



HAL
open science

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

Björn Stelbrink, Romy Richter, Frank Köhler, Frank Riedel, Ellen E Strong, Bert Van Bocxlaer, Christian Albrecht, Torsten Hauffe, Timothy J. Page, David C. Aldridge, et al.

► To cite this version:

Björn Stelbrink, Romy Richter, Frank Köhler, Frank Riedel, Ellen E Strong, et al.. Global Diversification Dynamics Since the Jurassic: Low Dispersal and Habitat-Dependent Evolution Explain Hotspots of Diversity and Shell Disparity in River Snails (Viviparidae). *Systematic Biology*, 2020, 69, pp.944 - 961. 10.1093/sysbio/syaa011 . hal-02917167

HAL Id: hal-02917167

<https://hal.science/hal-02917167>

Submitted on 13 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 This manuscript has been accepted for publication in Systematic Biology, 69(5): 944-961
2 with DOI:10.1093/sysbio/syaa011. The published version is available at:
3 <https://academic.oup.com/sysbio/article-abstract/69/5/944/5736565>.

4

5

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

9

10 Running title: BIOGEOGRAPHY AND SHELL EVOLUTION IN RIVER SNAILS

11

12 Authors: Björn Stelbrink^{1,2*}, Romy Richter³, Frank Köhler⁴, Frank Riedel^{5,6}, Ellen E. Strong⁷,
13 Bert Van Bocxlaer^{8,9}, Christian Albrecht¹, Torsten Hauffe¹, Timothy J. Page¹⁰, David C.
14 Aldridge¹¹, Arthur E. Bogan¹², Li-Na Du¹³, Marivene R. Manuel-Santos¹⁴, Ristiyanti M.
15 Marwoto¹⁵, Alena A. Shirokaya¹⁶ & Thomas von Rintelen³

16

17 ¹Systematics & Biodiversity Lab, Department of Animal Ecology and Systematics, Justus
18 Liebig University Giessen, Giessen, Germany

19 ²Zoological Institute, Department of Environmental Sciences, University of Basel, Basel,
20 Switzerland

21 ³Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin,
22 Germany

23 ⁴Australian Museum, Sydney, New South Wales, Australia

24 ⁵Palaeontology, Institute of Geological Sciences, Freie Universität Berlin, Berlin, Germany

25 ⁶Institute for Ecological Research and Pollution Control of Plateau Lakes, School of Ecology
26 and Environmental Science, Yunnan University, Kunming, China

27 ⁷Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian
28 Institution, Washington, DC, USA

29 ⁸CNRS, Univ. Lille, UMR 8198 Evo-Eco-Paleo, Lille France

30 ⁹Limnology Unit, Department of Biology, Ghent University, Ghent, Belgium

31 ¹⁰Australian Rivers Institute, Griffith University, Nathan, Queensland, Australia

32 ¹¹Aquatic Ecology Group, Department of Zoology, Cambridge University, Cambridge, UK

33 ¹²Research Laboratory, North Carolina State Museum of Natural Sciences, Raleigh, USA

34 ¹³State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology,
35 Chinese Academy of Sciences, Kunming, China

36 ¹⁴Zoology Division, National Museum of the Philippines, Manila, Philippines

37 ¹⁵Zoology Division (Museum Zoologicum Bogoriense), Research Center for Biology, LIPI,
38 Cibinong, Bogor, Indonesia

39 ¹⁶Limnological Institute, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia

40

41 *To whom correspondence should be addressed:

42 Present address: Björn Stelbrink, Zoological Institute, Department of Environmental Sciences,

43 University of Basel, Basel, Switzerland. Tel: +41 61 2075723, Fax: +41 61 2070301. Email:

44 bjoern.stelbrink@allzool.bio.uni-giessen.de, bjoern.stelbrink@unibas.ch

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 mm³ 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+ Γ , COI^{1st} =
222 GTR+I+ Γ , COI^{2nd} = GTR+I+ Γ , COI^{3rd} = HKY+I+ Γ , H3^{1st} = GTR+ Γ , H3^{2nd} = GTR+I, and

223 H3^{3rd} JC+I, whereas the Bayesian information criterion (BIC) favoured a similar but slightly
224 less complex partitioning scheme: 28S rRNA+ H3^{2nd} = GTR+I+ Γ , COI^{1st} = GTR+ Γ , COI^{2nd} =
225 GTR+I+ Γ , COI^{3rd} = HKY+I+ Γ , H3^{1st} = K80+ Γ , and H3^{3rd} 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+ Γ 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+ Γ , COI^{1st}+COI^{2nd}+COI^{3rd} = GTR+I+ Γ , H3^{1st} =
253 K80+I+ Γ , H3^{2nd}+H3^{3rd} = 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-HabER-ShellARD
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 *Glaucostracia* 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 *Bellamya*,
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 *Bellamya*, 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 *Bellamya* 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.

833 REFERENCES

- 834 Annandale N. 1919. The gastropod fauna of old lake-beds in Upper Burma. Rec. Geol. Surv.
835 India 50:209–240.
- 836 Annandale N. 1924. The evolution of the shell-sculpture in fresh-water snails of the family
837 Viviparidae. Proc. R. Soc. London B 96:60–76.
- 838 Arldt T. 1917-1922. Handbuch der Palaeogeographie. Volume I (Palaeaktologie) and Volume
839 II (Palaeogeographie). Leipzig: Gebrüder Borntraeger.
- 840 Bandel K. 1991. Gastropods from brackish and fresh water of the Jurassic-Cretaceous
841 transition (a systematic reevaluation). Berliner Geowissenschaftliche Abhandlungen,
842 Reihe A 134:9–55.
- 843 Bartsch P. 1907. The Philippine pond snails of the genus *Vivipara*. Proc. United States Natl.
844 Museum 32:135–150.
- 845 Bensasson D., Zhang D.-X., Hartl D.L., Hewitt G.M. 2001. Mitochondrial pseudogenes:
846 evolution's misplaced witnesses. Trends Ecol. Evol. 16:314–321.
- 847 Bouchet P., Rocroi J.-P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M.,
848 Strong E.E. 2017. Revised classification, nomenclator and typification of gastropod and
849 monoplacophoran families. Malacologia 61:1–526.
- 850 Briggs J.C. 2009. Darwin's biogeography. J. Biogeogr. 36:1011–1017.
- 851 Carini G., Hughes J.M. 2006. Subdivided population structure and phylogeography of an
852 endangered freshwater snail, *Notopala sublineata* (Conrad, 1850) (Gastropoda:
853 Viviparidae), in Western Queensland, Australia. Biol. J. Linn. Soc. 88:1–16.
- 854 Carini G., Hughes J.M., Bunn S.E. 2006. The role of waterholes as “refugia” in sustaining
855 genetic diversity and variation of two freshwater species in dryland river systems
856 (Western Queensland, Australia). Freshw. Biol. 51:1434–1446.
- 857 Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in

858 phylogenetic analysis. *Mol. Biol. Evol.* 17:540–552.

859 Che J., Zhou W.-W., Hu J.-S., Yan F., Papenfuss T.J., Wake D.B., Zhang Y.-P. 2010. Spiny
860 frogs (Paini) illuminate the history of the Himalayan region and Southeast Asia. *Proc.*
861 *Natl. Acad. Sci. USA* 107:13765–13770.

862 Chiu Y.W., Chen C.A., Chen H.C. 2002. Genetic variation of the viviparid snail, *Sinotaia*
863 *quadrata* (Gastropod: Viviparidae), in Taiwan. *Acta Zool. Taiwanica* 13:1–10.

864 Colgan D.J., Ponder W.F., Beacham E., Macaranas J. 2007. Molecular phylogenetics of
865 Caenogastropoda (Gastropoda: Mollusca). *Mol. Phylogenet. Evol.* 42:717–737.

866 Cowie R.H., Holland B.S. 2008. Molecular biogeography and diversification of the endemic
867 terrestrial fauna of the Hawaiian Islands. *Philos. Trans. R. Soc. London B* 363:3363–
868 3376.

869 Crayn D.M., Costion C., Harrington M.G. 2015. The Sahul-Sunda floristic exchange: dated
870 molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *J.*
871 *Biogeogr.* 42:11–24.

872 Crisp M.D., Trewick S.A., Cook L.G. 2011. Hypothesis testing in biogeography. *Trends Ecol.*
873 *Evol.* 26:66–72.

874 Davis G.M. 1982. Historical and ecological factors in the evolution, adaptive radiation, and
875 biogeography of freshwater mollusks. *Am. Zool.* 22:375–395.

876 de Bruyn M., Stelbrink B., Morley R.J., Hall R., Carvalho G.R., Cannon C.H., van den Bergh
877 G., Meijaard E., Metcalfe I., Boitani L., Maiorano L., Shoup R., von Rintelen T. 2014.
878 Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity.
879 *Syst. Biol.* 63:879–901.

880 de Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends*
881 *Ecol. Evol.* 20:68–73.

882 Drummond A.J., Suchard M.A., Xie D., Rambaut A. 2012. Bayesian phylogenetics with

883 BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29:1969–1973.

884 Du L., Yang J., von Rintelen T., Chen X., Aldridge D. 2013. Molecular phylogenetic
885 evidence that the Chinese viviparid genus *Margarya* (Gastropoda: Viviparidae) is
886 polyphyletic. *Chinese Sci. Bull.* 58:2154–2162.

887 Dupin J., Matzke N.J., Särkinen T., Knapp S., Olmstead R.G., Bohs L., Smith S.D. 2017.
888 Bayesian estimation of the global biogeographical history of the Solanaceae. *J. Biogeogr.*
889 44:887–899.

890 du Toit A.L. 1937. Our wandering continents: an hypothesis of continental drifting. London:
891 Oliver & Boyd.

892 FitzJohn R.G. 2012. Diversitree: comparative phylogenetic analyses of diversification in R.
893 *Methods Ecol. Evol.* 3:1084–1092.

894 Garland T., Dickerman A.W., Janis C.M., Jones J.A. 1993. Phylogenetic analysis of
895 covariance by computer simulation. *Syst. Biol.* 42:265–292.

896 Geary D.H., Staley A.W., Müller P., Magyar I., Spring N. 2002. Iterative changes in Lake
897 Pannon *Melanopsis* reflect a recurrent theme in gastropod morphological evolution.
898 *Paleobiology* 28:208–221.

899 Gillespie R.G., Baldwin B.G., Waters J.M., Fraser C.I., Nikula R., Roderick G.K. 2012.
900 Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol. Evol.* 27:47–
901 56.

902 Gorthner A. 1992. Bau, Funktion und Evolution komplexer Gastropodenschalen in Langzeit-
903 Seen. Mit einem Beitrag zur Paläobiologie von *Gyraulus "multiformis"* im Steinheimer
904 Becken. *Stuttgarter Beiträge zur Naturkunde, Serie B* 190:1–173.

905 Gu Q.-H., Husemann M., Ding B., Luo Z., Xiong B.-X. 2015a. Population genetic structure of
906 *Bellamya aeruginosa* (Mollusca: Gastropoda: Viviparidae) in China: weak divergence
907 across large geographic distances. *Ecol. Evol.* 5:4906–4919.

908 Gu Q.-H., Zhou C.-J., Cheng Q.-Q., Li X.-J., Zhu G.-R., Zhang M., Gao Y.-N., Dong J.
909 2015b. The perplexing population genetic structure of *Bellamyia purificata* (Gastropoda:
910 Viviparidae): low genetic differentiation despite low dispersal ability. *J. Molluscan Stud.*
911 81:466–475.

912 Gu Q.H., Husemann M., Wu H.H., Dong J., Zhou C.J., Wang X.F., Gao Y.N., Zhang M., Zhu
913 G.R., Nie G.X. 2019. Phylogeography of *Bellamyia* (Mollusca: Gastropoda: Viviparidae)
914 snails on different continents: contrasting patterns of diversification in China and East
915 Africa. *BMC Evol. Biol.* 19:82.

916 Guindon S., Dufayard J.F., Lefort V., Anisimova M., Hordijk W., Gascuel O. 2010. New
917 algorithms and methods to estimate maximum-likelihood phylogenies: assessing the
918 performance of PhyML 3.0. *Syst. Biol.* 59:307–321.

919 Hall R. 2009. Southeast Asia’s changing palaeogeography. *Blumea* 54:148–161.

920 Hallam A. 1981. Plate tectonics, biogeography and evolution. *Nature* 293:31–32.

921 Hayes K.A., Cowie R.H., Thiengo S.C. 2009. A global phylogeny of apple snails:
922 Gondwanan origin, generic relationships, and the influence of outgroup choice
923 (Caenogastropoda: Ampullariidae). *Biol. J. Linn. Soc.* 98:61–76.

924 Heath T.A., Hedtke S.M., Hillis D.M. 2008a. Taxon sampling and the accuracy of
925 phylogenetic analyses. *J. Syst. Evol.* 46:239–257.

926 Heath T.A., Zwickl D.J., Kim J., Hillis D.M. 2008b. Taxon sampling affects inferences of
927 macroevolutionary processes from phylogenetic trees. *Syst. Biol.* 57:160–166.

928 Hirano T., Saito T., Chiba S. 2015. Phylogeny of freshwater viviparid snails in Japan. *J.*
929 *Molluscan Stud.* 81:435–441.

930 Hirano T., Saito T., Tsunamoto Y., Koseki J., Prozorova L., Do V.T., Matsuoka K., Nakai K.,
931 Suyama Y., Chiba S. 2019a. Role of ancient lakes in genetic and phenotypic
932 diversification of freshwater snails. *Mol. Ecol.* 28:5032–5051.

- 933 Hirano T., Saito T., Tsunamoto Y., Koseki J., Ye B., Do V.T., Miura O., Suyama Y., Chiba S.
934 2019b. Enigmatic incongruence between mtDNA and nDNA revealed by multi-locus
935 phylogenomic analyses in freshwater snails. *Sci. Rep.* 9:6223.
- 936 Ho S.Y.W., Tong K.J., Foster C.S.P., Ritchie A.M., Lo N., Crisp M.D. 2015. Biogeographic
937 calibrations for the molecular clock. *Biol. Lett.* 11:20150194.
- 938 Huckriede R. 1967. Molluskenfaunen mit limnischen und brackischen Elementen aus Jura,
939 Serpulit und Wealden NW-Deutschlands und ihre paläogeographische Bedeutung.
940 Beihefte zum Geol. Jahrb. 67:1–244.
- 941 Hudleston W.H. 1887-1896. A monograph of the inferior Oolite Gasteropoda. Being part I of
942 the British Jurassic Gasteropoda. London: Palaeontological Society London.
- 943 Huelsenbeck J.P., Nielsen R., Bollback J.P. 2003. Stochastic mapping of morphological
944 characters. *Syst. Biol.* 52:131–158.
- 945 Hug L.A., Roger A.J. 2007. The impact of fossils and taxon sampling on ancient molecular
946 dating analyses. *Mol. Biol. Evol.* 24:1889–1897.
- 947 Johnson S.G., Bragg E. 1999. Age and polyphyletic origins of hybrid and spontaneous
948 parthenogenetic *Campeloma* (Gastropoda: Viviparidae) from the southeastern United
949 States. *Evolution* 53:1769–1781.
- 950 Johnson S.G., Leefe W.R. 1999. Clonal diversity and polyphyletic origins of hybrid and
951 spontaneous parthenogenetic *Campeloma* (Gastropoda: Viviparidae) from the south-
952 eastern United States. *J. Evol. Biol.* 12:1056–1068.
- 953 Jones E.J.W., Cande S.C., Spathopoulos F. 1995. Evolution of a major oceanographic
954 pathway: the equatorial Atlantic. *Geol. Soc. London, Spec. Publ.* 90:199–213.
- 955 Katoh K., Standley D.M. 2013. MAFFT multiple sequence alignment software version 7:
956 improvements in performance and usability. *Mol. Biol. Evol.* 30:772–780.
- 957 Katoh K., Toh H. 2008. Recent developments in the MAFFT multiple sequence alignment

958 program. *Brief. Bioinform.* 9:286–298.

959 Klaus S., Morley R.J., Plath M., Zhang Y.P., Li J.T. 2016. Biotic interchange between the
960 Indian subcontinent and mainland Asia through time. *Nat. Commun.* 7:12132.

961 Köhler F., Glaubrecht M. 2010. Uncovering an overlooked radiation: molecular phylogeny
962 and biogeography of Madagascar’s endemic river snails (Caenogastropoda:
963 Pachychilidae: *Madagasikara* gen. nov.). *Biol. J. Linn. Soc.* 99:867–894.

964 Lanfear R., Calcott B., Ho S.Y.W., Guindon S. 2012. PartitionFinder: combined selection of
965 partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.*
966 29:1695–1701.

967 Lanfear R., Frandsen P.B., Wright A.M., Senfeld T., Calcott B. 2016. PartitionFinder 2: new
968 methods for selecting partitioned models of evolution for molecular and morphological
969 phylogenetic analyses. *Mol. Biol. Evol.* 34:772–773.

970 Li G., Steel M., Zhang L. 2008. More taxa are not necessarily better for the reconstruction of
971 ancestral character states. *Syst. Biol.* 57:647–653.

972 Lohman D.J., de Bruyn M., Page T., von Rintelen K., Hall R., Ng P.K.L., Shih H.T., Carvalho
973 G.R., von Rintelen T. 2011. Biogeography of the Indo-Australian archipelago. *Annu.*
974 *Rev. Ecol. Evol. Syst.* 42:205–226.

975 Marshall C.R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.

976 Matsukawa M., Ito M., Nishida N., Koarai K., Lockley M.G., Nichols D.J. 2006. The
977 Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial
978 ecosystems in Asia. *Cretac. Res.* 27:199–225.

979 Matzke N.J. 2013a. Probabilistic historical biogeography: new models for founder-event
980 speciation, imperfect detection, and fossils allow improved accuracy and model-testing.
981 *Front. Biogeogr.* 5:242–248.

982 Matzke N.J. 2013b. BioGeoBEARS: BioGeography with Bayesian (and Likelihood)

983 evolutionary analysis in R scripts. University of California, Berkeley, CA.

984 Matzke N.J. 2014. Model selection in historical biogeography reveals that founder-event
985 speciation is a crucial process in island clades. *Syst. Biol.* 63:951–970.

986 McIntyre S.R.N., Lineweaver C.H., Groves C.P., Chopra A. 2017. Global biogeography since
987 Pangaea. *Proc. R. Soc. London B* 284:20170716.

988 Metcalfe I. 2011. Palaeozoic-Mesozoic history of SE Asia. In: Hall R., Cottam M.A., Wilson
989 M.E.J., editors. *The Southeast Asian Gateway: history and tectonics of Australia-Asia*
990 *collision*. London: The Geological Society of London. p. 7–35.

991 Miller M.A., Pfeiffer W., Schwartz T. 2010. Creating the CIPRES Science Gateway for
992 inference of large phylogenetic trees. *Proceedings of the Gateway Computing*
993 *Environments Workshop (GCE)*:1–8.

994 MolluscaBase. 2019. *Viviparidae* Gray, 1847. Accessed at:
995 <http://www.molluscabase.org/aphia.php?p=taxdetails&id=154000> on 2020-01-23.

996 Nabhan A.R., Sarkar I.N. 2012. The impact of taxon sampling on phylogenetic inference: a
997 review of two decades of controversy. *Brief. Bioinform.* 13:122–134.

998 Nugraha A.M.S., Hall R. 2018. Late Cenozoic paleogeography of Sulawesi, Indonesia.
999 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 490:191–209.

1000 Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the
1001 comparative analysis of discrete characters. *Proc. R. Soc. London B* 255:37–45.

1002 Parham J.F., Donoghue P.C.J., Bell C.J., Calway T.D., Head J.J., Holroyd P.A., Inoue J.G.,
1003 Irmis R.B., Joyce W.G., Ksepka D.T., Patané J.S.L., Smith N.D., Tarver J.E., van Tuinen
1004 M., Yang Z., Angielczyk K.D., Greenwood J.M., Hipsley C.A., Jacobs L., Makovicky
1005 P.J., Müller J., Smith K.T., Theodor J.M., Warnock R.C.M., Benton M.J. 2012. Best
1006 practices for justifying fossil calibrations. *Syst. Biol.* 61:346–59.

1007 Pickford M. 2004. Palaeoenvironments of Early Miocene hominoid-bearing deposits at

1008 Napak, Uganda, based on terrestrial molluscs. *Ann. Paléontologie* 90:1–12.

1009 Ponder W.F., Colgan D.J., Healy J.M., Nützel A., Simone L.R.L., Strong E.E. 2008.

1010 Caenogastropoda. In: Ponder W.F., Lindberg D.R., editors. *Phylogeny and evolution of*

1011 *the Mollusca*. Berkeley: University of California Press. p. 331–383.

1012 Posilović H., Bajraktarević Z. 2010. Functional morphological analysis of evolution of

1013 ribbing in Pliocene viviparid shells from Croatia. *Lethaia* 43:457–464.

1014 Prashad B. 1928. Recent and fossil Viviparidae. A study in distribution, evolution and

1015 palaeogeography. *Mem. Indian Museum* 8:153–251.

1016 Quan C., Fu Q., Shi G., Liu Y., Li L., Liu X., Jin J. 2016. First Oligocene mummified plant

1017 Lagerstätte at the low latitudes of East Asia. *Sci. China Earth Sci.* 59:445–448.

1018 Radley J.D., Allen P. 2012. The Wealden (non-marine Lower Cretaceous) of the Weald Sub-

1019 basin, southern England. *Proc. Geol. Assoc.* 123:245–318.

1020 Rambaut A., Drummond A.J. 2007. Tracer v. 1.5. Accessed at:

1021 <http://tree.bio.ed.ac.uk/software/tracer>.

1022 Rasser M.W., Covich A.P. 2014. Predation on freshwater snails in Miocene Lake Steinheim:

1023 a trigger for intralacustrine evolution? *Lethaia* 47:524–532.

1024 R Core Team. 2018. R: a language and environment for statistical computing. R Foundation

1025 for Statistical Computing, Vienna, Austria.

1026 Ree R.H., Smith S.A. 2008. Maximum likelihood inference of geographic range evolution by

1027 dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57:4–14.

1028 Revell L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other

1029 things). *Methods Ecol. Evol.* 3:217–223.

1030 Rohrbach F. 1937. Oekologische und morphologische Untersuchungen an *Viviparus*

1031 (*Bellamya*) *capillatus* Frauenfeld und *Viviparus* (*Bellamya*) *unicolor* Olivier, unter

1032 Berücksichtigung anderer tropischer Formen und im Hinblick auf phyletische

- 1033 Beziehungen. Arch. für Molluskenkd. 69:177–218.
- 1034 Ronquist F., Sanmartín I. 2011. Phylogenetic methods in biogeography. Annu. Rev. Ecol.
1035 Evol. Syst. 42:441–464.
- 1036 Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu
1037 L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic
1038 inference and model choice across a large model space. Syst. Biol. 61:539–542.
- 1039 Rysiewska A., Hofman S., Osikowski A., Beran L., Pešić V., Falniowski A. 2019. *Viviparus*
1040 *mammillatus* (Küster, 1852), and partial congruence between the morphology-,
1041 allozyme- and DNA-based phylogeny in European Viviparidae (Caenogastropoda:
1042 Architaenioglossa). Folia Malacol. 27:43–51.
- 1043 Salisbury B.A., Kim J. 2001. Ancestral state estimation and taxon sampling density. Syst.
1044 Biol. 50:557–564.
- 1045 Salzburger W., Van Bocxlaer B., Cohen A.S. 2014. Ecology and evolution of the African
1046 Great Lakes and their faunas. Annu. Rev. Ecol. Evol. Syst. 45:519–545.
- 1047 Schultheiß R., Van Bocxlaer B., Riedel F., von Rintelen T., Albrecht C. 2014. Disjunct
1048 distributions of freshwater snails testify to a central role of the Congo system in shaping
1049 biogeographical patterns in Africa. BMC Evol. Biol. 14:42.
- 1050 Schultheiß R., Wilke T., Jørgensen A., Albrecht C. 2011. The birth of an endemic species
1051 flock: demographic history of the *Bellamya* group (Gastropoda, Viviparidae) in Lake
1052 Malawi. Biol. J. Linn. Soc. 102:130–143.
- 1053 Sclater J.G., Hellinger S., Tapscott C. 1977. The paleobathymetry of the Atlantic Ocean from
1054 the Jurassic to the Present. J. Geol. 85:509–552.
- 1055 Scotese C.R. 2014a. Atlas of Jurassic Paleogeographic Maps (Mollweide Projection), Maps
1056 32-42, Volume 4, The Jurassic and Triassic, PALEOMAP Atlas for ArcGIS,
1057 PALEOMAP Project, Evanston, IL.

1058 Scotese C.R. 2014b. Atlas of Early Cretaceous Maps (Mollweide Projection), Maps 23-31,
1059 Volume 2, The Cretaceous, PALEOMAP Atlas for ArcGIS, PALEOMAP Project,
1060 Evanston, IL.

1061 Scotese C.R. 2014c. Atlas of Paleogene Paleogeographic Maps (Mollweide Projection), Maps
1062 8-15, Volume 1, The Cenozoic, PALEOMAP Atlas for ArcGIS, PALEOMAP Project,
1063 Evanston, IL.

1064 Scotese C.R. 2014d. Atlas of Neogene Paleogeographic Maps (Mollweide Projection), Maps
1065 1-7, Volume 1, The Cenozoic, PALEOMAP Atlas for ArcGIS, PALEOMAP Project,
1066 Evanston, IL.

1067 Sengupta M.E., Kristensen T.K., Madsen H., Jorgensen A. 2009. Molecular phylogenetic
1068 investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift
1069 Valley area of Africa. *Mol. Phylogenet. Evol.* 52:797–805.

1070 Shaw K.L., Gillespie R.G. 2016. Comparative phylogeography of oceanic archipelagos:
1071 hotspots for inferences of evolutionary process. *Proc. Natl. Acad. Sci. USA* 113:7986–
1072 7993.

1073 Sil M., Aravind N.A., Karanth K.P. 2019. Role of geography and climatic oscillations in
1074 governing into-India dispersal of freshwater snails of the family: Viviparidae. *Mol.*
1075 *Phylogenet. Evol.* 138:174–181.

1076 Soares A.E.R., Schrago C.G. 2015. The influence of taxon sampling on Bayesian divergence
1077 time inference under scenarios of rate heterogeneity among lineages. *J. Theor. Biol.*
1078 364:31–39.

1079 Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of
1080 large phylogenies. *Bioinformatics* 30:1312–1313.

1081 Stanton T.W. 1903. A new fresh-water molluscan faunule from the cretaceous of Montana.
1082 *Proc. Am. Philos. Soc.* 42:188–199.

- 1083 Stelbrink B., Albrecht C., Hall R., von Rintelen T. 2012. The biogeography of Sulawesi
1084 revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous
1085 island"? *Evolution* 66:2252–2271.
- 1086 Stelbrink B., von Rintelen T., Albrecht C., Clewing C., Naga P.O. 2019. Forgotten for
1087 decades: Lake Lanao and the genetic assessment of its mollusc diversity. *Hydrobiologia*
1088 843:31–49.
- 1089 Stiller M., Knapp M., Stenzel U., Hofreiter M., Meyer M. 2009. Direct multiplex sequencing
1090 (DMPS) – a novel method for targeted high-throughput sequencing of ancient and highly
1091 degraded DNA. *Genome Res.* 19:1843–1848.
- 1092 Strong E.E., Colgan D.J., Healy J.M., Lydeard C., Ponder W.F., Glaubrecht M. 2011.
1093 Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules.
1094 *Zool. J. Linn. Soc.* 162:43–89.
- 1095 Strong E.E., Gargominy O., Ponder W.F., Bouchet P. 2008. Global diversity of gastropods
1096 (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* 595:149–166.
- 1097 Tian Y., Fürsich F.T., Schneider S. 2013. Giant Viviparidae (Gastropoda: Architaenioglossa)
1098 from the Early Oligocene of the Nanning Basin (Guangxi, SE China). *Neues Jahrb. für*
1099 *Geol. und Paläontologie, Abhandlungen* 267:75–87.
- 1100 Tian Y., Shaw D., Schneider S. 2018. Oligocene fossil assemblages from Lake Nanning
1101 (Yongning Formation; Nanning Basin, Guangxi Province, SE China): biodiversity and
1102 evolutionary implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 505:100–119.
- 1103 Tozer E.T. 1956. Uppermost Cretaceous and Paleocene non-marine molluscan faunas of
1104 western Alberta. *Geol. Surv. Canada Mem.* 280:1–125.
- 1105 Tracey S., Todd J.A., Erwin D.H. 1993. Mollusca: Gastropoda. In: Benton M.J., editor. *The*
1106 *fossil record* 2. London: Chapman and Hall. p. 131–167.
- 1107 Upchurch P. 2008. Gondwanan break-up: legacies of a lost world? *Trends Ecol. Evol.*

- 1108 23:229–236.
- 1109 Vail V.A. 1977. Comparative anatomy of 3 viviparid gastropods. *Malacologia* 16:519–540.
- 1110 Van Bocxlaer B., Strong E.E. 2019. Viviparidae, Gray 1847. In: Lydeard C., Cummings K.S.,
1111 editors. *Freshwater mollusks of the world: a distribution atlas*. Baltimore: Johns Hopkins
1112 University Press. p. 43–50.
- 1113 Van Bocxlaer B., Strong E.E., Richter R., Stelbrink B., von Rintelen T. 2018. Anatomical and
1114 genetic data reveal that *Rivularia* Heude, 1890 belongs to Viviparinae (Gastropoda:
1115 Viviparidae). *Zool. J. Linn. Soc.* 182:1–23.
- 1116 Van Damme D., Pickford M. 1999. The late Caenozoic Viviparidae (Mollusca, Gastropoda)
1117 of the Albertine Rift Valley (Uganda-Congo). *Hydrobiologia* 390:171–217.
- 1118 Vermeij G.J., Covich A.P. 1978. Coevolution of freshwater gastropods and their predators.
1119 *Am. Nat.* 112:833–843.
- 1120 von Rintelen T., Stelbrink B., Marwoto R.M., Glaubrecht M. 2014. A snail perspective on the
1121 biogeography of Sulawesi, Indonesia: origin and intra-island dispersal of the viviparous
1122 freshwater gastropod *Tylomelania*. *PLoS ONE* 9:e98917.
- 1123 Wegener A. 1912a. Die Entstehung der Kontinente. *Petermanns Geogr. Mitt.*:185–195.
- 1124 Wegener A. 1912b. Die Entstehung der Kontinente. *Petermanns Geogr. Mitt.*:253–256.
- 1125 Wegener A. 1912c. Die Entstehung der Kontinente. *Petermanns Geogr. Mitt.*:305–309.
- 1126 Wiley E.O. 1988. Vicariance biogeography. *Annu. Rev. Ecol. Syst.* 19:513–542.
- 1127 Wilke T., Schultheiß R., Albrecht C. 2009. As time goes by: a simple fool’s guide to
1128 molecular clock approaches in invertebrates. *Am. Malacol. Bull.* 27:25–45.
- 1129 Willmann R. 1985. Responses of the Plio-Pleistocene freshwater gastropods of Kos (Greece,
1130 Aegean sea) to environmental changes. *Lect. Notes Earth Sci.* 1:295–321.
- 1131 Winnepeninckx B., Backeljau T., De Wachter R. 1993. Extraction of high molecular weight
1132 DNA from molluscs. *Trends Genet.* 9:407.

- 1133 Woodruff D.S. 2010. Biogeography and conservation in Southeast Asia: how 2.7 million
1134 years of repeated environmental fluctuations affect today's patterns and the future of the
1135 remaining refugial-phase biodiversity. *Biodivers. Conserv.* 19:919–941.
- 1136 Yen T.-C. 1950. Fresh-water mollusks of Cretaceous age from Montana and Wyoming. *Geol.*
1137 *Surv. Prof. Pap.* 233-A:1–20.
- 1138 Yen T.-C. 1952. Molluscan fauna of the Morrison Formation. *U.S. Geol. Surv. Prof. Pap.*
1139 223:21–51.
- 1140 Yu Y., Harris A.J., Blair C., He X. 2015. RASP (Reconstruct Ancestral State in Phylogenies):
1141 a tool for historical biogeography. *Mol. Phylogenet. Evol.* 87:46–49.
- 1142 Zhang L.-J., Chen S.-C., Yang L.-T., Jin L., Köhler F. 2015. Systematic revision of the
1143 freshwater snail *Margarya* Nevill, 1877 (Mollusca: Viviparidae) endemic to the ancient
1144 lakes of Yunnan, China, with description of new taxa. *Zool. J. Linn. Soc.* 174:760–800.
- 1145 Zielske S., Ponder W.F., Haase M. 2017. The enigmatic pattern of long-distance dispersal of
1146 minute freshwater gastropods (Caenogastropoda, Truncatelloidea, Tateidae) across the
1147 South Pacific. *J. Biogeogr.* 44:195–206.

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

1151 FUNDING

1152 This work was supported by DFG (German Science Foundation) grants to B.S. (DFG STE

1153 2460/1-1 and STE 2460/2-1) and T.v.R. (DFG RI 1738/3-1). B.V.B. was supported by ANR-

1154 JCJC-EVOLINK of the French Agence Nationale de la Recherche. Sampling in Russia was

1155 partly funded by the Russian federal project no. 0345-2019-0009 to A.A.S.

1156 ACKNOWLEDGEMENTS

1157 We thank Giovanella Carini and Ben Cook (Griffith University, Brisbane, Australia), Reuben
1158 Clements (Sunway University, Selangor, Malaysia), David Dudgeon (University of Hong
1159 Kong, China), Jeffrey Garner (Alabama Department of Conservation and Natural Resources,
1160 USA), Matthias Glaubrecht (Universität Hamburg, Centrum für Naturkunde, Germany), Paul
1161 Johnson (Alabama Aquatic Biodiversity Center, USA), Larisa Prozorova (Far Eastern Branch
1162 Russian Academy of Sciences, Vladivostok, Russia), Suriani Surbakti (Universitas
1163 Cenderawasih, Jayapura, Indonesia) and Daisy Wowor (Research Center for Biology, LIPI,
1164 Cibinong, Indonesia) for field assistance, providing specimens, and species determination.
1165 Nicholas J. Matzke (Australian National University, Canberra, Australia) provided useful
1166 advice on the biogeographical analyses and commented on a previous version of the
1167 manuscript. Catharina Clewing (Justus Liebig University Giessen, Germany) and Christine
1168 Zorn (Museum für Naturkunde Berlin, Germany) took pictures of additional voucher
1169 specimens. André Billion (Fraunhofer Institute for Molecular Biology and Applied Ecology,
1170 Giessen, Germany) kindly provided computer resources to run the biogeographical analyses.
1171 Further computational resources were provided by the BMBF-funded (Federal Ministry of
1172 Education and Research, Germany) de.NBI Cloud within the German Network for
1173 Bioinformatics Infrastructure (de.NBI). Finally, we thank Bryan Carstens and two anonymous
1174 reviewers for their helpful comments on improving this manuscript.

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_{ER}-Shell_{ARD}) 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).







