 DISCUSSION



546 *Taxon Sampling and Robustness of Phylogenetic Inference and Downstream Analyses*  
547 Whereas only ~50% of recognized viviparid species are represented in our analysis (61 out of  
548 c. 125-150 recognized species or 74 OTUs), our dataset at the genus level is more  
549 comprehensive and covers 24 out of the 28 currently valid genera. The missing genera are  
550 *Amuropaludina* Moskvicheva, 1979 (Far East Russia), *Boganmargarya* Thach, 2018  
551 (Myanmar) as well as *Eyriesia* P. Fischer, 1885 and *Glaucotrancia* Ancey, 1898 from  
552 Australia. However, all these geographical regions are represented in our dataset and thus the  
553 inferred regional and global biogeographical patterns should remain robust. At the species  
554 level, the inclusion of additional taxa is generally considered to improve phylogenetic  
555 accuracy and ancestral state reconstructions (e.g., Salisbury and Kim 2001; Hug and Roger  
556 2007; Heath et al. 2008a, 2008b; but see Nabhan and Sarkar 2012 for a recent review on this  
557 debate). However, evolutionary rates and thus time estimates seem to be robust to differences  
558 in taxon sampling if rate variation among branches is low (Soares and Schrago 2015), and we  
559 did not observe systematic differences among sampled clades and genera for any of the  
560 genetic markers used (Supplementary Fig. S5 available on Dryad). A potentially more critical  
561 issue is how even taxa were sampled across the phylogeny and thus how tree shape may be  
562 affected by missing data (e.g., Li et al. 2008). For our dataset, most of the missing (extant)  
563 taxa belong to terminal nodes and thus we assume that the general tree shape should remain  
564 robust. Moreover, shell morphologies and geographical areas are well covered in our dataset,  
565 suggesting that missing taxa would not bias biogeographical and morphological  
566 reconstructions. For example, all members of the Lioplacinae and Viviparinae occur in the  
567 same geographical region (see Fig. 1) and are also morphologically very similar, at least in  
568 terms of the defined shell sculpture types. Within the Bellamyinae, the majority of missing  
569 species belong to the genera *Bellamya*, *Cipangopaludina*, *Idiopoma*, *Mekongia*, *Notopala*,  
570 *Sinotaia*, and *Taia*. However, these genera are all represented in the phylogeny and the

571 missing species mainly occur in the same geographical area and possess shell features similar  
572 to their sampled congeners. The case of *Mekongia* is somewhat different. Because it  
573 represents a more widespread genus (we included two species from Indochina and Borneo,  
574 respectively), additional *Mekongia* species may improve biogeographical reconstructions.

575         Very importantly, our simulations on the models of habitat-shell evolution, which are  
576 generally more sensitive to incomplete taxon sampling compared to the biogeographical  
577 models due to higher number of free parameters, supported a robust model selection.  
578 Accordingly, both best-fit models and levels of transition rates simulated for a taxon-complete  
579 phylogeny were also identified by our reduced dataset. Besides the general robustness of this  
580 approach, the random pruning of taxa from the simulated taxon-complete phylogenies also  
581 recovered almost all genera examined. We are therefore convinced that our findings very  
582 likely reflect the evolutionary history of River Snails.

583

#### 584 *Phylogenetic Relationships and Systematic Implications*

585 The present study provides strong molecular support for the classical, mainly anatomy-based,  
586 subdivision of the Viviparidae into the three subfamilies Bellamyinae, Lioplacinae, and  
587 Viviparinae (Rohrbach 1937; Vail 1977; Bouchet et al. 2017) (Fig. 2). Of these subfamilies, a  
588 sister group relationship between Lioplacinae and Viviparinae was returned in most but not  
589 all phylogenetic analyses, although it is not highly supported. The phylogeny further confirms  
590 the placement of *Tulotoma* and *Rivularia* within the Viviparinae, as already proposed for  
591 *Tulotoma* based on comparative anatomy (Vail 1977) and for *Rivularia* by considering both  
592 anatomical and restricted molecular data (Van Bocxlaer et al. 2018). Contrary to Bouchet et  
593 al. (2017), our analysis also suggests that Campelomatinae is a synonym of Lioplacinae rather  
594 than Viviparinae. The genus *Viviparus* as traditionally conceived, with both European and  
595 North American representatives, was recovered as polyphyletic. The North American species

596 are more closely related to the American *Tulotoma*, and the European species more closely  
597 related to the Asian *Rivularia*. The genus-group name *Callinina* Thiele, 1931 (a replacement  
598 name for *Callina* Hannibal, 1912 *non* Lowe, 1855), with *Viviparus intertextus* (Say, 1829) as  
599 type species by typification of a replaced name, is available for the American species of  
600 *Viviparus*.

601 Traditionally, the systematics of viviparids at both the genus and species level has  
602 been based largely on shell characters. However, the analysis of character evolution indicates  
603 that the current shell morphology-based taxonomy does not accurately reflect phylogenetic  
604 relationships in this group. At the genus level, several cases of paraphyly and polyphyly were  
605 identified. However, this finding is understandable in the light of multiple independent origins  
606 of such morphological features. In some reconstructions, the genus *Filopaludina* was found to  
607 be monophyletic with low support, whereas in others (see Fig. 2), it was paraphyletic, with *F.*  
608 *tricostata* as sister to a clade that includes representatives of *Angulyagra*, *Larina*, and  
609 *Notopala*, but also with low support. Similarly, the monophyly of *Torotaia* remains uncertain  
610 owing to the ambiguous placement of *Angulyagra costata* between the different phylogenetic  
611 analyses. Assessing the monophyly of these genera will require the inclusion of additional  
612 taxa and more informative molecular markers. Moreover, in several cases resolving the  
613 systematic status of the species will require the inclusion of types. For example, both  
614 *Cipangopaludina* and *Angulyagra* were supported as polyphyletic, but resolving the question  
615 of which clade carries the genus name awaits inclusion of the respective type species. These  
616 systematic implications highlight the need for an integrative taxonomic revision of the  
617 Viviparidae, as recently initiated for the polyphyletic genus *Margarya* from China (see Du et  
618 al. 2013; Zhang et al. 2015). The present molecular phylogeny provides a robust family-level  
619 framework for such an endeavour on a global scale.

620

621 *The Fossil Record and Evolutionary Centre of River Snails*

622 Both the unconstrained and fossil-constrained analyses reconstructed very similar  
623 biogeographical histories for the Viviparidae, except for the origin of the family and  
624 subsequent diversification events within the Lioplacinae and Viviparinae (Fig. 3). In our  
625 opinion, the incorporation of fossil constraints considerably improved the overall plausibility  
626 of ancestral area estimations (see also Matzke, 2013a) and thereby allowed a more robust  
627 biogeographical reconstruction for River Snails. Note, however, that the majority of  
628 cladogenetic events discussed below were not constrained by fossils (see Fig. 3).

629         Based on the biogeographical analyses, ancestral lineages that gave rise to the  
630 Lioplacinae and Viviparinae originated on the Laurasian supercontinent (i.e., Europe and  
631 North America; Fig. 3). Whereas a Laurasian origin contradicts the hypothesis of a Pangaeon  
632 origin for Viviparidae (see e.g., Strong et al. 2008), the former interpretation is supported by  
633 the fossil record: River Snails first appeared in Middle Jurassic deposits of western Europe  
634 (Hudleston 1896; Tracey et al. 1993). Initial diversification of the Viviparidae during the  
635 Jurassic-Cretaceous transition (Huckriede 1967; Bandel 1991; Radley and Allen 2012; see  
636 Scotese 2014a, 2014b and Supplementary Fig. S11a,b available on Dryad) was followed by  
637 the colonization of large areas of Laurasia (Valanginian; see Scotese 2014b and  
638 Supplementary Fig. S11c available on Dryad), North America (Stanton 1903; Yen 1950,  
639 1952; Tozer 1956), and far east Eurasia (Matsukawa et al. 2006) during the Early Cretaceous.  
640 The oldest *Campeloma* was described from the Early Cretaceous (Aptian; see Scotese 2014b  
641 and Supplementary Fig. S11d available on Dryad) of Montana, USA (Yen 1952) providing  
642 evidence of the rise of the Lioplacinae during that period.

643

644 *Age Estimates and Biogeographical Implications*

645 The split between North American genera and the remaining members of the Viviparinae  
646 (95% HPD = 67.8-148.3) was inferred to have been caused by vicariance. However, the large  
647 credibility interval (error bar) does not allow to make a final conclusion of whether the onset  
648 of spreading in the North Atlantic c. 95-110 Ma (e.g., Sclater et al. 1977; Jones et al. 1995)  
649 caused the initial separation within the Viviparinae (i.e., *Viviparus* + *Rivularia* vs. *Viviparus*  
650 [= *Callinina*] + *Tulotoma*; Fig. 3) or whether other geological events can be associated with  
651 this split.

652         Within the Viviparinae, a close relationship between the European *Viviparus* species  
653 and the Chinese *Rivularia auriculata* is strongly supported (see also Van Bocxlaer et al.  
654 2018). Our analyses indicate that this split was either caused by vicariance or a jump-dispersal  
655 event (Fig. 3). The most parsimonious explanation would be a single colonization by a  
656 founder population out of Europe. Alternatively, *Rivularia auriculata*, which is currently  
657 restricted to the Hunan Province, could represent a relic of an ancestral lineage that expanded  
658 its range into East Asia during the Eocene (Fig. 3). Following the India-Asia and the Asia-  
659 Australia collision during the Eocene and Oligocene, respectively (see Scotese 2014c and  
660 Supplementary Fig. S11e,f available on Dryad), this region changed considerably in terms of  
661 its geology, geography, climate, and fauna (see e.g., Lohman et al. 2011; de Bruyn et al.  
662 2014). European and Asian populations may have become geographically separated from  
663 each other (vicariance) as a consequence of these changes. However, given the absence of  
664 both extinct lineages and additional extant populations of *Rivularia*, we consider both  
665 scenarios equally likely.

666         Based on the present analyses, Bellamyinae-clade A probably originated in Indochina  
667 + East Asia, whereas clade B emerged in Indochina (Fig. 3). Similar patterns have been found  
668 in spiny frogs within the Dicroglossidae in the East Asian-Indochinese transition zone (Che et  
669 al. 2010). The interplay of geological and climatic dynamics during the Oligocene and

670 Miocene related to the uplift of the Tibetan Plateau has been hypothesized to have facilitated  
671 the diversification of these amphibians. However, the split between the two clades of  
672 Bellamyinae was estimated to have occurred in the Late Cretaceous c. 87.2 Ma (95% HPD =  
673 63.3-113.9). Because of the complex palaeogeographical and climatic history of Southeast  
674 Asia, it remains difficult to identify the exact cause of this divergence.

675         The biogeographical analyses further revealed some remarkable jump-dispersal  
676 events, including the colonization of Africa and India from Indochina in the Early and Late  
677 Miocene, respectively (Fig. 3); each of these events was followed by subsequent  
678 diversification in these regions. Whereas our study supports the proposed Asian Miocene  
679 origin of the African clade (Sengupta et al. 2009; Schultheiß et al. 2014; Van Bocxlaer et al.  
680 2018), it rejects the hypothesis that the Bellamyinae are of Gondwanan origin (*sensu* Davis  
681 1982; see also Sengupta et al. 2009) as has been hypothesized for other widespread freshwater  
682 gastropod families such as the Ampullariidae, Pachychilidae, Pomatiopsidae, and Thiaridae  
683 (e.g., Davis 1982; Strong et al. 2008; Hayes et al. 2009). Moreover, the probable Miocene  
684 origin of the Australian and Indian species implies that the Cretaceous fossils described from  
685 these areas likely do not represent members of the Viviparidae (see Supplementary Material  
686 available on Dryad for details).

687         Whereas the recent study of Sil et al. (2019) estimated comparatively similar  
688 divergence times for the Bellamyinae, their calibration strategy based on two considerably  
689 young fossil calibration points (i.e., Miocene for *Bellamyia* and Pleistocene for *F. bengalensis*)  
690 suggested a much younger (Paleocene) origin for the Viviparidae and considerably larger  
691 credibility intervals towards the base of the phylogeny. This pattern is very similar to the  
692 divergence time estimates obtained from our modified BEAST analysis, in which only CP3-  
693 CP5 were enforced (Supplementary Fig. S6 and Supplementary Table S5 available on Dryad).  
694 Significantly younger ages for both the Bellamyinae and the Viviparidae have been suggested

695 by Gu et al. (2019) and Hirano et al. (2019a). These authors focussed on African *Bellamy*,  
696 mainly Chinese *Sinotaia* species (Gu et al. 2019), and other East Asian taxa (Hirano et al.  
697 2019a). According to both studies, the Bellamyinae and even the Viviparidae originated as  
698 recently as the Early Miocene (c. 20 Ma). However, the dataset of Gu et al. (2019) is  
699 taxonomically very incomplete, *Filopaludina* and *Sinotaia* species have been misplaced in  
700 *Bellamy*, taxa previously recognized as belonging to the ingroup (i.e., *Neothauma*  
701 *tanganyicense*; see Sengupta et al. 2009; Schultheiß et al. 2014) have been forced into the  
702 outgroup, and their three geological and fossil calibration points are questionable and do not  
703 follow the guidelines of Parham et al. (2012). Moreover, the authors used a COI substitution  
704 rate for calibrating the tree as an alternative calibration strategy, but this rate was reported  
705 explicitly for relatively small, annual species and is likely saturated for diversification events  
706 older than 10 million years (My; see Wilke et al. 2009). Likewise, Hirano et al. (2019a)  
707 applied the fast COI rate inferred from the fossil-calibrated *Bellamy* phylogeny of Schultheiß  
708 et al. (2014) to East Asian taxa. Whereas Gu et al. (2019) refrained from discussing their age  
709 estimates in the light of the fossil record, Hirano et al. (2019) suggested that all pre-Miocene  
710 viviparid lineages either went extinct or were simply misidentified. Substitution saturation  
711 may also have affected the divergence time estimation by Hirano et al. (2019a) and in any  
712 case led to the considerably younger divergence estimates compared to our study. This  
713 comparison highlights the challenge of incorporating fossil information in molecular  
714 phylogenies, particularly for taxa with a long evolutionary history.

715

#### 716 *Biogeographical Patterns in the IAA*

717 With the possible exception of *Mekongia* sp. from Borneo, the colonization of insular  
718 Southeast Asia occurred comparatively late, from the Middle Miocene to the Plio-Pleistocene  
719 and thus closely reflects the dynamic geological history of this area (e.g., de Bruyn et al.

720 2014; see also Scotese 2014d and Supplementary Fig. S11 g,h available on Dryad). East Asia  
721 and Indochina, which were identified as the main source for emigration events, have largely  
722 been established since the Middle Jurassic (e.g., Metcalfe 2011), allowing the accumulation of  
723 species over a long geological period. In contrast, several islands in the IAA were largely  
724 submerged during the Miocene and later (e.g., Java and Sumatra) or had not yet formed (e.g.,  
725 the Philippines and Sulawesi; see e.g., de Bruyn et al. 2014; Nugraha and Hall 2018). The  
726 intensified colonization of the archipelago since the Late Miocene, facilitated by the extensive  
727 formation of land bridges across the IAA (see e.g., Hall 2009; de Bruyn et al. 2014), is thus  
728 consistent with palaeogeographical reconstructions and with inter-island colonization patterns  
729 observed in other invertebrates and vertebrates (Stelbrink et al. 2012; de Bruyn et al. 2014).

730         The analyses also identified multiple independent long-distance dispersal events from  
731 East Asia, Indochina and the Sunda Shelf into the Philippines, Sulawesi, and the Sahul Shelf  
732 (New Guinea and Australia; Fig. 3) that again highlight the permeability of renowned ‘faunal  
733 boundaries’ (i.e., Wallace’s Line and Lydekker’s Line; see e.g., Lohman et al. 2011).  
734 Moreover, the OTU-based tree used to infer biogeographical processes was constructed very  
735 conservatively, resulting in the grouping of genetically divergent island populations (Fig. 3).  
736 Consequently, some of the species, particularly within the genus *Filopaludina*, were treated as  
737 widespread and thus covered three to four of the predefined geographical areas. It is thus  
738 likely that the number of dispersal events is underestimated and that colonization within the  
739 IAA (particularly between islands within Sundaland) can be attributed to dispersal at the  
740 species level.

741         Whereas major, particularly older, speciation events are compatible with a vicariant  
742 hypothesis, dispersal seems to be more frequent in River Snails as previously thought (see  
743 e.g., Prasad 1928), despite their size and mobility. The biogeographical analyses showed that  
744 jump-dispersal was the most frequent range-changing cladogenetic process, whereas



745 anagenetic dispersal was rare (Supplementary Table S6 available on Dryad). Current global  
746 biodiversity patterns in River Snails can thus be only partly attributed to dispersal, as may  
747 perhaps be expected for such an ancient taxon. The most important process in shaping  
748 biodiversity hotspots in the Viviparidae, however, was *in situ* diversification (i.e., sympatry;  
749 see Fig. 3), particularly in isolated (and comparatively ancient) systems such as the African  
750 Great Lakes and the islands within the IAA.

751

### 752 *Patterns and Drivers of Shell Evolution*

753 Diversification within the Viviparidae was accompanied by major habitat shifts. The present  
754 study suggests that River Snails evolved from a lotic and smooth-shelled ancestor (Fig. 4).  
755 This scenario is supported in both unconstrained and fossil-constrained analyses, and it is also  
756 confirmed by the fossil record: the oldest fossil viviparids from the Jurassic and Cretaceous  
757 all lack spiral shell sculpture (Hudleston 1896; Stanton 1903; Yen 1950; Huckriede 1967;  
758 Bandel 1991; Tracey et al. 1993; Radley and Allen 2012), with the possible exception of the  
759 North American *Tulotomops* and *Lioplacodes*, both of which cannot be unambiguously  
760 assigned to Viviparidae (see also Supplementary Material available on Dryad). However, as  
761 the habitat type for fossils is often questionable (see Supplementary Material available on  
762 Dryad), the environmental settings in which these earliest representatives originated remain  
763 uncertain.

764       Species with unsculptured shells predominate in extant River Snails, particularly in the  
765 oldest subfamilies Lioplacinae and Viviparinae, and smooth shells were also estimated to be  
766 the most likely ancestral state for all three major clades (Fig. 4). In contrast, the highest  
767 variability in shell sculpture is found in the Bellamyinae, particularly within clade A.  
768 Interestingly, various extinct taxa also evolved heavily sculptured shells. Renowned examples  
769 include the morphologically disparate Plio-Pleistocene fauna of the genus *Viviparus* from

770 Greece (Willmann 1985), the African fossil assemblage of *Neothauma* since the Miocene (see  
771 e.g., Van Damme and Pickford 1999; Salzburger et al. 2014), and heavily sculptured  
772 *Margarya* forms identified from Oligocene deposits in China (e.g., Tian et al. 2013, 2018).  
773 The present results thus strongly indicate that such fine and heavily sculptured shells evolved  
774 multiple times independently across various viviparid lineages (Fig. 4), providing the first  
775 phylogenetic evidence for iterative shell evolution in River Snails. However, the repeated  
776 evolution of shell sculpture in both the extant and extinct faunas raises the question of  
777 whether underlying factors can be identified.

778         Shell sculpture in freshwater gastropods may not necessarily represent an adaptive  
779 response (see e.g., Gorthner 1992), but it has often been attributed to limnological parameters  
780 including habitat differences (e.g., Annandale 1919, 1924) and predatory pressure (e.g.,  
781 Vermeij and Covich 1978; Geary et al. 2002; Rasser and Covich 2014). Whereas the latter  
782 factor cannot be addressed here, habitat information available for the extant and some of the  
783 fossil species used to calibrate the phylogeny allows a discussion on environmental  
784 differences. In extant River Snails, species with smooth or finely sculptured shells mainly  
785 inhabit lotic habitats (Fig. 4). In contrast, those with coarse spiral sculpture are exclusively  
786 found in lentic environments (except for *Tulotoma magnifica*), and predominantly in  
787 (putative) ancient lakes (i.e., Yunnan Plateau lakes, China: *Anularya*, *Margarya*, and  
788 *Tchangmargarya*; Lake Inlé, Myanmar: *Taia*; Lake Poso, Indonesia: *Celetaia*; and Lake  
789 Lanao, Philippines: *Torotaia*). These species mainly belong to the Bellamyinae-clade A,  
790 which may also be characterized by larger and more slender shells compared to clade B  
791 (Supplementary Fig. S8 and Supplementary Table S7 available on Dryad). However, these  
792 apparent differences are not supported by the phylogenetic ANOVAs, suggesting that neutral  
793 morphological evolution explains the observed size differences.

794 The present analysis of habitat-shell evolution suggests that the evolution of  
795 sculptured shells was associated with major habitat shifts in some cases (Fig. 4). This is most  
796 noticeable in Bellamyinae-clade A, in which the highest shell disparity is found today (Fig.  
797 4). In contrast, a habitat transition from lotic to lentic identified in the extant Lake Malawi  
798 species flock of *Bellamyia* (clade B; see also Schultheiß et al. 2011), for example, did not give  
799 rise to a similar extant variability in shell sculpture. This pattern can be best explained by the  
800 estimated habitat-shell transition rates (Fig. 4, inset). According to the best-fit model (and  
801 other well supported models; Supplementary Table S8 available on Dryad), shell transitions  
802 were habitat-dependent, i.e., they differed between lentic and lotic environments. Moreover,  
803 the best-fit model revealed very low habitat transition rates. This finding suggests that  
804 changes in shell form mainly occurred *in situ*. However, in lotic habitats, coarsely sculptured  
805 shells ('LoC') were solely gained via habitat shifts and never derived *in situ*. Because  
806 transition rates between habitats were considerably lower than those between shell forms,  
807 coarse sculpture is very rare in lotic species and in extant viviparids only represented by  
808 *Tulotoma magnifica* (Viviparinae; see Fig. 4). This low prevalence is further affected by high  
809 transition rates from 'coarse' to 'smooth' via 'finely' sculptured shells  
810 ('LoC'→'LoB'→'LoA'), resulting in a net increase of smooth shells in lotic habitats. In  
811 lentic habitats, however, the highest transition rates were reciprocal between smooth and  
812 finely sculptured shells ('LeA'↔'LeB'), and the magnitude of these shell transition rates was  
813 much higher than those in lotic habitats. This finding implies an evolutionary versatility  
814 between these two shell types as a response to different environmental conditions in lentic  
815 habitats.

816 Similar to our results, data from the viviparid fossil record, for example, on European  
817 *Viviparus* (e.g. Willmann 1985; Posilović and Bajraktarević 2010), indicates that changes  
818 from smooth to sculptured shells relate to a change between lotic and lentic habitats. Whereas

819 our findings suggest a link between habitat and sculpture, more research is required to  
820 understand the mechanisms driving shell sculpture and how these processes are affected by  
821 abiotic and biotic factors. High rates of gain and loss in shell sculpture explain why coarsely  
822 sculptured shells are predominantly found in Bellamyinae–clade A in several independent  
823 lineages, and not more extensively in clade B, which comprises various extinct species from  
824 the African Great Lakes that are renowned for their high shell disparity (see e.g., Van Damme  
825 and Pickford 1999; Salzburger et al. 2014). Such high rates of shell evolution also explain the  
826 sympatric occurrence of closely related but morphologically disparate species in a single lake  
827 system such as Lake Inlé in Myanmar (Annandale 1919) and Lake Lanao in the Philippines  
828 (Bartsch 1907; Stelbrink et al. 2019), and why both weakly and heavily sculptured genera  
829 (*Sinotaia* vs. *Margarya*) co-occur in several Yunnan Plateau lakes (see e.g., Zhang et al.  
830 2015). Whereas the generally low dispersal ability together with high transition rates in lentic  
831 habitats triggered both *in situ* diversification and a high versatility in shell evolution, a  
832 selective pressure towards smooth shells seems to predominate in lotic habitats.

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1148 SUPPORTING INFORMATION

1149 Data available from the Dryad Digital Repository: [http://dx.doi.org/10.5061/dryad.\[NNNN\]](http://dx.doi.org/10.5061/dryad.[NNNN]).

1150

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1175 FIGURE CAPTIONS

1176 FIGURE 1. Distribution map of River Snails (Viviparidae) and their subfamilies (modified  
1177 from Van Bocxlaer and Strong 2019; see Figure S1 for a detailed map of samples collected in  
1178 Asia/Australia). White circles represent sample sites of specimens used in the present study.  
1179 Note that *Viviparus* occurs in both North America (= *Callinina*; see Discussion) and the  
1180 western Palearctic and that the monotypic genus *Rivularia* reported from the Hunan Province  
1181 of China belongs to the Viviparinae (see Van Bocxlaer et al. 2018). Bold numbers represent  
1182 number of extant genera described and sampled in our study.

1183

1184 FIGURE 2. OTU-based tree of Viviparidae created from the original BEAST MCC tree based  
1185 on the genes 28S rRNA, COI, and H3 including node ages, error bars (95% HPD), and  
1186 support values (posterior probabilities).

1187

1188 FIGURE 3. Unconstrained vs. fossil-constrained biogeographical analysis of Viviparidae based  
1189 on 13 predefined geographical areas, the best-fit biogeographical model (both DEC+J), and  
1190 error bars (95% HPD) obtained from the BEAST analysis. For simplicity, ancestral states are  
1191 only shown when they differ from the ancestral node. Colour-coded branches and nodes refer  
1192 to different cladogenetic and anagenetic events identified by the different analyses.

1193

1194 FIGURE 4. Ancestral state estimation of Viviparidae for habitat type and shell sculpture using  
1195 stochastic character mapping and the best-fit model (HabDep-Hab<sub>ER</sub>-Shell<sub>ARD</sub>) for the fossil-  
1196 constrained analysis (see text for details). For simplicity, ancestral states for the unconstrained  
1197 analysis are only shown if they differ considerably from the fossil-constrained analysis.  
1198 Colour gradients across the branches represent habitat transitions identified by the fossil-  
1199 constrained analyses. Representative shell images for each of the three spiral sculpture

1200 categories (from left to right): *Viviparus* cf. *contectus* ('absent'), *Torotaia* cf. *lanaonis*  
1201 ('fine'), and *Celetaia persculpta* ('coarse'). The upper inset shows the transition rates  
1202 calculated with the best-fit model for the six predefined habitat-shell states obtained from the  
1203 fossil-constrained analysis: 'LeA', 'LeB', 'LeC', 'LoA', 'LoB', and 'LoC'. Horizontal arrows  
1204 denote equally constrained transition rates for habitat transitions; transition rates between  
1205 shell types were all allowed to be different as indicated by the colours (see text for details).









