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Historical Drainage Evolution and Water Level Fluctuations in the African Great Lakes Shaped Phylogeny and Biogeography of Freshwater Gastropods

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ABSTRACT

Aim: The role of historical drainage connectivity and the influence of water level fluctuations in African lakes on the evolution and distribution of macroinvertebrates remain poorly understood. This is partly because evolutionary biology research has largely focused on mobile vertebrates, such as cichlids. Here, we studied an African freshwater snail genus and assessed its phylogenetic relationships and phylogeographic patterns, and determined its colonisation history in African waters.

Location: African Great Lakes (AGL).

Taxon: *Gabbiella* (Gastropoda: Bithyniidae).

Methods: We applied a multi-locus molecular phylogenetic approach combining two mitochondrial DNA markers (COI and 16S) and two nuclear DNA markers (H3 and 28S) based on samples covering six AGL, their major connected rivers, and two crater lakes in western Uganda. Using maximum likelihood (ML) and Bayesian inference (BI) approaches, we inferred a dated phylogeny of *Gabbiella* and estimated the ancestral areas of the *Gabbiella humerosa* subspecies using BioGeoBEARS. We used statistical parsimony haplotype networks and genetic *p*-distances to investigate phylogeography and quantify genetic divergence within and between *Gabbiella* clades.

Results: The ML and BI analyses yielded nearly identical topologies. Our BEAST analysis suggests that *Gabbiella* probably originally diversified in the Miocene and later in the Pliocene and Pleistocene, too. We found high genetic distance among *Gabbiella* species and typical intraspecific genetic distance among *G. humerosa* subspecies. Phylogenetic inferences suggest that the most recent common ancestor (MRCA) of all *G. humerosa* subspecies originated in the Kivu–Tanganyika region during the Late Pleistocene. The MRCA of the Nilotic *G. humerosa* subspecies was most likely distributed in the Lake Kivu and Lake Albert regions.

Main Conclusions: The timing of diversification of *Gabbiella* coincides with significant geological events, such as rifting, historical drainage changes and lake-level fluctuations. These events suggest that the tectonic and climatic history of the region plays an integral role in diversification. Following each episode of vicariance, dispersal rather than extinction seems to determine the distribution patterns, underlining the high ecological tolerance of *G. humerosa*. The spatial diversification patterns of *Gabbiella* show similarities with those of other African molluscs and several fish taxa, suggesting that diversification is influenced by common underlying factors.

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1 | Introduction

Formed by tectonic activity that split the earth's crust, creating deep depressions that were later filled with water, the African Great Lakes (AGL) are located in the rift valleys between East and Central Africa (Cohen et al. 1997; Danley et al. 2012; Ogutu-Ohwayo et al. 2020). Together they cover a catchment area of over 850,000 km² in seven large lake basins: lakes Tanganyika, Kivu, Edward, Albert, Victoria, Turkana and Malawi (also known as Nyasa or Niassa) (Salzburger et al. 2014; Cowx and Ogutu-Ohwayo 2019). The AGL represent the largest freshwater lake system in the tropics (Plisnier et al. 2023), an invaluable resource at local, regional and global scales. They provide water, support biodiversity, enable food security, drive economic activities and regulate the climate (Daley 2003; Salzburger et al. 2014). The AGL are known as biodiversity hotspots due to their exceptional species diversity, making them of great interest to evolutionary biologists (e.g., Brooks 1950; Martens et al. 1994; Martens 1997; Rossiter and Kawanabe 2000). The lakes' structure, age, and habitat diversity have given rise to unique and endemic organisms (Salzburger et al. 2014). Their drainage history, shaped by tectonic activities and climatic changes, has had a lasting impact on the speciation and dispersal patterns of aquatic organisms (Salzburger et al. 2014; Daniels et al. 2015; Ogutu-Ohwayo et al. 2020). For example, genetic evidence suggests that tectonically induced drainage reversals have played a crucial role in the evolution and dispersal of cichlids and other endemic AGL species (Verheyen et al. 2003). The formation of a cichlid superclade following the drying events in Lake Victoria indicates historical drainage connectivity, which is defined here as former surface water linkages between basins, among lakes Albert, Edward and Kivu (Elmer et al. 2009; Vranken et al. 2022; Meier et al. 2023). These connections are now mainly restricted to the Nile River (Schultheiß et al. 2014). Lake Malawi, which is part of the Zambezi River system, has remained isolated from the other AGL (Salzburger and Meyer 2004). However, several authors have suggested a connection between the Congo River system and Lake Malawi (Van Bocxlaer et al. 2015; Schultheiß, Ndeo, et al. 2011; Schultheiß, Wilke, et al. 2011; Ortiz-Sepulveda et al. 2020).

While much of the research in evolutionary biology has focused on fish such as the famous cichlids, catfish and killifish (Verheyen et al. 2003; Seehausen 2006; Friedman et al. 2013; Day et al. 2013; Van der Merwe et al. 2021; Meier et al. 2023), less is known about macroinvertebrates. Most fish are highly mobile and can disperse over long distances. They can move against the current, cross barriers, and use temporary water connections in wet conditions (Hohausová et al. 2010). This mobility leads to dispersal patterns that are often very different from those of other invertebrates (Tonkin et al. 2018). In addition, human-induced relocations of fish can blur natural biogeographical patterns (e.g., Van Steenberge et al. 2020). Biogeographical studies of less mobile invertebrates could enable more accurate reconstructions of drainage connectivity through time. Their restricted movement subjects them to localised evolutionary pressures, making them valuable for biogeographic studies and the reconstruction of drainage connections (Mahulu et al. 2021). Recent studies found some freshwater molluscs particularly valuable for studying ancient evolutionary

processes (Ortiz-Sepulveda et al. 2020; Van Bocxlaer et al. 2021; Mahulu et al. 2021). However, none of these studies covered the AGL entirely or their connected rivers.

Gabbiella is a genus of freshwater gastropods belonging to the family Bithyniidae. Here it serves as a model for reconstructing phylogeographic patterns because it is widely distributed in African lakes and rivers, less commonly in permanent small water bodies, and rarely in habitats that dry out frequently (Mandahl-Barth 1968; Brown 1994). Each AGL harbours an endemic *Gabbiella* species or subspecies (Mandahl-Barth 1968; Brown 1994). This strong pattern of local endemism is likely due to limited dispersal ability and strict habitat specificity. *Gabbiella* species are freshwater specialists with narrow ecological tolerances (Mandahl-Barth 1968; Brown 1994). They depend on stable, localised habitats such as fine substrates or rocky littoral zones (Brown 1994), making them highly sensitive to historical changes in drainage connectivity. The oldest fossil record of *Gabbiella* dates to the Miocene (12.5–10.5 Ma) from the pre-Obweruka or Kisege stage (Van Damme and Pickford 2003), and other fossils are found in African paleo-lakes (see Table S3). The *Gabbiella* genus is divided into three subgenera, of which two subgenera, *Gabbiella* sensu stricto and *Conogabbia*, are distributed across the AGL and surrounding waters (Mandahl-Barth 1968). *Gabbiella humerosa* is very diverse in the AGL of East Africa and comprises six subspecies: *G. h. tanganyicensis* (Lake Tanganyika), *G. h. kivuensis* (Lake Kivu), *G. h. edwardi* (Lake Edward), *G. h. alberti* (Lake Albert), *G. h. kyogae* (Lake Kyoga & Victoria Nile River), and *G. h. humerosa* (Lake Victoria) (Mandahl-Barth 1968). *Gabbiella kichwambae* occurs in the crater lakes of western Uganda and is morphologically similar to *G. humerosa* but larger (Brown 1994). Lake Albert harbours not only *G. h. alberti*, but also two other endemic *Gabbiella* species: *G. candida* and *G. walleri* (Mandahl-Barth 1968). Lake Malawi is home to the endemic *G. stanleyi*, while Lake Turkana hosts the endemic *G. rosea* (Mandahl-Barth 1968).

Knowledge of the Bithyniidae in sub-Saharan Africa remains limited as populations are not extensively surveyed and species richness and taxonomy are still primarily based on shell and radula morphology and distribution patterns (Mandahl-Barth 1968; Brown 1994). To date, no comprehensive large-scale phylogenetic analysis of the *Gabbiella* genus has been conducted.

In this context, we sampled *Gabbiella* species in the AGL (Figure 1 and Figure S3). We (1) determined the phylogenetic relationships, genetic variability, and phylogeographic patterns of *Gabbiella* species in the AGL. We (2) determined the geographical origin and colonisation history of the subspecies of *G. humerosa* in the AGL of East Africa, and we (3) assessed the impact of drainage changes and water level fluctuations on the dispersal and adaptive radiation of *Gabbiella* species. Although most *Gabbiella* species are restricted to large lakes, the evolutionary links between these lakes remain unresolved, particularly the question of whether lacustrine species evolved from widespread riverine ancestors or by dispersal between lakes.

To address these objectives, we used a multi-locus molecular phylogenetic approach, constructed haplotype parsimony networks, and reconstructed ancestral ranges. We discuss the diversification patterns of *Gabbiella* in the context of AGL basin evolution, water level fluctuations, and large-scale biogeographical

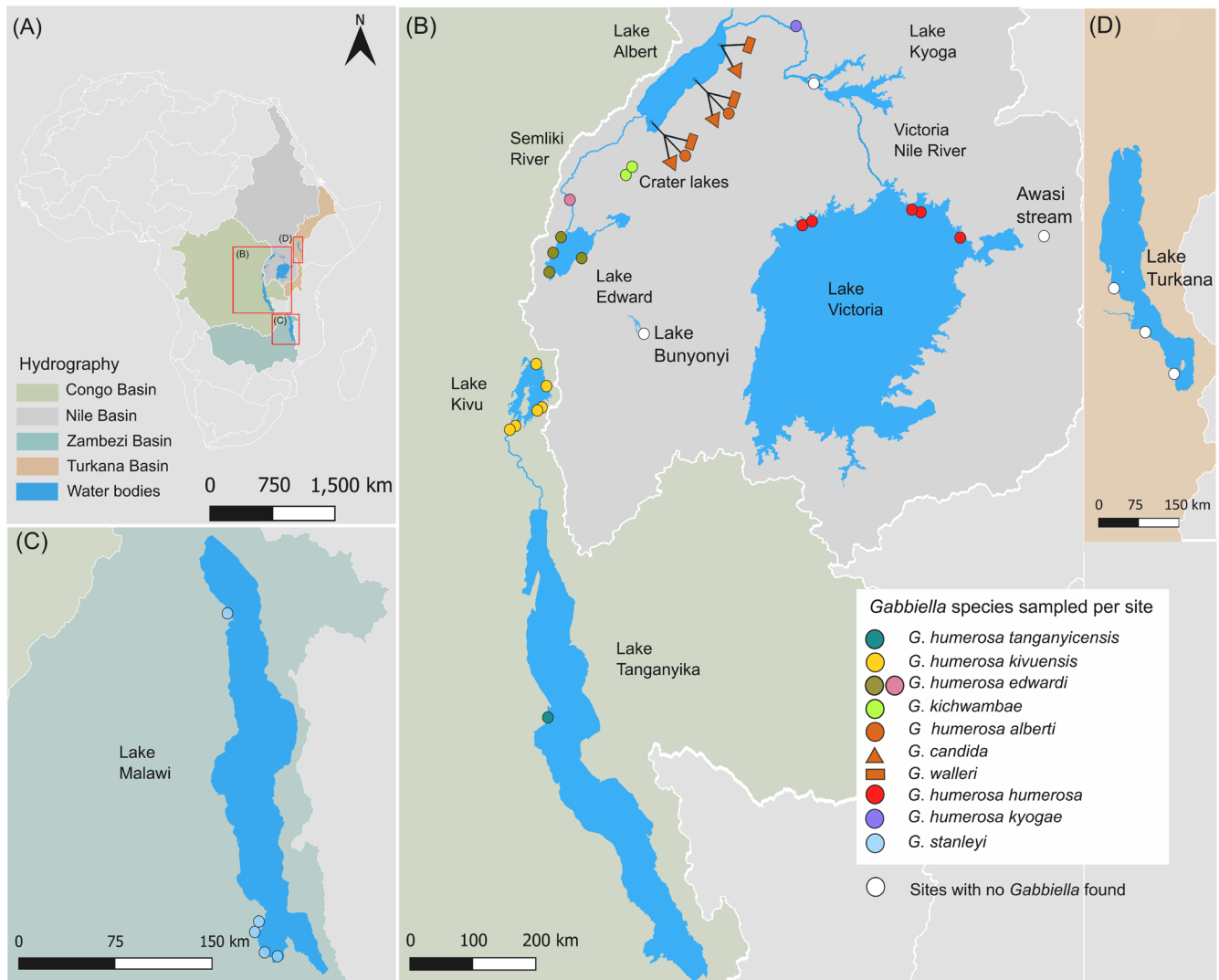


FIGURE 1 | Map of Africa highlighting the African Great Lakes and rivers (in red frame) within their respective drainage basins where *Gabbiella* spp. were sampled (A). The sampled *Gabbiella* spp. are shown at their locations in the map (B) and (C) and the colour codes represent their lakes of origin. White dots in the map (C) and (D) indicate locations where no *Gabbiella* spp. were found.

patterns in Africa. Finally, we compare our results with patterns in cichlid fishes and other freshwater molluscs.

2 | Material and Methods

2.1 | Data Collection and Morphological Identification

A targeted sampling of *Gabbiella* was carried out, specifically focusing on type localities summarised by Mandahl-Barth (1968). Fieldwork was conducted at Lake Tanganyika (LT), Lake Kivu (LK), Lake Edward (LE), Lake Albert (LA), Lake Kyoga (LKY), Lake Victoria (LV), the Victoria Nile River (VNR), the Semliki River (SR), Lake Malawi (LM), Lake Turkana (LTK), Lake Bunyonyi (LB), several crater lakes in western Uganda (CL), and a stream in the Kano Plain near Awasi (SKA) in western Kenya. The samples were taken in a survey carried out in 2022 and 2023. Additional *Gabbiella* spp. material from multiple previous collections spanning from 2006 to 2018, stored in the UGSB (University Giessen

Systematic & Biodiversity) collection at the Justus Liebig University Giessen (Germany), complemented this study. Specimens were hand-picked from hard substrates in shallow waters on stones and rocks, while scoop nets and dredges were used on soft substrates. Sampling was extended to deeper parts of the littoral zone (down to depths of 40 m) using an Ekman grab and a dredge. All specimens were preserved in 80% ethanol. We then used the relevant literature of Mandahl-Barth (1962) and Brown (1994) for morphological taxonomic identification. Prior to DNA extraction, high-resolution images were taken using a digital microscope (Keyence VHX-2000).

2.2 | DNA Isolation, Amplification and Sequencing

DNA was extracted from two specimens per species per locality, resulting in a total of 120 *Gabbiella* specimens, using either an entire specimen or a foot tissue sample (for larger specimens) using the CTAB protocol described by Wilke et al. (2006). Fragments of two mitochondrial markers, cytochrome *c* oxidase subunit I (COI) and large subunit ribosomal RNA (16S), were amplified using the

primers LCO1490 and HCO2198 (Folmer et al. 1994), and 16Sar and 16Sbr (Palumbi et al. 1991), respectively. In addition, two nuclear markers, histone 3 (H3) and large subunit ribosomal RNA (28S), were amplified with the primers H3F and H3R (Colgan et al. 2000), and D23F and D6R (Park and Foighil 2000), respectively. PCR conditions are described in the Table S4. DNA vouchers and, where available, shells and tissue remains are stored in the UGSB collection. Sanger sequencing was performed on an ABI 3730xl DNA analyser using the BigDye Terminator Kit (Life Technologies, LGC Genomics GmbH, Berlin, Germany).

2.3 | Dataset Compilation and Alignment

Additional Bithyniidae sequences for all four genetic markers were downloaded from the NCBI GenBank database (see Table S1). We used *Bythinella pannonica* (COI: FJ029077; 16S: FJ028877; 28S: FJ028895) and *Lithoglyphus naticoides* (COI: AF4445332; 16S: FJ160287; 28S: FJ160290) as outgroup taxa. Alignments for the protein-coding 66 sequences (49 newly generated) of COI (658bp) and 25 sequences (15 newly generated) of H3 (328bp) were performed using ClustalW implemented in BioEdit version 7.2.5 (Hall 1999). The non-coding gene fragments with 37 sequences (22 newly generated) of 16S (516bp) and 22 sequences (10 newly generated) of 28S (820bp) were aligned using the online program MAFFT version 7.0 (Katoh and Standley 2013; default settings). Ambiguous sites within the 28S alignment were removed using Gblocks version 0.91b (Castresana 2000) with the settings for a less stringent selection (i.e., allowing smaller final blocks, gap positions within the final blocks, and less strict flanking positions). The final alignment of 28S was 677bp long, representing 82.5% of the original 820 positions. All new sequences are deposited in GenBank (accession numbers are given in Table 1). A concatenated dataset was created using SequenceMatrix version 1.7.8 (Vaidya et al. 2011), resulting in a dataset composed of 66 taxa with a total length of 2179 bp.

2.4 | Phylogenetic and Molecular-Clock Analyses

The phylogenetic relationships were reconstructed using both maximum likelihood (ML) and Bayesian inference (BI). Prior to the analyses, we used jModelTest version 2.1.10 (Darriba et al. 2012) to select the best-fit substitution model for each gene partition. The models were selected based on the corrected Akaike information criterion (AICc) and Bayesian information criterion (BIC). For the 28S and 16S partitions, the AICc and BIC selected the GTR+I+ Γ model, while for the COI and H3 partitions, the HKY+I+ Γ and GTR+I models were selected, respectively. The ML analysis was performed for the concatenated dataset ($N=66$) using IQ-TREE version 2.2.2.6 (Minh et al. 2020). The node supports were evaluated using 10,000 ultra-fast bootstrap iterations.

The estimation of divergence times was performed with BEAST version 1.8.4 (Drummond et al. 2012) using a concatenated dataset reduced to unique haplotypes ($N=49$). The following settings were used: speciation=birth–death process; number of MCMC generations=40,000,000 and a sample frequency=2000. Due to uncertainty about the age and identification of the fossils (see Table S3), fossil calibrations were not used. Instead, we applied a mean molecular-clock rate ranging from 0.0124 to 0.0157

(substitutions per site and My) proposed for the COI gene for different Protostomia groups referring to the substitution models HKY and HKY+I+ Γ , respectively (Wilke et al. 2009). A uniform prior was applied to this range. Two different clock models, the strict-clock model and the uncorrelated lognormal relaxed-clock model, were used. These clock models were compared in BEAST using the marginal likelihood estimation based on path sampling (PS) and stepping-stone (SS) sampling (Baele et al. 2012). Based on marginal likelihood comparison, the relaxed clock model was favoured (see Table S5) and a maximum clade credibility (MCC) tree was generated with TreeAnnotator version 1.8.4 (BEAST package; node heights=mean heights) with a 50% burn-in. To address convergence issues with more complex substitution models (major ESS values <25), the less complex HKY substitution model was applied to the 16S, 28S and H3 partitions (28S and 16S=HKY+I+ Γ ; H3=HKY+I), reaching stationarity and increasing the effective sample size (ESS) values for all parameters. The ESS values were visualised on Tracer version 1.5 (Rambaut and Drummond 2007) revealing for both clock models values >300.

Species delimitation was based on congruence between shell morphological identification and phylogenetic structure inferred from the phylogenetic analyses.

2.5 | Phylogeographical Analyses

To explore the phylogeographic patterns of *Gabbiella* spp., we performed a statistical parsimony network analysis based on COI newly generated sequences using TCS version 1.21 (Clement et al. 2000; connection limit=95%). In addition, uncorrected genetic p -distances between groups of different *Gabbiella* (sub)species were calculated using the COI gene fragment in MEGA 11 (Tamura et al. 2021).

2.6 | Ancestral Area Estimation

To infer the biogeographical history of the *G. humerosa* group (see Figure 2), we used the R package BioGeoBEARS version 1.1.3 (Matzke 2013a, 2013b) for the R statistical environment 4.4.2 (R Core Team 2024). Six biogeographical models were tested and compared using the AICc: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BayAreaLIKE and BayAreaLIKE+J (Landis et al. 2013; Ree et al. 2005; Ree and Smith 2008; Ronquist 1997; Matzke 2014). The geographic distribution of each subspecies was coded based on occurrences of the sampled populations, resulting in seven regions (see 2.1.): LT (A), LK (B), LE (C), LA (D) and LV (E), as well as SR (F) and VNR (G). The maximum number of ancestral areas possibly inhabited was set to two. Prior to the analyses, the BEAST maximum clade credibility (MCC) tree was pruned to a *G. humerosa* subspecies (OTU-like) tree in BioGeoBEARS.

3 | Results

3.1 | Species Richness and Communities

Of the 13 type localities surveyed, five *Gabbiella* spp. were found at 9 localities (Figure 1). No *Gabbiella* spp. were found in LTK, which harboured only other snail shells during sampling.

TABLE 1 | Sampling sites for the studied *Gabbiella* species, including specimen codes, location information (country, region, name of waterbody, coordinates), haplotype number, and GenBank accession numbers. Abbreviations for lakes are as follows: LA—Lake Albert, LE—Lake Edward, LK—Lake Kivu, LT—Lake Tanganyika, LV—Lake Victoria, CL—Lake Nyinabugha and Lake Lyantonde (crater lakes), LM—Lake Malawi. GenBank accession numbers will be provided upon acceptance.

Specimen code	Country	Location	Coordinates		Species	Haplo-type no.	Voucher no.	GenBank accession no.			
			Latitude (°N)	Longitude (°E)				COI	16S	28S	H3
LA01/1	Uganda	Butiaba, Lake Albert	1.81914	31.32879	<i>G. candida</i>	H01	UGSB 28863	PX149791		PX169358	PX204858
LA02/1	Uganda	Ntoroko, Lake Albert	1.03089	30.51656	<i>G. candida</i>	H01	UGSB 28834	PX149792			PX204859
LA03/1	Uganda	Butiaba, Lake Albert	1.81475	31.31992	<i>G. candida</i>	H01	UGSB 28861	PX149793			
LA04/1	Uganda	Ntoroko, Lake Albert	1.03166	30.51738	<i>G. candida</i>	H01	UGSB 28868	PX149794			
LA05/1	Uganda	Hoima, Lake Albert	1.58376	31.10286	<i>G. candida</i>	H02	UGSB 28839	PX149795			
LA05/2	Uganda	Hoima, Lake Albert	1.58376	31.10286	<i>G. candida</i>	H03	UGSB 28840	PX149796			
LA05/3	Uganda	Hoima, Lake Albert	1.58376	31.10286	<i>G. humerosa alberti</i>	H04	UGSB 28837	PX149797	PX169336		
LA05/4	Uganda	Hoima, Lake Albert	1.58376	31.10286	<i>G. humerosa alberti</i>	H04	UGSB 28842	PX149798			
LA06/1	Uganda	Hoima, Lake Albert	1.58120	31.12238	<i>G. humerosa alberti</i>	H04	UGSB 28847	PX149799			
LA07/1	Uganda	Ntoroko, Lake Albert	1.05228	30.53475	<i>G. humerosa alberti</i>	H05	UGSB 28843	PX149800	PX169337		
LA04/2	Uganda	Ntoroko, Lake Albert	1.03166	30.51738	<i>G. humerosa alberti</i>	H06	UGSB 28852	PX149801	PX169338		
LA03/2	Uganda	Butiaba, Lake Albert	1.81475	31.31993	<i>G. humerosa alberti</i>	H07	UGSB 28858	PX149802			
LE01/1	DR Congo	Lunyasenge, Lake Edward	−0.30085	29.45000	<i>G. humerosa edwardi</i>	H08	UGSB 28885	PX149803			
LE02/1	DR Congo	Lunyasenge, Lake Edward	−0.49245	29.33960	<i>G. humerosa edwardi</i>	H09	UGSB 28887	PX149804			
LE02/2	DR Congo	Lunyasenge, Lake Edward	−0.49245	29.33960	<i>G. humerosa edwardi</i>	H10	UGSB 28888	PX149805	PX169339		
SR01/1	DR Congo	Kyavinyonge, Semliki River	−0.11697	29.57148	<i>G. humerosa edwardi</i>	H11	UGSB 28892	PX149806	PX169340		PX204860

(Continues)

TABLE 1 | (Continued)

Specimen code	Country	Location	Coordinates		Species	Haplo- type no.	Voucher no.	GenBank accession no.			
			Latitude (°N)	Longitude (°E)				COI	16S	28S	H3
LE03/1	Uganda	Rwenshana, Lake Edward	-0.38809	29.75127	<i>G. humerosa edwardi</i>	H12	UGSB 28894	PX149807	PX169341		
LK01/1	Rwanda	Nyamasheke, Lake Kivu	-2.31244	29.13772	<i>G. humerosa kivuensis</i>	H13	UGSB 27868	PX149808	PX169342	PX169359	PX204861
LK02/1	Rwanda	Nyamasheke, Lake Kivu	-2.29037	29.15549	<i>G. humerosa kivuensis</i>	H14	UGSB 27869	PX149809	PX169343		PX204862
LK03/1	Rwanda	Kigufi, Lake Kivu	-1.73938	29.27026	<i>G. humerosa kivuensis</i>	H15	UGSB 27871	PX149810			
LK04/1	Rwanda	Gitesi, Lake Kivu	-2.07361	29.35914	<i>G. humerosa kivuensis</i>	H15	UGSB 27873	PX149811			PX204863
LK05/1	Rwanda	Cyangugu, Lake Kivu	-2.47920	28.89837	<i>G. humerosa kivuensis</i>	H15	UGSB 27877	PX149812	PX169344		
LK06/1	Rwanda	Cyangugu, Lake Kivu	-2.47921	28.89836	<i>G. humerosa kivuensis</i>	H15	UGSB 28071	PX149813			
LT01/1	Congo	Kasanga, Lake Tanganyika	-5.73446	29.36347	<i>G. humerosa tanganyicensis</i>	H16	UGSB 17452	PX149814	PX169345	PX169361	PX204864
LT01/2	Congo	Kasanga, Lake Tanganyika	-5.73446	29.36347	<i>G. humerosa tanganyicensis</i>	H16	UGSB 17453	PX149815	PX169346	PX169362	PX204865
LT01/3	Congo	Kasanga, Lake Tanganyika	-5.73446	29.36347	<i>G. humerosa tanganyicensis</i>	H16	UGSB 17454	PX149816	PX169347		
LT01/4	Congo	Kasanga, Lake Tanganyika	-5.73446	29.36347	<i>G. humerosa tanganyicensis</i>	H16	UGSB 17455	PX149817	PX169348		
VN01/1	Uganda	Atura, Victoria Nile River	2.12852	32.32919	<i>G. humerosa kyogae</i>	H17	UGSB 28870	PX149818	PX169349		PX204866
LV01/1	Uganda	Ssese Archipelago, Lake Victoria	0.00735	32.35314	<i>G. humerosa humerosa</i>	H17	UGSB 28897	PX149819	PX169351		
LV02/1	Uganda	Dagusi Island, Lake Victoria	0.15662	33.56414	<i>G. humerosa humerosa</i>	H18	UGSB 28939	PX149820			
LV03/1	Uganda	Ssese Archipelago, Lake Victoria	0.05037	32.39346	<i>G. humerosa humerosa</i>	H19	UGSB 28896	PX149821	PX169350	PX169360	PX204868

(Continues)

TABLE 1 | (Continued)

Specimen code	Country	Location	Coordinates		Species	Haplo-type no.	Voucher no.	GenBank accession no.		
			Latitude (°N)	Longitude (°E)				COI	16S	28S
LV04/1	Uganda	Dagusi Island, Lake Victoria	0.13707	33.60149	<i>G. humerosa humerosa</i>	H20	UGSB 28898	PX149822		
CL01/1	Uganda	Isunga, Lake Nyinambuga (crater lake)	0.48092	30.28825	<i>G. kichwambae</i>	H21	UGSB 28974	PX149823	PX169352	
CL02/1	Uganda	Nyakasunsa, Lake Lyantonde (crater lake)	0.48716	30.28048	<i>G. kichwambae</i>	H21	UGSB 29660	PX149824		
LM01/1	Malawi	Chilumba, Lake Malawi	−10.43677	34.26531	<i>G. stanleyi</i>	H22	UGSB 29376	PX149825	PX169353	PX169363
LM02/1	Malawi	Chilumba, Lake Malawi	−10.43593	34.26424	<i>G. stanleyi</i>	H22	UGSB 31033	PX149826		
LM03/1	Malawi	Chilumba, Lake Malawi	−10.43675	34.26533	<i>G. stanleyi</i>	H23	UGSB 29377	PX149827	PX169354	PX169364
LM04/1	Malawi	Pemba, Lake Malawi	−13.90833	34.62748	<i>G. stanleyi</i>	H24	UGSB 0096	PX149828		
LM05/1	Malawi	Kalonga, Lake Malawi	−10.43593	34.26425	<i>G. stanleyi</i>	H25	UGSB 0111	PX149829		
LM05/2	Malawi	Kalonga, Lake Malawi	−10.43593	34.26425	<i>G. stanleyi</i>	H26	UGSB 31032	PX149830		
LM06/1	Malawi	Pemba, Lake Malawi	−13.90055	34.63010	<i>G. stanleyi</i>	H27	UGSB 0058	PX149831		
LM06/2	Malawi	Pemba, Lake Malawi	−13.90055	34.63010	<i>G. stanleyi</i>	H28	UGSB 31034	PX149832		
LM07/1	Malawi	Mangochi, Lake Malawi	−14.25548	34.80618	<i>G. stanleyi</i>	H29	UGSB 0176	PX149833		
LM08/1	Malawi	Kalonga, Lake Malawi	−10.42556	34.25018	<i>G. stanleyi</i>	H30	UGSB 0216	PX149834		
LA08/1	Uganda	Hoima, Lake Albert	1.69745	31.06365	<i>G. walleri</i>	H31	UGSB 28849	PX149835		
LA09/1	Uganda	Ntoroko, Lake Albert	1.06135	30.53561	<i>G. walleri</i>	H31	UGSB 28862	PX149836	PX169355	PX169365
LA09/2	Uganda	Hoima, Lake Albert	1.69745	31.06365	<i>G. walleri</i>	H31	UGSB 28850	PX149837		
LA09/3	Uganda	Hoima, Lake Albert	1.69745	31.06365	<i>G. walleri</i>	H31	UGSB 28865	PX149838	PX169356	PX169366
LA09/4	Uganda	Hoima, Lake Albert	1.69745	31.06365	<i>G. walleri</i>	H32	UGSB 28864	PX149839	PX169357	PX169367

co-occurring with *G. humerosa alberti* (Figure 1). Lake Albert is thus the only lake with more than a single *Gabbiella* species. *Gabbiella kichwambae* was found in the CL (lakes Nyinambuga and Lyantonde), and *G. stanleyi* was recorded from various locations across LM, but was not found in the tributaries.

3.2 | Phylogenetic Relationships and Estimation of Divergence Times

The ML and BI trees yielded nearly identical topologies, except for the position of *G. kichwambae* from the crater lakes of western Uganda and *Hydrobioides* sp. from Myanmar, the latter position rendering the genus *Gabbiella* non-monophyletic (see taxonomic implications in Appendix S1). Overall, strongly supported phylogenies were obtained (Figure 2A and Figure S1). The *Gabbiella* samples from the AGL yielded three major clades with Bayesian posterior probabilities (BPP) above 0.95 and bootstrap values (BS) of 1.00 for clade 1 and clade 2, and BPP of 0.98 and BS of 0.74 for clade 3 (Figure 2A and Figure S1). Clade 1 consists of *G. humerosa* (incl. all six subspecies) and *G. kichwambae*, and is the sister of clade 2, which consists of *G. candida* (BPP = 1.00 and BS = 100). Clade 3, comprising *G. stanleyi* and *G. walleri* (BPP = 1.00 and BS = 100), is sister to *Hydrobioides* sp. from Myanmar. Clade 3 and *Hydrobioides* sp. form a sister group to clades 1 and 2, and all three clades form a sister group to the remaining bithyniid.

According to the Bayesian divergence time estimates, the split between *Gabbiella* (including *Hydrobioides* from Myanmar) and the Eurasian bithyniids occurred in the Late Oligocene 25.03 Ma [95% highest posterior density (HPD) = 18.16–32.22 Ma] (Figure 2A). The most recent common ancestor (MRCA) of *G. stanleyi* and *G. walleri* (lakes Malawi and Albert, respectively) and *Hydrobioides* sp. (Myanmar) split in the Middle Miocene 17.31 Ma (95% HPD = 11.88–23.62 Ma). The MRCA of *G. candida*, *G. kichwambae*, and *G. humerosa* was estimated to be 14.35 million years old (95% HPD = 9.43–19.91 Ma). The split between *G. stanleyi* and its sister species (*G. walleri*) is estimated to be 3.36 Ma (95% HPD = 1.99–4.80 Ma) and thus dates back to the Pliocene. The *G. humerosa* subspecies originated in the Early Pleistocene 1.50 Ma (95% HPD = 0.94–2.26 Ma).

3.3 | Phylogeographical Patterns

The statistical parsimony network analysis resulted in 32 unique haplotypes out of 49 COI sequences organised in seven single networks (Figure 3 and Table 1). *Gabbiella humerosa alberti* (LA) clustered together with *G. humerosa humerosa* (LV) and *G. humerosa kyogae* (VNR) in group A, which comprised eleven specimens separated by a maximum of four mutational steps (Figure 3A). Two specimens from LV and the VNR share the same haplotype (H17), showing that *G. humerosa humerosa* (LV) and *G. humerosa kyogae* (VNR) are genetically identical. *Gabbiella humerosa kivuensis* (LK) clustered together with *G. humerosa edwardi* (LE) in group B, which comprised 11 specimens separated by a maximum of seven mutational steps (Figure 3B). The *G. humerosa edwardi* haplotype (H11) from the SR was separated by one mutational step from specimens

from LE. Four specimens of *G. humerosa tanganyicensis* (LT) formed a single haplotype (group C; Figure 3C) and did not cluster with any other *G. humerosa* subspecies. *Gabbiella kichwambae* formed an independent cluster comprising two specimens from the crater lakes Nyinambuga and Lyantonde (group D; Figure 3D). *Gabbiella candida* and *G. walleri* from Lake Albert ($N=6$ and $N=5$, respectively) formed the independent networks (see Figure 3E,F). The haplotypes from LM were clustered in group G (see Figure 3G), which comprised 10 specimens of *G. stanleyi*, with populations from the southern basin (H24, H27–H29) connected to those from the northern basin (H22, H23) by a maximum of 18 mutational steps.

The *p*-distance between the group A (*G. h. alberti*, *G. h. humerosa* and *G. h. kyogae*) and the group B (*G. h. kivuensis* and *G. h. edwardi*) was 2.8%, while the *p*-distance to group C (*G. h. tanganyicensis*) was 2.5% and 3.3%, respectively (Table 2). The *p*-distance between *G. humerosa* (groups A, B, C) and *G. kichwambae* (group D) ranged between 3.6% and 4.7%. The genetic *p*-distance between *G. candida* (group E) and *G. walleri* (group F) and *G. humerosa* subspecies ranged between 16.6% and 18.2% (Table 2), while the *p*-distance between the two sister taxa *G. walleri* (group F) and *G. stanleyi* (group G) was 7.7%.

3.4 | Ancestral Area Estimation

According to the AICc as implemented in BioGeoBEARS, the best-fit biogeographical model was DIVALIKE ($d=0.5781$; $e=0.4158$; $j=0$; $\text{LnL}=-14.66$; Figure S2). The MRCA of *G. humerosa* probably inhabited the area of LT and LK (Figures 2B, 4 and Figure S2). A vicariant event around 1.17 Ma (95% HPD = 0.76–1.59 Ma) gave rise to the ancestor of all Nilotic subspecies (*G. h. alberti*, *G. h. humerosa*, *G. h. kyogae*, *G. h. kivuensis* and *G. h. edwardi*) and the LT subspecies (*G. h. tanganyicensis*; see Figures 2B, 4). Subsequently, the ancestral area of all Nilotic subspecies was expanded via anagenetic dispersal from the LK region into the LA area. Around 1.00 Ma (95% HPD = 0.64–1.4 Ma) another vicariant event separated the ancestral populations inhabiting LK and LA, which both expanded their range to LK + LE and LA + LV, respectively, via anagenetic dispersal. Both ancestral areas (LK + LE and LA + LV) were further subdivided via vicariance c. 400 ka (95% HPD = 0.20–0.61 Ma) and c. 300 ka (95% HPD = 0.12–0.4 Ma), respectively, giving rise to all currently known Nilotic subspecies.

4 | Discussion

4.1 | Species Diversity, Phylogenetic Relationships and Divergence Times

The present study provides the first molecular-based approach to *Gabbiella* species diversity in the AGL and major connected rivers. Our analyses identified the presence of five *Gabbiella* species and five of the six *G. humerosa* subspecies at their type localities (Figure 1, note that *G. h. kyogae* is with *G. h. humerosa*). Our results also confirm the occurrence of *G. humerosa edwardi* in the SR, which is consistent with earlier findings by Schultheiß,

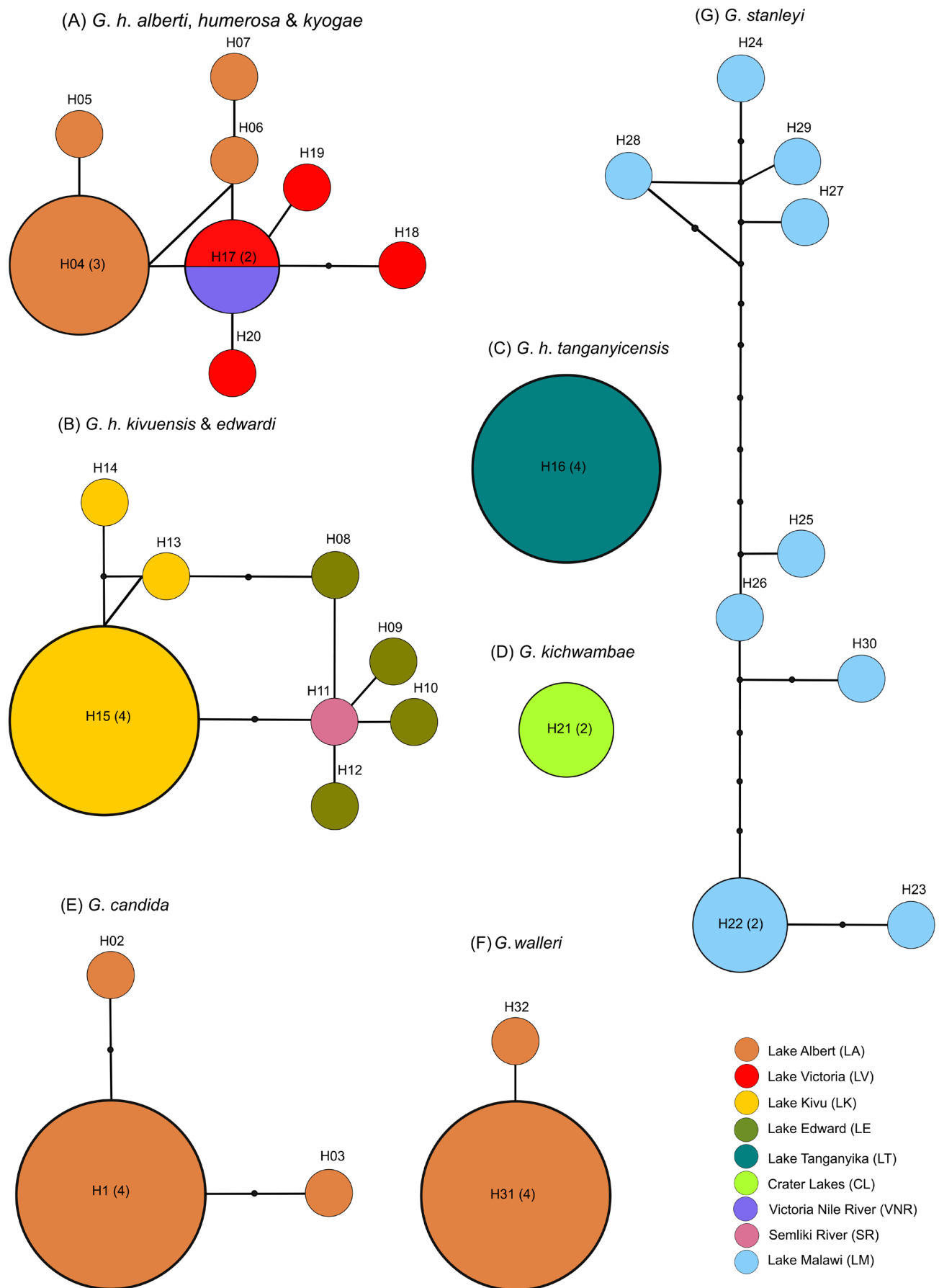


FIGURE 3 | Legend on next page.

FIGURE 3 | Phylogeography of *Gabbiella* spp. using statistical parsimony haplotype networks implemented in TCS (95% connection limit). 32 unique haplotypes of the COI gene fragment are colour-coded according to lakes and rivers (Figure 1). Seven clusters were identified. The size of the circles is proportional to the number of specimens sharing the same haplotype.

TABLE 2 | Uncorrected genetic *p*-distances between *Gabbiella* species groups, based on COI dataset (658 bp).

Group	<i>G. candida</i>	<i>G. h. alberti, humerosa & kyogae</i>	<i>G. h. kivuensis & edwardiensis</i>	<i>G. kichwambae</i>	<i>G. h. tanganyicensis</i>	<i>G. walleri</i>
<i>G. candida</i>						
<i>G. h. alberti, humerosa & kyogae</i>	16.6					
<i>G. h. kivuensis & edwardiensis</i>	16.7	2.8				
<i>G. kichwambae</i>	15.9	3.7	4.7			
<i>G. h. tanganyicensis</i>	16.2	2.5	3.3	3.6		
<i>G. walleri</i>	18.6	18.2	16.9	18.5	17.8	
<i>G. stanleyi</i>	17.3	18.1	17.2	17.8	17.7	7.7

Ndeo, et al. (2011) and Schultheiß, Wilke, et al. (2011). Our phylogenies reveal the presence of three highly divergent *Gabbiella* clades aligned with taxonomic classifications rather than geographic distribution (i.e., samples from LA do not form a cluster). Importantly, the phylogenetic relationships within the clades (except clade 1) and between the clades are not reflected in the classification of *Gabbiella* into different subgenera based on morphological, anatomical, and radula characters from previous studies (see taxonomic implications in the Appendix S1; Mandahl-Barth 1968; Brown 1994). Our multi-gene phylogenies strongly support a close relationship within the subspecies of *G. humerosa* found in the AGL, as recognised by Mandahl-Barth (1968), and support a close relationship of *G. humerosa* and *G. kichwambae* from the western Uganda crater lakes (Figure 2A and Table 2). The uncorrected genetic *p*-distance between subspecies of *G. humerosa* of 2.5% to 3.3% corresponds to the intraspecific *p*-distance of 1.5% to 5.0% in *Bythinella pannonica*, which is thought to be comparatively high due to a spatial distribution characterised by habitat fragmentation and dispersal over long distances (Fehér et al. 2013). The *p*-distance between *G. kichwambae* and *G. humerosa* ranging between 3.6% and 4.7% corresponds to interspecific *p*-distances from the family Hydrobiidae (Beran et al. 2022) and thus supports a close relationship between *G. humerosa* and *G. kichwambae* as recognised by Mandahl-Barth (1968).

Interestingly, unlike other AGL, where each lake harbours a single endemic *Gabbiella* species, LA contains three highly distinct species. The uncorrected *p*-distance between these species exceeds the *p*-distance observed in hydrobiids (Delicado et al. 2019). It is similar to the family or subfamily divergence observed in the Truncatelloidea (Wilke et al. 2001, 2023). These species are not closely related and thus do not represent a species flock, but rather a species scatter resulting from multiple

colonisation events (Hauswald et al. 2008). Similar situations for Bithyniidae have so far only been found in temperate, potentially ancient lakes Trichonis and Prespa (Albrecht et al. 2009, 2012). While formal taxonomic changes are beyond the scope of this study, our results emphasise the need for a comprehensive phylogenetic re-evaluation of the genus *Gabbiella* (see taxonomic implications in Appendix S1). Compared to other smaller AGL such as LE and LK, LA hosts a relatively high molluscan diversity. Similarly, the western Uganda crater lakes exhibit a comparatively high molluscan diversity, including a potentially endemic *Gabbiella* species, raising questions about the origins and colonisation mechanisms of species in these isolated water bodies. The inferred sister relationship between *G. walleri* (LA) and *G. stanleyi* (LM) should be interpreted with caution due to the incomplete sampling.

The fossil record of *Gabbiella* is summarised (Table S3), but the actual dating, taxonomic classification, and age of most of the records are uncertain, limiting their applicability in determining their precise placement on the phylogenetic tree. Such uncertainties reduce the trustworthiness of using the fossil record as a reference for dating evolutionary relationships. Therefore, we used the mean molecular-clock rate for the COI gene according to Wilke et al. (2009), which closely matches clock rates determined by fossil calibrations in freshwater molluscs (Schultheiß et al. 2014; Tumwebaze et al. 2022). As such, the suggested divergence time of *Gabbiella* from the Eurasian bithyniids (Figure 2A) thus predates the geological evidence for the closure of the Tethys Seaway (18–20 Ma; Okay et al. 2010) and aligns with the earliest evidence for mammalian exchange between Africa and Eurasia (Rögl 1999; Harzhauser et al. 2007; Harzhauser and Piller 2007). Moreover, a significant portion of the eastern branch of the East African Rift System developed somewhat later, approximately 20 Ma (Pickford 1982;

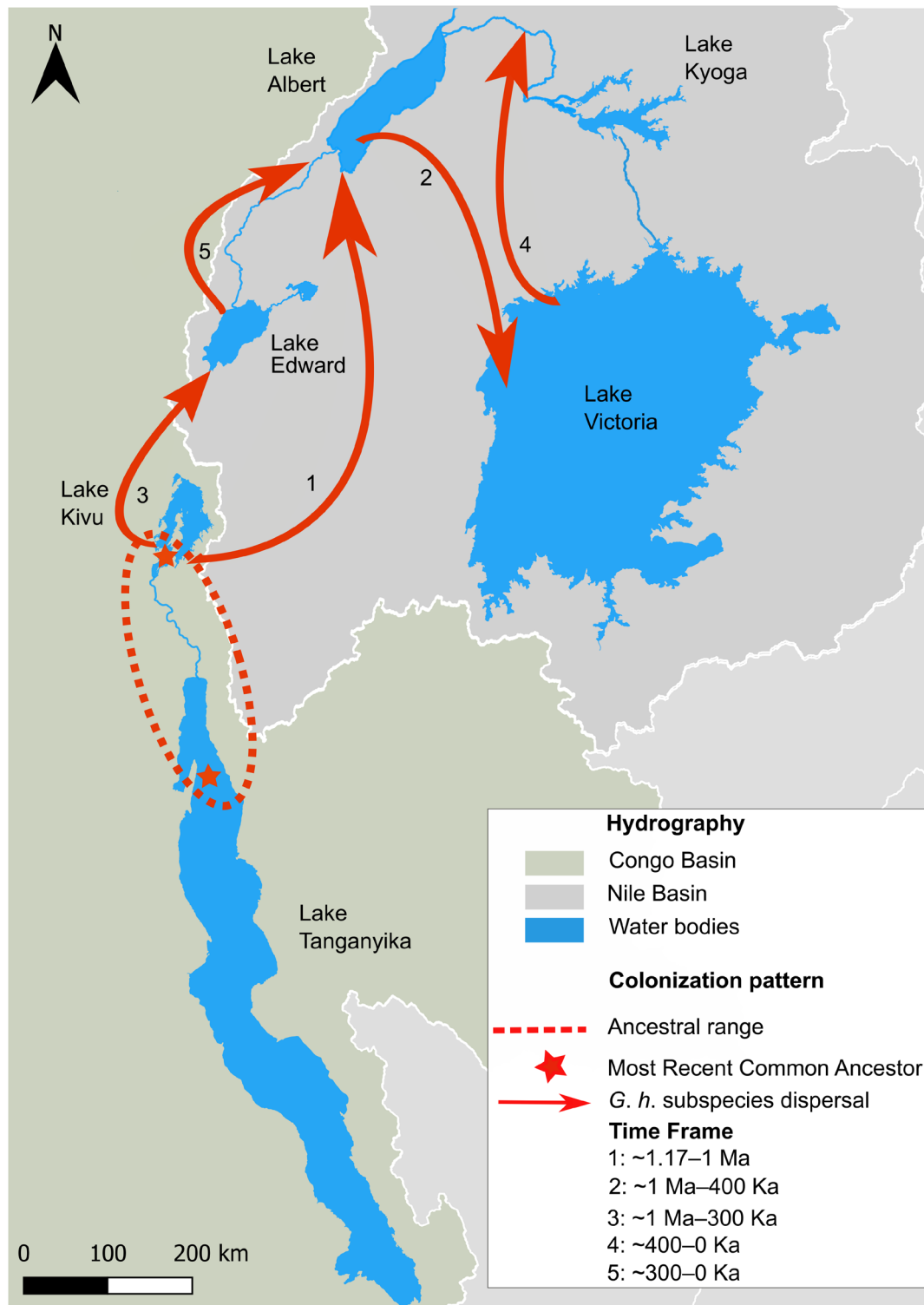


FIGURE 4 | Biogeographical history scenario of *Gabbiella humerosa* subspecies from the Early Pleistocene to the present. Map of the African Great Lakes and the rivers in their respective drainage basins in which samples of *Gabbiella humerosa* subspecies were found. The dotted ellipse shows the distribution area of the ancestor (red star), while the red arrow indicates the origin of the subspecies' dispersal and the time frame indicating the range of dispersal is shown (see Figure 2B).

Chorowicz 2005). The colonisation of *Gabbiella* in the African region began later than that of co-occurring freshwater molluscs like *Lanistes* (Mahulu et al. 2021) and freshwater crabs of the Potamonautidae, which originated during the Eocene (Daniels et al. 2015). However, it aligns with that of *Melanoides* in the Early Miocene (Genner et al. 2007) and fish genera, such

as *Distichodus* in the Late Oligocene (Arroyave et al. 2020). The split of *G. stanleyi* and *G. walleri* (clade 3) from the Asian *Hydrobioides* (Myanmar) coincides with a period of significant climatic and geological changes in Africa during the Middle Miocene, with the climatic optimum around 15–17 Ma representing a warmer phase with a peak in precipitation (Zachos

et al. 2001). This may have increased the connectivity of African rivers, facilitating divergence and diversification. Other fish genera have also been identified as having diversified around the same period, including spiny eels (*Mastacembelus*) and killifish (*Nothobranchius*) during the Miocene (Day et al. 2017; Van der Merwe et al. 2021) as well as the Early Miocene onset of diversification within Haplochromini cichlids (Schedel et al. 2019). It is noteworthy that *Gabbiella*'s diversification occurred earlier than that of *Bellamya* snails (Schultheiß, Ndeo, et al. 2011; Schultheiß, Wilke, et al. 2011; Schultheiß et al. 2014) and *Coelatura* bivalves (Ortiz-Sepulveda et al. 2020). The *G. candida* from LA diverged from the *G. humerosa* subspecies and *G. kichwambae* in the Middle Miocene, 14.35 Ma (95% HPD = 9.43–19.91). The relatively long branch likely indicates prolonged isolation and an absence of further diversification. Alternatively, we could also miss taxa because they are either extinct or have not been sampled. The initial colonisation of the paleo-lake Obweruka occurred during the Kisegi stage (12.0 and 10.5 Ma), where the oldest fossils of *Gabbiella* were discovered (Van Damme and Pickford 2003) overlap the timing of the split of *G. candida*. By 2.0 Ma, however, all Albertine endemics had gone extinct, leaving only the widespread thiarids remaining in the Kairo and Luso paleo-lakes (Van Damme and Pickford 2003). Identifying and classifying older fossils within a modern DNA-based phylogenetic framework is challenging (Wilke et al. 2009). Using such older fossils with uncertain phylogenetic placement as calibration points can lead to significant errors (Nguyen and Ho 2020). The SR, which formed a connection between LE and LA about 10 ka ago (Beadle 1981), adds to the difficulty of accurately placing the associated fossil record. Similarly, the estimated age of the *G. stanleyi* fossils from paleo-lake Chiwondo in the Malawi Basin is unclear (Van Damme and Gautier 2013). Our estimate for the initial start of diversification within *G. stanleyi* in the Middle Pleistocene, 930 ka (95% HPD = 0.48–1.46 Ma), coincides with *Lanistes* (Schultheiß et al. 2009; Mahulu et al. 2021), *Bellamya* (Schultheiß, Ndeo, et al. 2011; Schultheiß, Wilke, et al. 2011; Schultheiß et al. 2014), and thus supports the founder flush pattern recognised by Schultheiß et al. (2009). Lake Malawi was most likely dry during long periods between 1.6 Ma and 800 ka (see figure 5; Delvaux 1995; Lyons et al. 2015; Ivory et al. 2016), and it is likely that *G. stanleyi*, among other taxa, recolonised the lake after the crisis (Van Damme and Gautier 2013).

4.2 | Biogeography and Phylogeographic Patterns

The phylogeny of *G. humerosa* from the AGL suggests a strong connection between the region's historical drainages and underscores the impact of vicariance and dispersal on biogeographical patterns. Each evolutionary divergence in *G. humerosa* is associated with a discrete episode of drainage evolution, which either separated ancestral populations into new habitats or facilitated their dispersal. This was likely driven by rifting or climatic change. Our phylogenetic framework suggests similar patterns of colonisation of the AGL by *G. humerosa* and the cichlid fish of the LV Region Superflock (LVRS; cichlids of LV and the nearby LA, LKY, LE and LK; Verheyen et al. 2003; Meier et al. 2023). A slight difference with other molluscs such as *Bellamya* and *Coelatura* exists (Schultheiß, Ndeo, et al. 2011; Schultheiß, Wilke, et al. 2011; Schultheiß et al. 2014; Ortiz-Sepulveda et al. 2020; Van

Bocxlaer et al. 2021). Notably, *Bellamya* and *Coelatura* are absent in LK (Brown 1994; Mandahl-Barth 1988; Dusabe et al. 2024), and *Bellamya* is absent in LE and Lake George (Brown 1994; Schultheiß, Ndeo, et al. 2011; Schultheiß, Wilke, et al. 2011). Apart from these absences, the phylogeographic patterns of *G. humerosa* closely match those of the molluscs mentioned above.

The MRCA of *G. humerosa* inhabited LK and LT in the Early Pleistocene 1.50 Ma (95% HPD = 0.94–2.26 Ma; Figure 2A). With the progression of rifting, a vicariance likely disrupted the drainage connection between LK and LT around 1.17 Ma (95% HPD = 0.76–1.59 Ma). This period coincides with increasing aridity and climate variability across Africa, as documented by Trauth et al. (2021) for the period from 1.9 to 1.4 Ma. Faunal fluctuation must have occurred on a larger African scale around 2.0 to 1.75 Ma (Bibi and Kiessling 2015) and 0.75 to 0.50 Ma (Cohen, Du, et al. 2022). The vicariance also matches the time when the water level of LT dropped significantly, reaching up to 600 m in Plio-Pleistocene (Russell et al. 2020) or even 650–700 m below present-day levels by 1.1 Ma (Figure 5; Lezzar et al. 1996). In addition, the final uplift of the northern LT boundary fault, which occurred around 1.0 Ma, further corroborates the vicariance (Lezzar et al. 2002; Wright et al. 2020). This vicariance led to the initial allopatric speciation of *G. humerosa* (Figure 2B), giving rise to the ancestor of all Nilotic subspecies (*G. h. kivuensis*, *G. h. alberti*, *G. h. humerosa*, *G. h. kyogae* and *G. h. edwardi*) and the LT subspecies (*G. h. tanganyicensis*; see Figures 2B and 4). The ancestral area of all Nilotic subspecies expanded via anagenetic dispersal from the LK region into the LA area within a timeframe of ~1.17–1 Ma (Figure 4). Around 1.00 Ma (95% HPD = 0.64–1.4 Ma), a vicariance event occurred, separating the ancestral populations inhabiting the LK and LA regions. This separation likely resulted from the cooling and drying of climate in East Africa between 1.7 and 1.0 Ma (Peter 2004; Hoag and Svenning 2017), which likely triggered ecological fragmentation and genetic isolation. The time of the vicariance also corresponds with the estimated age of the MRCA of cichlids in the LVRS (913 ka; Meyer et al. 2017). However, the MRCA of viviparid snails in the LV ecoregion is older, at approximately 2.50 Ma (Schultheiß et al. 2014; Van Bocxlaer et al. 2020). Following this divergence, the descendant populations appear to have expanded their range to the LK + LE region (timeframe: ~1 Ma–300 ka) and to the LA + LV region (timeframe: ~1 Ma–400 ka).

Notably, the LK's inclusion in the MRCA of other Nilotic AGL *Gabbiella* species aligns with prior research highlighting the pivotal role of LK in the cichlids distribution within the Nilotic AGL (Verheyen et al. 2003; Meier et al. 2023). This also highlights the historical drainage connections between the LK and other Nilotic lakes (Beadle 1981; Ross et al. 2014). However, the dispersal pattern of the catfish *Clarias gariepinus* tells a different story. The ancestors of the LK catfish were distributed throughout the Congo Province, reflecting the current drainage system through which the LK flows into the Congo River via the LT (Van Steenberge et al. 2020). Both ancestral areas (LA + LV and LK + LE) were further subdivided by vicariance around 400 ka (95% HPD = 0.20–0.61 Ma) and 300 ka (95% HPD = 0.12–0.4 Ma), respectively, giving rise to

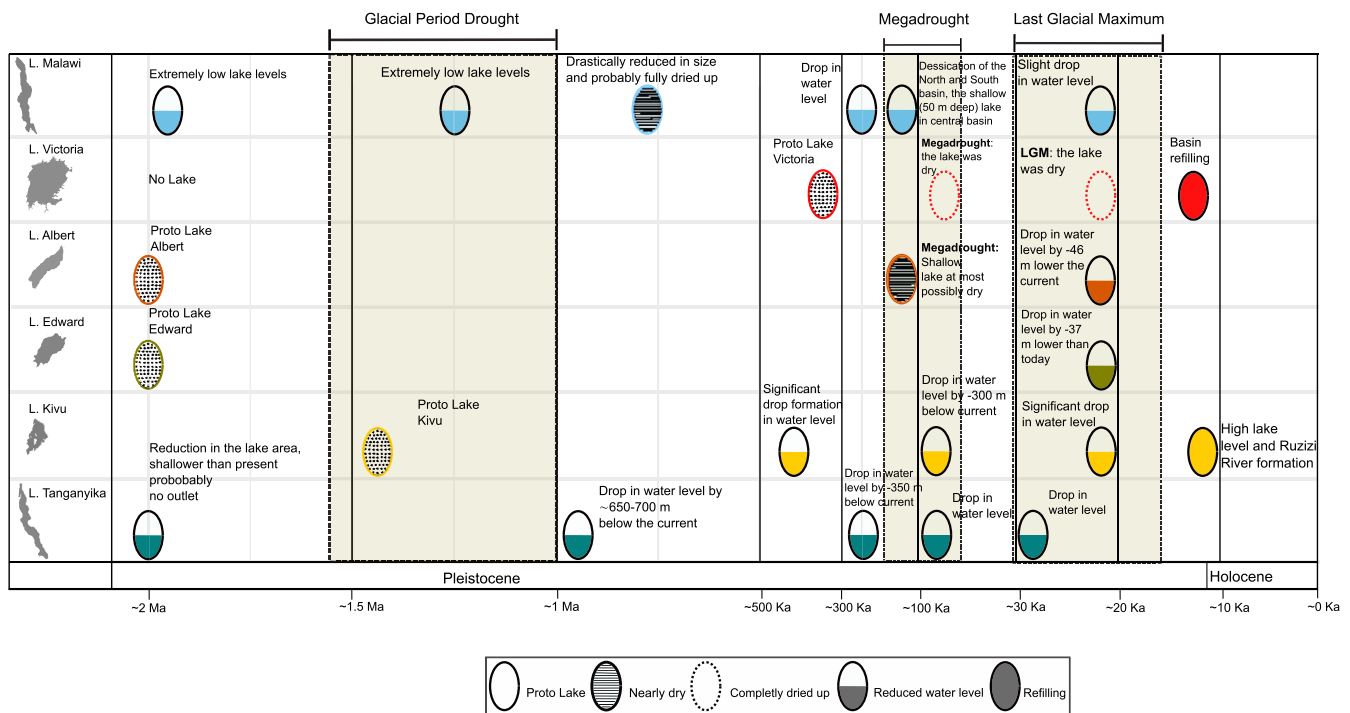


FIGURE 5 | The water level fluctuations of the African Great Lakes from the Early Pleistocene to the present, dominated by three types of droughts (glacial drought, megadrought, and last glacial maximum) (This figure was created based on the detailed information in Table S2).

all the Nilotic subspecies known today. The vicariance event that separated LA + LV at 400 ka corresponds to the estimated origin of LV (Johnson et al. 1996; Talbot and Williams 2009; Danley et al. 2012; Salzburger et al. 2014) and corroborates the mitochondrial divergence time of the cichlid LVRS (Schedel et al. 2019). The LA and LV subspecies cluster in the same haplotype network, separated by a maximum of four mutational steps (Figure 3A), suggesting a recent common ancestor that nevertheless experienced some divergence with persistent gene flow. Lake Victoria may have completely desiccated during the megadroughts (Beverly et al. 2020; Renaut and Owen 2023) or experienced widespread desiccation with localised seasonal wetlands during the Last Glacial Maximum (Wienhues et al. 2024; Tryon et al. 2015). Survival of organisms would potentially require that a source area existed in the vicinity of LV during arid phases and that recolonisation happened when the lake refilled. Lake Victoria is currently connected to the LA via the VNR and LKY. However, the VNR is estimated to be only about 11.2 ka (Beuning et al. 1997; Johnson et al. 2000; Table S2C), which corroborates the timeframe of species dispersal between the LV and VNR. This dispersal likely began with the formation of the VNR (see Figure 2B). Mandahl-Barth (1968) and Brown (1994) recorded the occurrence of *G. humerosa kyogae* in the VNR. Our phylogeographic analysis shows that *G. humerosa kyogae* shares the same haplotype with *G. humerosa humerosa* (Figure 3A). Due to the absence of clear genetic, morphological, and ecological differences (see Figure S3B,C), we hypothesise that these populations represent a single, contiguous lineage and are not independently evolving subspecies.

The vicariance event that separated LK + LE at 300 ka coincides with the Middle Pleistocene lava flows (300–350 ka), which caused a flow reversal in the paleo-Nyabarongo River

system. This diversion of water from the Kivu Rift into the Nile system occurred as a result of the lava flows (Holzförster and Schmidt 2007). A significant drop in the LK water level around 475 ka preceded this event and may have set the stage for genetic and ecological divergence (figure 5; Wood and Scholz 2017). The clustering of the LK and LE subspecies within the same haplotype network, separated by a maximum of seven mutational steps (Figure 3B), emphasises their close phylogenetic relationship and historical connectivity of their drainage systems. According to geological evidence, the SR did not flow out of the LE until the Late Pleistocene (Beadle 1981), which supports the timeframe of population dispersal between these areas (Figure 2B). Recent immigration is evident (Figure 3B), and slight genetic differentiation is likely due to local adaptation to the riverine habitat.

Gabbiella stanleyi (LM) harbours distantly related haplotypes from the north separated by more than 18 mutational steps to the south of the lake (Figure 3G). The LM has experienced several prolonged lake level fluctuations, which may have led to habitat fragmentation (figure 5; Delvaux 1995; Lyons et al. 2015; Ivory et al. 2016). Thus, for several thousand years, the lake was confined to a single paleo-lake in the northern half of the depression, where the current water depth reaches more than 700 m (Delvaux 1995; Johnson et al. 2016; Ivory et al. 2016). The distantly related haplotypes observed in *G. stanleyi* may therefore indicate prolonged isolation, reflecting cryptic speciation or independently evolving species that may have been shaped by historical isolation from refugia during low lake levels.

The interpretations of historical drainage changes and lake-level fluctuations referenced here are drawn from published geological literature (see Table S2). An increasing number of

deep-drilling campaigns across Africa will likely provide a higher temporal resolution of patterns in paleolimnological configurations (Cohen, Campisano, et al. 2022; Cohen, Du, et al. 2022). This information will be invaluable for interpreting future biogeographical patterns of aquatic taxa across the continent. Although reticulate evolution, resulting from mechanisms such as hybridisation or introgression, could theoretically explain the patterns of shared genetic variation, the resolution of our multilocus dataset does not allow rigorous inference of admixture. The strong spatial structure and consistency with historical drainage patterns also make passive dispersal unlikely. Many species have low tolerance for desiccation, low survival rates during overland transport, and require specific habitats for successful colonisation. Thus, the observed endemism reflects the isolation of catchments after the termination of hydrological connectivity. Our results are consistent with those of other studies on the historical drainage changes in the AGL. These studies demonstrate that historical drainage changes and water-level fluctuations impact the evolution of organisms in the AGL (Salzburger et al. 2014; Seehausen 2015; Cohen et al. 2013). The biogeography of *G. humerosa*, in particular, serves as one of the most informative models for drainage evolution in the AGL during the Pleistocene.

5 | Conclusion

This study provides the first molecular phylogeny for freshwater bithyniids of the genus *Gabbiella* inhabiting the AGL. Accordingly, ancestors of *Gabbiella* from the AGL date back to the early Miocene. The spatial patterns of diversification of *Gabbiella* show similarities with those of other molluscs and various fish taxa. This suggests that diversification is influenced by common underlying factors and corroborates various events such as rifting, historical drainage changes, and climate fluctuations. Our analysis shows that the current diversity and distribution of the AGL *Gabbiella humerosa* subspecies result from vicariance and dispersal patterns caused by rifting and associated historical drainage changes during the Pleistocene. A taxonomic revision of *Gabbiella* spp. is necessary, as the previous morphological classification is not reflected in the phylogenetic classification. This study provides new insights into the patterns and process of diversification of *Gabbiella* in the African Great Lakes and contributes to phylogeographic studies of freshwater biodiversity in Africa.

Author Contributions

M.C.D. carried out fieldwork, performed laboratory work and analyses, created figures, and wrote the first draft of the manuscript. C.C. checked the quality of the sequences, helped with data compilation, and analysed data. G.K.-R. helped with fieldwork and permits. M.R. assisted with field and lab work; O.W.N. and J.T. collected materials. C.A. conceived the study, collected material, advised in the data analyses, and revised the manuscript. All authors contributed to drafting and reviewing the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All sequences are deposited in GenBank of the manuscript under the accession numbers given in Table 1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jbi70074-sup-0001-supinfo.docx.