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Enigmatic distribution patterns of the Bithyniidae in the Balkan Region (Gastropoda: Rissooidea)

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> Abstract

We give an overview of 21 species of the freshwater gastropod family Bithyniidae occurring in the Balkans and Asia Minor and discuss their enigmatic distribution in this region. Some large lakes are inhabited by up to three distinct species, while the famous ancient Lake Ohrid is free of bithyniid species. All species, except *B. radomani*, live as endemics in lakes or drainage systems. Possible reasons are on the one hand the retarded passive dispersal because of a special reproduction strategy and, on the other hand, a small niche width of the species. We also describe four new species: *Pseudobithynia kirka* n. sp., *P. panetolis* n. sp., *P. trichonis* n. sp., and *Bithynia kastorias* n. sp.

> Kurzfassung

Wir geben einen Überblick über 21 Arten der Süßwassergastropoden-Familie Bithyniidae vom Balkan und Kleinasien und diskutieren ihre ungewöhnliche Verbreitung in dieser Region. In einigen große Seen kommen bis zu drei unterschiedliche Arten vor, während der Langzeitsee Ohrid frei ist von *Bithynia*-Arten. Mit Ausnahme von *B. radomani*, leben alle Arten endemisch in den Seen oder Fließgewässersystemen. Der Grund liegt vermutlich einerseits in der reduzierten Ausbreitungsgeschwindigkeit durch besondere Vermehrungsstrategien und anderseits in der kleineren speziellen Nischenweite der Arten. Außerdem beschreiben wir vier neue Arten: *Pseudobithynia kirka* n. sp., *P. panetolis* n. sp., *P. trichonis* n. sp. und *Bithynia kastorias* n. sp.

> Key words

Balkan, enigmatic distribution, ancient lakes, Bithyniidae, *Pseudobithynia kirka* n. sp., *P. panetolis* n. sp., *Bithynia kastorias* n. sp.

Introduction

The Balkan Region is among the world hot spots of biodiversity (Griffith et al. 2004). Especially the Balkan freshwater fauna has long been recognized as highly diverse with remarkable degrees of endemism in practically all major taxa (Bănărescu 2004). In spite of numerous investigations into the freshwater mollusc fauna of the Balkan Region, the research on the biodiversity and distribution, especially as to the Bithyniidae, is in its infancy. For the Bithyniidae from Turkey, Glöer & Pešić (2006, 2007) as well as Glöer & Yildirim (2006) pointed out that many more species exist than currently known. Part of the problem is that previous many names of Central European species were widely applied to taxa from e.g., Asia Minor or the Balkans (e.g. Westerlund & Blanc 1879). Schütt (1987) was right, when he wrote that *Bithynia tentaculata* and *B. leachii*, which live in Central Europe, are only distributed north of the Alps, but his two-species concept (*B. graeca* and *B. candiota*) for Greece remains doubtful (for the most recent checklist see Bank 2006).

Intrinsic and extrinsic factors determine the range of any taxon (Gaston 2003). In contrast to pulmonate gastropods, caenogastropods often have less dispersal capabilities and consequently, as a rule, smaller ranges (Ponder & Colgan 2002). However, range restriction to a small drainage system or single lake entity is rare on a worldwide scale. Long-term permanency of a habitat is believed to be a pre-requisite for the proliferation of many taxa after in situ evolution. Our ongoing investigations show that most of the *Bithynia* species that live in the Balkans are narrow-range endemics. Furthermore, our data indicate that no *Bithynia* species inhabits Lake Ohrid while in other lakes, e.g. Lake Skadar, which is connected to the Ohrid Lake by the Drim River, three species occur.

It is the purpose of that paper i) to review the current knowledge on bithyniid diversity in the Balkans, ii) to introduce four new species: *Pseudobithynia kirka* n. sp., *P. panetolis* n. sp., *P. trichonis* n. sp., and *Bithynia kastorias* n. sp., and iii) to discuss the enigmatic distribution pattern of the Bithyniidae in the Balkan Region.

Material and methods

The snails were collected by dredging or by hand, and samples stored in 75% ethanol. The dissections and measurements of genital organs and shells were carried out using a Stemi Zeiss SV6 stereo microscope with an eyepiece-micrometer; the photographs were made with a Nikon D70 digital camera. All type material is deposited at the Zoological Museum of Hamburg (ZMH).

For comparison, additional type material (syntypes, paratypes, topotypes) was obtained from the Natural History Museum Göteborg, the Naturmuseum Senckenberg Frankfurt/M., and the Hungarian Natural History Museum, Budapest.

Results

The Bithyniidae of the Balkan Region can be assigned to the genera *Pseudobithynia* and *Bithynia*. The latter is usually divided into the subgenera *Bithynia* s. str. and *Codiella*. Acknowledging that this classification is not universally accepted, we found that three species of the subgenus *Bithynia* s. str. and all others, except four *Pseudobithynia* spp. (*Pseudobithynia kirka* n. sp., *P. westerlundi*, *P. falniowskii, P. panetolis* n. sp.), belong to the subgenus *Codiella* (Fig. 1.). The species which belong to the subgenus *Bithynia* s. str. only occur in the Dinaric Region: *Bithynia* (*Bithynia*) *cettinensis* Clessin, 1885, *B.* (*B.*) *mostarensis* Moellendorf, 1873, and *B.* (*B.*) *radomani* Glöer & Pešić, 2007. All other *Bithynia* species that occur in the Balkans are small, have a deep suture and a rounded operculum and, therefore, belong to the subgenus *Codiella*. While the occurrence of *B. cettinensis* is restricted to the Cetina river system, and that of *B. mostarensis* to the Neretva drainage system, the latter, could also be found near Omiš (Croatia). *B. radomani* is distributed throughout Montenegro and seems to vicariate with *B. tentaculata*. The shell of *B. radomani* is similar to *B. tentaculata,* which often leads to confusion as to their correct identification. *B. radomani* lives in the Skadar Lake and therefore also in Albania. Maybe the findings of *B. tentaculata* in Albania mentioned by DHORA & WELTER-SCHULTES (1996) actually refer to *B. radomani*.

Another field of debate is the relationship of *B. tentaculata* and *B. mostarensis*. Though, the latter has shouldered whorls with a deep suture and an opened umbilicus. Another species from the Dinaric Region is *B. majewskyi,* which can be distinguished from *B. tentaculata* by an opened umbilicus. However, despite intensive search, we were unable to find this species and can therefore not comment on its distribution. FRAUENFELD (1862) described this species on the basis of juvenile specimens, as he did when he described *B. schwabii* (see SCHÜTT 1987).

In Krka National Park a new *Pseudobithynia, P. kirka* n. sp, was found on the travertine terrasses, directly at the main waterfalls. This is the northwestern most sampling site of a *Pseudobithynia* known so far (Fig. 1.). The closest sampling sites are Lake Pamvotis near Ioannina (Greece, *P. westerlundi* Glöer & Pešić, 2006) and Lake Trichonis (Greece, *P. falniowskii* Glöer & Pešić, 2006).

While in the northwestern part of the Balkans only *Bithynia* species of *tentaculata* type occur, the southern part is inhabited by representatives of the subgenus *Codiella*, locally distributed in selected lakes and seemingly narrow-range endemics. Interestingly, the ancient Lake Ohrid is free of *Bithynia*, though it is connected by the Drim River to Lake Skadar, which is inhabited by three *Bithynia* spp. Lake Skadar, a presumably younger ancient lake (GLÖER & PEŠIĆ in press) turned out to be a hot spot of *Bithynia* evolution, and so did Lake Trichonis. Lake Vegoritis is also free of bithyniids as is most likely Lake Amvrakia, while in ancient Lake Dojran, *Bithynia leachii* was mentioned (STANKOVIĆ 1985). Lake Pamvotis and Krka National Park are the only sampling sites known so far where we could find species of the genus *Bithynia* and *Pseudobithynia*, in sympatry (see Fig. 1.). Recently, we only found *Pseudobithynia westerlundii* in Lake Pamvotis. However, in the 19th century, WESTERLUND & BLANC (1879) found that *B. graeca* occurred there as well (loc. typ.). Both species can be found in Westerlund's collection (GLÖER & PEŠIĆ 2006). This disjunctive distribution of several *Bithynia* and *Pseudobithynia* species continues into Turkey (Fig. 6).

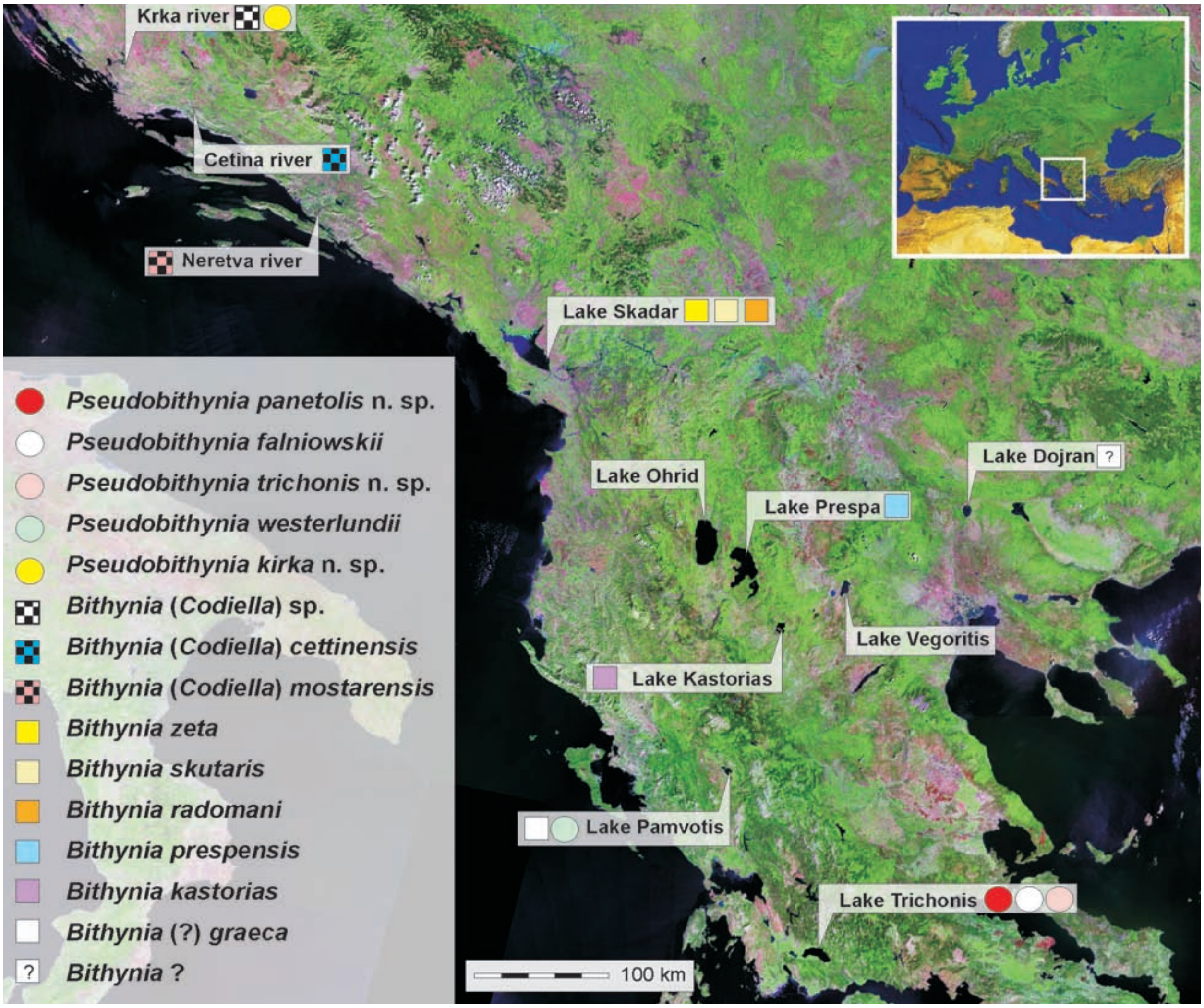

Fig. 1. Sampling sites in the Balkans and composition of bithyniid fauna.

Description of the species from continental Greece

Westerlund & Blanc (1879, p. 136–137) mentioned from Greece the species *Bithynia orsinii* (Küster, 1852), *B. goryi* (Bourguignat, 1856), *B. boissieri* (Küster, 1852), as well as *B. graeca* (Westerlund, 1879). The loc. typ. of *B. orsinii* is situated in Italy (Falkner & Boeters 2003, as *Paludina orsinii*) as well as the loc. typ. of *B. boissieri*, while the loc. typ. of *B. goryi* is the River Nil (Egypt). Except for *Bithynia graeca*, the species mentioned above do not occur in Greece. In his 'Fauna of the Palaearctic Region', Westerlund (1886) also mentions *Bithynia badiella* var. *candiota* Westerlund, 1886 and *B. rubens* (Menke, 1830). *Bithynia badiella* var. *candiota* was described from Crete and considering the syntypes of Westerlund's collection (Göteborg), we can say that this species is distinct to all other *Bithynia* spp. discussed here (Fig. 7.16). *Bithynia rubens* has its loc. typ. in Sicilia and most likely does not occur in Greece.

The following species were described from Corfu, a region which is not under discussion here: *B. corcyrense* Letourneux, 1879, *B. renei* Letourneux 1887, *B. servainiana* Letourneux 1887, *B. viridis* Letourneux 1887, *B. stossichiana* Locard 1894, and *B. phaeacina* Locard 1894.

It remains unclear which species was meant when Kobelt (1891, p. 67, icono. 860) described *B.* (*orsinii* var. ?) *hellenica* Kobelt, 1891. He reported this taxon from Greece and the isles of the archipelago. The shell of this species is similar to *B. candiota* and has nothing in common with *B. orsinii* from the region of Rome. This problem will be discussed in a separate paper. No species found by us corresponds to his original description or to the given drawing.

However, we were able to locate another species, *Bithynia gracilis* (Locard, 1894) (loc. typ. Lysimachia, Vrachoury nord de Missolonghi, Greece). But this species name is preoccupied by *Bithynia gracilis* (Sandberger, 1863), a species with an angulated *tentaculata*-like aperture. We do not know which species was

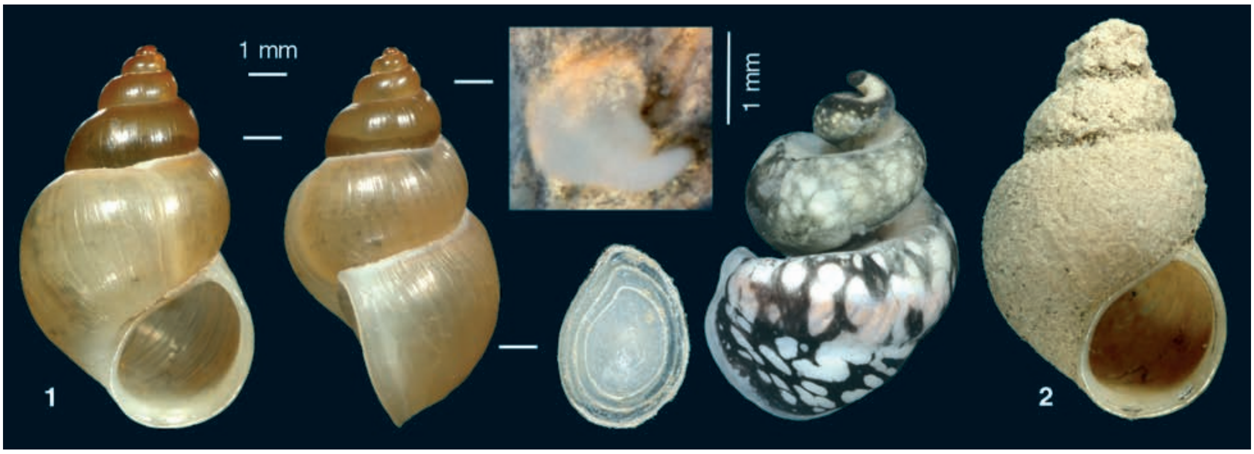

Fig. 2. *Pseudobithynia kirka* n. sp. **1:** Holotype (shell, penis, operculum), **2:** Paratype (softbody, shell).

meant when Stanković (1985) reported *B. leachii* from Lake Dojran, recently it could not be found by us.

Family Bithyniidae Troschel, 1857

Genus *Pseudobithynia* Glöer & Pešić, 2006

Type species: *Pseudobithynia irana* Glöer & Pešić, 2006

Pseudobithynia kirka n. sp.

Material examined: 4 specimens from locus typicus, leg. 7 June 2006 C. Albrecht.
Holotype: Shell height 10.5 mm, shell width 3.2 mm, Holotypus ZMH 51022 (Fig. 2.1).
Paratypes: Penis in ethanol, ZMH 51023, 1 specimen in coll. Glöer, 2 specimens in coll. JLU Giessen (BA.2006.02).
Locus typicus: Krka National Park, Croatia, Skradin, 43.805480°N, 15.963934°E.
Habitat: Travertine terraces directly at major fall on stones in highly oxygenated water.
Etymology: Named after the type locality Krka National Park.
Description: Shell glossy, yellowish horn-coloured, umbilicus closed, apex small and blunt, 5.5 regular enlarging whorls, spire to body whorl = 2.8 : 10, shallow suture whitish at the body whorl, border of aperture regularly thickened and whitish, outer margin of the aperture sinuated, operculum at nucleus concave.
Penis morphology: Penis simple with a small swelling.

Pseudobithynia panetolis n. sp.

Material examined: 15 specimens from locus typicus, leg. 6 September 2005 C. Albrecht & R. Schultheiß.
Holotype: Shell height 4.4 mm, shell width 2.8 mm, Holotype ZMH 51028.
Paratypes: Male, 3.8 mm, 2.6 mm, Paratype ZMH 51029.
Locus typicus: Lake Trichonis, Greece, E of Panetolion (Panaitolio), NW shore; 38.58893°N, 21.46703°E.
Habitat: 1 m depth on rocks covered with microalgae.
Etymology: Named after the nearest village to the sampling site.
Description: Shell glossy and fine striated, suture deep, whorls slightly convex, Umbilicus open, apex obtuse, spire to shell height = 2 : 6, edge of aperture sharp, outer margin of aperture a little sinuated, 4.0–4.5 whorls; shell height to width: male 3.5–3.8 : 2.2–2.6 mm, female: 4.4–6.9 : 2.8–4.0 mm; nucleus of operculum cochleate, convex bended.
Male copulatory organ: Penis simple.

Pseudobithynia trichonis n. sp.

Material examined: 9 specimens Lake Trichonis, 3 specimens stream between lakes Trichonis and Lysimachia; leg. 7/8 September 2005 C. Albrecht & R. Schultheiß.
Holotype: Shell height 3.3 mm, shell width 2.0 mm, Holotype ZMH 51026.
Paratypes: Shell height 3.5 mm, width 2.4 mm, Paratype ZMH 51027.
Locus typicus: Lake Trichonis, Greece, Etoloakarnania, NE shore; 38.52763°N, 21.65608°E.
Habitat: Depth 1 m, on stones covered with microalgae.
Etymology: Named after the locus typicus, Lake Trichonis.

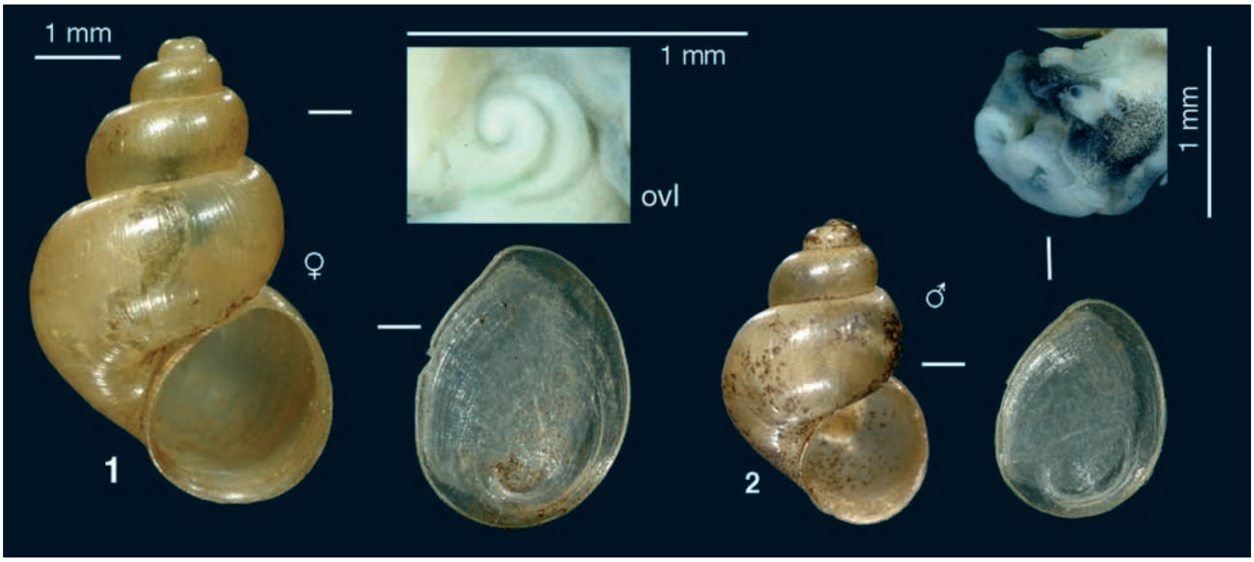

Fig. 3. *Pseudobithynia panetolis* n. sp. **1**: Holotype (shell, operculum, and ovl = oviductual loop), **2**: Paratype (shell, operculum, head with penis).

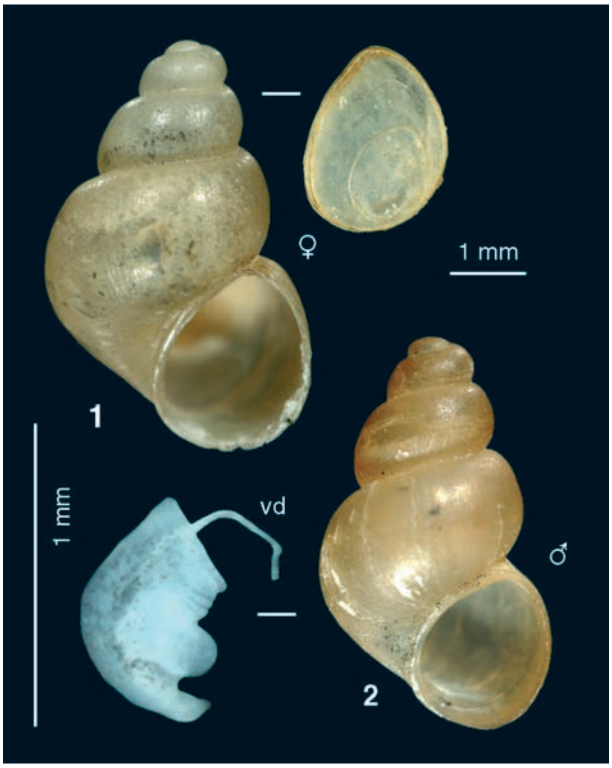

Fig. 4. *Pseudobithynia trichonis* n. sp. (shell, operculum, and penis, vd = vas deferens).

Description: Apex obtuse, shell silky, 4 whorls regularly convex, first whorl flat, suture deep, spire to shell height = 1.1 : 3.5, edge of aperture sharp, outer margin of aperture sinuated, operculum convex and not bended, nucleus of operculum cochleate; males more slim than females.
Male copulatory organ: Penis simple with a thick swelling in the middle part.

Genus *Bithynia* Leach, 1818

Type species: *Bithynia tentaculata* (Linnaeus, 1758)

Bithynia kastorias n. sp.

Material examined: 18 specimens, leg. 14 May 2005 C. Albrecht & T. Wilke.
Holotype: Female, shell height 6.5 mm, shell width 4.4 mm, Holotype ZMH 51024.
Paratypes: Male, shell height 4.1 mm, shell width 2.5 mm, Paratype ZMH 51025.
Locus typicus: Kastorias Lake (Orestiada), Greece, 40.55092°N, 21.27237°E.
Habitat: Littoral zone on rocks (0.5–0 m depth), eutrophic lake.
Associated molluscs: *Lymnaea stagnalis*, *Galba truncatula, Radix auricularia, Planorbis planorbis*, *Planorbarius corneus, Segmentina nitida, Valvata* sp.
Etymology: Named after the locus typicus, Lake Kastorias.
Description: Shell glossy and light horn-coloured, suture very deep, apex blunt, whorls shouldered, umbilicus opened to slit-like, border of aperture slightly thickened and outer margin sinuated, 4.5 whorls, spire to shell height = 1.8 : 6.5, nucleus of operculum cochleate and obliquely concave, at the upper margin slightly bended, otherwise planar; shell height to width: female 6.1–6.5 mm : 3.9–4.4 mm, male 4.1 mm : 2.5 mm.
Male copulatory organ: Penial appendix very long, distal penis part very short, flagellum ca. 7 × longer than penis.

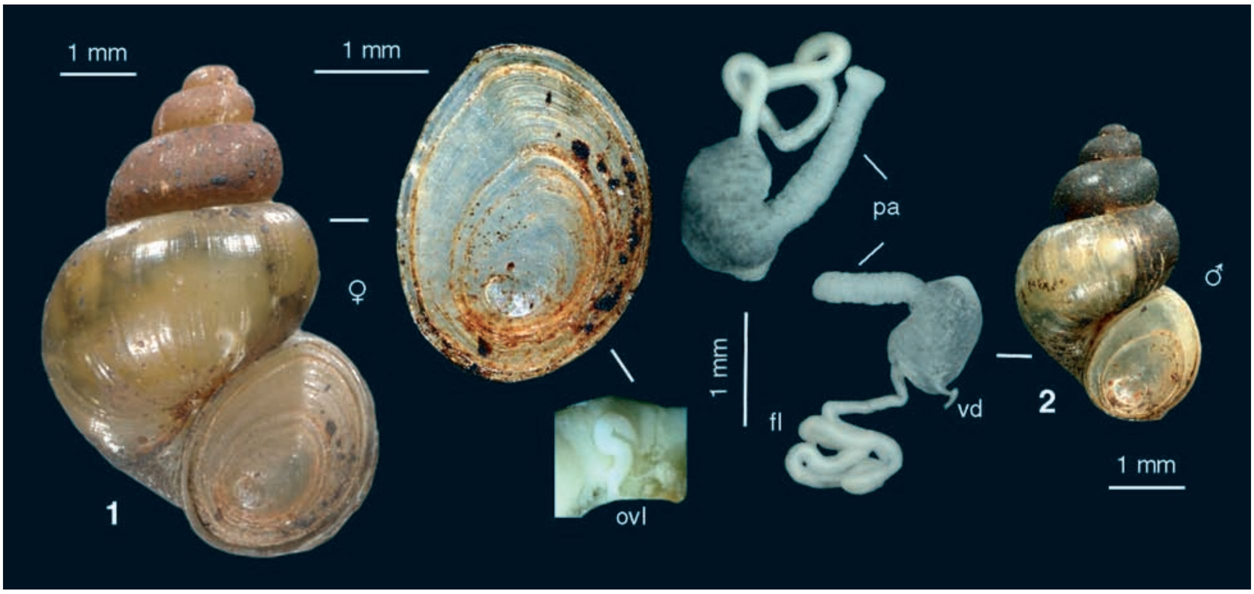

Fig. 5. *Bithynia kastorias* n. sp. **1**: Holotype, female (shell, operculum, and ovl = oviductual loop), **2**: Paratype, male (shell with operculum, fl = flagellum, pa = penial appendix, vd = vas deferens).

Differential diagnosis

Pseudobithynia kirka is much larger in shell height (10 mm) than the other *Pseudobithynia* species of the Balkans (3–7 mm) and the shell shape is similar to *B. tentaculata*. In *P. falniowskii* and *P. panetolis*, the females are clearly larger than the males. In *P. trichonis*, the males and females are of similar size but the latter are broader than the males. In *P. falniowskii* the ratio between shell height and width is 1.43 and in females 1.58 in males, in *P. panetolis* 1.53 in females and 1.40 in males, so the shells of males of the latter species are slimmer. The oviductual loop in *P. panetolis* is coiled and in *P. falniowskii* it is loop-like.

The penis morphology of *Bithynia kastorias* is distinct to all other *Bithynia* spp. from the Balkans known so far, and the difference lies in the very long penial appendix and the very short distal penis part. The body whorl of *B. kastorias* is more prominent than in *B. graeca*.

Discussion

Unanticipated diversity

One reason for the unanticipated species richness in many Balkan waters is the degree of research efforts that have been attributed to the family Bithyniidae. While the remaining hydrobioid fauna was in focus for decades (e.g. Radoman 1983, 1985), bithyniids were studied in some detail only occasionally (e.g. Hadžišče 1958). Another fact complicating the situation is the somewhat cryptic nature of the species under concern and the adoption of a mere Central European taxonomic framework by many authors studying the Balkan bithyniid fauna. Only extensive sampling in each lake systems and its tributaries could lead to the discovery of the new species. We are convinced that there are more bithyniid species to be discovered in Balkan waters. Nevertheless, the described diversity is already much higher in the Balkans than in northern and Central Europe (Glöer 2002). One reason could be less pronounced extinction events in the area during the last glacial periods. A detailed phylogeographical analysis could enlighten potential refugia and migration pathways. Preliminary data suggest that the morphological diversity described here is also reflected in the genetics of the taxa (Wilke & Albrecht, unpublished data). Interestingly, the new species described are not restricted to the ancient lakes in the Balkans, but also occur in river systems. However, the highest number of co-occurring species is found in ancient lakes like Skutari, Pamvotis or Trichonis. Small bithyniid radiations are also known from other ancient lakes in the world, e.g. the Lake Albert *Gabiella* spp. (Brown 1994). However, a striking finding is the absence of any bithyniid in the Ohrid Basin. We do not know whether bithyniids never occurred in the primary and secondary basins that later on formed the recent Ohrid setting (cf. Radoman 1985) or whether ancestral populations got wiped out when other major radiations rised. Examples include e.g., some hydrobioid groups like the Pyrgulinae (Radoman 1985, Wilke & Albrecht 2006). There is no gastropod fossil record in the Lake Ohrid basin that could help to elucidate the question of former bithyniid occurrence. The nearest quarternary bithyniid records are from Philippi (Schütt 1987) and the Ptolemais formation in northern Greece (A. Kossler, pers. comm.).

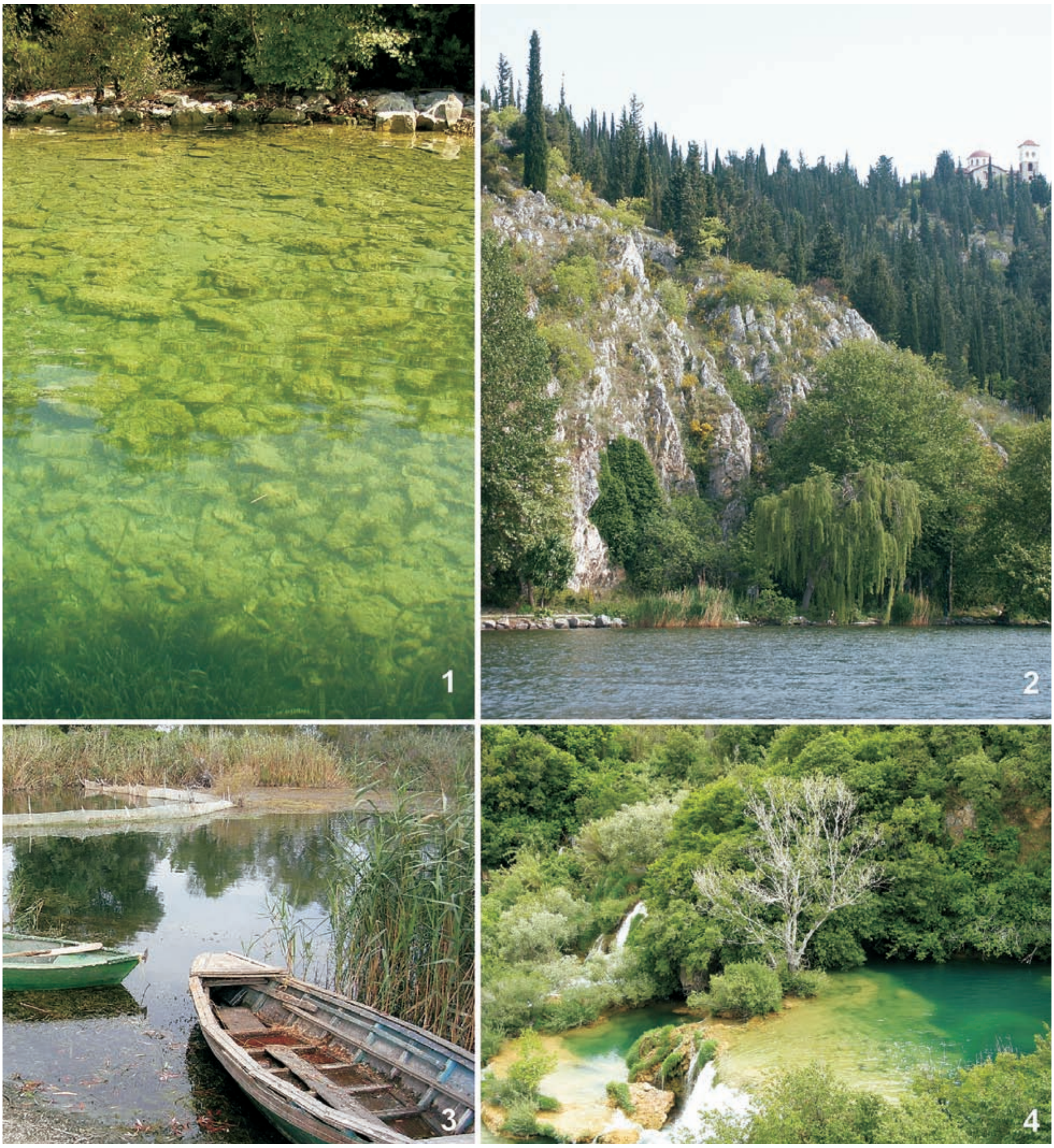

Fig. 6. Localities of the bithyniid species studied. **1**: Littoral of Lake Trichonis (*Pseudobithynia panetolis* n. sp.), **2**: Lake Kastorias near Kastoria (*Bithynia kastorias* n. sp.), **3**: Outflow of Lake Trichonis (*Pseudobithynia trichonis* n. sp.), **4**: Krka water falls in Krka National Park (*Pseudobithynia kirka* n. sp.).

It is a well recognized pattern in caenogastropod radiations in ancient lakes that either thiarid like taxa or hydrobioids radiate (Boss 1978, Michel 1994). This "exclusion rule" could also apply to the hydrobioids and Bithyniidae in the case of Lake Ohrid. On the contrary, absence of major hydrobioid radiations in other lakes like Skutari, Pamvotis or Trichonis could have triggered diversification in bithyniids. Habitat diversity and long-term stability and isolation lead to endemic species in other gastropod taxa of those lakes (see Glöer & Pešić 2007, Frogley & Preece 2004, Albrecht & Glöer 2007). As Radoman (1985) pointed out, no author could offer a conclusive explanation for the low degree of faunal exchange (immigration and emigration) of Lake Ohrid and neighbouring water systems. He believed in an inherent structure of the biocenosis itself that prevents such events. The conditions in the lake produced a highly adapted fauna, which is a major source of competition for immigrants. There are other examples of species rich genera that are absent in Lake Ohrid. Four species of *Orientalina* spp. occur in Lake Skadar (Glöer

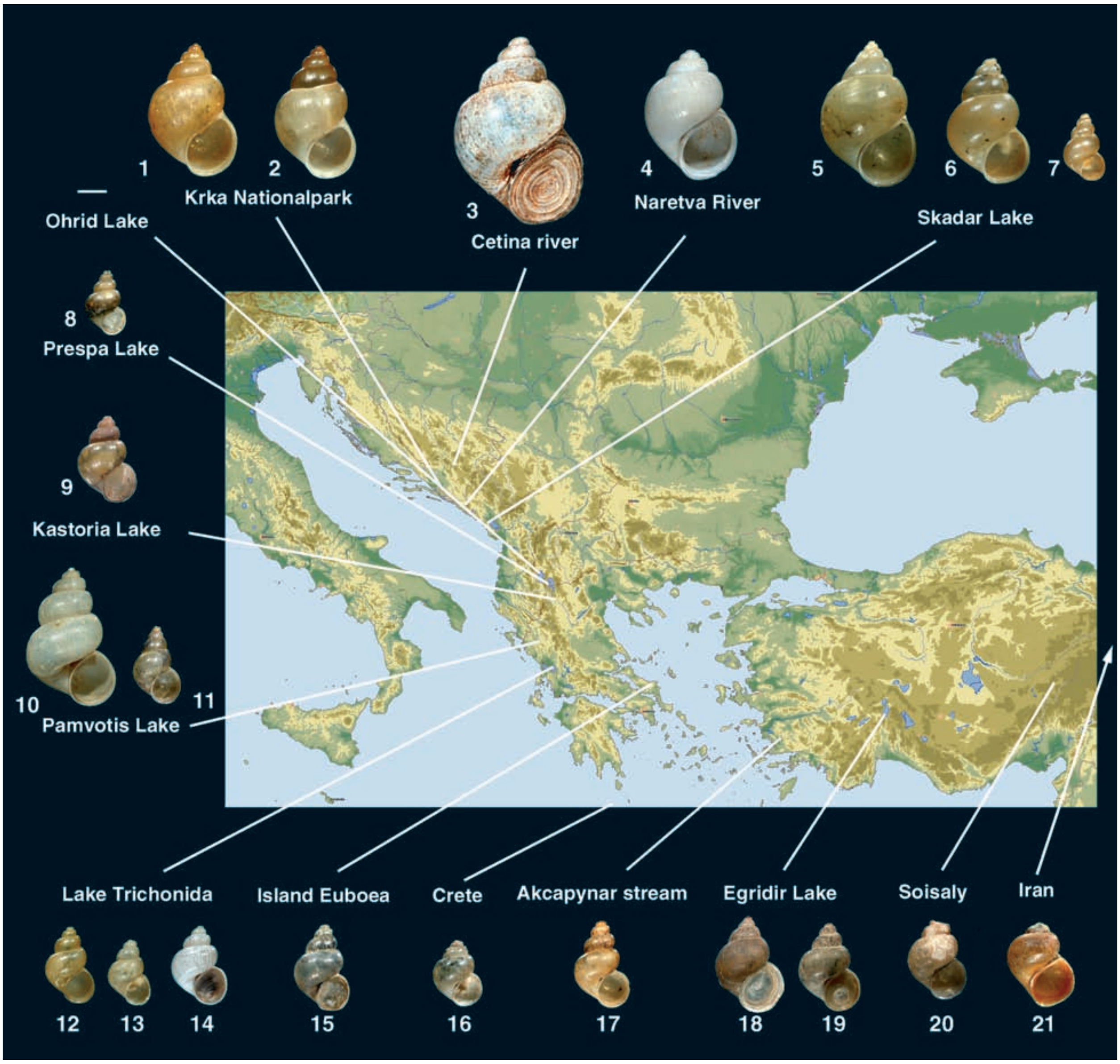

Fig. 7. Diversity of the Bithyniidae in the Balkans and Asia Minor; **Krka National Park:** (1) *Bithynia* sp. (coll. Natural Hist. Museum Budapest), (2) *Pseudobithynia kirka* n. sp.; **Cetina river:** (3) *B. cettinensis* (Syntype, Senckenberg Museum), **Naretva river:** (4) *B. mostarensis* (Syntype, Senckenberg Museum); **Lake Skadar:** (5) *B. radomani*, (6) *B. skutaris*, (7) *B. zeta*; **Lake Prespa:** (8) *B. prespensis*, **Kastoria Lake**: (9) *B. kastorias* n. sp.; **Lake Pamvotis:** (10) *B.* (?) *graeca*, (11) *P. westerlundii*; **Lake Trichonis:** (12) *P. panetolis* n. sp., (13) *Pseudobithynia trichonis* n. sp., (14) *P. falniowskii*; **Island Euboea:** (15) *B.* sp. (*B. goryi* sensu Westerlund, coll. Westerlund, Göteborg), **Crete:** (16) *B. candiota* (Syntype, coll. Westerlund, Göteborg), **Akçapýnar Stream:** (17) *B. pesicii*; **Lake Eğridir:** (18) *B. pseudemmericia*, (19) *B.* sp.; **Soislay:** (20) *B. pentheri*; **Iran:** (21) *P. irana*.

& PEŠIĆ in press) and one species even in springs surrounding Lake Ohrid. However in the lake itself they are absent (RADOMAN 1985). The latter author attributes ecological barriers and the "specific nature of the lacustrine biocenosis" as reasons for the pattern found. Bithyniids in general are adapted to rather different ecological settings, unfortunately we do not know enough about ecological requirements of Balkan bithyniids and an explicit discussion would therefore be premature. It is also striking that in Lake Ohrid groups of gastropods radiated that are usually not prone to extended speciation, namely the pulmonates. An example was recently studied for the endemic *Ancylus* spp. (ALBRECHT et al. 2006). Distinct niches are a necessary prerequisite for coexistence of sympatric species (HARDIN 1960). Small-scale ecological studies must address niche width and degree of sympatry and in-lake allopatry in Balkan waters in order to understand why bithyniids diversified in certain localities to the extent described here.

Narrow ranges

Isolation and restricted dispersal avenues for freshwater organism in Balkan waters are certainly factors contributing to the distribution pattern found in this study. There is no major linkage between the drainage systems and actual basins. Therefore, no boat traffic can enhance spread of freshwater organisms, this was already mentioned for the restricted dispersal of two *Dreissena* mussel species in the Balkans (Albrecht et al. submitted). Even the River Drim is not believed to be a major route of faunal exchange between Lakes Ohrid and Skutari (Radoman 1985). Also, topography of the Balkans is not favoring interdrainage dispersal. In the lowlands, small waterbodies are colonised by a new species every nine years (Boycott 1936) with an immigration rate v_I=0.11 taxa/a, which decreases in the isle of Sylt, a small island in the North Sea, to 0.04 taxa/a (Reise & Glöer 2006). Recent biogeographical studies on the Åland islands revealed 4 types of lakes based on the mollusc communities, among them a "*Bithynia*"-type (Carlsson 2001), with *Bithynia tentaculata* as a frequent immigrant. The immigration rate should be, however, much lower in the Balkans. One reason could be the reproductive strategy of some taxa in this region, which retards the immigration rate. Usually spreading happens by passive dispersal of spawn mass, laid on submerged vegetation. In the Balkans, however, some species lay their egg-strings onto their own shells (Albrecht 2006, Glöer & Pešić 2006). Dispersal of dioecious taxa like bithyniids would require the simultaneous transport of at least two individuals in order to survive, reproduce and establish a new population. This restricted dispersal capacity in combination with unfavourable opportunities outlined above, decreases the likelihood of such events. Nevertheless, dispersal happens occasionally as evidenced by the presence of a *Bithynia* species in artificial lakes like Lake Kerkini in Greek Makedonia (Eleutheriadis & Lazaridou-Dimitriadou 1997). On the other hand, the large natural Lake Vegoritis seems to be free of bithyniids. It is not clear whether altitudinal aspects play a role in the present distribution pattern. However in one of the highest Balkan lakes, Lake Prespa, there is the endemic *Bithynia prespensis*. Nevertheless, the highest sympatric diversity is found in lowland lakes. The complex paleogeographic circumstances of the Balkan itself as strong historical component have certainly influenced distributional patterns seen in current faunas.

As far as we know, the bithyniid species in the Balkans, except for *B. radomani*, are all endemic to a lake or a drainage system. If one considers the bithyniids of Asia Minor in a biogeographical context (Fig. 6), it is possible to compare patterns derived from other gastropod groups. Radoman (1985) distinguished 3 major groups of lakes in the Balkans and Asia Minor: the Adriatic-Ionian lake group, the Prespa system, and the Aegean-Anatolian lake group. Given our recent knowledge on bithyniid diversity and distributions, no clear-cut pattern as proposed by Radoman (1985) can be observed. Also, it is intriguing that no *Pseudobithynia* has been found so far in the Aegean-Adriatic lake group or the Prespa system. Also, the restriction of *Codiella* spp. to the northern Dinaric Region is interesting. Further comparative studies including phylogeographical approaches are necessary to elucidate the complex history of freshwater gastropod faunal evolution in the Balkans.

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