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MOLLUSC BIODIVERSITY AND ENDEMISM IN THE POTENTIAL ANCIENT LAKE TRICHONIS, GREECE

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ABSTRACT

Ancient lakes are hotspots of biodiversity, often harboring a large number of endemic species that make them prime model systems for evolutionary biologists. Besides such well-recognized ancient or long-lived lakes as Baikal, Biwa, Ohrid, and Tanganyika, there are other potentially old and biodiverse lakes in the world with poorly specified ages and under-studied faunas. We here report on the mollusc fauna of one such lake, Lake Trichonis in continental Greece. This graben lake is situated in a highly tectonized area, characterized by karst features and probably of middle to late Pliocene origin. Lake Trichonis is deep, oligotrophic, and rich in such specific habitat types as macrophyte meadows, rocky shores and sublacustrine spring systems. Moreover, it is a hotspot of freshwater biodiversity in Greece, particularly in molluscs.

After reviewing newly collected material and the published mollusc records, we found that at least 33 mollusc species occur in Lake Trichonis, with 24 gastropod and 9 bivalve species currently being recognized. This is 24% of the total freshwater mollusc diversity of Greece; 21% of the gastropods (five species) are endemic to Lake Trichonis. If the whole Trichonis Basin is considered, which also includes neighboring Lake Lysimachia, eight species (33%) of the total fauna appear to be endemic. Taking lake surface areas into account, the index of gastropod endemism of 0.442 ($\log N_{\text{endemic species}}/\log A_{\text{surface area}}$) for the Lake Trichonis Basin resembles on a world-wide scale values known for Lake Baikal, Russia, and Lake Biwa, Japan, and is only exceeded by Lake Ohrid, Macedonia/Albania, and ancient lakes of Sulawesi, Indonesia.

Despite the limited knowledge about the lake's evolutionary history, the suggested age of origin, the palaeogeographical characteristics, and the potential timing of phylogenetic events reviewed here support the presumed status of Lake Trichonis as an ancient lake.

From a conservational standpoint, more research, management and conservation efforts are necessary because ancient lakes are among the most vulnerable and threatened ecosystems on earth. Effects of human-induced environmental change are already noticeable in Lake Trichonis. Recognition of Lake Trichonis as a unique system with an unusually high biodiversity may help promoting conservation efforts.

Key words: Ancient lake, Balkan, diversity, endemism, conservation.

INTRODUCTION

Ancient lakes are commonly hotspots of biodiversity, often harboring remarkable radiations that make them important targets for study by evolutionary biologists (e.g., Brooks, 1950; Martens et al., 1994; Martens, 1997; Rossiter & Kawanabe, 2000). Although ancient lakes may have different origins and characteristics, it is the diversity and endemism of their organisms that separate them from short-lived, post-glacial lakes. The latter parameters often serve as proxies for the recognition of such lakes (Martens, 1997). However, longevity at least since before the last glacial period (i.e., ~120,000 years ago) or even since before the Pleistocene some 1.8 Million years ago (Mya) (Wilke et al., 2008; Frank Riedel, personal communication) is often considered to be the only objective criterion for the recognition of ancient lakes (Gorthner, 1994; Martens, 1997). Unfortunately, often the age of a given lake is poorly constrained, resulting in confusion about its designation as an ancient lake. Moreover, a lake may have come into existence a long time ago but may not have existed continuously

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(e.g., Lake Victoria; Seehausen, 2006), thus not qualifying as ancient lake.

This and restricted knowledge of the faunas partly account for the existence of a number of unrecognized ancient lakes in the world that are outshone by their famous counterparts. Both the Balkan Peninsula and Asia Minor possess such candidate lakes, which all show some degree of endemism (e.g., Albrecht et al., 2006a; Wilke et al., 2007; Albrecht & Wilke, 2008). In the Balkans, there is the outstanding and well-known ancient Lake Ohrid, which has been in focus of evolutionary biology research for more than 100 years (review: Albrecht & Wilke, 2008). Less recognized are Lake Prespa (Crivelli & Catsadorakis, 1997) and almost all other Balkan lakes, such as Lake Skutari (Reed et al., 2004; Glöer & Pešić, 2008a), Lake Dojran (Griffith et al., 2002), and Lake Pamvotis (Frogley & Preece, 2004, 2007). Most of these lakes share a relatively high degree of endemic biodiversity, particularly in gastropods. However, they also have in common poorly understood systematics of the resident species. Taxonomic uncertainty (Rintelen et al., 2007) or the presence of cryptic species (Gomez et al., 2002; see also Wilke & Falniowski, 2001) can lead to an underestimation of the actual degree of diversity and endemism. To infer evolutionary processes in lacustrine systems, to understand ecological interactions, and to make informed conservation decisions, a robust taxonomic framework is required.

A candidate ancient lake for such studies is the western Greek Lake Trichonis (the old Greek name), which is also called Lake Trichonida (the new Greek name), or Lake Vrakhori (from the medieval name for the city of Agrinio located northwest of the lake). We use here the old name, since it is predominant in the current literature. The lake, situated in the South Adriatic-Ionian biogeographic region (Bănărescu, 2004), is the largest and deepest natural lake in Greece (Tafas et al., 1997).

The biodiversity and endemism of some of its faunal elements, particularly endemic molluscs, have received increasing attention in the past years (e.g., Reischütz & Reischütz, 2003; Szarowska et al., 2005; Albrecht et al., 2007; Glöer et al., 2007; Hauswald et al., 2008; Radea et al., 2008). Yet information is still sparse and partly controversial, due to the absence of a comprehensive faunal assessment for the lake in particular and for Greek freshwater molluscs in general. Only recently, has an attempt been made to summarize present knowledge (Bank, 2006). A principal problem in the study of Balkan freshwater molluscs is the adoption of a central European taxonomic framework. Thus, distinct taxa in this southwestern European region often remain unrecognized.

During ongoing studies of the evolution and diversity of molluscs in European ancient lakes (e.g., Albrecht et al., 2006a, b; Albrecht & Wilke, 2008), we surveyed most large natural lakes on the Balkans, among them Lake Trichonis. During this field work and a survey of the published mollusc record for the lake, we realized that Lake Trichonis, in terms of mollusc biodiversity and endemism, is among the most outstanding but largely ignored lakes in the Balkans.

We therefore attempt in the present review to (a) re-evaluate the lake's mollusc fauna, (b) to compare its molluscan biodiversity and endemism on a Balkan and a global scale, (c) to discuss the potential ”ancient” character of Lake Trichonis, and (d) assess the conservation status of the lake's mollusc fauna.

GEOLOGY AND LIMNOLOGY OF LAKE TRICHONIS

Lake Trichonis (Fig. 1) has been classified as a warm, monomictic and karstic water body (Zacharias et al., 2002), embedded within a complex hydrogeological system (Tafas et al., 1997a, b; Zacharias et al., 2003; Elias & Ierotheos, 2006), and situated in a highly tectonized area (Poulimenos & Doutsos, 1997). Many different rock formations account for the complex regional geology of the Trichonis Basin containing Lake Trichonis and neighboring Lake Lysimachia. The basin is bounded by a major north-dipping fault system on the south side (Goldsworthy et al., 2002). According to Zacharias et al. (2003), fissured limestone dominates in the catchment of the basin, whereas

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FIGS. 1–4. Lake Trichonis and selected characteristic habitat types. FIG. 1: View from North of the lake; FIG. 2: Oligotrophic conditions with hard substrates in the upper littoral followed by a typical *Chara* belt; FIG. 3: Rocky shore at the NE steep parts of Lake Trichonis with marks of different water levels visible at the rock's surface; FIG. 4: Lakes Trichonis and Lysimachia (Greece) and collecting points of the 2005 and 2007 surveys. Bathymetric lines according to Zacharias et al. (2003).

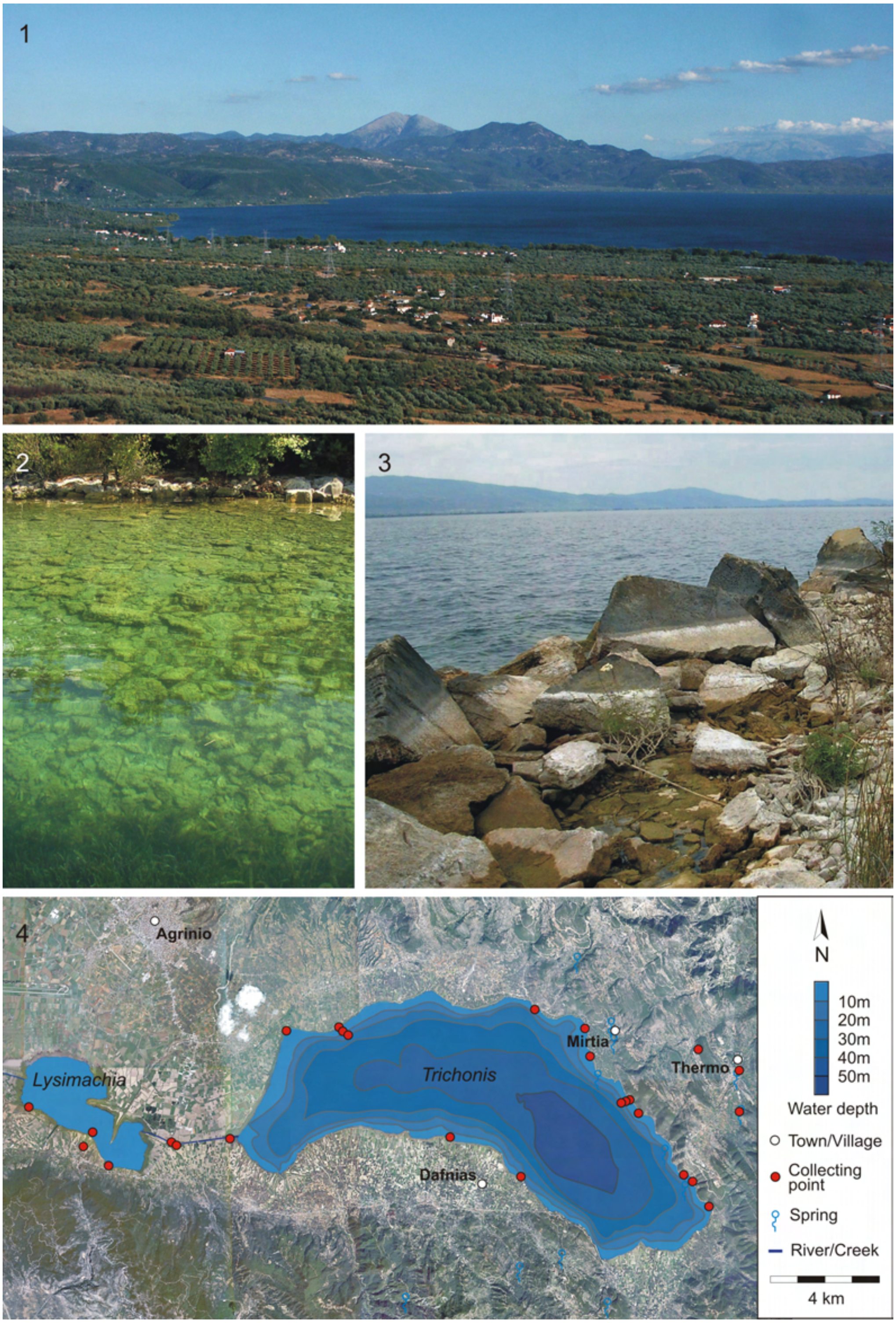
1
2
3
4
Agrinio
Lysimachia
Trichonis
Mirtia
Thermo
Dafnias
N
10m
20m
30m
40m
50m
Water depth
Town/Village
Collecting point
Spring
River/Creek
4 km

TABLE 1. Selected characteristics of Lake Trichonis (*data from Tafas et al., 1997; **data from Zacharias et al., 2002).

	Lake Trichonis
Location	38.508°–38.603°N; 21.445°–21.657°E
Altitude	16 m a.s.l.
Maximum Length	17.8 km
Maximum Width	6.5 km
Maximum Depth	58 m*
Mean Depth	30.45 m*
Volume	2.93 km^3**
Shore length	52.07 km
Surface area	94.24 km^2
Retention time	9.4 years**
Secchi depth (min/max)	8.5/13.0 m**
Catchment area	421 km^2**
Annual water level fluctuation	1 m*
Climate type	Csa (Koeppen)

fault uplifts folded Miocene flysch deposits and Eocene limestones in its footwall, with some young lacustrine sediments occurring in the western part of the footwall, which steps to the north (Goldsworthy et al., 2002).

With a maximum depth of 58 m and a surface area of 92.4 km^2, Lake Trichonis is the deepest and largest natural lake in Greece (Table 1, Figs. 1–4). Preferential groundwater flows are enhanced by karstic conditions characteristic for the area. Faulting processes are most pronounced in the northeast of the lake (Zacharias et al., 2003).

Chemically, Lake Trichonis is considered as a carbonate type, low conductivity lake, with relatively low nitrogen and phosphorous concentrations (Tafas et al., 1997; Tafas & Economou-Amilli, 1997).

Today's water balance of Lake Trichonis is characterized by inflows from approximately 30 seasonal streams, direct precipitation on the lake surface, and subaquatic karstic springs (Elias & Ierotheos, 2006). It is considered to be an oligotrophic water body, with a maximum Secchi disk depth of 13 m and a residence time of 9.4 years (Zacharias et al., 2002). Output occurs via a connection to neighboring Lake Lysimachia and from there via the River Acheloos into the Adriatic Sea (Overbeck et al., 1982).

Annual lake level changes of approximately one meter are caused by the lake's hydraulic relation with karst aquifers, by evaporation during the hot, dry summer, and by intensive irrigation and water extraction (Tafas et al., 1997; Tafas & Economou-Amilli, 1997; Fig. 3). Water extraction increased considerably when a hydraulic infrastructure was constructed in 1957 (Elias & Ierotheos, 2006).

The littoral of the lake is characterized by a variety of habitats, including large zones of macrophytes, as well as rocky and sandy shores (Figs. 1–3). The vertical (bathymetrical) zonation of major habitat types in the lake shows the same differentiation described for other ancient Balkan lakes, such as Lake Ohrid (Radoman, 1985; Albrecht & Wilke, 2008): a rocky or sandy upper littoral (Fig. 2), the *Chara*-belt, a shell zone with both dead and live *Dreissena* specimens, a sandy and silty zone without shells, and the profundal. However, compared to Lake Ohrid, there is a bathymetric shift of these zones towards shallower water depths. Whereas, for example, the shell zone in Lake Ohrid extends to 35 m (Albrecht & Wilke, 2008), in Lake Trichonis it typically only extends to 20 m (Wilke et al., unpublished data).

These geological and limnological features of Lake Trichonis – an likely old basin combined with a relatively large size and considerable depth, as well as a diverse watershed (including springs and temporal streams), and a clear horizontal and vertical zonation of the lake proper – have contributed to a relatively high degree of freshwater biodiversity and endemism in the lake, particularly in molluscs.

MOLLUSC BIODIVERSITY AND ENDEMISM

Mollusc Biodiversity

For Lake Trichonis, a total of 45 extant mollusc taxa is mentioned in the literature, of which we consider at least 33 species (24 gastropod and 9 bivalve species) to occur in the lake today (Table 2). The difference of 12 species is due to both changed taxonomy and nomenclature, but also decline and potential loss, as well as recognition of new species. All taxa with authorships are listed in Table 2. For the entire freshwater fauna of Greece, Bank (2006) listed a total of 112 gastropod and 25 bivalve species (and subspecies). Thus, Lake Trichonis is home to 21% of the Greek freshwater gastropod diversity and 36% of the bivalve diversity (24% of total freshwater mollusc fauna).

Two species of the gastropod genus *Pseudobithynia* – *P. falniowskii*, *P. panetolis*, – as

TABLE 2. Comparative species list and type of endemism of mollucs occurring in Lake Trichonis. Literature records: S – Schütt (1962, 1980), RR – Reischütz & Reischütz (2003), R – Radoman (1983, 1985); FS – Dyduch-Falniowska (1989), Falniowski & Szarowska (1995), Falniowski (1999), Falniowski et al. (1988, 1997), Szarowska et al. (2005); RLE – Radea et al. (2008); KPT – Koussouris & Pugh-Thomas (1982); ASWHW – Albrecht & Schultheiß (September 2005) and Wilke, Hauffe, Wolff (September 2007). Nomenclature largely follows Bank (2006). Presence/validity: Critical evaluation of the published record and new field data. ()species for which no recent record exists. Levels of endemicity: $E_{Trichonis}$ – endemic to Lake Trichonis; $E_{TriLysOzPam}$ - endemic to Lakes Trichonis and/or Lysimachia and/or Ozeros and/or Pamvotis; E_{Greece} – endemic to continental Greece (Bank, 2006), i.e. the southern Balkans.

Species	S	R	RR	FS	KPT	RLE	ASWHW	Presence/ validity	Scale of endemism
Neritimorpha									
Theodoxus varius callosus (Deshayes, 1835)			x				x	x	E_{Greece}
Theodoxus danubialis (C. Pfeiffer, 1828)	x[1]				x[1]				
Caenogastropoda									
Viviparus ater hellenicus (Clessin, 1879)	x		x	x	x		x	x	E_{Greece}
Viviparus cf. *viviparus* (Linnaeus, 1758)			x[2]		x[2]				
Bithynia graeca (Westerlund ,1879)			x[3]						
Bithynia majewskyi Frauenfeld, 1862	x[4]								
Pseudobithynia falniowskii (Glöer & Pešić, 2006)							x	x	$E_{Trichonis}$
Pseudobithynia sp.							x	x	$E_{Trichonis}$
Pseudobithynia trichonis (Glöer, Albrecht & Wilke, 2007)							x	x	E_{TriLys}
Pseudobithynia panetolis (Glöer, Albrecht & Wilke, 2007)							x	x	$E_{Trichonis}$
Potamopyrgus antipodarum J. E. Gray, 1843						x		x	
Trichonia trichonica Radoman, 1973		x						(x)	E_{TriPam}
Pseudoislamia balcanica Radoman, 1979		x[5]						x	$E_{Trichonis}$
Islamia trichoniana Radoman, 1979		x	x					(x)	$E_{Trichonis}$
Belgrandiella haesitans (Westerlund, 1881)	x							x	E_{Greece}
Dianella thiesseana (Clessin, 1878)	x	x	s	x			x	x	E_{TriLys}

(continues)

(continued)

Species	S	R	RR	FS	KPT	RLE	ASWHW	Presence/ validity	Scale of endemism
Heterobranchia									
Valvata cristata O. F. Müller, 1774	x		x		x		s	x	
Valvata cf. *macrostoma* Mörch, 1864			s						
Valvata piscinalis (O. F. Müller, 1774)	x		s	x	x		s	x	
Valvata klemmi Schütt, 1962	x		s		x		x	x	$E_{TriLysOz}$
Acroloxus lacustris (Linnaeus, 1758)	x		x					x	
Galba truncatula (O. F. Müller, 1774)			x				x	x	
Stagnicola cf. *fuscus* (C. Pfeiffer, 1821)			s						
Radix auricularia (Linnaeus, 1758)			x[6]						
Radix balthica (Linnaeus, 1758)				x[7]					
Radix labiata (Rossmässler, 1835)					x[8]				
Radix sp.							x	x	E_{TriLys}
Haitia acuta (Draparnaud, 1805)			x				x	x	
Planorbarius corneus (Linnaeus, 1758)			x					x	
Ferrissia wautieri (Mirolli, 1960)			s				x	x	
Planorbis carinatus O. F. Müller, 1774	x		s		x			x	
Planorbis planorbis (Linnaeus, 1758)			x				x	x	
Gyraulus laevis (Alder, 1838)	x[9]				x[9]				
Gyraulus sp. juv.			x						
Hippeutis complanatus (Linnaeus, 1758)	x		s				s	x	

(continues)

(continued)

Species	S	R	RR	FS	KPT	RLE	ASWHW	Presence/ validity	Scale of endemism
Bivalvia								x	
Unio crassus ionicus Drouët, 1879			x				s	x	E_{Greece}
Pisidium amnicum (O. F. Müller, 1774)			x	x				x	
Pisidium casertanum (Poli, 1791)				x				x	
Pisidium personatum Malm, 1855			x					x	
Pisidium nitidum Jenyns, 1832			x	x				x	
Pisidium subtruncatum Malm, 1855				x				x	
Pisidium tenuilineatum Stelfox, 1918				x				x	
Pisidium annandalei Prashad, 1925				x				x	
Dreissena blanci Westerlund, 1890	x		x				x	x	
Dreissena polymorpha (Pallas, 1771)					x[10]				

[1]*T. danubialis* is not known to occur in Greece (Bank, 2006) and is most likely mistaken by the authors.
[2]Cited as "*V. fasciatus* Mull." which appears to be usually a synonym of *Viviparus viviparus*. This species, however, is restricted to the lowlands N of the Alps. It most likely does not occur in Lake Trichonis.
[3]Since no other recent study found *B. graeca* in Lake Trichonis (Glöer & Pešić, 2006) we consider this to be likely a *Pseudobithynia* sp.
[4]Species from Croatia not recognized for Greek fauna (Bank, 2006).
[5]Spelled as *balkanica* by Radoman (1983: 83); see Bank (2006) for the taxonomy of that species.
[6]*Radix auricularia* not found during recent collections at Lake Trichonis, likely belonging to *Radix* sp.
[7]*Radix balthica* not found during recent collections in the southern Balkans, maybe belonging to *Radix* sp.
[8]Cited as *Radix peregra* f. *ovata*, most likely *Radix* sp.
[9]Considering Meier-Brook (1983: 38), it is unlikely that *Gyraulus laevis* occurs in the Mediterranean region.
[10]Today regarded as *Dreissena blanci* (see Albrecht et al., 2007).

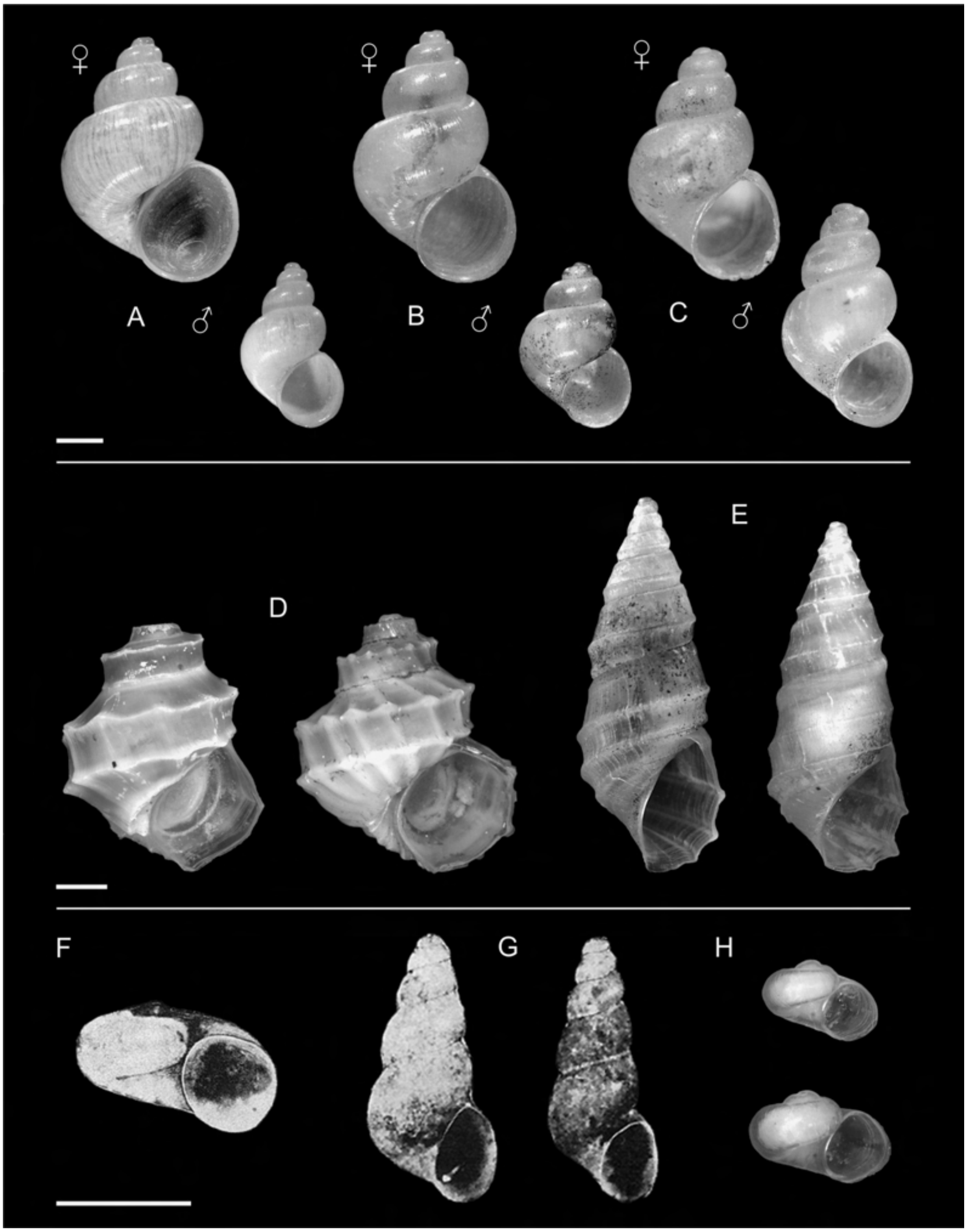

FIG. 5. Endemic gastropod species of Lake Trichonis. A: *Pseudobithynia falniowskii*; B: *Pseudobithynia panetolis*; C: *Pseudobithynia trichonis*; D: *Valvata klemmi*; E: *Dianella thiesseana*; F: *Islamia trichoniana*; G: *Trichonia trichonica*; H: *Pseudoislamia balcanica* - juvenile on top, subadult on bottom. Images of the bithyniid species are taken from original descriptions of Glöer & Pešić (2006) and Glöer et al. (2007). *Trichonia trichonica* and *Islamia trichoniana* reproduced from Radoman (1983; Plate V, No. 82, 83, page 220; Plate IX, No. 153, page 228). Scale bar = 1 mm.

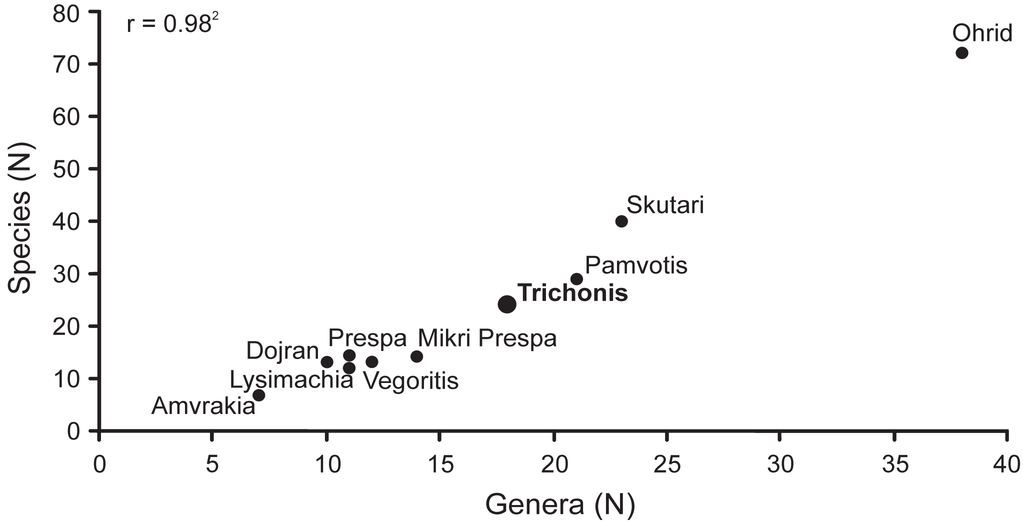

FIG. 6. Correlation between species and generic diversity in selected recognized and potential ancient lakes on the Balkan Peninsula.

well as *Pseudoislamia balcanica* and *Islamia trichoniana* are considered to be endemics to Lake Trichonis (Fig. 5). In addition, two taxa are considered to be new for science and endemic to the lake: *Radix* sp. and *Pseudobithynia* sp. (Glöer, personal communication).

Dianella thiesseana and *Pseudobithynia trichonis* only occur in Lake Trichonis and neighboring Lake Lysimachia. *Valvata klemmi* is now known from lakes Trichonis, Lysimachia and Ozeros (Wilke et al., unpublished data). *Trichonia trichonica*, a species previously found exclusively at its type locality in Lake Trichonis, was recently found at Lake Pamvotis (Frogley & Preece, 2007). The remaining known faunal elements from Lake Trichonis are either subspecies considered to be regionally distributed (i.e., *Theodoxus varius callosus*, *Viviparus ater hellenicus*, and *Unio crassus ionicus*) or widespread species.

Lake Trichonis has a greater number of both gastropod species and genera compared to many other Balkan lakes, such as Prespa. However, Lake Trichonis has less taxonomic diversity than lakes Pamvotis, Skutari or Ohrid (Fig. 6). It should be noted that the intensity of faunistic studies has varied greatly among those lakes. Thus, numbers presented here for other Balkan lakes should be regarded as preliminary.

In the case of Lake Trichonis, it is not unlikely that new collections will reveal new mollusc species. For example, the bithyniid *Pseudobithynia falniowskii* was formerly subsumed under *Bithynia graeca* and only recently recognized as new and endemic for Lake Trichonis (Glöer & Pešić, 2006). In fact, almost none of the assumed widespread taxa of Lake Trichonis have yet been studied in a detailed phylogenetic context, with the possible exception of *Dreissena* "*polymorpha*" (Table 2; see also Albrecht et al., 2007). The phenomenon of undetected diversity is not restricted to molluscs or invertebrates in this system. Even the already diverse and well-studied fish fauna of Lake Trichonis was recently enlarged by a new species of blenny, *Salaria economidisi* Kottelat, 2004 (Wirtz, 2006).

More molluscan endemics are likely to be discovered in Greek lakes. Only such detailed studies as those of Frogley & Preece (2004, 2007) in Lake Pamvotis may eventually close the gaps in knowledge.

Gastropod Endemism

Endemism in freshwater habitats is subject to intense studies (e.g., Dudgeon et al., 2006) and, as endemism can occur at different spatial scales, especially narrow-range taxa have been of interest to researchers (e.g., Ponder & Colgan, 2002).

At the lake scale, 21% of the gastropods (five out of 24 species) are endemic to Lake Trichonis. At the scale of the Trichonis Basin, 33% (eight species) of the total fauna appear to be endemic.

TABLE 3. Gastropod endemism in selected Balkan and world-wide ancient lakes compared to Lake Trichonis.

Lake	Total N species	N endemic species	Endemism (%)	Surface area (km²)	Index [log $N_{endemic\ species}$/log $A_{surface\ area}$]	Source of endemism data
Worldwide ancient lakes						
Baikal	147	114	78	31,500	0.457	Strong et al. (2008)
Biwa	38	19	50	674	0.452	Strong et al. (2008)
Malawi	28	16	57	29,600	0.269	Rintelen et al. (2007)
Malili lakes	61	58	95	753	0.613	Rintelen et al. (2007)
Poso	25	23	92	323	0.543	Rintelen et al. (2007)
Tanganyika	73	66	90	32,600	0.403	West et al. (2004)
Titicaca	24	15	63	8448	0.300	Dejoux & Iltis (1992)
Balkan lakes						
Amvrakia	7	2	29	14.2	0.261	Albrecht et al. (2006a)
Dojran	13	1	8	42.8	0.000	Stankovic (1985)
Lysimachia	12	0 (3)[1]	0 (25)[1]	13.5	0.000 (0.422)[1]	Reischütz & Reischütz (2003)
Mikri Prespa	14	2	14	53	0.175	Radoman (1985), Albrecht & Wilke unpublished data
Trichonis	24	5 (8)[2]	21 (33)[2]	96.5	0.352 (0.442)[2]	this study
Ohrid	72	56	78	358	0.685	Albrecht & Wilke (2008)
Pamvotis	29	2 (5)[3]	7 (17)[3]	22	0.224 (0.521)[3]	Frogley & Preece (2004, 2007)
Prespa	14	6	43	266	0.321	Radoman (1985), Albrecht & Wilke unpublished data
Skutari	40	7	18	600[4]	0.304	Glöer & Pešić (2008a, b), Glöer in litt.
Vegoritis	13	2	15	53	0.175	Schütt (1962, 1985), Albrecht et al. (2006a), Albrecht & Wilke unpublished data

[1]Number in brackets if sister Lake Trichonis is considered.
[2]Number in brackets if sister Lake Lysimachia is considered.
[3]Data for Lake Pamvotis are equivocal with the estimated minimum endemism and maximum endemism including taxa of unclear status (Frogley & Preece, 2007).
[4]Average maximum surface area.

Given the tentative value of 33% gastropod endemism, Lake Trichonis Basin is far exceeded by the famous Balkan lakes Ohrid (78%) and Prespa (43%). However, it is considerable higher than other Balkan lakes, such as Lake Skutari (18%) (Table 3).

On a global scale, gastropod endemism in Lake Trichonis does not reach the levels of > 50% found in such ancient lakes as lakes Baikal, Poso, Tanganyika, Titicaca, or the Malili lakes (Table 3). However, compared to these lakes, Lake Trichonis is relatively small. Thus, for comparative reasons, and applying island biogeographic theory to freshwater gastropod biodiversity (e.g., Lassen, 1975), the respective area (e.g., lake surface or watershed) may be incorporated into calculation of endemic biodiversity indices. Taking lake sizes into account, a double log value of 0.442 of number of endemic species per lake surface areas results for the Lake Trichonis Basin. With this relatively high value, Lake Trichonis is second on the Balkan scale and even far exceeds such famous lakes as Malawi and Titicaca (Table 3).

In addition to geographical scale, it might be informative to assess the taxonomical ex-

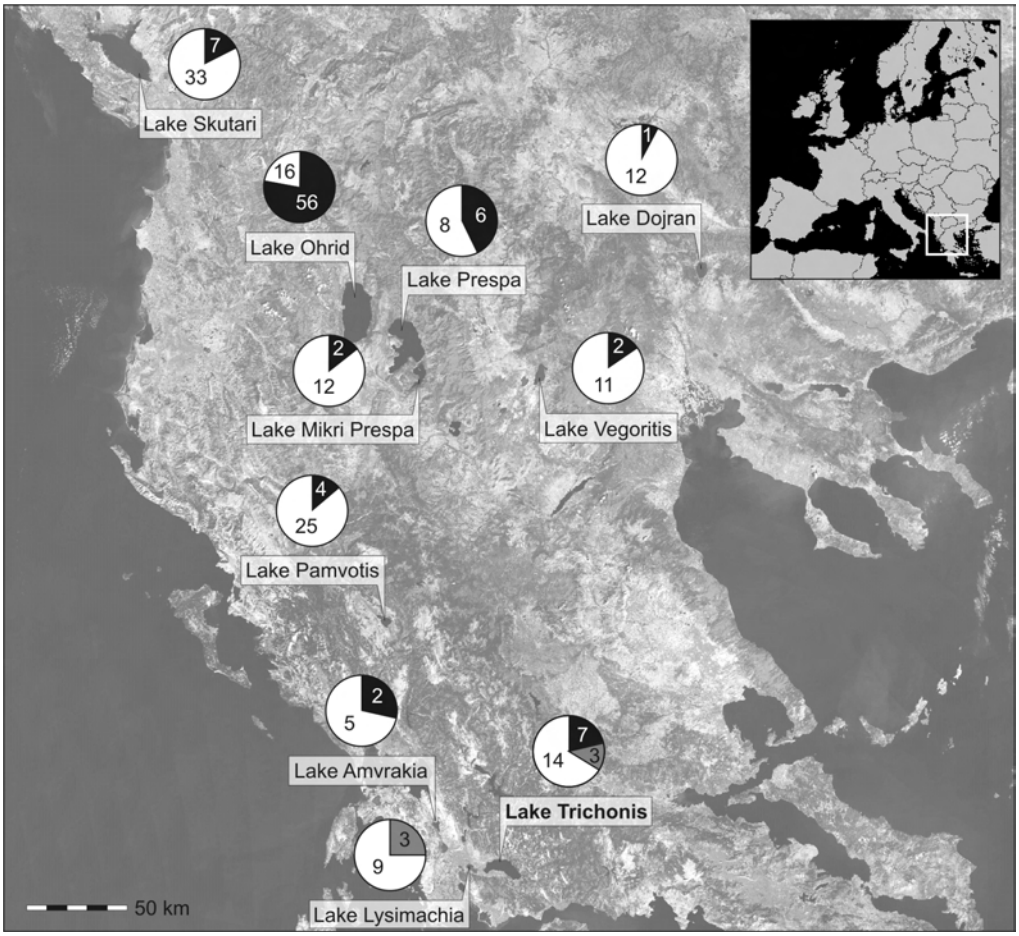

FIG. 7. Gastropod endemism in selected recognized and potential ancient lakes on the Balkan Peninsula. Black slices indicate percentage of endemic species (references see Table 3), total numbers are plotted. Data for Lake Pamvotis represent the maximum endemism including taxa of unclear status (Frogley & Preece, 2007). In Lake Trichonis, black indicates strict endemics while grey accounts for species also occurring in the sister Lake Lysimachia (see Table 1). Lake Lysimachia shares 3 endemics with its sister Lake Trichonis.

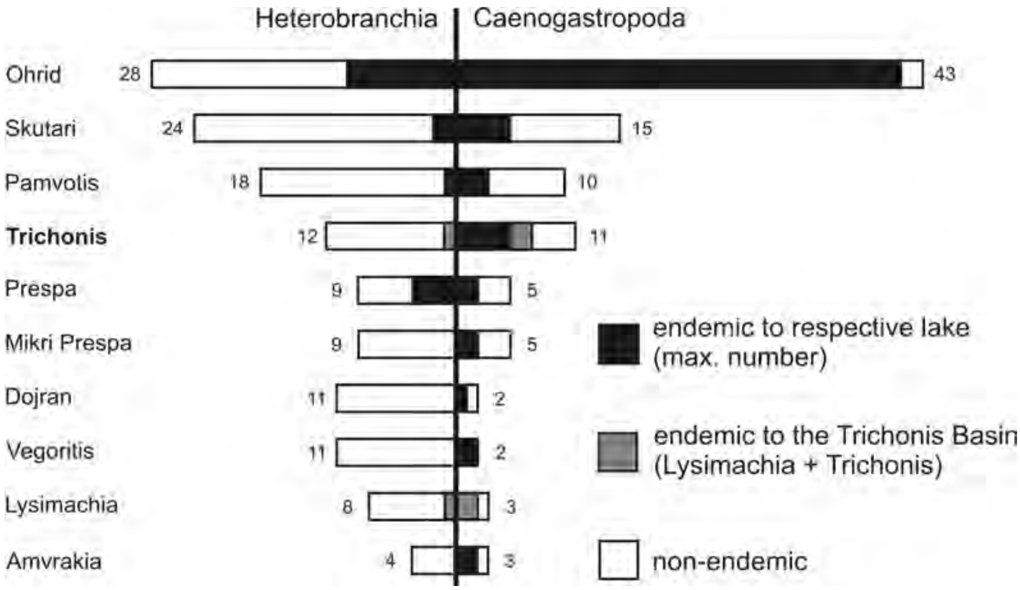

FIG. 8. Gastropod taxonomic composition in selected recognized and potential ancient lakes on the Balkan Peninsula. Note that this statistics is restricted to the two major clades Caenogastropoda and Heterobranchia but does not include *Theodoxus* spp. Data for Lake Pamvotis are maximum estimates of endemism including taxa of unclear status (Frogley & Preece, 2007). In Lake Trichonis, black indicates strict endemics while grey accounts for species also occurring in the sister Lake Lysimachia (see Table 1).

tent of endemism, that is, whether endemism occurs at the supraspecific level. Such well-recognized ancient lakes as Baikal or Ohrid are characterized by endemic genera or even family-level taxa.

Lake Trichonis harbors the endemic and monotypic hydrobiid genus *Pseudoislamia* Radoman, 1978. Beside lakes Ohrid and Trichonis, there are only two other Balkan lakes, Prespa and Mikri Prespa, that currently have an endemic genus each. Endemicity at the generic level, however, is difficult to assess in the absence of thorough phylogenetic and systematic analyses of a given biogeographical region.

Nonetheless, endemism at and above the species level in Lake Trichonis hints at a high degree of mollusc diversification both for the lake itself as well as for the Trichonis Basin (Figs. 4, 7).

Although eutrophic Lake Lysimachia and oligotrophic Lake Trichonis appear very different in their current limnological characteristics (Overbeck et al., 1982), they are sister lakes due their close proximity and direct hydrological connection, which is also evident in a fair degree of shared faunistic elements (for a discussion of ancient sister lakes, see Albrecht et al., 2008b).

A striking difference in the mollusc fauna composition of Lake Trichonis compared to lakes Ohrid, Tanganyika or the lakes on Sulawesi is the absence of species flocks, that is, monophyletic and endemic groups of species. However, there are other recognized ancient lakes in the world that also lack gastropod radiations. It remains to be studied whether the four endemic species of *Pseudobithynia* (Glöer & Pešić, 2006; Glöer et al., 2007) in Lake Trichonis represent a small species-flock.

In addition to elevated endemism, another common feature among ancient lake gastropod species is a higher shell sculpture index compared to ubiquitous species (Gorthner, 1992). A keel, for example, is a prominent shell feature not only of *Dianella thiesseana* from Lake Trichonis, but also of many pyrgulinid gastropod taxa, such as *Chilopyrgula sturanyi*, *Ohridopyrgula macedonica* and *Prespopyrgula prespensis* from the Balkan lakes Ohrid and Prespa, or *Falsipyrgula* from Lake Egirdir in Asia Minor (Wilke et al., 2007). *Valvata klemmi*

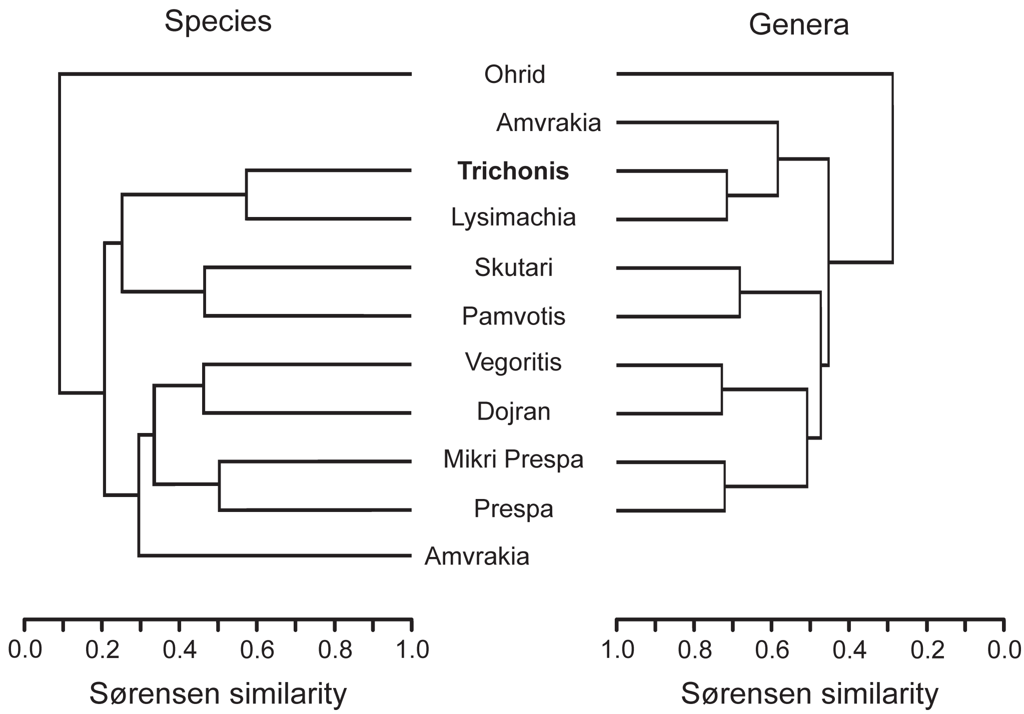

FIG. 9. Cluster analysis of faunal relationships at species (N = 147) and genus level (N = 61). The paired-group method and Sørensen-similarity were used and the analyses conducted in PAST 1.83 (Hammer et al., 2001).

is another Trichonis species with ornate shell sculpture resembling congeners endemic to Lake Ohrid (Fig. 5). A recent molecular study, however, raised doubts concerning the species status of that taxon (Hauswald et al., 2008).

The question whether certain gastropod clades are more prone to speciation in ancient lakes has been treated repeatedly (reviewed in Michel, 1994). Comparing the two major clades, that is, Caenogastropoda and Heterobranchia, the general trend of higher percentage endemism in the Caenogastropoda becomes evident in the Balkan lakes. Lake Trichonis is no exception (Fig. 8). With the exception of Lake Ohrid, Lake Trichonis ranks well with the other Balkan lakes Pamvotis, Skutari, and Prespa. The endemism of mainly pulmonates, however, is significantly higher in the latter.

Lake Trichonis endemism is not restricted to molluscs but is also evident in fishes. The well-studied fish fauna (Leonardos, 2004) holds interesting species, including the endemic *Economidichthys trichonis* (Gobiidae), the smallest known freshwater fish species of Europe (Economidis & Miller, 1990; Miller, 1990). Endemism also occurs in phytoplankton and periphyton (e.g., Kristiansen, 1980; Economou-Amilli, 1982; Falniowski et al., 1988; Economou-Amilli & Tafas, 2000).

Given the still scarce data on the living world of Lake Trichonis, the currently recognized degree of endemism in different taxa is remarkable. Future detailed studies of, for example, macrozoobenthic taxa would certainly give new insights into endemism, biogeography, and evolutionary history of Lake Trichonis.

Faunal Relationships among Balkan Lakes

The faunal relationships of the Lake Trichonis malacofauna was analyzed at species and generic levels (Fig. 9). Both analyses support the sister lake relationship to Lake Lysimachia. Based on presence/absence of genera, Lake Amvrakia is the most closely related lake to those sister lakes. In the species-level analysis, lakes Trichonis and Lysimachia clustered as sister group to lakes Skutari and Pamvotis.

Radoman (1985) classified Lake Trichonis as belonging to the so-called Adriatic-Ionian lake group. His analysis was based on species of the “Hydrobioidea” only and did not include all lakes considered here. Direct comparisons are thus not possible.

LAKE TRICHONIS AS ANCIENT LAKE

As mentioned above, longevity at least since before the last glacial period (ancient lakes *sensu lato*) or even since before the Pleistocene (ancient lakes *sensu stricto*) is often considered to be the only objective criterion for ancient lakes.

Given recent progress in studies of the palaeogeographical evolution of the Balkans (Steininger & Rögl, 1984; Popov et al., 2004), hydrological data available for Lake Trichonis, as well as existing dated phylogenetic data for some of its endemic taxa, it is possible to comment on the status of Lake Trichonis as ancient lake.

Unfortunately, there are no detailed geological and/or limnological data available for the exact age of extant Lake Trichonis. However, Economidis & Miller (1990) hypothesized the tectonic origin of the lake in the Late Pliocene. Khondkarian et al. (2004) suggested that the Trichonis Basin could have been formed in the southernmost edge of a freshwater/lowland area east of the Hellenids in the Middle to Late Pliocene (i.e., some 3.4 to 1.8 Mya).

The oligotrophic and relatively deep Lake Trichonis is situated in the Trichonis Graben in a highly tectonized area with Karst limnology. These characteristics: oligotrophic status, which often is associated with low sedimentation rates, large original depth, and tectonic origin are also typical characteristics of other ancient lakes on the Balkans (e.g., Lake Ohrid; Albrecht & Wilke, 2008). These conditions allow for a compensation of sedimentation by subduction. In addition, Karst conditions assure water input during periods of low precipitation and thus might prevent desiccation.

Recent molecular clock analyses suggested the split of *Dianella thiesseana* (subfamily Pyrgulinae) from Lake Trichonis and its sister taxon, the Lake Ohrid pyrgulinid species flock, to be between 2.6 ± 0.3 My (Wilke et al., 2009) and 2.8 ± 0.3 My old (Wilke et al., 2007). Moreover, Trichonis populations of the fish genus *Leuciscus* are estimated to have separated from river populations 2.2 Mya (Doadrio & Carmona, 1998).

Although timing of these events cannot be used as direct evidence for the ancient character of Lake Trichonis, they hint at Plio-Pleistocene divergence events, possibly associated with the origin of Lake Trichonis and at the distinctness of some of its taxa. In fact, Doadrio & Carmona (1998) even consider Lake Trichonis (including River Evinos) to form a biogeographical subregion within Greece.

Although detailed paleostratigraphic studies remain to be done on Lake Trichonis, biological information both from taxonomic uniqueness of the fauna and molecular divergence of selected taxa indicate a Plio-Pleistocene age or older. Thus, it qualifies as an ancient lake *sensu lato*, and possibly even as an ancient lake *sensu strictu*.

CONSERVATION ISSUES

Many ancient lakes in the world are famous for their extraordinarily high degree of mollusc endemism. However, these faunas are frequently under extreme anthropogenic pressure (Coulter et al., 2006). Therefore, more research, management and conservation efforts are necessary because ancient lakes are among the most vulnerable and threatened ecosystems (Lévêque et al., 2005).

The endemic mollusc species of many of the Balkan lakes were described only a few decades ago. The decline and potential loss of endemic mollusc diversity in lakes in Montenegro, Albania, Macedonia and Greece has been described by Bouchet et al. (1999). The urgency of conservation measures was highlighted by Albrecht et al. (2006a) as lakes in circum-Mediterranean countries are under ever increasing anthropogenic pressure. Major causes are dramatic changes in water levels due to massive extraction for agribusiness. At the same time, the eutrophication-level of most lakes increased during the past decades due to a combination of water use, fishery, pollution, toxification, and climatic extremes, especially during summer. These factors lead to direct or indirect habitat destruction and loss. As a consequence, communities change and eventually complete food webs become disrupted. Highly adapted and specialized species cannot cope with these environmental changes, which can happen very quickly in some cases, for example, during a single season.

From a conservation point of view, it is necessary to assess the current status of the endemic species of Lake Trichonis. Reischütz

TABLE 4. Ecology and conservation measures of endemic gastropods of Lake Trichonis. This table includes described endemic species only. Distribution and habitat characteristics are taken from Radoman (1983), Schütt (1962, 1980) but also include own observations.

Species	Distribution	Habitat	Depth range	Conservation status
Trichonia trichonica Radoman, 1973	NE shore near Mirtia (Radoman, 1983), S coast (Schütt, 1980)	rocky bank	sublittoral (Schütt, 1980)	no recent records
Pseudoislamia balcanica Radoman, 1979	NE shore near Mirtia	rocky bank	1 m	critically endangered
Islamia trichoniana Radoman, 1979	NE shore near Mirtia	stony	unknown	no recent records
Pseudobithynia falniowskii (Glöer & Pešić, 2006)	Southern shore	gravel, *Dreissena* beds, including macrophytes	5 m	endangered
Pseudobithynia trichonis (Glöer, Albrecht & Wilke, 2007)	NE shore	stones	1 m	endangered
Pseudobithynia panetolis (Glöer, Albrecht & Wilke, 2007)	E of Panetolion	rocks	1 m	endangered
Dianella thiesseana (Clessin, 1878)	NE shore	gravel sand	10–27	critically endangered
Valvata klemmi Schütt, 1962	S shore and S shore of Lake Lysimachia (Schütt, 1962); NW and NE shore of Lake Trichonis and Lake Ozeros (this study)	stones, gravel, pebble, sand, mud	0–27	endangered

& Reischütz (2003) only found shells of *Dianella thiesseana*, whereas Szarowska et al. (2005) could collect very few specimens. During our survey in 2007 and 2008, we could find this taxon at only one sampled locality. Little over 20 years ago, Radoman (1985) reported that *D. thiesseana* was very common in Lake Trichonis, which is certainly not the case anymore. A similar situation is present for other hydrobiid endemics. *Trichonia trichonica* and *Islamia trichoniana,* as well as *Pseudoislamia balcanica*, all described from rocky or stony bank parts of the lake, were assumed to be extinct (Szarowska, 2006). We found only *Pseudoislamia balcanica* in very low abundances at two localities near Mirtia on the northeastern rocky shore of Lake Trichonis.

Effects of human-induced environmental changes are evident for Lake Trichonis (Bertahas et al., 2006), with water level loss and eutrophication (mostly due to increased phosphorous loads) being the most serious threats. These processes are particularly severe for microsnails living in a narrow stretch of the littoral (Table 4). Fast water level and/or biofilm changes have a great impact on these highly adapted communities.

Changes are recognizable in the whole ecosystem, for example, by the presence of invasive fish species (Leonardos et al., 2008). Invasive gastropod species become more and more important in ancient lakes, as outlined for *Physa acuta* in Lake Titicaca (Albrecht et al., 2008b), a species also present in Lake Trichonis. The very recent appearance of another globally invasive gastropod species, *Potamopyrgus antipodarum*, in Lake Trichonis is of even greater concern (Radea et al., 2008). These circumstances and the reported decline in endemic gastropod diversity, should trigger efforts to save this sensitive lake ecosystem. By 2008, none of the Trichonis lake endemic molluscs are listed in the IUCN Red List of Threatened Species.

A critical point in all conservation efforts related to Balkan lakes is public awareness of the uniqueness of these ecosystems, which may help increasing the acceptance of, for example, management plans for controlled water extraction. Sewage treatment systems should be installed along the actual lakes and all tributary systems. Agricultural practices should become more sustainable with reduction of fertilizer and pesticide use as ultimate goal. However, all these practices can only be effective if concerted action plans are implemented in the immediate future. A first step was achieved by listing the wetlands surrounding Lake Trichonis as Natura 2000 Environmental Protection Area.

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