A REVIEW OF THE AQUATIC MOLLUSCA FROM LAKE PAMVOTIS, IOANNINA, AN ANCIENT LAKE IN NW GREECE

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Abstract *Lake Pamvotis (= Lake Ioannina) is an ancient lake in NW Greece famous for its long geological record, which has furnished some of the most detailed Quaternary palaeoclimate records from Europe. Unlike some other Balkan lakes, which exhibit spectacular faunal radiations, Lake Pamvotis (and its surrounding habitats) supports just two (but maybe up to five) endemic gastropods but is the type locality for two other valid species of aquatic molluscs and for two taxa now regarded as junior synonyms. It was also an important locality where Schläfli collected specimens later described by Mousson in 1859. These shells, now in Zürich Museum, have been revised as part of a new study of the aquatic fauna of the lake. Four species represented in this collection are not otherwise known from Greece, raising the suspicion that shells from different localities have become mixed. The status of a further two species, known elsewhere in Greece, remains unclear since they have not been re-discovered at Ioannina. A systematic review is given of the 29 species of gastropod and 8 species of bivalve now known from Lake Pamvotis and its surrounding marshlands and springs.* Trichonia trichonica *is reported from only its second known site and* Pisidium obtusale *and* Gyraulus *cf.* piscinarum *are recorded from Greece for the first time. Illustrations of critical taxa are presented.* Planorbis janinensis *is transferred to the genus* Gyraulus*. Eight species of mollusc have been recovered from Holocene sediments beneath the lake; the records for four of these can be traced back to at least 200,000 years.* Dreissena stankovici *seems to have been present at Ioannina throughout the Quaternary.*

Key words *Lake Pamvotis, Ioannina, aquatic molluscs, endemism, Mousson*

INTRODUCTION

The molluscan faunas of the Balkans (and Greece in particular) have been the subject of study for at least the last two centuries (e.g. Butot & Welter-Schultes, 1994). Isolated ancient lakes from the region, such as Ohrid and Prespa, have often been a focus for detailed investigation, because of their remarkable endemic faunas (e.g. Hadžiščhe, 1956; Hubendick & Radoman, 1959; Stanković, 1960; L'vova & Starobogatov, 1982; Meier-Brook, 1983; Stanković, 1985; Schütt, 1987; Sattmann & Reischütz, 1988). Despite this, the malacology of many other key localities from the area still remains poorly documented.

One such site is Lake Pamvotis (39°45'N, 20°51'N), situated 470 m above sea-level in the Ioannina basin on the western flank of the Pindus Mountain Range, in the region of Epirus (figs 1 and 2). It is thought that solution of the Mesozoic limestone basement in the Plio-Pleistocene created a depression known as a polje which, coupled with tectonic subsidence along a series of boundary faults, led to the development of the lake basin. Extensive coring by the Greek Institute of Geology and Mineral Exploration (IGME) has revealed that the floor of the basin was sealed by braided river deposits that were quickly succeeded by lacustrine sediments (IGME, unpubl. data). Evidence from lignite bands suggests that several sub-basins developed, each of which was subject to a variable tectonic history.

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There have been few studies on the fossil molluscan fauna of the lake. Dollfus (1922) described eight species from Upper Pliocene lacustrine sediments from a site south-west of the village of Katsikas, in the south of the basin. This site was subsequently resampled by Aubouin (1959), Gillet (1962) and Guernet *et al.* (1977), bringing the total number of fossil molluscs recorded from this location to fifteen. More recently, a pilot study was carried out on the basal lake sediments from a 130 m long borehole taken from the margin of the basin south-east of Katsikas (core I-256, fig. 1). The basal section of the core reached bedrock and, on the basis of palaeomagnetic and faunal evidence, was thought to be Plio-Pleistocene in age (Frogley, 1997). The sediments yielded five aquatic molluscan taxa, all of which had previously been recorded from the Katsikas sediments. Finally, Reischütz & Reischütz (2002) identified fifteen taxa (including three new pyrgulids) from lake sediments of indeterminate age near to Perama.

Studies of the modern fauna are similarly limited (table 1). The earliest and most comprehensive was published by Mousson (1859), who described material collected by Alexander Schläfli, a military doctor posted to

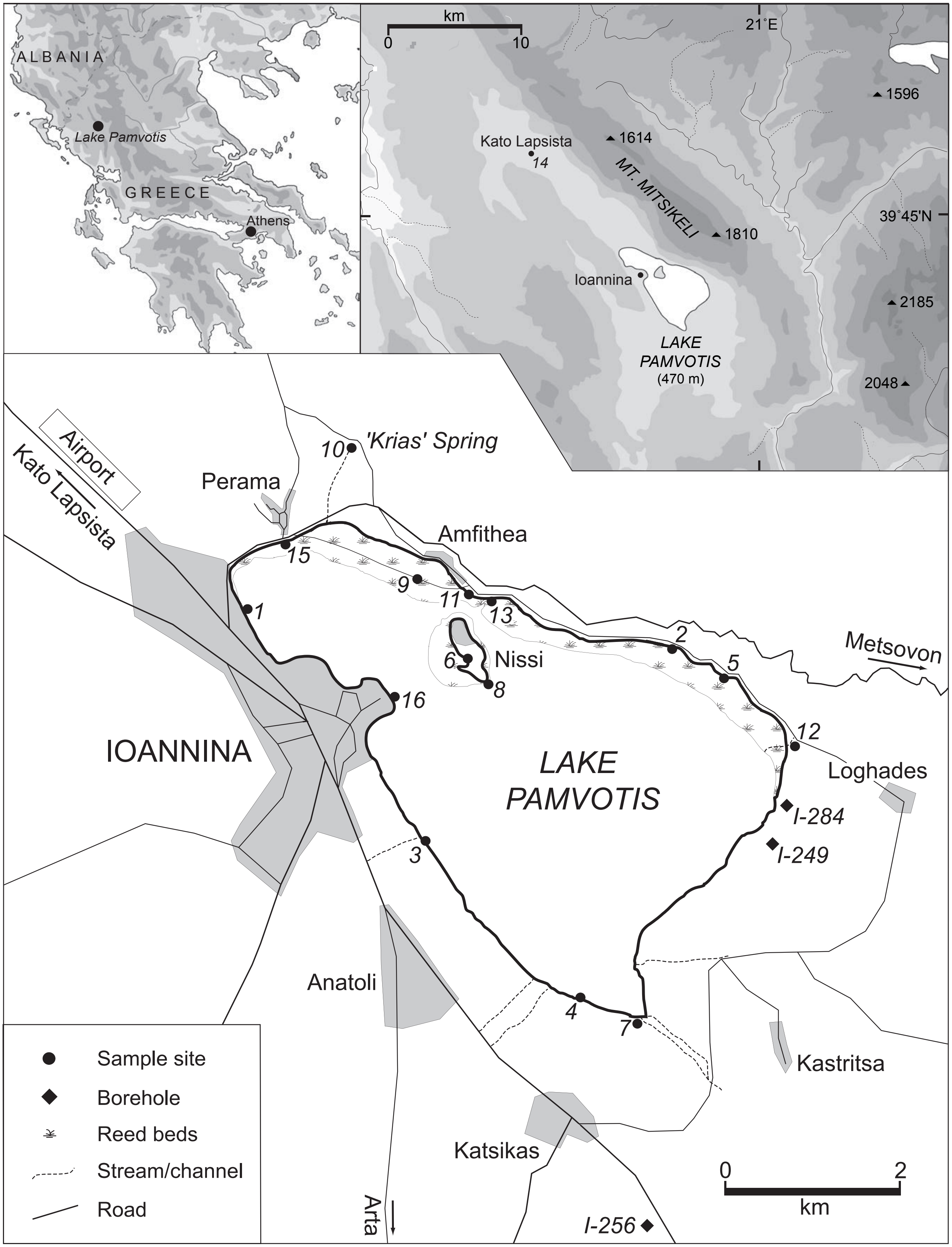

Fig. 1 Location map, showing sampling stations and borehole sites (adapted from Lawson *et al.*, 2004).

the Ioannina garrison from 1856 to 1860 (Meier, 1994). A total of thirty-eight (modern) molluscan species were collected and identified, of which thirteen were aquatic. In 1918, Marius Dalloni collected eight species from the lake, a list of which was subsequently published by Dollfus (1922) as part of a wider discussion of the fossil taxa known from the Katsikas site. Schütt (1962, 1980) described four species of hydrobiid collected from the northern shore of the lake, Pamvotis being the type site for three of these. More recently, whilst on a recent field tour of the Epirus region of north-western Greece, Reischütz & Sattmann (1990) visited Ioannina and collected thirty molluscan taxa, of which eleven were aquatic. Finally, as part of a review of fossil material found in Pamvotis lake sediments, Reischütz & Reischütz (2002) published a list of fourteen aquatic taxa currently living in the lake.

The importance of the present study is therefore twofold. The antiquity of the lake, whilst not unique to the region, is certainly unusual. Its long history has enabled several endemic taxa to evolve, all of which have been poorly described. In addition, it provides an opportunity to update and revise the few existing malacological studies on the lake. This new work is based on fieldwork carried out during September 1994, April 1998, July 2005 and on the faunal content of sediments derived from a 319 m long borehole (core I-284, fig. 1), taken from what appears to be the deepest sub-basin.

Lake Pamvotis

The modern lake, sometimes called Lake Ioannina, currently has a maximum depth of around 10 m and an areal extent of around 23 km^2 (fig. 2). It is approximately 8 km in length (along its longest axis) and has a maximum width of approximately 5 km. Throughout historical times, the lake was more extensive than it is today. At the end of the nineteenth century, part of the lake and the marsh around Kato Lapsista in the northern part of the basin (approximately 5 km NW of the present extent of the lake) were artificially drained for agricultural purposes (fig. 1). There is little surrounding natural vegetation remaining in the basin due to cultivation, logging and over-grazing of the land by domestic animals. These activities have also largely contributed to the destabilisation and erosion of the soils from the limestone bedrock. Around the lake itself, the vegetation consists largely of the free-standing reeds *Phragmites communis* (particularly common around the northern and eastern shores), along with *Potamogeton perfoliatus*, *Typha augustifolia*, *Scirpus holoschoenus*, *S. lacustris*, *Cyperus longus*, and *Sparganium erectum* amongst others (Higgs *et al.*, 1967, Bottema, 1974). Sparse open-canopy brushwoods and low thickets (dominated by the evergreen oak, *Quercus coccifera*) are the main vegetation types on the lower uncultivated slopes of the basin below about 1,000 m (Higgs *et al.*, 1967). Other taxa include *Juniperus oxycedrus*, *Pistacia terebinthus*, *Ostrya carpinifolia* and several other kinds of thorny shrub.

The city of Ioannina, with a population of approximately 100,000 inhabitants, is situated on the western shore of the lake. The agricultural area of the basin (approximately ~54,000 hectares) is mostly planted with corn, tobacco and vegetables (Albanis *et al.*, 1986). Lake Pamvotis itself is a typical temperate, freshwater, eutrophic lake (average pH ~7.6, average salinity ~0.35 ‰), with a water chemistry dominated by calcium (Ca^{2+}) and bicarbonate (HCO_3^-) ions (Overbeck in Anagnostidis & Economou-Amilli, 1980; Frogley, 1997). Abundant phytoplankton in the surface waters thrive as a result of the pollutants introduced from various human and industrial sources, as well as from agricultural pesticides. Falling fish stocks and the constant presence of unpleasant dark green algal blooms mean that pollution of the lake is becoming a serious ecological concern (e.g. Albanis *et al.*, 1986, Kalogeropoulos *et al.*, 1994).

Material Examined

Modern Fauna An attempt was made to sample qualitatively from a wide range of microhabitats around the edge of the lake and the island in its centre (fig. 1). Additionally, surface samples were recovered from the former lake bed soils around Kato Lapsista. For the purposes of this investigation they were considered to contain 'modern' fauna, since these sediments are less than ~100 years old. The characteristics of the sixteen principal collecting stations are detailed in table 2.

Table 1 Comparison of lists of aquatic molluscan fauna from Lake Pamvotis. Taxa in brackets (+) denote occurrences that were originally either misidentified or unrecognized (see text). T = species with their type locality at Lake Pamvotis or its immediate environs; E = endemic taxa. [1]Although the varietal name *graeca* had subsequently been applied to material in the Mousson collection, these shells differ from Westerlund's type specimen (see text).

		Mousson (1859)	Dollfus (1922)	Schütt (1962, 1980)	Reischütz & Sattmann (1990)	Reischütz & Reischütz (2002)	This study: Holocene	This study: modern
Gastropoda								
Prosobranchia								
Theodoxus (*Neritaea*) *varius varius* (Rossmässler, 1835)		–	–	–	–	+	–	–
Viviparus ater hellenicus (Clessin, 1879)		–	–	–	–	+	–	–
Viviparus contectus (Millet, 1813)		–	–	–	+	+	–	–
Viviparus mamillatus (Küster, 1852)		(+)	(+)	–	(+)	(+)	+	+
Bithynia (*Codiella*?) *graeca* (Westerlund, 1879)	?E	(+)[1]	–	–	–	–	–	–
Pseudobithynia westerlundii Glöer & Pešić, 2006	?E	(+)	(+)	–	(+)	(+)	+	+
Heleobia (*Semisalsa*) *steindachneri* (Westerlund, 1902)	T	–	–	+	+	–	–	–
Trichonia trichonica Radoman, 1973		(+)	–	–	–	–	–	+
Belgrandiella haesitans (Westerlund, 1881)		–	–	+	+	–	–	–
Paladilhiopsis janinensis (Schütt, 1962)	E	–	–	+	+	–	–	–
Islamia epirana (Schütt, 1962)	T	–	–	+	+	+	–	+
Valvata (*Valvata*) *cristata* Müller, 1774		–	–	–	+	–	+	+
Valvata (*Cincinna*) sp.	?E	(+)	–	–	–	–	+	+
Pulmonata								
Stagnicola corvus (Gmelin, 1791)		–	–	–	–	–	–	+
Radix cf. *ampla* (Hartmann, 1821)		–	–	–	–	+	–	–
Radix auricularia (Linnaeus, 1758)		(+)	+	–	–	–	–	+
Radix peregra (Müller, 1774)		+	–	–	+	–	–	–
Lymnaea stagnalis (Linnaeus, 1758)		+	+	–	–	–	–	+
Physella (*Costatella*) *acuta* (Draparnaud, 1805)		–	–	–	–	+	–	+
Planorbarius corneus (Linnaeus, 1758)		+	+	–	–	+	–	+
Ferrissia (*Pettancylus*) *clessiniana* (Jickeli, 1882)		–	–	–	–	+	–	+
Planorbis (*Planorbis*) *carinatus* Müller, 1774		+	+	–	–	–	–	+
Planorbis (*Planorbis*) *planorbis* (Linnaeus, 1758)		+	–	–	+	–	+	+
Gyraulus cf. *piscinarum* (Bourguignat, 1852)		(+)	–	–	–	–	–	+
Gyraulus janinensis (Mousson, 1859)	E	+	–	–	–	–	+	+
Gyraulus (*Armiger*) *crista* (Linnaeus, 1758)		–	–	–	–	–	–	+
Hippeutis complanatus (Linnaeus, 1758)		–	–	–	–	–	–	+
Segmentina nitida (Müller, 1774)		–	–	–	–	–	–	+
Ancylus cf. *fluviatilis* Müller, 1774		+	–	–	+	–	–	–
Bivalvia								
Anodonta (*Anadonta*) *anatina* (Linnaeus, 1758)		–	+	–	–	+	–	+
Anodonta (*Anodonta*) *cygnea* (Linnaeus, 1758)		+	–	–	–	+	–	+
Musculium (*Musculium*) *lacustre* (Müller 1774)		–	–	–	–	–	–	+
Pisidium (*Euglesa*) *casertanum* (Poli, 1791)		–	–	–	+	–	–	–
Pisidium (*Cyclocalyx*) *obtusale* (Lamarck, 1818)		–	–	–	–	–	–	+
Pisidium (*Cingulipisidium*) *milium* Held, 1836		–	–	–	–	–	–	+
Pisidium (*Cingulipisidium*) *nitidum* Jenyns, 1832		–	–	–	–	–	+	+
Dreissena (*Dreissena*) *stankovici* L'vova & Starobogatov, 1982		(+)	(+)	–	–	(+)	+	+

Fig. 2 View of Lake Pamvotis looking north from site 4.

Fossil Fauna Specimens were recovered from the Holocene interval of a 319 m core (I-284), drilled by IGME in 1989 on the eastern shore of the existing lake (fig. 1). An age model was established for this sequence (Frogley, 1997; Lawson *et al.*, 2004), based on: (1) correlation with the pollen stratigraphy from an adjacent core (I-249) situated in the same sub-basin (Tzedakis, 1994); (2) nineteen accelerator mass spectrometry (AMS) radiocarbon determinations from the upper part of the core; (3) a set of U-series dates from the last interglacial interval (Atkinson *et al., in prep*.); and (4) detailed palaeomagnetic data. On the basis of this chronology, the I-284 record appears to extend back approximately 400,000 years. Only the top ~145 m contains molluscan remains, most of which are too poorly preserved for confident identification, although three discrete beds of *Dreissena*, indicating periods of lowered lake level, were present in the later part of the last glacial stage. Better material occurs throughout the Holocene interval of the core (approximately the top 15 m) and this is reviewed here.

Modern and fossil specimens were deposited in the University Museum of Zoology, Cambridge (UMZC) as both spirit and dry material (M. R. Frogley Collection). All of the aquatic taxa from the Mousson Collection, archived at Zürich Museum of Zoology (ZMZ), were also examined; a complete review and taxonomic reassessment of this material is contained herein.

SYSTEMATIC REVIEW

A general description of all the modern and Holocene aquatic molluscan taxa that have been found in Lake Pamvotis is now given (see also table 1). The original citation is given for each species, followed by a synonymy that refers only to usage in relation to material from Lake Pamvotis. Nomenclature and taxonomic order follows Bank (2007), except for the treatment of the Lymnaeidae where a more conservative approach is adopted. Many of the species are well-known European forms and are thus described only briefly. In considering distribution, emphasis is placed on European (and in particular, Balkan) occurrences.

CLASS GASTROPODA
SUBCLASS ORTHOGASTROPODA
ORDER NERITOPSINA
FAMILY NERITIDAE
Genus *Theodoxus* Montfort, 1810
Subgenus *Neritaea* Roth, 1855

Theodoxus (*Neritaea*) *varius varius* (Rossmässler, 1835)

1835 *Neritina varia* Rossmässler *Icon*., (1) 1 (2), p. 18.
2002 *Theodoxus varius varius* (Rossmässler). Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges.* **10**, p. 3.

Remarks This species was listed from Lake Pamvotis by Reischütz & Reischütz (2002). It was found in the reed belt north of the departure point to the island, to the north-west of Amfithea (P. Reischütz, *pers. comm*. 2004).

ORDER ARCHITAENIOGLOSSA
FAMILY VIVIPARIDAE
Genus *Viviparus* Montfort, 1810

Viviparus ater hellenicus (Clessin, 1879)

1879 *Vivipara hellenica* Clessin, *Malakozool. Bl., Neue Folge*, **1**: 3-4, plate 1 fig. 1 (shell).
2002 *Viviparus hellenicus* (Clessin). Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges.* **10**, p. 3.
2006 *Viviparus ater hellenicus* (Clessin). Bank, *Heldia*, **6** (1/2), p. 2.

Table 2 Characteristics of sampling stations in this study. Collection dates refer to either September 1994, April 1998 or July 2005.

	Site	Date	Description
1	N 039°40′42.1″ E 020°50′31.0″	1994/ 1998	Limnopoula beach. Gently dipping coarse sandy beach. Sparse aquatic vegetation.
2	N 039°40′39.6″ E 020°54′24.3″	1994	Lake edge, northern shore. Steeply dipping grassy bank adjacent to reed beds. Used by cattle and goats for drinking and grazing.
3	N 039°38′47.1″ E 020°52′26.5″	1994	Lake edge, southern shore. Shallow, flat-lying muddy / grassy area. Abundant aquatic vegetation.
4	N 039°38′16.5″ E 020°53′07.5″	1994	Lake edge, southern shore. Low-lying grassy area, surrounded by reed beds. Abundant aquatic vegetation.
5	N 039°40′27.2″ E 020°54′51.9″	1994/ 1998	Lake edge, northern shore. Low-lying grassy area, surrounded by reed beds. Sparse aquatic vegetation.
6	N 039°40′27.3″ E 020°52′33.1″	1994	Marsh area, southern coast of island. Shallow, rocky shore, gives way to marshy conditions; surrounded by reed beds.
7	N 039°38′59.5″ E 020°53′53.0″	1998	Marsh area, adjacent to SE corner of lake. Stagnant water, muddy substrate, thick algal covering, abundant vegetation.
8	N 039°40′24.0″ E 020°52′41.8″	1994	South-eastern tip of island. Shallow, rocky shoreline, little aquatic vegetation.
9	N 039°41′05.1″ E 020°52′16.5″	1994/ 1998	Reed beds, road between Amfithea and Perama. Steeply dipping shore, abundant aquatic vegetation.
10	N 039°42′07.3″ E 020°51′27.2″	1998	'Krias' spring, northern extent of lake. Clear water, some vegetation, sandy substrate.
11	N 039°41′02.4″ E 020°52′31.3″	1994/ 1998	Reed beds, adjacent to the ferry access channel. Shallow, muddy backwater area in reed beds.
12	N 039°40′03.3″ E 020°55′47.6″	1994/ 1998	Channel to pumping station. Limestone lining to deep channel, covered with algae. Also sampled adjacent shallow ditch.
13	N 039°40′59.4″ E 020°52′40.5″	1998	Spring adjacent to café on northern shore. Deep, clear pool, little vegetation, sandy substrate; walls to pool covered in algae.
14	N 039°45′11.1″ E 020°44′06.4″	1998	Surface samples collected from Kato Lapsista, 5km NW of present-day lake. Part of lake prior to artificial drainage (see text).
15	N 039°41′23.0″ E 020°50′51.9″	2005	Perama beach. Gently dipping shore, muddy substrate, some localised reeds.
16	N 039°40′25.0″ E 020°51′39.8″	2005	Shore immediately adjacent to eastern edge of Citadel promontory; rocks at foot of retaining wall to lake edge.

Remarks This species was listed from Lake Pamvotis by Reischütz & Reischütz (2002). The record is based on two specimens from the vicinity of Perama. They were detected amongst hundreds of *mamillatus* by their small, slender shells with flattened whorls. They have probably been introduced from Lake Trichonis (P. Reischütz, *pers. comm.* 2004). Further specimens have also been found at Ioannina by T. Wilke (*pers. comm.* 2006).

Viviparus contectus (Millet, 1813)

1813 *Cyclostoma contectum* Millet. *Moll. Maine & Loire* p. 5.

1990 *Viviparus contectus* (Millet). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 256.

Remarks This species has been listed on several occasions from Lake Pamvotis. Many of the earlier records appear to be misidentifications

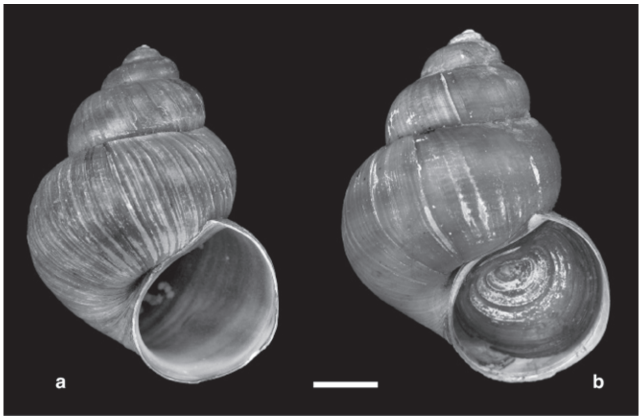

Fig. 3 *Viviparus mamillatus* from Ioannina: **a** Frogley Collection (UMZC), collected in 1994 from site 12 (fig. 1); **b** Mousson Collection (ZMZ524578), labelled '*Paludina inflata* Villa'. Scale bar = 1 cm.

of *mamillatus* but there are some recent records of *contectus* that appear to be genuine (Reischütz & Sattmann, 1990; Reischütz & Reischütz, 2002). 'Typical' specimens of *contectus* have been found near Perama and in a channel leading into the lake from Neohori (P. Reischütz, *pers. comm.* 2004).

Viviparus mamillatus (Küster, 1852)
Fig. 3

1852 *Paludina mamillata* Küster, Martini & Chemnitz, *Syst. Conch. Cabinet* 1 part **21**, p. 9, pl. 2, figs. 1-5; p. 20, pl. 4, fig. 5.
1859 *Paludina inflata* var *janinensis* Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 280.
1877 *Paludina fasciata* var *janinensis* (Mousson). Kobelt in Rossmässler, *Icon. Land. Süss-Moll.*, **5** (4-5), p. 74, pl. 138, fig. 1372. (synonym of *gigantea* Parreyss ms).
1879 *Paludina vivipara janinensis* (Mousson). Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 135.
1880 *Vivipara janinensis* (Mousson). Bourguignat, *Récens. Vivipares syst. Européen*, p. 27.
1886 *Paludina contecta janinensis* (Mousson). Westerlund, *Fauna Paläarct. Region*, **6**, p. 5.
1909 *Vivipara mamillata janinensis* (Mousson). Kobelt in Martini & Chemnitz, *Syst. Conch. Cabinet*, **21a**, p. 346, pl.70, fig. 1; pl. 71, figs. 1-2.
1922 *Viviparia janinensis* (Mousson). Dollfus, *Bull. Soc. Géol. Fr.*, **22** (4), p. 123.
1955 *Viviparus mamillatus janinensis* (Mousson). Zilch, *Arch. Moll.*, **84** (1), p. 55, pl. 4, fig. 22.
2002 *Viviparus viviparus janinensis* (Mousson). Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges.* **10**, p. 3.
2004 *Viviparus mamillatus janinensis* (Mousson). Frogley & Preece, *Balkan biodiversity*, p. 248.
2007 *Viviparus mamillatus* (Küster). Bank, *Heldia*, **6** (1/2), p. 3.

Material examined UMZC: numerous modern shells (sites 1, 2, 6, 12); rare Holocene material. Mousson Collection: ZMZ52457 (collected 1856), 3 shells (labelled '*Paludina inflata* Villa'); ZMZ524578 (collected 1859), 5 shells (labelled '*Palud. inflata* Villa').

Diagnosis Shell large (mean height = 54.9 mm, mean breadth = 40.1 mm, n = 16), semi-transparent, broadly conical, olive green–brown in colour. Umbilicus absent. Spire tapers to a moderately pointed apex. Surface covered with growth-lines; three chestnut-brown bands visible on body whorl, two bands on the others. Sutures moderately deep and whorls convex. Whorls 5-6. Body-whorl large, swollen, nearly 75% of the total shell height. Aperture large, ear-shaped, with rounded outer margin. Operculum has concentric structure, with distinct nucleus.

Occurrence *V. mamillatus* is distributed throughout the western Balkans from Croatia southwards into Epirus (Boettger, 1955).

Ecology Little detailed information exists on the ecology of *V. mamillatus*. Most of the specimens collected from the modern lake were dead shells recovered from the shore (sites 1, 2 and 6). However, specimens from site 12 were found living on the thick algal covering of limestone blocks used to line a quiet, relatively deep water channel serving a pumping station.

Remarks There appears to be some confusion in the literature concerning the species of *Viviparus* found in Lake Pamvotis. Mousson (1859) considered that, despite a tapering apex, his specimens did not represent a form of *achatina* Draparnaud (a synonym of *fasciata* Müller) but a large form of *Paludina inflata* Villa, a synonym of *V. contectus* (Millet). Kobelt (1877), however, attributes the Pamvotis specimens to the *mamillatus* (Küster) group, suggesting that *janinensis* is synonymous with *gigantea* Parreyss.

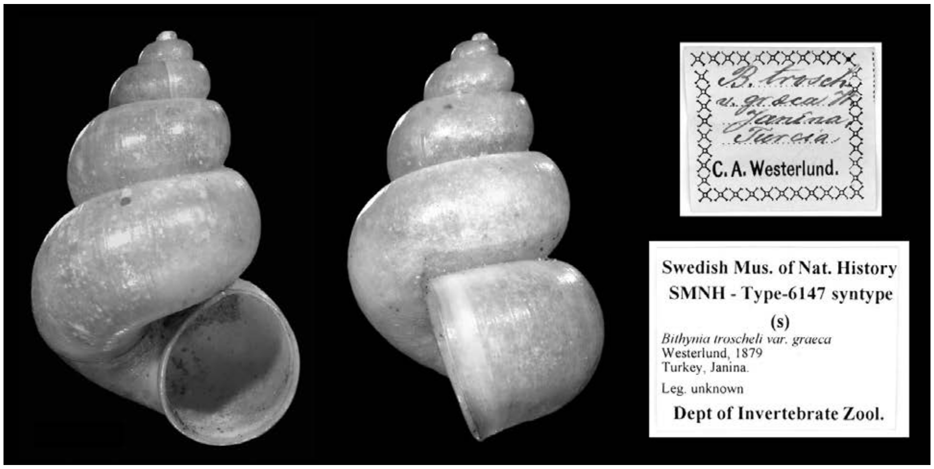

Fig. 4 *Bithynia graeca*. Type specimen in the Westerlund Collection in the Swedish Museum of Natural History, Stockholm. Note that "Janina" (= Ioannina) is in Greece and not Turkey, as labelled. Height of shell = 11mm. Figure reproduced from Glöer & Pešić (2006, fig. 2).

Westerlund & Blanc (1879) also considered Mousson's original designation to be misplaced, suggesting that whilst the species in question was clearly a variety of '*fasciata*', it was significantly different from *mamillatus*. Kobelt returned to the problem in 1909, when he suggested that Westerlund & Blanc had described juvenile specimens and, by means of illustrations to support his argument, reaffirmed his opinion that the species found in Lake Pamvotis was a form of *mamillatus*. This position was echoed by Zilch (1955), in his review of the viviparids held by the Senckenberg Museum in Frankfurt.

Critical comparison of both the Mousson specimens and those collected during this study with relevant figures published in the literature suggests that the Pamvotis species is indeed a large form of *mamillatus*. Whilst juvenile forms display morphological characteristics that are similar to *contectus* (such as deep sutures and a pointed apex), those of the adult specimens (particularly its larger size, the shape of the mouth and a more broadly tapering spire) are clearly closer to *mamillatus*. Bank (2007) does not even separate *janinensis* as a sub-species, simply listing it in the synonymy of *V. mamillatus.*

Order Neotaenioglossa
Family Bithyniidae
Genus *Bithynia* Leach, 1818
Subgenus *Codiella* Locard, 1894

Bithynia* (*Codiella*?) *graeca (Westerlund, 1879)
Fig. 4

1879 *Bythinia graeca* Westerlund, in Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 137.

1886 *Bythinia troscheli graeca* (Westerlund), *Fauna Paläarct. Region*, **6**, p. 18.

Material Examined None. Illustration of type specimen (Swedish Museum of Natural History, Stockholm, SMNH-Type-6147) reproduced here (courtesy of Dr P Glöer).

Remarks Until recently, *Bithynia graeca*, which has its type locality at Lake Pamvotis, was thought to be the most common bithyniid in the lake. However, Glöer & Pešić (2006) examined two lots of specimens in the Westerlund Collection from Lake Pamvotis labelled "*B. leachii* var. *graeca*" (from the Natural History Museum, Göteborg) and "*B. troscheli* var. *graeca*" from the Swedish Museum of Natural History, Stockholm). The latter taxon is relatively large (11 mm high x 6.75 mm wide), has a round mouth and rounded whorls, separated by a deep suture (fig. 4), which conforms more closely to Westerlund's original description. Consequently, Glöer & Pešić (2006) restricted the use of the name *B. graeca* for this taxon, which appears to be known only from the type specimen (collector unknown), although see fig. 5d and discussion below. *B. leachii* var. *graeca* has been referred to a new taxon, *Pseudobithynia westerlundii* (see below). The name *B. graeca* has been applied to specimens from a number of localities in Greece (e.g. Schütt, 1987; Eleutheriadis & Lazaridou-Dimitriadou, 2001), but in the light of this new taxonomic revision, their true identity requires clarification.

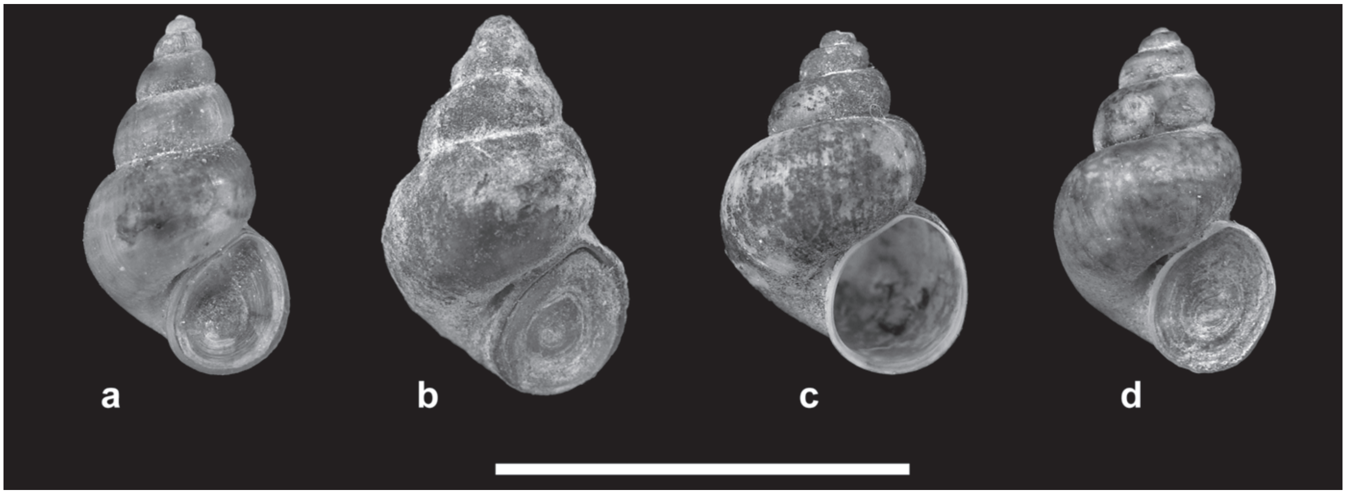

Fig. 5 Bithyniidae from the Mousson Collection (ZMZ523973), labelled '*Bythinia troscheli* Ch.': **a** *Pseudobithynia westerlundii*; **b** *Bithynia tentaculata*; **c** and **d** *Bithynia* (*Codiella*) sp. Scale bar = 5 mm.

Genus *Pseudobithynia* Glöer & Pešić , 2006

Pseudobithynia westerlundii Glöer & Pešić, 2006
Fig. 5a

1859 *Bythinia similis* Draparnaud (in part) Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 280.
1922 *Bithynia boissieri* Küster. Dollfus, *Bull. Soc. Géol. Fr*., **22** (4), p. 123.
1990 *Bithynia graeca* (Westerlund). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 256.
2006 *Pseudobithynia westerlundii* Glöer & Pešić, *Malak. Abh.,* **24**, p. 33-34.

Material examined UMZC: numerous modern shells (sites 1, 3, 8, 9, 10, 13, 14, 15); common Holocene material. Mousson Collection: ZMZ523965 (collected 1856), 1? shell (labelled '*B. graeca* West.?'); ZMZ523966 (collected 1856), 1 shell (labelled '*B. graeca* West.?'); ZMZ523973 (collected 1861), 25 shells (labelled '*Bythinia Troscheli* Ch.'); ZMZ523974 (collected 1856), 24 shells (labelled '*Bithinia Troscheli* Ch.'); ZMZ523975 (collected 1858), 42 shells (labelled '*Palud. troscheli*').

Remarks Glöer & Pešić (2006) have recently investigated the identities of several bithyniid species that occur in Greece and Iran, including material from Lake Pamvotis. They showed that the specimens from Ioannina do not belong to the genus *Bithynia* because they lack a penial appendix and a flagellum. Furthermore, the egg capsules are solid, hexagonal structures that are laid in double rows onto the shells of members of the same species. These characters are sufficiently different to justify the erection of a new genus, *Pseudobithynia* (Glöer & Pešić , 2006), that appears to contain several species in the Balkans (P. Glöer, *pers. comm.*).

As mentioned above, Glöer & Pešić (2006) recognise two bithyniid species from Lake Pamvotis, *B. graeca* (known only from the type specimen) and a second taxon that they have named *Pseudobithynia westerlundii*. The latter, which appears to be the most common bithyniid living in the lake today, is represented by two size classes. This feature was first noted by Mousson (1859), who recognised a small form, with a shell height of 5 mm and a larger form with a shell height of 11 mm ("la *B. Troscheli* Charp.": p. 280). He claimed that these forms did not differ in shape, only size, and referred them both to "*Bythinia similis* Drap.", although he noted that they were more slender than specimens from Germany. The name *similis* has a complicated nomenclatural history, since Draparnaud's name has also been applied to a species of *Mercuria*, but Mousson was here clearly referring to a *Bithynia*. We have been unable to match such a size distinction in the Mousson material but also noted that their shells fell into two size categories. For example, in lot ZMZ523974 the larger group measured 7.58 x 4.13 mm (n = 13) and the smaller 6.62 x 3.68 mm (n = 9), both of which

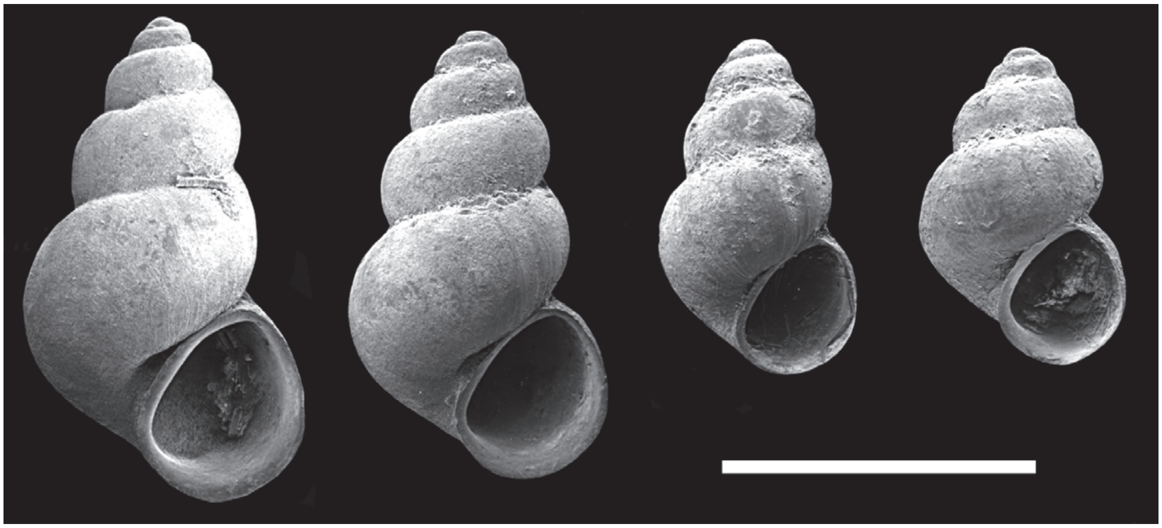

Fig. 6 *Trichonia trichonica* from the Mousson Collection (ZMZ524358), labelled '*Bithinella* (*Bithinella*) *janinensis* Mousson'. Identification of specimens verified by H. Schütt. Scale bar = 1 mm.

are larger but narrower than measurements of 6.0 x 4.3 mm given by Glöer & Pešić (2006) for *P. westerlundii*.

Dollfus (1922) identified a modern bithyniid from Lake Pamvotis as a form of *B. leachii*, which he called *B. boissieri* Küster, 1852. No specimens of "*B. boissieri*" from Lake Pamvotis could be found in the Dollfus collection in the Muséum National d'Histoire Naturelle, Paris, so we are unable to establish the identity of this taxon. Given that *P. westerlundii* is the most common bithyniid species in the lake, it is likely that Dollfus was referring to this taxon.

Ecology In Lake Pamvotis, *P. westerlundii* was found living on pond-weed in clear, well-oxygenated habitats, including the areas around the two springs.

Family Hydrobiidae
Subfamily Cochliopinae
Genus *Heleobia* Stimpson, 1865
Subgenus *Semisalsa* Radoman, 1974

Heleobia* (*Semisalsa*) *steindachneri
(Westerlund, 1902)

1894 *Hydrobia* nov. spec.? Sturany, *Ann. Naturhist. Mus. Wien.* **9**, p. 383, 390, pl. 18, figs. 32-33.
1902 *Hydrobia steindachneri* Westerlund, *Nachr. Bl. dtsch. malak. Ges.*, 34, p. 47.
1980 *Semisalsa steindachneri* (Westerlund). Schütt, *Arch. Moll*. **110** (4), p. 117, pl. 9, figs. 4-5.
2007 *Heleobia (Semisalsa) steindachneri* (Westerlund). Bank, *Heldia* **6** (1/2), p. 4.

Remarks *S. steindachneri* is restricted to western parts of Epirus and several western Greek islands, including Corfu, Kefalonia, Kerkira, Lefkada and Zakinthos (Schütt, 1980; Bank, 2007). Its type site is Lake Pamvotis, where it has been found associated with karstic streams around the lake (Schütt, 1980). It was not found during this study.

Subfamily Belgrandiinae
Genus *Trichonia* Schütt, 1980

Trichonia trichonica Radoman, 1973
Fig. 6

1973 *Trichonia trichonica* Radoman, *Prir. Muz. Beograd*, **32**, p. 22.
2004 *Trichonia trichonica* Radoman. Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells from site 10. Mousson Collection: ZMZ524358 (collected 1856), numerous shells (labelled '*Bithinella* (*Bithinella*) *janinensis* Mousson').

Occurrence *T. trichonica* has only previously been recorded from its type locality, Lake Trigonis (Schütt, 1980).

Ecology Schütt (1980) states that this species has only previously been found in the sublittoral zone of the stony southern shore of Lake Trigonis. In Lake Pamvotis, it was found living on stones and aquatic vegetation at the mouth of the Krias spring (site 10).

Remarks The Mousson specimens were not mentioned in his 1859 publication, probably because much of his cataloguing did not commence until he had retired some years later (T. Meier, ZMZ, *pers. comm*.). *Bithinella* (*Bithinella*) *janinensis* Mousson appears to be a *nomen museorum*. Their identification has been verified by H. Schütt (*pers. comm*.).

Genus *Belgrandiella* A. J. Wagner, 1928

Belgrandiella haesitans (Westerlund, 1881)

1881 *Hydrobia haesitans* Westerlund, *K. Vet. Ak. Forh*. **4**, p. 68.
1980 *Belgrandiella (Belgrandiella) haesitans* (Westerlund). Schütt, *Arch. Moll*. **110** (4), p. 126, pl. 9, figs. 16-19.
1990 *Belgrandiella haesitans* (Westerlund). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien* **91**B, p. 256.

Remarks *B. haesitans* has a reasonably broad distribution across the southern Balkans, especially from northern and north-western Greece (Schütt 1980). It has also been recorded from Lefkada and Zakinthos (Bank, 2007). At Ioannina it lives in the karstic streams around the shore of the lake, but it was not found during this study.

Genus *Paladilhiopsis* Pavlović, 1913

Paladilhiopsis janinensis (Schütt, 1962)

1962 *Paladilhiopsis janinensis* Schütt, *Arch. Moll*. **91**, p. 164, figs. 6 and 11.
1970 *Paladilhiopsis (Paladilhiopsis) janinensis* Schütt, *Arch. Moll*. **100**, p. 307, pl. 15, fig. 19.

Remarks Good illustrations of this species are provided by Schütt (1962, figs. 6 and 11; 1970, pl. 15, fig. 19; 1980, pl. 9, fig. 10). *P. janinensis* lives in the subterranean karstic caves associated with the springs along the northern shore of Lake Pamvotis (H. Schütt, *pers. comm*.). It is endemic to this locality and has not been found elsewhere (Schütt, 1980). It was not found during this study.

Genus *Islamia* Radoman, 1973

Islamia epirana (Schütt, 1962)

1962 *Horatia (Neohoratia) epirana* Schütt, *Arch. Moll.* **91**, p. 161, figs. 4 and 10
1990 *Horatia epirana* Schütt. Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien* **91**B, p. 256.
2002 *Horatia* cf. *epirana* Schütt. Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges*. **10**, p. 3.
2007 *Islamia epirana* (Schütt). Bank, *Heldia* **6** (1/2), p. 6.

Material examined UMZC: a single modern shell from site 9.

Remarks *I. epirana* has previously been collected from its type locality in the streams on the northern shore of Pamvotis (Schütt, 1962, 1980) and only a few other sites, including Lake Ambrakia at Arta (Radoman, 1973) and in streams on the Greek island of Lefkada (Schütt, 1980).

ORDER ECTOBRANCHIA
FAMILY VALVATIDAE
Genus *Valvata* Müller, 1773
Subgenus *Valvata* Müller, 1773

Valvata* (*Valvata*) *cristata Müller, 1774

1774 *Valvata cristata* Müller, *Verm. Hist*., **ii**, p. 198.
1990 *Valvata cristata* Müller. Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 256.

Material examined UMZC: numerous modern shells (sites 9 and 11); rare Holocene material.

Occurrence The distribution of *V. cristata* ranges across most of Europe and parts of northern Asia (Økland, 1990). It is a common Quaternary fossil in the Balkans (e.g. Schütt, 1987; Butot & Welter-Schultes, 1994).

Ecology *V. cristata* prefers fresh-water habitats, such as lakes and slow-flowing rivers, that are rich in aquatic vegetation (Økland, 1990). This was the case in Lake Pamvotis, where it was associated with plant macrophytes at site 9.

Remarks At Lake Pamvotis, *V. cristata* has previously been found only by Reischütz & Sattmann (1990).

Subgenus *Cincinna* Hübner, 1810

Valvata (Cincinna) sp.

1859 *Valvata piscinalis* (Müller). Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 281.

Material examined UMZC: numerous modern shells (sites 1, 3, 4, 9); specimens from Holocene levels (upper 15 m of I-284) and older shells (marine isotope stage 6/7) at 127-129 m. Mousson Collection: ZMZ524875 (collected 1858), 64 shells; ZMZ524876 (collected 1856), 53 shells.

Remarks There is some uncertainty regarding the identity of this species at Ioannina. Elsewhere, we have followed Mousson (1859) and attributed it to *Valvata piscinalis* (Frogley & Preece, 2004) but the Ioannina shells are smaller and have a wider umbilicus than typical *V. piscinalis* and may belong to an undescribed taxon. Moreover, there are also some anatomical differences, particularly with respect to the width of the snout (P. Glöer, *pers. comm.*). Molecular phylogenetic investigations are currently being undertaken by T. Wilke.

Order Pulmonata
Family Lymnaeidae
Genus *Stagnicola* Leach, 1830

Stagnicola corvus (Gmelin, 1791)

1791 *Helix corvus* Gmelin. C. Linnaeus … *Systema Naturae* ed. 13, p. 3665.
2004 *Stagnicola palustris* (Müller). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 7, 9, 11, 12 and 14).

Remarks The identity of specimens from site 11 was confirmed by dissection. The identification was based on the very short penis sheath and a transverse section of the prostate, which contains many folds (only one in *palustris* and two in *fuscus*). Detailed distributional information about this species is incomplete because it has only recently been recognized as a true species within the *palustris* complex. *S. corvus* is known from mainland Greece (Bank, 2007) but has not been previously recorded from Lake Pamvotis.

Genus *Radix* Montfort, 1810
Radix* cf. *ampla (Hartmann, 1821)

1821 *Limneus ampla* Hartmann, Neue Alpina, **1**, p. 251, pl. 2, fig. 29 (shell).

Remarks Listed from Lake Pamvotis by Reischütz & Reischütz (2002).

Radix auricularia (Linnaeus, 1758)

1758 *Helix auricularia* Linnaeus, *Syst. Nat*., ed. 10, p. 774, no. 617.
1922 *Limnea auricularia* (Linnaeus). Dollfus, *Bull. Soc. Géol. Fr.*, **22** (4), p. 123.
2004 *Radix auricularia* (Linnaeus). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 1, 2, 4, 5, 13, 15). Mousson Collection: ZMZ520591 (collected 1859), 18 shells labelled '*Radix ovata* (Draparnaud, 1805)'.

Occurrence *R. auricularia* occurs throughout Europe, Asia, northern Africa and Alaska and has been introduced to the continental United States (Økland, 1990). It is widespread throughout the Balkans and has numerous modern and fossil records from Greece (e.g. Schütt *et al.*, 1985; Schütt, 1987; Sattmann & Reischütz, 1988; Butot & Welter-Schultes, 1994).

Ecology *R. auricularia* generally inhabits standing fresh-water bodies, particularly lakes in hard-water areas (Macan, 1969; Økland, 1990). In Lake Pamvotis, it was particularly abundant at shallow, vegetation-rich littoral sites with muddy substrates.

Remarks *R. auricularia* was not originally recorded by Mousson (1859) and it is possible that the specimens were, perhaps, collected too late to be included in the published faunal list.

Radix peregra (Müller, 1774)

1774 *Buccinum peregrum* Müller, *Verm. Hist.* **ii**, p. 130.
1859 *Limnaeus vulgaris* (Müller). Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 278.
1879 *Limnaea lagotis attica* Roth. Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 125.
1990 *Lymnaea peregra* (Müller). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 257.

Material examined Mousson Collection: ZMZ 520334 (collected 1865), 21 shells, labelled '*Radix peregra* var. *rivularis* Hartmann'

Occurrence *R. peregra* is widespread throughout Europe, northern and middle Asia and north-western Africa (Økland, 1990). It is also widespread in the Balkans and has a fossil record that extends back at least to the Lower Quaternary in Greek Macedonia (Schütt, 1987).

Ecology *R. peregra* prefers lakes and slow-flowing rivers rich in aquatic vegetation (Økland, 1990). No living examples were found in Lake Pamvotis during this study but it was found by Mousson (1859) and Reischütz & Sattman (1990).

Remarks The nomenclatural history of this species is complex and has been extensively reviewed elsewhere (Falkner *et al*., 2001). Alternative names have been suggested but '*peregra*' is listed as a conserved name by the ICZN and this name is retained here.

Genus *Lymnaea* Lamarck, 1799

Lymnaea stagnalis (Linnaeus, 1758)

1758 *Helix stagnalis* Linnaeus, *Syst. Nat*., ed. 10, p. 774, no. 612.
1859 *Limnaeus stagnalis* (Linnaeus). Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 278.
1879 *Limnaea stagnalis attica* (Linnaeus). Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 123.
1922 *Limnea stagnalis* (Linnaeus). Dollfus, *Bull. Soc. Géol. Fr.*, **22** (4), p. 123.
2004 *Lymnaea stagnalis* (Linnaeus). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 1, 4, 6, 11). Mousson Collection: ZMZ520685 (collected 1859), 5 shells.

Occurrence *L. stagnalis* has a holarctic distribution, occurring throughout Europe, Asia, North America and parts of northern Africa. It is well-known in both modern and fossil records from Greece (e.g. Schütt *et al.*, 1985; Schütt, 1987; Sattmann & Reischütz, 1988; Eleutheriadis *et al.*, 1993; Butot & Welter-Schultes, 1994).

Ecology *L. stagnalis* can be found in most freshwater habitats, but has a preference for lakes in hard-water areas with abundant macrophytic vegetation (Macan, 1969; Økland, 1990). At Lake Pamvotis, living specimens were abundant in shallow, vegetation-rich backwater sites.

FAMILY PHYSIDAE
Genus *Physella* Haldeman, 1842
Subgenus *Costatella* Dall, 1870

Physella (_Costatella_) _acuta_ (Draparnaud, 1805)

1805 *Physa acuta* Draparnaud, *Hist. Moll. France*, p. 55, pl. iii, figs. 10 and 11.
2002 *Physella acuta* (Draparnaud). Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges.* **10**, p. 3.

Material examined UMZC: numerous modern shells (sites 1, 4, 5, 7, 11, 13, 15).

Occurrence *P. acuta* is a Mediterranean species that occurs throughout the Balkans. It is known in eastern Greece as far back as the Lower Pleistocene (Schütt, 1987).

Ecology *P. acuta* favours marshy or fresh-water bodies rich in vegetation, particularly lakes (Macan, 1969; Eleutheriadis *et al.*, 1993). In Lake Pamvotis, live specimens were abundant in shallow littoral areas with abundant vegetation.

FAMILY PLANORBIDAE
SUBFAMILY BULININAE
Genus *Planorbarius* Froriep, 1806

Planorbarius corneus (Linnaeus, 1758)
Fig. 7

1758 *Helix cornea* Linnaeus, *Syst. Nat*., ed. 10, p. 770, no. 587.
1859 *Planorbis etruscus* Ziegl. MS.: Bouguignat,

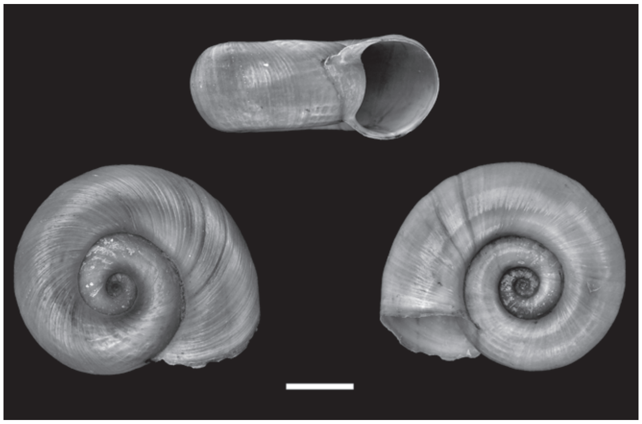

Fig. 7 *Planorbarius corneus* from the Mousson Collection (ZMZ520873), labelled '*Planorbis* (*Coretus*) *etruscus* Villa'. Scale bar = 1 cm.

Rev. & Mag. Zool., Sér. II, **xi**, p. 514.

1859 *Planorbis corneus* (Linnaeus). Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 278.

2002 *Planorbarius corneus* (Linnaeus). Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges.* **10**, p. 3.

Material examined UMZC: numerous modern shells (sites 1, 2, 6, 9, 12, 13 and 14). Mousson Collection: ZMZ520873 (collected 1858), 10 shells (labelled '*Planorbis* (*Coretus*) *etruscus* Villa'); ZMZ520878 (collected 1856), 3 shells (labelled '*Planorbis* (*Coretus*) *etruscus* Villa').

Occurrence *P. corneus* is common throughout most of Europe (except the north), as well as large parts of Asia (Økland, 1990) and the Balkans (e.g. Stanković, 1960; Stanković, 1985; Sattmann & Reischütz, 1988). On the Greek mainland, it is widespread, except in the Peleponnese, although it has been found in Pleistocene deposits from that region (Schütt *et al.*, 1985). It is also known from a range of Quaternary deposits from elsewhere in Greece (e.g. Schütt, 1987).

Ecology *P. corneus* can be found in lakes and ponds, although it appears to favour smaller fresh-water bodies rich in macrophytic vegetation (Økland, 1990). At Lake Pamvotis, live specimens were particularly abundant in vegetation-rich backwater sites such as 6, 9 and 12.

Remarks Specimens of *P. corneus* from Lake Pamvotis are unusually large (adults are commonly ~40 mm in diameter, compared with the ~30 mm diameter of more typical specimens). Similarly large specimens, referred to as *Planorbarius corneus grandis* Dunker, 1850, occur in the southern Balkan Peninsula and in Anatolia (Frank & Kinzelbach, 1986; Schütt, 1987; Sattmann & Reischütz, 1988).

Genus *Ferrissia* Walker, 1903
Subgenus *Pettancylus* Iredale, 1943

Ferrissia* (*Pettancylus*) *clessiniana (Jickeli, 1882)

1882 *Ancylus clessinianus* Jickeli, *Jahrb. dtsch. malakozool. Ges.*, **9** (4), p. 366.

2004 *Ferrissia* sp. Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: two dead modern shells (site 6), both juvenile.

Remarks Our specimens were too small for confident identification but Reischütz & Reischütz (2002) list this species from Lake Pamvotis. *F. clessiniana* is a synonym of *F. wautieri* (Mirolli, 1960), a name widely used in European literature.

Subfamily Planorbinae
Genus *Planorbis* Müller, 1773
Subgenus *Planorbis* Müller, 1773

Planorbis* (*Planorbis*) *carinatus Müller, 1774

1774 *Planorbis carinatus* Müller, *Verm. Hist.*, **ii**, p. 157.

1859 *Planorbis carinatus* Müller. Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 279.

Material examined UMZC: numerous modern shells (sites 9, 10, 12 and 14). Mousson Collection: ZMZ521079 (collected 1858), 2 shells.

Occurrence *P. carinatus* is common in a range of lakes rich in aquatic vegetation across most of Europe and parts of Asia (Meier-Brook 1983, Økland 1990).

Ecology *P. carinatus* inhabits hard-water lakes that are rich in aquatic vegetation (Økland 1990). In Lake Pamvotis, it was found associated with macrophytes either adjacent to springs (sites 10 and 12), or near to a fresh-water input (site 9).

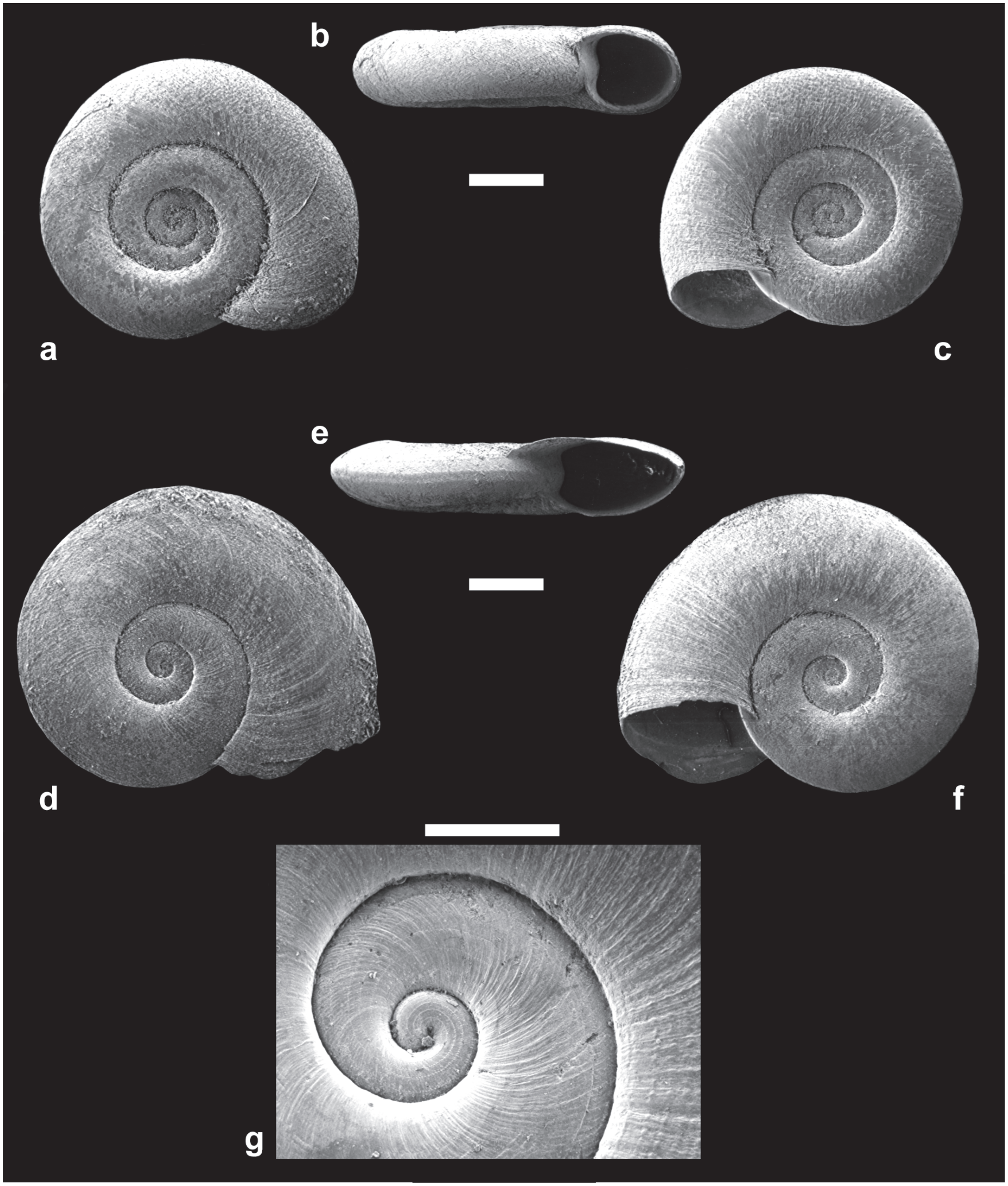

Fig. 8 **a-c** *Gyraulus* cf. *piscinarum* (UMZC), collected in 1998 from site 7, bordering Lake Pamvotis (fig. 1). **d-g** *Gyraulus janinensis* from the Mousson Collection (ZMZ521189). Scale bar a-f = 1 mm; scale bar g = 0.5 mm.

Planorbis (_Planorbis_) _planorbis_ (Linnaeus, 1758)

1758 *Helix planorbis* Linnaeus, Syst. Nat., ed. 10, p. 769, no. 578.
1859 *Planorbis marginatus* Draparnaud. Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 279.
1990 *Planorbis planorbis* (Linnaeus). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 257.

Material examined UMZC: several modern shells (site 9); rare Holocene material. Mousson Collection: ZMZ521036 (collected 1856), 10 shells (labelled '*Planorbis* (*Anysus*) *marginatus* Draparnaud'); ZMZ521190 (collected 1859), 1 juvenile shell.

Occurrence *P. planorbis* is distributed across most of Europe, western and northern Asia and parts of North Africa (Meier-Brook, 1983; Økland, 1990). It is well-known from the Balkans and from the Quaternary records of the region (e.g. Schütt *et al.*, 1985; Schütt, 1987).

Ecology *P. planorbis* is common in a range of lakes and ponds rich in aquatic vegetation. This was confirmed by its occurrence at site 9 in Lake Pamvotis.

Genus *Gyraulus* Charpentier, 1837

Gyraulus cf. _piscinarum_ (Bourguignat, 1852)
Fig. 8a-c

1852 *Planorbis piscinarum* Bourguignat, *Test. nov.*, p. 22.
2004 *Gyraulus* cf. *piscinarum* (Bourguignat). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (site 7). Mousson Collection: ZMZ521189 (collected 1861) 8 shells among material labelled '*Planorbis janinensis*'.

Remarks The exact affinities of the specimens recovered from a marsh immediately adjacent to Lake Pamvotis and the 8 shells in the Mousson Collection recognized amongst one lot of *Gyraulus janinensis* are unclear. Two of the recently collected specimens were dissected by C. Meier-Brook, who tentatively ascribed them to *G. piscinarum* on the basis of shell morphology and penis sheath/preputium ratios (between 1.14 and 1.825). *G. piscinarum* has been widely recorded from south and east Asia, but its range may have been exaggerated by confusion with other species (Meier-Brook, 1983). If correctly identified, its occurrence at Ioannina would constitute its most westerly record (C. Meier-Brook, *pers. comm*.).

Gyraulus janinensis (Mousson, 1859)
Fig. 8d-g

1859 *Planorbis janinensis* Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 279.
2004 *Gyraulus janinensis* (Mousson). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 3, 8, 9 and 14); common Holocene material. Mousson Collection: ZMZ521189 (collected 1861), 70 shells (labelled '*Planorbis janinensis*'); ZMZ521190 (collected 1859), 12 shells (labelled '*Planorbis janinensis*').

Diagnosis Shell discoidal, thin and translucent, yellowish-brown with faint greenish tint. Shell surface bears a series of moderately coarse transverse ridges, crossed by a weakly developed spiral sculpture, occasionally developed as beading (fig. 8g). Whorls 3-4, increasing gradually and evenly, rounded above, slightly flattened below, no deflection of last whorl. Sutures moderately deep. Aperture depressed, oval. Peripheral margin bluntly angulated, with distinctive double periostracal seam (fig. 8e). Mean breadth = 5 mm, mean height = 1.7 mm (n = 5).

Occurrence *G. janinensis* appears to be endemic to Lake Pamvotis.

Ecology No ecological information is available for *G. janinensis*. It is likely, however, that in common with other planorbids it prefers lake habitats rich in aquatic vegetation. Dead shells were found at a variety of sites in Lake Pamvotis, making it difficult to assess any specific ecological preferences.

Remarks Endemic species of *Gyraulus* occur in a number of lakes in the Balkans. For example, five

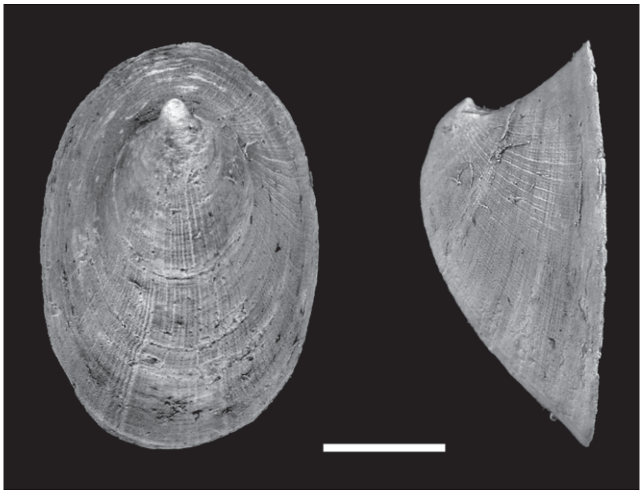

Fig. 9 *Ancylus* cf. *fluviatilis* from the Mousson Collection (ZMZ521352), labelled '*Ancylus janinensis*'. Scale bar = 1 mm.

endemic species have been recorded from Lakes Ohrid and Prespa (e.g. Hubendick & Radoman, 1959), although these have all now been assigned to the subgenus *Carinogyraulus* Polinski, 1929 (Meier-Brook, 1983). The shell morphology of the form from Ioannina suggests that it belongs to the genus *Gyraulus*. It appears to be closely related to *G. albidus* Radoman from Lake Ohrid but further work is needed to establish whether they are conspecific (C. Meier-Brook, *pers. comm.*).

Subgenus *Armiger* W. Hartmann, 1843

Gyraulus* (*Armiger*) *crista (Linnaeus, 1758)

1758 *Nautilus crista* Linnaeus, *Syst. Nat.*, ed. 10, p. 709, no. 234.
2004 *Gyraulus crista* (Linnaeus). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined Several dead shells from surface samples taken from the former lake-bed at Kato Lapsista (site 14).

Occurrence *G. crista* is common throughout Europe, parts of north America and large parts of Asia (Meier-Brook, 1983; Økland, 1990). It is well documented from the Balkans at both modern and fossil sites (e.g. Schütt *et al.*, 1985; Stanković, 1985; Schütt, 1987; Butot & Welter-Schultes, 1994). This is the first record of *G. crista* from Lake Pamvotis.

Ecology *G. crista* prefers fresh-water habitats such as lakes and ponds that are rich in aquatic vegetation and have fairly high pH values (Økland, 1990).

Genus *Hippeutis* Charpentier, 1837

Hippeutis complanatus (Linnaeus, 1758)

1758 *Helix complanata* Linnaeus, *Syst. Nat.*, ed. 10, p. 769, no. 579.
2004 *Hippeutis complanatus* (Linnaeus). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 9, 11, 12 and 14).

Occurrence *H. complanatus* is distributed across most of Europe and Asia (Økland, 1990). This is the first record of this species from Lake Pamvotis.

Ecology *H. complanatus* prefers fresh-water habitats such as lakes and ponds that are rich in aquatic vegetation and have fairly high pH values (Økland, 1990). This was confirmed in Lake Pamvotis, where specimens were found associated with submerged macrophytes at sites 9 and 12.

Genus *Segmentina* Fleming, 1818

Segmentina nitida (Müller, 1774)

1774 *Planorbis nitidus* Müller, *Verm. Hist.* **ii**, p. 163.
2004 *Segmentina nitida* (Müller). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous modern shells (sites 7, 9, 12, 13).

Occurrence *S. nitida* has a range that covers most parts of Europe, as well as northern and middle Asia (Økland, 1990). It is common throughout the Balkans, including the Quaternary fossil record (e.g. Schütt *et al.*, 1985; Schütt, 1987). This is the first record from Lake Pamvotis.

Ecology *S. nitida* prefers fresh-water habitats such as lakes and ponds that are rich in aquatic

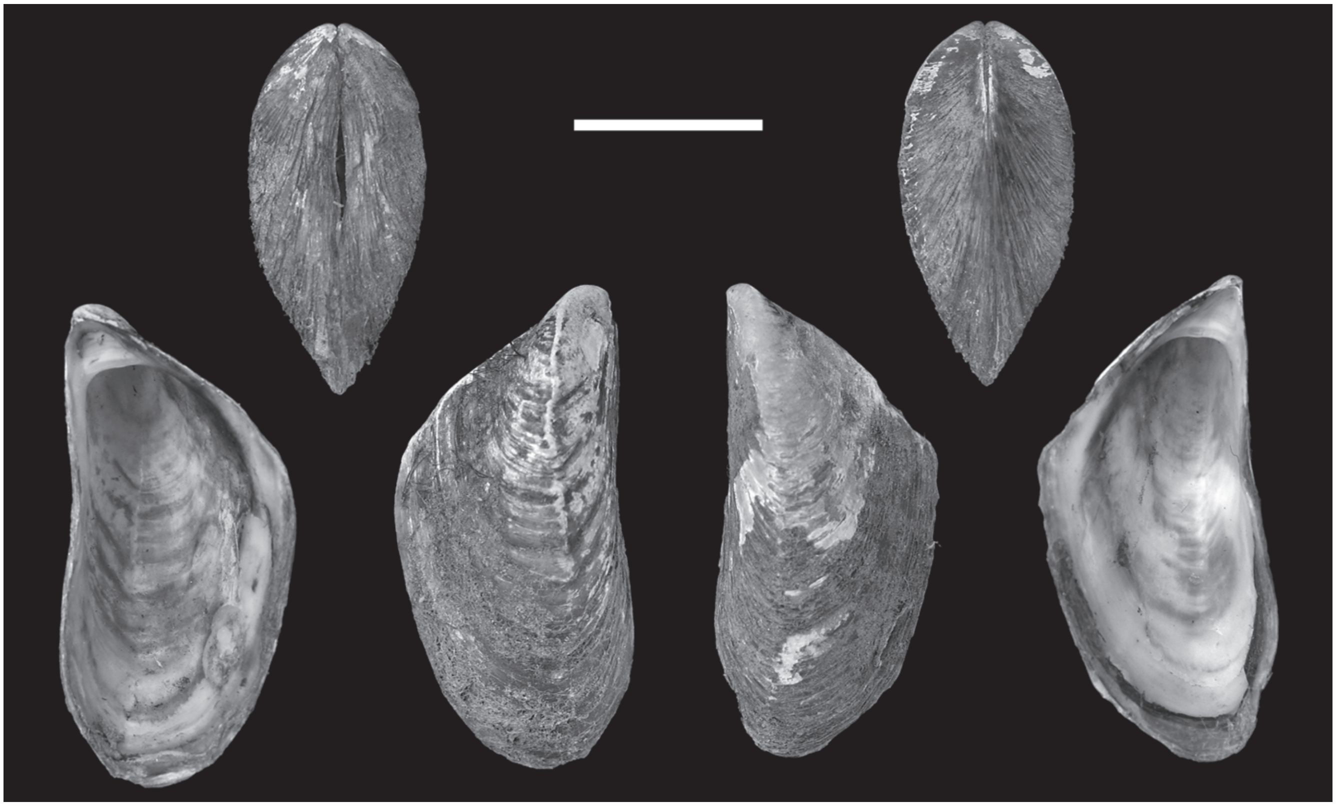

Fig. 10 *Dreissena* (*Dreissena*) *stankovici* from the Mousson Collection (ZMZ530008), labelled '*Mytilus* (*Dreissena*) *polymorpha* Pallas'. Scale bar = 0.5 cm.

vegetation (Økland, 1990). This was reflected in Lake Pamvotis, since sites 7, 9 and 12 were all rich in plant macrophytes. Site 13, however, was a pool associated with a spring feeding the lake; whilst there was relatively little aquatic vegetation, live specimens were recovered from algae-covered stone walls.

Genus *Ancylus* Müller, 1773

Ancylus* cf. *fluviatilis Müller, 1774
Fig. 9

1774 *Ancylus fluviatilis* Müller, *Verm. Hist*., **ii**, p. 201.
1859 *Ancylus* radiolatus Küster. Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 280.
1862 *Ancylus janinensis* Bourguignat. *Spicilèges malacologiques*, *Paris* **15**, p. 155.
1882 *Ancylus janinensis* Clessin. *Syst. Conch. Cabinet*, (1) **6** (316), p. 74, pl. 9, fig. 7.
1990 *Ancylus fluviatilis* Müller. Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 257.

Material examined Mousson Collection: ZMZ 521351 (collected 1861), 74 shells (labelled '*Ancylus* (*Ancylastrum*) *strictus* Morelet'); ZMZ521352 (collected 1861), 233 shells (labelled '*Ancylus janinensis* Mousson').

Remarks No specimens were found in the Mousson Collection labelled *A. radiolatus* but it appears that only one species of *Ancylus* occurs at Ioannina (Fig. 9), although we were unable to refind it during this study. The phylogeny of *A. fluviatilis* has recently been investigated using mitochondrial DNA sequences from 16S ribosomal RNA, cytochrome *c* oxidase subunit I (COI) and nuclear DNA from internal transcribed spacer (ITS-1) regions from 103 populations across Europe (Pfenninger *et al*., 2003). This revealed the existence of four highly divergent lineages representing a cryptic species complex. The clade representing the nominal taxon *A. fluviatilis* occurred mainly in central and northern Europe, so the taxonomic status of *Ancylus* populations from southern Europe, including those from Ioannina, require clarification.

Class Bivalvia
Subclass Eulamellibrachia
Order Unionoida
Family Unionidae

SUBFAMILY ANODONTINAE
Genus *Anodonta* Lamarck, 1799
Subgenus *Anodonta* Lamarck, 1799

Anodonta* (*Anodonta*) *anatina (Linnaeus, 1758)

1758 *Mytilus anatinus* Linnaeus, *Syst. Nat*., ed. 10, p. 706, no. 219.
1922 *Anodonta anatina* (Linnaeus). Dollfus, *Bull. Soc. Géol. Fr*., **22** (4), p. 123.

Material examined UMZC: several (dead) modern shells (site 2).

Occurrence *A. anatina* has a broad palaearctic distribution (Ellis, 1978) and is known throughout the Balkans as part of the modern and fossil record (e.g. Butot & Welter-Schultes, 1994).

Ecology *A. anatina* prefers fresh-water habitats such as rivers, canals and lakes with sandy substrates in which it can bury itself (Ellis, 1978). In Lake Pamvotis it was only found at site 2, a relatively shallow backwater area with a muddy substrate. It is probable that the dead shells were transported to this site and washed ashore by wave action.

Anodonta* (*Anodonta*) *cygnea (Linnaeus, 1758)

1758 *Mytilus cygneus* Linnaeus, *Syst. Nat*., ed.10, p. 706, no. 218.
1859 *Anadonta cellensis* (Schröter). Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4** (3), p. 282.
1879 *Anodonta gravida* Drouët. Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 148.
2002 *Anodonta cygnaea* (Linnaeus) agg. Reischütz & Reischütz, *Nachr. Erst. Vor. malakozool. Ges*. **10**, p. 3.
2004 *Anodonta cygnea* (Linnaeus). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: several modern (dead) shells (sites 1 and 12). Mousson Collection: ZMZ531955 (collected 1861), 3 articulated pairs of valves, 6 disarticulated valves; ZMZ532009 (collected 1861), 1 articulated pair of valves (labelled '*A. piscinalis* Nilsson').

Occurrence *A. cygnea* has a broad palaearctic distribution (Ellis, 1978). It is widespread throughout the Balkans and is also known from the Quaternary fossil record from Greece (e.g. Schütt, 1987).

Ecology *A. cygnea* prefers fresh-water habitats such as rivers, canals and lakes with muddy substrates (Ellis, 1978).

Remarks One pair of articulated valves present in the Mousson Collection were mistakenly labelled '*A. piscinalis* Nilsson', which is a synonym of *A. anatina*.

ORDER VENEROIDA
FAMILY SPHAERIIDAE
SUBFAMILY PISIDIINAE
Genus *Musculium* Link, 1807
Subgenus *Musculium* Link, 1807

Musculium* (*Musculium*) *lacustre (Müller, 1774)

1774 *Tellina lacustris* Müller, *Verm. Hist*. **ii**, p. 204.
2004 *Musculium lacustre* (Müller). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: several modern shells (sites 9, 12 and 14).

Occurrence *M. lacustre* has a broad, palaearctic distribution and is well-known from the Balkans (Ellis, 1978; Schütt *et al*., 1985). This is the first record of this species from Lake Pamvotis.

Ecology *M. lacustre* can be found in habitats up to 1,400 m altitude and prefers small lakes, ponds and ditches. It can tolerate a wide range of conditions and often occurs in assemblages with low species diversity (Ellis, 1978). This happened at Lake Pamvotis, where it was found at only two sites, the still (relatively low salinity) waters behind the roadway barrage of site 9, and in a drainage ditch adjacent to site 12.

Genus *Pisidium* Pfeiffer, 1821
Subgenus *Euglesa* Jenyns, 1832

Pisidium* (*Euglesa*) *casertanum (Poli, 1791)

1791 *Cardium casertanum* Poli, *Test. utr. Silicae*, **i**, ord. II, p. 65, pl. xvi, fig. 1.
1990 *Pisidium casertanum* (Poli). Reischütz & Sattmann, *Ann. Naturhist. Mus. Wien*, **91B**, p. 258.

Occurrence *P. casertanum* is a widely distributed species that occurs throughout Europe, parts of Asia, Africa, North America and New Zealand (Ellis, 1978). It is recorded as both a modern and Quaternary fossil species from the Balkans (e.g. Schütt *et al.,* 1985). It has only been found previously in Lake Pamvotis by Reischütz & Sattmann (1990).

Ecology *P. casertanum* is a hardy, eurytopic species that can be found in a wide variety of various fresh-water habitats at altitudes up to 2,500 m and at depths down to 40 m (Ellis, 1978).

Subgenus *Cyclocalyx* Dall, 1903

Pisidium* (*Cyclocalyx*) *obtusale (Lamarck, 1818)

1818 *Cyclas obtusalis* Lamarck, *Hist. nat Anim. sans Vert*., **v**, p. 559.
2004 *Pisidium obtusale* (Lamarck). Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: several shells (site 9).

Occurrence *P. obtusale* has a broad holarctic distribution, being found in North America (including Alaska), parts of Russia (including Siberia) and throughout Europe and the Balkans (Ellis, 1978). This is not only the first record of this species from Lake Pamvotis but also from Greece (cf. Bank, 2007). The specimens were identified by Dr M.P. Kerney.

Ecology This species is known from a range of fresh-water habitats, though often prefers ditches, marshes and ponds rather than larger water bodies and streams (Ellis, 1978).

Subgenus *Cingulipisidium* Pirogov & Starobogatov, 1974

Pisidium* (*Cingulipisidium*) *milium Held, 1836

1836 *Pisidium milium* Held, *Isis*, **xxix**, Hft. 4, col. 281.
2004 *Pisidium milium* Held. Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: several shells (site 9).

Occurrence This species can be found across most of Europe, the Balkans, northern Africa and North America (Ellis, 1978). It is also known from the fossil record, for example, from Quaternary deposits in Greek Macedonia (Schütt, 1987). This is the first record of *P. milium* from Lake Pamvotis.

Ecology *P. milium* prefers lakes and ponds over more stagnant habitats (Ellis, 1978). This was confirmed at Lake Pamvotis, where it was found at site 9, a relatively fresh water habitat, with some aquatic vegetation.

Pisidium* (*Cingulipisidium*) *nitidum Jenyns, 1832

1832 *Pisidium nitidum* Jenyns, *Trans. Camb. Phil. Soc.*, **iv**, p. 304, pl. xx, figs. 7 and 8.
2004 *Pisidium nitidum* Jenyns. Frogley & Preece, *Balkan biodiversity*, p. 248.

Material examined UMZC: numerous (dead) shells (sites 3 and 9); rare Holocene material.

Occurrence *P. nitidum* is widespread throughout Europe and parts of North America (Ellis, 1978). It is also well known from the fossil record, for example from Lower Pleistocene deposits in north-eastern Greece (Schütt, 1987) and the Megalópolis Basin (Schütt *et al.,* 1985). This is the first record of *P. nitidum* from Lake Pamvotis.

Ecology *P. nitidum* can be found in most lakes, streams, rivers and ponds, though prefers harder water areas (Ellis, 1978). In Pamvotis it was only found as dead shells at the lake edge, making more specific conclusions concerning its ecology difficult.

FAMILY DREISSENIDAE
Genus *Dreissena* Van Beneden, 1835
Subgenus *Dreissena* Van Beneden, 1835

Dreissena* (*Dreissena*) *stankovici L'vova & Starobogatov, 1982
Fig. 10

1859 *Dreissena polymorpha* Pallas. Mousson, *Vierteljahrschr. Naturf. Gesell. Zürich*, **4 (3)**, p. 282.
1879 *Dreissena chemnitzi* Rossmässler. Westerlund & Blanc, *Aper. Faune Mal. Gréce*, p. 148.
1922 *Dreissena polymorpha* var. *chemnitzi* Rossmassler. Dollfus, *Bull. Soc. Géol. Fr.*, **22** (4), p. 123, Fig. 8
1982 *Dreissena* (*Carinodreissena*) *stankovici* L'vova & Starobogatov, *Zoologicheskij Zhurnal*, **61** (11), p. 1749, fig. 1.
1993 *Driessena blanci* Westerlund. Schütt, *Arch. Moll*. **122**, p. 327.
2004 *Dreissena* (*Carinodreissena*) sp. Frogley & Preece, *Balkan biodiversity* p. 247.

Material examined UMZC: numerous specimens (sites 1, 3 and 16); abundant Holocene material. Mousson Collection: ZMZ530008 (collected 1856), 43 disarticulated valves, 8 articulated valves (labelled '*Mytilus* (*Dreissena*) *polymorpha* Pallas').

Remarks *Dreissena* was recorded as part of the modern fauna from Lake Pamvotis by Mousson (1859) as *D. polymorpha* Pallas and by Westerlund & Blanc (1879) as *D. chemnitzi*, a synonym of *D. polymorpha*. The *Dreissena* shells from Ioannina possess a distinctive sharp 'S'-shaped keel that is strongly twisted in the umbonal region (fig. 10), a feature which distinguishes them from *D. polymorpha*. The Ioannina shells have consequently been attributed to *D. blanci* Westerlund, 1890 (Schütt, 1993; Reischütz & Reischütz, 2002), a species that has a sharp keel (Fechter & Falkner, 1990). However, this feature, which has been used to characterise the subgenus *Carinodreissena* (L'vova & Starobogatov, 1982), is also present in other Balkan species, such as *D. stankovici* from Lake Ohrid. Published photographs of *D. blanci* (Fechter & Falkner, 1990) suggest greater similarity to *D. polymorpha* than to *D. stankovici* (Korniushin, 2004). The attribution of these keeled shells to a distinct subgenus was endorsed by Rosenberg & Ludyanskiy (1994), but others regard *Carinodreissena* as a synonym of *Dreissena* (Falkner *et al*., 2001). Korniushin (2004) also noted that *D. stankovici* differs from *D. polymorpha* in its anatomy (large papillae between siphons, numerous papillae on the inhalent siphon) and in the nature of the muscle scars (equilateral anterior adductor scar and a broad pedal retractor scar). The *Dreissena* from Ioannina are smaller than *D. stankovici* from Ohrid, with a mean length of approximately 23 mm (n = 16), as opposed to 40 mm (L'vova & Starobogatov, 1982). Nevertheless, preliminary genetic data from two Ioannina populations confirm their identity as *D. stankovici* (T. Wilke, *pers. comm*.). The molecular phylogeography of *D. stankovici* from Ohrid and Prespa, in relation to other species of *Dreissena* within their endemic range in the Ponto-Caspian Sea basin and in the Balkans, is discussed by Gelembiuk *et al*. (2006).

Dreissena has a long geological record at Ioannina, occurring sporadically throughout the upper 145 m of core I-284 (i.e. the last 200,000 years), and is present in much older sediments towards the base of another core (I-256), taken from the southern margin of the lake basin (fig. 1). These sediments are lake marls, with reversed palaeomagnetic polarity, containing a very different molluscan fauna (see Dollfus, 1922), suggesting a pre-Quaternary age.

DOUBTFUL TAXA

A number of taxa are represented in the Mousson collection that were not detected during recent surveys at Lake Pamvotis. Four of these are otherwise unknown from Greece, raising the suspicion that shells from different localities have become mixed. A further two species known from Greece require confirmation at Ioannina. Details are as follows:

Bithynia* (*Bithynia*) *tentaculata (Linnaeus 1758). Fig. 5b. ZMZ523965 (collected 1856), 9 shells (labelled '*B. graeca* West.?'); ZMZ523966 (collected 1856), 5 shells (labelled '*B. graeca* West.?'); ZMZ523973 (collected 1861), 2 shells (labelled '*Bythinia Troscheli* Ch.'); ZMZ523974 (collected 1856), 1? juvenile shell (labelled '*Bithinia Troscheli* Ch.'); ZMZ523975 (collected 1858), 2 shells (labelled '*Palud. troscheli*'). *B. tentaculata* is common throughout the western palaearctic but becomes rarer in northern latitudes (Graham, 1988; Økland, 1990). It is also known from both modern and Quaternary Balkan sites, where several sub-species have been recognized (see discussion by Schütt, 1987).

***Bithynia* (*Codiella*) sp.** Fig. 5c and d. ZMZ523973. Amongst the 30 shells included in this lot were two specimens that had more swollen, rounded whorls, deeper sutures and rounded apertures. One (fig. 5c) is squat with a shorter spire that approaches *B. troschelii* in general form (cf. Glöer, 2002), but this species is otherwise unknown in Greece, so its identity remains uncertain. The second specimen is more slender and resembles the type specimen of *B. graeca*, although we are not confident of this attribution.

Emmericia patula (Brumati, 1838). ZMZ523975. One specimen with an operculum was detected amongst 43 shells of *Bithynia* spp. Although the genus *Emmericia* occurs in the Adriatic region, there are no previous records of *E. patula* from Greece (Radoman, 1967).

Bythinella charpentieri (Roth, 1855). ZMZ524358. Two juvenile shells were included with specimens of *Trichonia trichonica* (labelled '*Bithinella* (*Bithinella*) *janinensis* Mousson'). The identifications were confirmed by H. Schütt. *B. charpentieri* has a broad distribution across the Balkans (Schütt, 1980).

***Corbicula* sp.** ZMZ532413. Amongst the specimens of *Sphaerium corneum* in this lot (labelled '*Sphaerium* (*Sphaerium*) *rivalis*') was a single juvenile valve of *Corbicula*.

Sphaerium* (*Sphaerium*) *corneum (Linnaeus, 1758). ZMZ532413. In the Mousson collection were 4 specimens (1 articulated pair, 2 disarticulated valves, 1 single valve, 1 juvenile valve). They are listed here as doubtful because no-one has re-found this species at Ioannina since.

Reischütz & Reischütz (2002) recently described three new species of pyrgulid (*Pyrgula falkneri*, *P. acicula* and *P. pambotis*) from Perama on Lake Pamvotis, but it is unclear whether these shells are fossils excavated from the lake beds or whether these species still inhabit the lake. Associated with these pyrgulids were a number of other species including *Valvata* cf. *macrostoma* Mörch, 1864 and two species of *Gyraulus*, although it is not clear how these relate to the two species of *Gyraulus* discussed above.

Conclusions

A total of 29 species of gastropod (13 prosobranchs and 16 pulmonates) and 8 species of bivalve are confirmed from Lake Pamvotis and its surrounding habitats (table 1), totals that may rise in the light of forthcoming molecular analyses. At least two species (*Paladhiliopsis janinensis* and *Gyraulus janinensis*) are endemic but a further three (*Bithynia graeca*, *Pseudobithynia westerlundii* and *Valvata* sp.) may also prove to be endemic. Lake Pamvotis and its environs is the type locality for two valid species (*Heleobia steindachneri* and *Islamia epirana*) and two other taxa (*Paludina inflata* var. *janinensis* and *Ancylus janinensis*) now regarded as junior synonyms.

Examination of Mousson's material in the Zürich Museum, coupled with the study of newly collected specimens, has allowed reappraisal of Mousson's taxonomy relating to aquatic molluscs from Lake Pamvotis. Two species (*Radix auricularia* and *Anodonta anatina*) were correctly identified but collected too late for inclusion in the original paper (Mousson, 1859). Two others (*Trichonia trichonica* and *Gyraulus* cf. *piscinarum*), present but unidentified in Mousson's collection, have been confirmed at Lake Pamvotis during this study. A further six taxa (*Bithynia tentaculata*, *Bithynia* sp., *Emmericia patula*, *Corbicula* sp., *Bythinella charpentieri* and *Sphaerium corneum*) have not been re-found at Lake Pamvotis; indeed all but the last two are unknown from any other site in Greece. Their occurrence in this lake therefore requires confirmation. This also applies to various species (*Pyrgula falkneri*, *P. acicula*, *P. pambotis* and *Valvata* cf. *macrostoma*) known only as dead shells, possibly fossils (Reischütz & Reischütz, 2002).

Whilst reasonably rigorous, the collecting techniques employed here were entirely qualitative, so the faunal list is therefore likely to be incomplete. Nevertheless, eight additional species can be added to the faunal list for Lake Pamvotis: *Stagnicola corvus*, *Gyraulus crista*, *Segmentina nitida*, *Hippeutis complanatus*, *Pisidium obtusale*, *P. milium*, *P. nitidum* and *Musculium lacustre*. *Trichonia trichonica* is reported from only its second site and the records of *Gyraulus* cf. *piscinarum* and *Pisidium obtusale* are new to Greece. Further work needs to be undertaken on the two endemic taxa (*Paladilhiopsis janinensis* and *Gyraulus janinensis*), neither of which was found alive during the present study.

Unlike the situation in some other ancient lakes in the Balkans, no extensive radiation in either gastropods or bivalves is now apparent in Lake Pamvotis. This situation is also reflected in the fossiliferous upper levels of borehole I-284. The eight molluscan taxa recognized in the Holocene section of the core (table 1), are identical to those still living in the lake today. Sparser records for four species (*Valvata* sp., *Viviparus* sp., *Pseudobithynia westerlundii* and *Dreissena stankovici*) from the late Middle Pleistocene (as far back as ~200,000 years) also belong to taxa still living in the lake. Molluscan fossils are absent from earlier intervals of this core, probably due to the profundal nature of the sediments. However, the basal 60 m of another borehole (I-256) recovered from a neighbouring sub-basin, located 5 km to the south of I-284, show that the lake once supported a very different and diverse molluscan fauna (Frogley & Preece, 2004). This corroborates earlier findings of this exotic fauna from other sites in the lake basin (Dollfus, 1922; Aubouin, 1959; Gillet, 1962; Guernet *et al*., 1977). Further study of marginal cores may well amplify details of the records for critical species.

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References

Albanis TA, Pomonis PJ & Sdoukos AT 1986 Seasonal fluctuations of organochlorine and triazine pesticides in the aquatic system of the Ioannina Basin (Greece). *The Science of the Total Environment* **58**: 243-253.

Anagnostidis K & Economou-Amilli A 1980 Limnological studies on Lake Pamvotis (Ioannina), Greece. *Archiv für Hydrobiologie* **89** (3): 313-342.

Atkinson TC, Rowe P, Frogley MR, Tzedakis PC & Preece RC (*in prep*.) The reliability of U-series isochrons derived from carbonate lacustrine sediments at Ioannina, NW Greece.

Aubouin J 1959 Contribution à l'étude géologique de la Grèce septentrionale: les confins de l'Épire at de la Thessalie. *Annales Géologiques des Pays Helléniques* **10**: 1-525.

Bank RA 2007 (in press) Towards a catalogue and bibliography of the freshwater Mollusca of Greece. *Heldia* **6** (1/2): 33pp.

Boettger CR 1955 Zoogeographische Betrachtungen über die europäischen Süßwasserschnecken der Gattung *Viviparus* Montfort. *Archiv für Molluskenkunde* **84** (1): 87-95.

Bottema S 1974 *Late Quaternary Vegetation History of Northwestern Greece*. Ph.D. thesis, University of Groningen.

Butot LJM & Welter-Schultes FW 1994 Bibliography of the mollusc fauna of Greece. *Schriften zur Malakozoologie* **7**: 1-160.

Dollfus GF 1922 Faune malacologique du Miocène supérieur de Janina en Epire. *Bulletin de la Societé Gèologique Français* **22** (4): 101-123.

Ehrmann P 1956 *Die Tierwelt Mitteleuropas II (1). Weichtiere, Mollusca*. Quelle & Meyer, Leipzig.

Eleutheriadis N, Hatziioannou M & Lazaridou-Dimitriadou M 1993 Contribution to the study of the biology of *Bithynia graeca* (Prosobranchia Gastropoda) and *Physa acuta* (Pulmonata Gastropoda) in Lake Kerkini (North Greece). *Biologia Gallo-hellenica* **20** (1): 267-272.

Eleutheriadis N & Lazaridou-Dimitriadou M 2001 The life cycle, population dynamics, growth and secondary production of *Bithynia graeca* (Westerlund, 1879) (Gastropoda) in Lake Kerkini, northern Greece. *Journal of Molluscan Studies* **67**: 319-328.

Ellis AE 1978 *British Freshwater Bivalve Mollusca. Synopsis of the British Fauna (N.S.) 11*. Academic Press, London.

Falkner G, Bank RA & von Proschwitz T 2001 Checklist of the non-marine Molluscan Species-group taxa of the States of Northern, Atlantic and Central Europe (CLECOM 1). *Heldia* **4**: 1-76.

Fechter R & Falkner G 1990 *Weichtiere. Europäische Meeres- und Binnenmollusken*. Mosaik Verlag, München.

Frank C & Kinzelbach R 1986 The distribution of the Great Ramshorn, *Planorbarius corneus grandis*, in the southern Balkan Peninsula and in Anatolia. *Zoology in the Middle East* **1**: 125-129.

Frogley MR 1997 *The biostratigraphy, palaeoecology and geochemistry of a long lacustrine sequence from NW Greece*. Ph.D. thesis, University of Cambridge.

Frogley MR & Preece RC 2004 A faunistic review of the modern and fossil molluscan fauna from Lake Pamvotis, Ioannina, an ancient lake in NW Greece: implications for endemism in the Balkans. In *Balkan Biodiversity: Pattern and Process in the European Hotspot* (HI Griffiths, B Kryštufek & JM Reed eds). Kluwer Academic Publishers, Dordrecht pp.243-260.

Gelembiuk GW, May GE & Lee CE 2006 Phylogeography and systematics of zebra mussels and related species. *Molecular Ecology* **15**: 1033-1050.

Gillet S 1962 Remarques sur des Gastropodes de quelques gisements du Pliocène et du Quaternaire d'Épire. *Praktika Akadamiae Athens* **37**: 260-273.

Glöer P 2002 *Bithynia leachii troschelii* (Paasch 1842) – die östliche Rasse von *B. leachii* (Sheppard 1823) (Gastropoda: Orthogastropoda: Bithyniidae). *Archiv für Molluskenkunde* **130**: 259-265.

Glöer P & Pešić V 2006 On the identity of *Bithynia graeca* Westerlund, 1879 with the description of three new *Pseudobithynia* n. gen. species from Iran and Greece (Gastropoda: Bithyniidae). *Malakologische Abhandlungen* **24**: 29-36.

Graham A 1988 *Molluscs: Prosobranch and Pyramidellid Gastropods. Synopsis of the British Fauna (N.S.)* 2. Universal Book Services / Dr W Backhuys Oegstgeest.

Guernet C, Sauvage J & Soulie-Marsche I 1977 Le Levantin de Joanina (Épire, Grèce): observations stratigraphiques et paléontologiques. *Géobios* **10** (2): 297-309.

Hadžišće S 1956 Beitrag zur Kenntnis der Gastropoden fauna des Ohridsees. *Recuil des Travaux, Skopje* **4** (1): 57-107.

Higgs ES, Vita-Finzi C, Harris DR & Fagg AE 1967 The climate, environment and industries of Stone Age Greece: Part III. *Proceedings of the Prehistoric Society* **33**: 1-29.

Hubendick B & Radoman P 1959 Studies on the *Gyraulus* species of Lake Ochrid. Morphology. *Arkiv för Zoologi Series 2*, **12** (16): 223-243.

Kalogeropoulos N, Karayannis MI, Vassilaki-Grimani M & Grimanis AP 1994 Application of trace element determination and multivariate statistics to a pollution study of Lake Pamvotis, NW Greece. *Fresnius Environmental Bulletin* **3**: 187-192.

Kobelt W. 1877 Iconographie der Land- & Süsswasser-Mollusken. In *Iconographie der Land- & Susswasser-Mollusken (1) 5 (4/6)* (EA Rossmässler ed). C.W Kriedel's Verlag, Wiesbaden pp.61-129.

Kobelt W 1909 Die Gattung *Paludina* Lam. (*Vivipara* Montfort). Neue Folge. In *Systematisches Conchylien-Cabinet von Martini & Chemnitz* (HC Küster ed). Verlag von Bauer & Raspe, Nürnburg pp.313-430.

Korniushin, AV 2004 The bivalve mollusc fauna of ancient lakes in the context of the historical biogeography of the Balkan region. In *Balkan Biodiversity: Pattern and Process in the European Hotspot* (HI Griffiths, B Kryštufek & JM Reed eds). Kluwer Academic Publishers, Dordrecht pp.219-241.

Lawson I, Frogley M, Bryant C, Preece R & Tzedakis P 2004 The Lateglacial and Holocene environmental history of the Ioannina basin, north-west Greece. *Quaternary Science Reviews* **23**: 1599-1625.

L'vova AA & Starobogatov YI 1982 Novyj vid drejsseny (Bivalvia, Dreissenida) iz Okhridskogo ozera. *Zoologicheskij Zhurnal* **61** (11): 1749-1752.

Macan, TT 1969 *A Key to the British Fresh- and Brackish-Water Gastropods*. Scientific Publication No.13, Freshwater Biological Association, Ambleside.

Meier T 1994 Albert Mousson (1805-1890) und seine Sammlung in Zürich. *Mitteilungen der Deutschen Malakozoologischen Gesellschaft* **54**: 9-10.

Meier-Brook C 1983 Taxonomic studies on *Gyraulus* (Gastropoda: Planorbidae). *Malacologia* **24** (1/2): 1-113.

Mousson A 1859 Coquilles Terrestres et Fluviatiles. Recueilles dans l'Orient par M. le Dr Alexandre Schlaefli. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* **4** (1): 12-36; **4** (3): 253-297. [Reprinted 1859 with modifications: Separatum, 72pp. Zürich (Zürcher & Furrer)]

Økland J 1990 *Lakes and Snails. Environment and Gastropoda in 1,500 Norwegian Lakes*. Universal Book Services / Dr W. Backhuys, Oegstgeest.

Petridis D & Sinis A 1994 Benthos of Lake Mikri Prespa (North Greece). *Hydrobiologia* **304**: 185-196.

Petridis D & Sinis A 1997 The benthic fauna of Lake Mikri Prespa. *Hydrobiologia* **351**: 95-105.

Pfeninnger M, Staubach, S, Albrecht C, Streit B & Scwenk K 2003 Ecological and morphological differentiation among cryptic evolutionary lineages in freshwater limpets of the nominal form-group *Ancylus fluviatilis* (O.F. Müller, 1774). *Molecular Ecology* **12**: 2731-2745.

Radoman P 1967 Speciation of the genus *Emmericia* (Gastropoda) in the Adriatic sea. *Basteria* **31**: 27-43.

Radoman P 1973 New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. *Prirodnjacki Muzej u Beogradu* **32**: 1-30.

Reischütz A & Reischütz PL 2002 Helleniká pantoía, 1: Pyrgulidae (Gastropoda: Prosobranchia) aus dem Limni Pamvotis (Epirus, Greichenland). *Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft* **10**: 1-4.

Reischütz PL & Sattmann H 1990 Beiträge zur Molluskenfauna des Epirus, II. *Annalen des Naturhistorischen Museums in Wien B* **91**: 253-272.

Rosenberg G & Ludyanskiy ML 1994 A nomenclatural review of *Dreissena* (Bivalvia: Dreissenidae), with identification of the quagga mussel *Dreissena bugensis*. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 1474-1484.

Sattmann H & Reischütz PL 1988 Beiträge zur Molluskenfauna Nordgreichenlands. *Annalen des Naturhistorischen Museums in Wien B* **90**: 203-214.

Schütt H 1962 Neue Süßwasser-Prosobranchier Greichenlands. *Archiv für Molluskenkunde* **91** (4): 157-166.

Schütt H 1980 Zur Kenntnis greichischer Hydrobiiden. *Archiv für Molluskenkunde* **110** (4): 115-149.

Schütt H 1987 Limnische Mollusken aus älterem Quartär Makedoniens. *Zoologische Mededelingen* **61** (8): 113-121.

Schütt H 1993 Die Gattung *Dreissena* im Quartär Anatoliens (Bivalvia Eulamellibranchiata: Dreissenacea). *Archiv für Molluskenkunde* **122** (Zilch Festschrift): 323-333.

Schütt H Velitzelos E & Kaouras G 1985 Die Quartärmollusken von Megalopolis (Greichenland). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **170** (2): 183-204.

Stanković S 1960 The Balkan Lake Ohrid and its living world. *Monographiae Biologicae* **9**: 1-357.

Stanković SV 1985 A contribution to the knowledge of Gastropods fauna of Dojran Lake and the surrounding waters. *Fragmenta Balcanica* **12** (13): 141-152.

Tzedakis PC 1994 Vegetation change through glacial – interglacial cycles: a long pollen sequence perspective. *Philosophical Transactions of the Royal Society B* **345**: 403-432.

Westerlund CA 1890 Fauna 7: Malacozoa Acephala, 1-319. Register 1-15, Lund.

Westerlund CA & Blanc H 1879 *Aperçu sur la Fauna Malacologique de la Grèce inclus l'Epire et la Thessalie Coquilles Extramarines.* Naples: 161pp.

Zilch A 1955 Die Typen und Typoide des Natur-Museums Senckenberg, 14: Mollusca, Viviparidae. *Archiv für Molluskenkunde* **84** (1): 45-86.