



Greece, a second hotspot of *Bythinella* spp. (Gastropoda: Bythinellidae) in Europe, with the description of two new species

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RESUM

Grècia, un segon punt calent de *Bythinella* spp. (Gastropoda: Bythinellidae) a Europa, amb la descripció de dues noves espècies. — Recentment, nombroses espècies del gènere *Bythinella* han estat descrites per a Grècia, fins arribar a 34 espècies conegudes. Noves investigacions van revelar dues noves espècies de les muntanyes de Lefkas i Parnassos. Per a la delimitació de les noves espècies es van fer servir caràcters morfològics i anàlisi multivariant de clústers, que van mostrar diferenciació dels dos taxons. Addicionalment, es dona una visió de conjunt de totes les espècies conegudes del gènere a Grècia, amb breus descripcions i fotografies de les conquilles. Aquest seria el segon punt calent de biodiversitat del gènere *Bythinella* a Europa, després de França, on es coneixen 52 espècies.

ABSTRACT

Greece, a second hotspot of *Bythinella* spp. (Gastropoda: Bythinellidae) in Europe, with the description of two new species. — Recently, many *Bythinella* species have been described from Greece, with the result that 34 species are already known in this country. New investigations revealed two additional species from Lefkas and Parnassos mountains. For the new species delimitation, morphometric characters and multivariate cluster analyses were used, which showed distinctiveness of the species. Additionally, an overview of all known species of Greece with pictures of the shells and short descriptions are given. This is the second highest species richness spot of *Bythinella* in Europe, after the 52 *Bythinella* species known in France.

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Introduction

The small freshwater spring snails from the genus *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Bythinellidae) are the most diverse of all hydrobioids in Europe (Radoman 1976, 1983; Ponder *et al.*, 2008). Representatives of the genus are distributed throughout continental Europe, from northern Germany to Sicily, and from North-Africa (Boeters, 1998) over Spain (Boeters, 2019) to Ukraine (Wilke *et al.*, 2010). They can also be found on some Mediterranean islands and as far as in the Asian part of Turkey (Yildirim *et al.* 2006). They are considered to have a center of highest species richness in France, with a total of 52 known species in this country (Bichain *et al.* 2007; Bank & Neubert 2017).

When Schütt (1980) studied the *Bythinella* species from Greece, he could only report on *Bythinella charpentieri* (Roth, 1855), but he added the species *Bythinella cretensis* Schütt, 1980, and *Bythinella kosensis* Schütt, 1980. In 1988, Reischütz described *Bythinella charpentieri cabirius* Reischütz, 1988 from Samothrace as new subspecies, and added in 2008, together with his son Alexander and W. Fischer, *Bythinella beckmanni* A. Reischütz *et al.*, 2018, and *Bythinella atypicos* A. Reischütz *et al.*, 2008. The authors reported that the species richness of *Bythinella* in the Peloponnese is higher than

initially believed. In 2011 the region of Greece has been interpreted by Benke *et al.* (2011) as a coldspot of species richness, with only 6 *Bythinella* species. In 2016 Szarowska *et al.* studied the *Bythinella* species composition of Greece by molecular genetics and found 16 clades, which could be interpreted as species, but unfortunately, they did not deal with species names. More recently, many species have been described as new, so 36 *Bythinella* species are already known, but only eight of these could be studied anatomically.

Haase *et al.* (2007) stated that the identification of *Bythinella* species has to be based on the integration of morphological, anatomical, and genetic investigations. On the other hand, Bichain *et al.* (2007) stated that analyses of ITS1 and COI in some clades of *Bythinella* are in conflict concerning taxonomic delineations, probably because of different genetic evolutionary histories. Nevertheless, they concluded by DNA sequencing that *Bythinella bicarinata* and *Bythinella dunkeri*, two obviously distinct species, are conspecific. The fact that distinct species can be genetically (COI) similar has been shown by Haase *et al.* (2007) for *B. robiciana*/*B. opaca* from Slovenia. Altogether, there is no clear delimitation of taxa, so new integrative research is urgently needed in this group.

This paper is intended to: (i) summarize the knowledge about the *Bythinella* species of Greece; (ii) describe two new *Bythinella* species from continental Greece and Lefkas; and (iii) provide a basis for future investigations.

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Table 1. The distinguishing features of *Bythinella* species of Greece.

Taxon	shell shape	aperture	umbilicus	Body whorl	suture	H/W	h/H	shell size
<i>B. alexpeteri</i>	2	2	0	0	0	1,68	0,47	1
<i>B. amira</i>	1	2	0	0	0	1,80	0,44	1
<i>B. atypicos</i>	2	2	0	0	0	1,70	0,45	1
<i>B. beckmanni</i>	1	1	0	0	0	1,90	0,38	0
<i>B. ch. charpentieri</i>	1	2	0	0	1	1,88	0,47	2
<i>B. charpentieri cabirius</i>	4	1	0	1	0	1,68	0,44	1
<i>B. corrosa</i>	1	1	0	0	0	1,88	0,42	1
<i>B. cretensis</i>	4	2	1	1	0	1,63	0,43	0
<i>B. dimitrosensis</i>	2	2	0	0	1	1,69	0,51	1
<i>B. eleousae</i>	3	0	1	0	0	1,31	0,47	2
<i>B. ellinikae</i>	4	1	0	1	0	1,72	0,46	1
<i>B. jozefgregoi</i>	4	1	0	1	1	1,76	0,45	1
<i>B. kambosensis</i>	1		0	0	1	1,22	0,47	2
<i>B. kastaliae</i>	2	1	0	0	0	1,62	0,43	1
<i>B. kastanolongosensis</i>	4	2	0	1	0	1,74	0,45	2
<i>B. kithiraensis</i>	4	1	0	1	0	1,71	0,42	1
<i>B. klimaensis</i>	4	1	0	0	0	1,81	0,40	2
<i>B. konstadinensis</i>	2	2	0	0	0	1,50	0,50	1
<i>B. kosensis</i>	1	1	0	0	1	1,68	0,45	1
<i>B. kwanti</i>	2	1	1	0	0	1,48	0,50	1
<i>B. kyriaki</i>	2	2	0	1	0	1,43	0,45	0
<i>B. liandinaensis</i>	4	2	1	0	0	1,80	0,44	1
<i>B. olymbosensis</i>	1	2	0	0	1	1,60	0,50	1
<i>B. perivoliensis</i>	4	1	0	0	1	1,68	0,46	1
<i>B. pesici</i>	2	0	0	0	0	1,61	0,46	1
<i>B. petrosensis</i>	2	1	0	0	0	1,65	0,42	0
<i>B. rachonica</i>	4	2	0	0	0	1,65	0,47	2
<i>B. reischuetzi</i>	2	1	0	0	1	1,52	0,50	0
<i>B. rethymnonensis</i>	4	1	0	0	0	1,12	0,48	1
<i>B. reuselaarsi</i>	4	1	0	0	0	1,68	0,49	2
<i>B. righaensis</i>	2	1	0	0	0	1,70	0,48	2
<i>B. sitiensis</i>	4	1	0	0	0	1,65	0,44	1
<i>B. taygetensis</i>	4	2	0	0	1	1,64	0,45	1
<i>B. walensae</i>	4	2	1	1	0	1,76	0,45	2
<i>B. lilaia n.sp.</i>	1	1	0	0	1	1,78	0,41	2
<i>B. palmosi n. sp.</i>	2	1	0	0	0	1,64	0,46	0

Shape of the shell: elongated ovate = 1, ovate = 2, broad ovate = 3, cylindrical = 4. Aperture: ovate = 0, rounded angled = 1, angled = 2. Umbilicus: closed = 0, slit-like = 1. Body whorl: convex = 0, straight = 1. Suture: deep = 0, shallow = 1. Shell size: <2.5mm = 0, >2.5mm<3.0mm = 1, >3mm = 2. h: aperture height; H: total shell height; W: shell width

Material and methods

In July and August 2021, the second author collected freshwater molluscs in Greece. The snails were collected by hand from the surface of dead leaves and small stones in spring not swallow water spots. The samples were put into 75% ethanol. The dissections and measurements of the genital organs and the shells were carried out

using a stereo microscope (Leica M205C); the photographs were made with a digital camera (Leica DMC5400). The multivariate cluster analysis was made using PAST4.03 (<https://past.en.lo4d.com/download>). The type material is stored in the Zoological Museum of Hamburg (ZMH).

The nomenclature of the male sex tract follows Begrenzer (1914) and Hershler & Ponder (1998).

Results

Determination of taxa belonging to the genus *Bythinella* is not easy because they are not equipped with a wealth of distinguishing characters. Nevertheless, it was possible to distinguish 36 *Bythinella* species by making use of a rather simple species concept: every species has at least one constant character that allows separation from other species. A constant distinguishing character shows that speciation has taken place. But this concept only works with samples that comprise a large number of individual specimens in order to account for the considerable variability. In addition, only adult shells with an identical number of whorls may be compared, because the shells of younger specimens or juveniles may look distinct from the adults, due to allometric growth. Thus, we only used differentiating characters, which differ in some species (Table 1).

With the characters mentioned in Table 1 we could work out a multivariate cluster analysis (Figure 1), which shows distinctiveness of the *Bythinella* taxa. Their distribution is presented in Figure 2.

Systematics

***Bythinella alexpeteri* Glöer & Hirschfelder, 2020 – Fig. 3.1**
 2008 *Bythinella* sp. 2 – Reischütz et al. [*Nachri.bl. Erst. Vorarlb. Malak. Ges.*, 15: 35-36].

2020 *Bythinella alexpeteri* Glöer & Hirschfelder, p. 64, fig. 2.5 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Arcadia, Mari, travertine spring at the northern end of the village, N 37°01'58.7" / E 22°49'33.5", 634 masl.

Description: shell ovate cylindrical, small apex, 4.5-5 whorls slightly convex with a deep suture; body whorl takes about 0.75 of shell height; aperture ovate, angled at the top with a sharp peristome, somewhat thickened at the columella; umbilicus closed. H = 2.6-2.9 mm, W = 1.7-1.8 mm.

Anatomy: unknown.

Distribution: known only from type locality.

Remarks: the sympatrically occurring *Bythinella beckmanni* was not found again in 2018. That species might be extinct as already suspected by Reischütz et al. (2008).

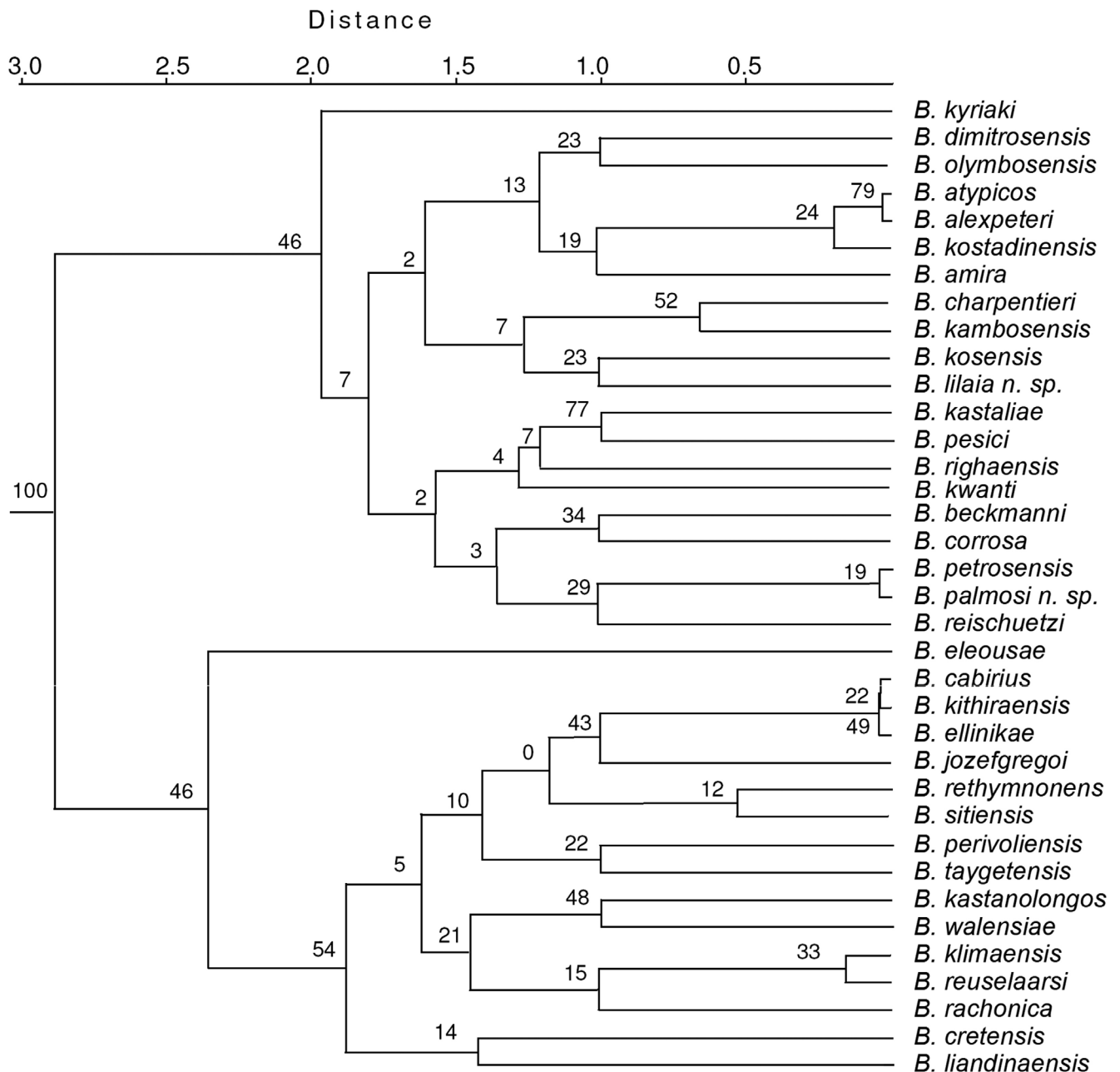


Figure 1. Multivariate cluster analysis (complete linkage) of the *Bythinella* species of Greece.

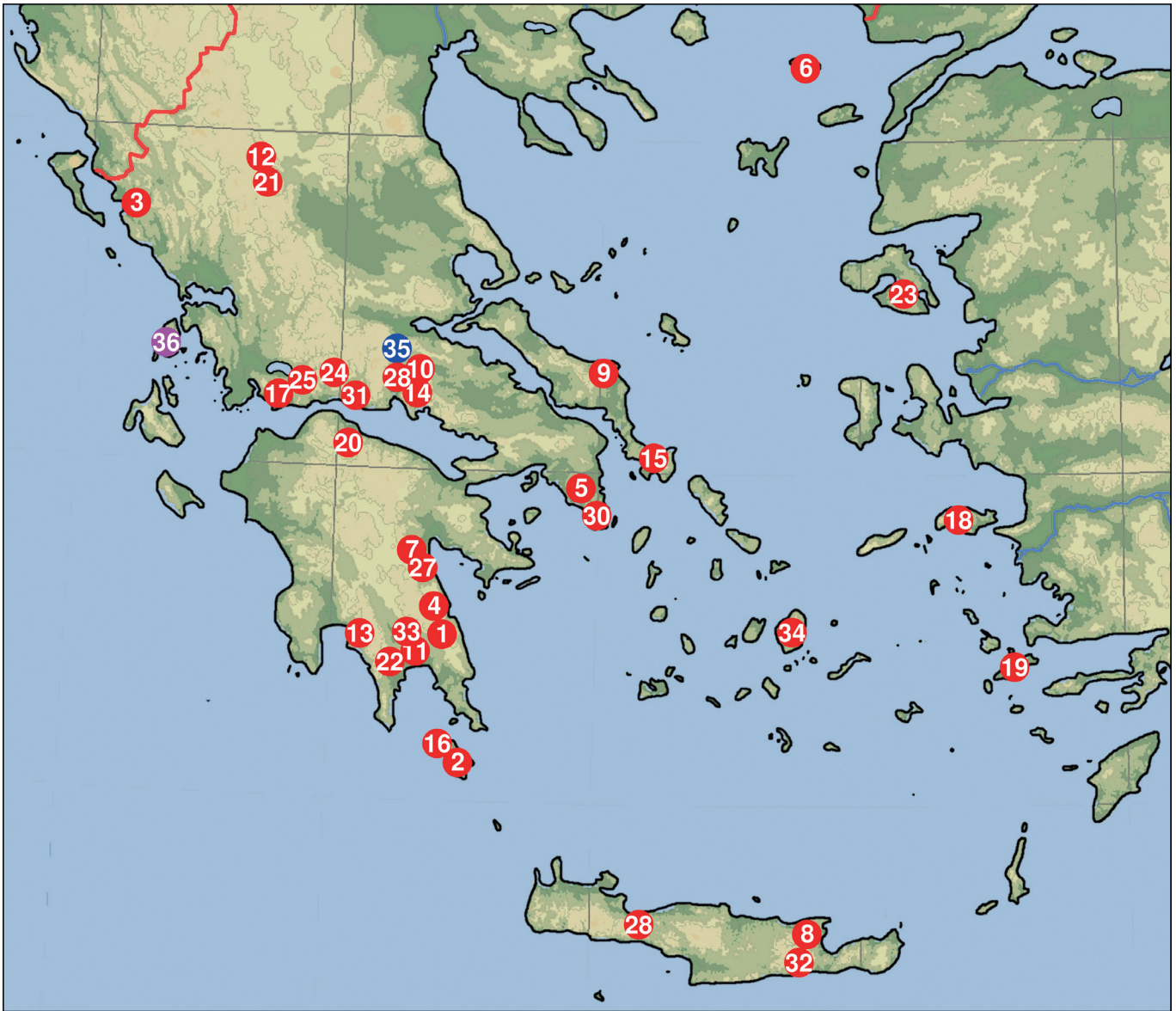


Figure 2. The distribution of the *Bythinella* species in Greece (in alphabetical order). 1: *B. alexpeteri*, 2: *B. amira*, 3: *B. atypikos*, 4: *B. beckmanni*, 5: *B. charpentieri*, 6: *B. charpentieri cabirius*, 7: *B. corrosa*, 8: *B. cretensis*, 9: *B. dimitrosensis*, 10: *B. eleousae*, 11: *B. ellinikae*, 12: *B. jozefgregoi*, 13: *B. kambosensis*, 14: *B. kastaliae*, 15: *B. kastanolongosensis*, 16: *B. kithiraensis*, 17: *B. klimaensis*, 18: *B. konstadinensis*, 19: *B. kosensis*, 20: *B. kwanti*, 21: *B. kyriaki*, 22: *B. liandinaensis*, 23: *B. olymbosensis*, 24: *B. perivoliensis*, 25: *B. pesici*, 26: *B. petrosensis*, 27: *B. rachonica*, 28: *B. reischuetzi*, 29: *B. rethymnonensis*, 30: *B. reuselaarsi*, 31: *B. righaensis*, 32: *B. sitiensis*, 33: *B. taygetensis*, 34: *B. walensae*, 35: *B. lilaia* n. sp. (blue circle), 36: *B. palmosi* n.sp. (magenta circle, Lefkas).

***Bythinella amira* Glöer & Hirschfelder, 2020 – Fig. 3.2**

2020 *Bythinella amira* Glöer & Hirschfelder, p. 65, fig. 2.7 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Kithira island, Karavas, spring-fed brook in Amir Ali, N 36°20'43.9" / E 22°56'57.4", 110 masl.

Description: shell cylindrical to slightly conical, apex small rounded, 4.5-5 convex whorls with deep suture; body whorl about 0.7 of shell height; aperture elongated ovate, with thickened peristome; umbilicus closed. H = 2.3-2.6 mm, W = 1.3-1.4 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella atypikos* A. Reischütz, P.L. Reischütz & W. Fischer, 2008 – Fig. 3.3**

2008 *Bythinella atypikos* A. Reischütz, P.L. Reischütz & W. Fischer, p. 36, fig. 5 [*Nach.bl. Erst. Vorarl. Malak. Ges.*, 15: 35-36].

Type locality: "Quelle in Faskomilia östl. Nea Figalia, nördl. der Neda, Nomos Ilia, Peloponnese, Griechenland."

Description: shell slim conical with 5 slightly convex whorls, deep suture; body whorl about one third of shell height, apex blunt; aperture ovate. H = 2.9 mm, W = 1.8 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella beckmanni* A. Reischütz, P.L. Reischütz & W. Fischer, 2008 – Fig. 3.4**

2008 *Bythinella beckmanni* A. Reischütz, P.L. Reischütz & W. Fischer, p. 35, fig. 3 [*Nachri.bl. Erst. Vorarl. Malak. Ges.*, 15: 35-36].

Type locality: „Quelle in Mari, südlich von Leonidion, Nomos Argolida, Peloponnese, Griechenland.“

Description: shell elongated-ovate, 4 slightly convex whorls, aperture ovate, peristome separated from the shell. H = 2 mm, W = 1.3 mm.

Anatomy: unknown.

Distribution: known only from type locality.

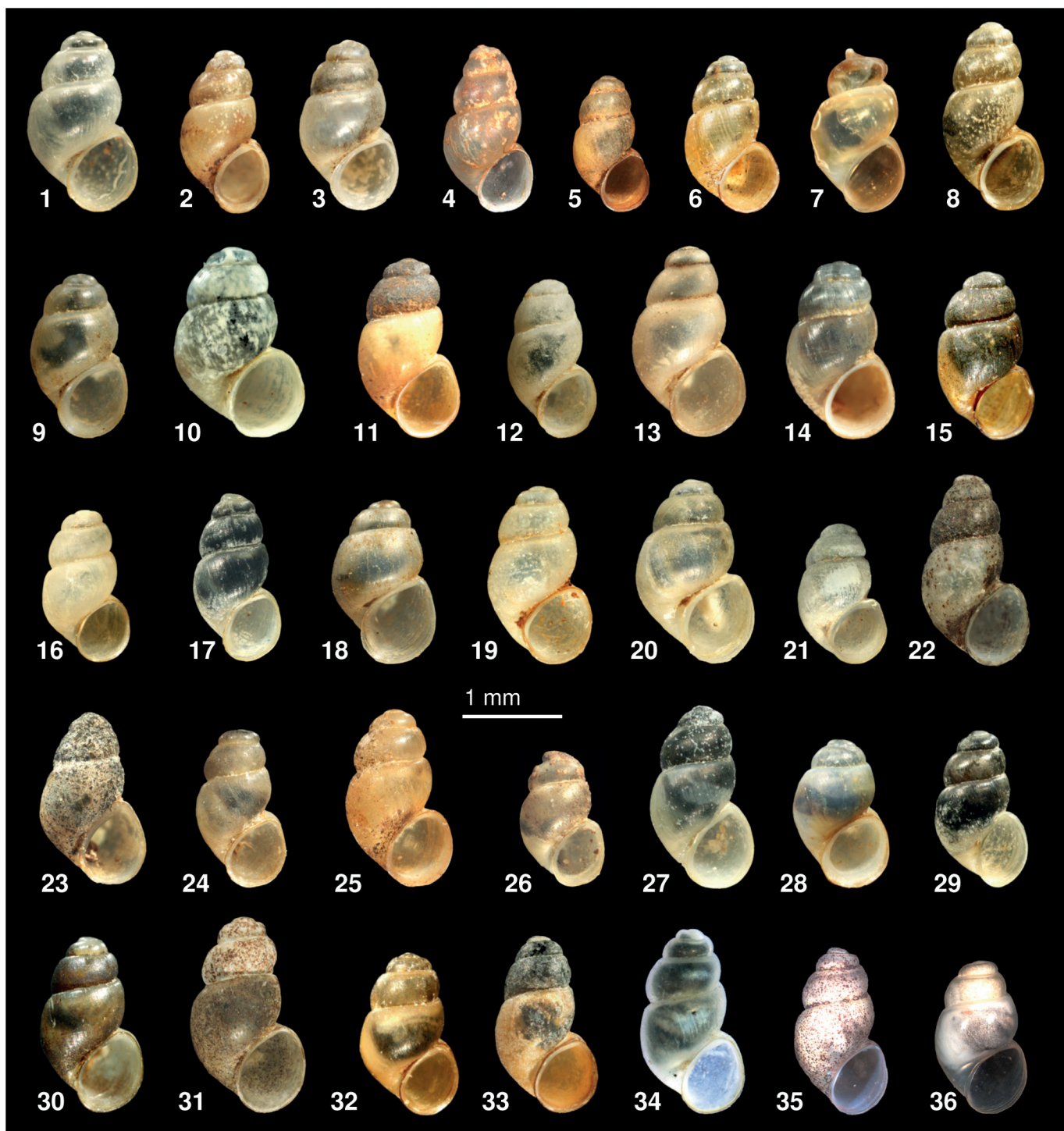


Figure 3. The shells of the *Bythinella* species of Greece (in alphabetical order). 1: *B. alexpeteri*, 2: *B. amira*, 3: *B. atypikos*, 4: *B. beckmanni*, 5: *B. charpentieri*, 6: *B. charpentieri cabirius*, 7: *B. corrosa*, 8: *B. cretensis*, 9: *B. dimitrosensis*, 10: *B. eleousae*, 11: *B. ellinikae*, 12: *B. jozefgregoi*, 13: *B. kambosensis*, 14: *B. kastaliae*, 15: *B. kastanolongosensis*, 16: *B. kithiraensis*, 17: *B. klimaensis*, 18: *B. konstadinensis*, 19: *B. kosensis*, 20: *B. kwanti*, 21: *B. kyriaki*, 22: *B. liandinaensis*, 23: *B. olymbosensis*, 24: *B. perivoliensis*, 25: *B. pesici*, 26: *B. petrosensis*, 27: *B. rachonica*, 28: *B. reischuetzi*, 29: *B. rethymnonensis*, 30: *B. reuselaarsi*, 31: *B. righaensis*, 32: *B. sitiensis*, 33: *B. taygetensis*, 34: *B. walensae* (after Falmiowski *et al.* 2016), 35: *B. lilaia* n. sp., 36: *B. palmosi* n. sp.

***Bythinella charpentieri* (Roth, 1855) – Figs 3.5, 4.5**

1855 *Amnicola Charpentieri* Roth, p. 52 [*Malacozologische Blätter*, 2: 17-58].

1856 *Paludinella charpentieri* – Frauenfeld [Sitz.-Bericht., *Akad. Wiss. Wien*, 22: 575, Griechenland“].

1863 *Paludinella charpentieri* – Frauenfeld [Verh. Zool.-bot. Ges. Wien, 13: 204, “von Athen und dem Hymettus”].

1883 *Bythinella charpentieri* – O. Boettger, [Jb. 10: 338].

1885 *Bythinella charpentieri* – O. Boettger [Jb. 12: 198].

1889 *Hydrobia (Bythinella) charpentieri* – Martens [Arch. Naturgesch., 1: 179, 210].

1892 *Bythinella charpentieri parnassia* O. Boettger, 1892.

1967 *Bythinella (Bythinella) charpentieri* – Jaekel in *Illies: Limnofauna Europaea*: 129 [no. 406, Balkan].

2016 *Bythinella charpentieri* – Szarowska *et al.* [*Hydrobiologia*, 765: 225–243].

2020 *Bythinella charpentieri* – Glöer & Porfyrus [*Ecol. Montenegrina* 38: 144-146].

Type locality: “Attika [Athens]” [Hymettos].

Description: shell cylindrical ovate, 4 convex whorls, body whorl prominent; umbilicus slit-like; aperture elongated ovate, angled at the top; peristome slightly reflexed. H = 3.5 mm, W = 1.7 mm.

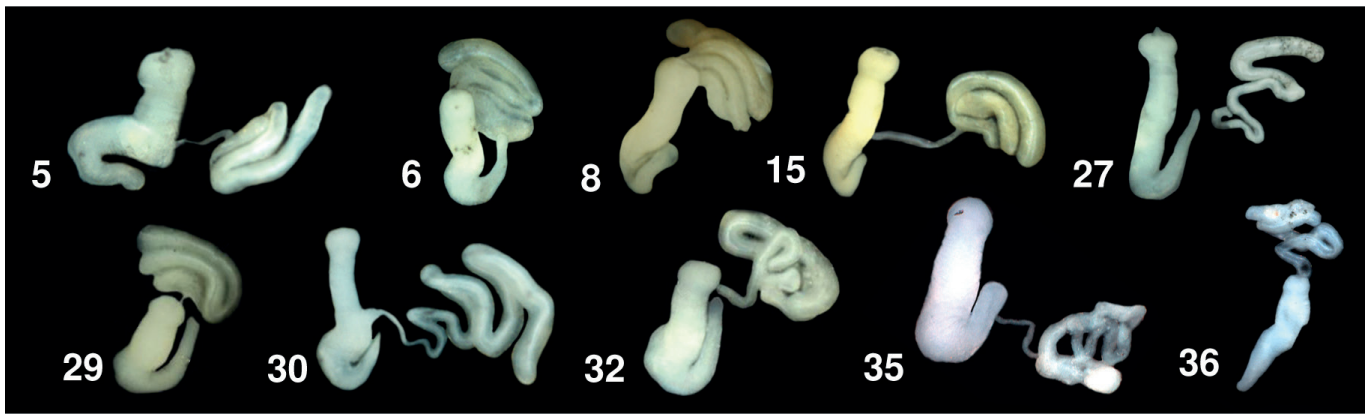


Figure 4. The penis morphologies known so far (numbers as in Figs 2, 3; different magnifications).

Anatomy: penis shorter than penial appendix, tubular gland very thin at proximal end and of same width along the distal part.

Distribution: known only from type locality.

Remark: Martens (1889) listed this species from “Korax-Gebirge” [Korakas (Κόρακας)] and Parnes in Attika and Karystos in southern Euboea, which are both far away from the type locality. Boettger (1885: 198) reported this species from Laconia, Elis, Achaia in Morea, Phthiotis and on Euboea as a “common species” but all these sites are far away from type locality. Szarowska *et al.* (2016) believe that the species Benke *et al.* (2011, their sample Kess from Kessariani) sequenced is *B. charpentieri*, though it was not collected at the type locality.

***Bythinella cabirius* P.L. Reischütz, 1988 – Figs 3.6, 4.6**

1988 *Bythinella charpentieri cabirius* P.L. Reischütz, p. 348 [Ann. Nat. Hist. Mus. Wien 90(B): 341-356].

Type locality: „Quelle an der Straße unterhalb von Palaiopolis, Samothrace“.

Description: shell elongated ovate, 4 slightly convex whorls with a deep suture; body whorl about two thirds of shell height; aperture ovate with sharp peristome, reflexed at the top and columella; umbilicus is slit-like. H = 2.5-2.7 mm, W = 1.2-1.3 mm.

Anatomy: penis shorter than penial appendix, tubular gland of same width over the full length.

Distribution: known only from Samothrace.

Remark: when Reischütz described this species it was believed, following Schütt (1980) that in this region only *B. charpentieri* occurs, but this was a wrong assessment, so there is no reason why it should be a subspecies of *B. charpentieri*.

***Bythinella corrosa* Glöer & Hirschfelder, 2020 – Fig. 3.7**

2020 *Bythinella corrosa* Glöer & Hirschfelder, p. 66, fig. 4 [Ecol. Montenegro 20: 10-23].

Type locality: Greece, Arcadia, Astros, spring 2.7 km south of Astros, below the main road to Leonidio on the bank of Limni Moustou, N 37°23'06.2" / E 22°44'36.5", 1 masl.

Description: shell with 3-3.5 tumid whorls, conical with the uppermost part of the embryonic whorl erected and detached; in some specimens two or more whorls detached with a corkscrew-like appearance; first whorls more or less strongly corroded; aperture ovate, sharp peristome; umbilicus closed. H = 1.8-2.6 mm, W = 1.3-1.5 mm.

Anatomy: unknown.

Distribution: known only from type locality.

Remark: all specimens are strongly corroded and more or less deformed. Out of more than 30 investigated specimens, no one showed a “normal” shape. The reason is unknown and could be due to parasitism or chemical influences. This species is the only one in Greece that lives at sea level.

***Bythinella cretensis* Schütt, 1980 – Figs 3.8, 4.8**

1889 *Hydrobia (Bythinella)* sp. Martens [Arch. Naturgesch., 55(1): 189 (Elos)].

1967 *Bythinella (Bythinella) badiella candiota* – Jaeckel in [Illies: Limnofauna Europaea].

1980 *Bythinella cretensis* Schütt, p. 130, pl. 10, fig 27 [Arch.Moll. 110: 115-149].

Type locality: “Insel Kreta: Quellbach in Mesa Potami, 25°31' N, 35°13' E, 900 m NN, 11.2-14.1 °C. [Remark: Schütt confused the coordinates N/E].

2011 Falniowski & Szarowska – *Bythinella cretensis* [Ann. Zool. Fennici, 48: 67-90].

2016 Szarowska *et al.* – *Bythinella cretensis* [Hydrobiologia 765:225-243].

Description: shell cylindrical with small apex, 4-4.5 slightly convex whorls with deep suture; body whorl prominent, especially in height; aperture ovate, narrowed at the top, with a peristome thickened at the columella; umbilicus slit-like to closed. H = 3.3 mm, W = 1.5-2.0 mm.

Anatomy: penis shorter than penial appendix, tubular gland regularly wide over the full length.

Distribution: known only from Crete.

Remark: the species Martens (1889) mentioned from Elos (Crete) could be sequenced by Falniowski as an unnamed *Bythinella*, *Bythinella (Bythinella) badiella candiota*, which Jaeckel listed in Fauna Europaea is a *Bithynia*. Szarowska *et al.* (2016) supported the idea that the species Benke *et al.* (2011, their sample Epis from Asigonia, road towards Episkopi) sequenced is *B. cretensis*, though it was not collected at the type locality.

***Bythinella dimitrosensis* Glöer & Reuselaars, 2020 – Fig. 3.9**

2020 *Bythinella dimitrosensis* Glöer & Reuselaars, p. 29, fig. 2.12 [Ecol. Montenegro 29: 20-33].

Type locality: spring of Aghios Dimitrios, island of Evia, Greece at 330 m altitude, 38° 06' 29.05401" N 24° 26' 12.21897" E.

Description: ovate shell with 4.5 slightly convex whorls, separated by a clear suture; apex pointed, aperture oblique ovate, angled at the top; peristome thickened at the columella; umbilicus closed; body whorl 0.77 of shell height. H = 2.4-2.7 mm, W = 1.5-1.7 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella eleousae* Glöer & Hirschfelder, 2020 – Fig. 3.10**

2020 *Bythinella eleousae* Glöer & Hirschfelder, p. 63, fig. 2.1 [Ecol. Montenegro 30: 60-67].

Type locality: Phocis, Parnassus Mountains, Polidrosos, Kifisou Spring at the ruins of the Byzantine church Agia Eleousa, 1.5 km SW of Polidrosos, N 38°37'45.1" E 22°31'12.4", 311 masl.

Description: cylindrical shell with a flat apex and relatively broad, 4.5-5 whorls slightly convex with a clear suture; body whorl about 0.75 of shell height; aperture ovate with sharp peristome; umbilicus slit-like. H = 2.8-3.1 mm, W = 1.8-1.9 mm broad.

Anatomy: unknown.

Distribution: known only from type locality on the northern slope of the Parnassos Mountains.

***Bythinella ellinikae* Glöer & Hirschfelder, 2020 – Fig. 3.11**

2020 *Bythinella ellinikae* Glöer & Hirschfelder, p. 64, fig. 2.6 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Laconia, Peloponnese, spring along the road from Xifias to Elliniko, 400 m east of Elliniko, N 36°36'35.0" E 22°59'15.3", 500 masl.

Description: cylindrical shell with small apex and 4.5-5 convex whorls with deep suture; body whorl about 0.6 of shell height; aperture ovate, slightly angled at the top with sharp peristome; umbilicus closed. H = 2.7-2.9 mm, W = 1.6-1.7 mm broad.

Anatomy: unknown.

Distribution: known only from type locality in southern Peloponnese.

***Bythinella jozefgregoi* Glöer & Reuselaars, 2020 – Fig. 3.12**

2020 *Bythinella gregoi* Glöer & Reuselaars (homonym), p. 26, fig. 2.2 [*Ecol. Montenegrina* 29: 20-33].

2020 *Bythinella jozefgregoi* Glöer & Reuselaars, p. 26, fig. 2.2 [*Ecol. Montenegrina* 29: 40].

Type locality: spring SW of Anthousa, Greece, at 1,000 masl, 39° 39' 31.97786" N 21° 12' 27.76905" E.

Description: slim ovate shell with slightly convex 4-4.5 whorls with clear suture; aperture ovate, slightly angled at the top; peristome thickened at the columella; umbilicus slit-like. H = 2.4-2.7 mm, W = 1.4-1.5 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella kambosensis* Glöer & Hirschfelder, 2020 – Fig. 3.13**

2020 *Bythinella kambosensis* Glöer & Hirschfelder, p. 64, fig. 2.4 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Messenia, western slope of the Taygetos Mountains, spring along the road between Akrogiali and Kambos, about 2.5 km from the turnoff from the coastal road, N 36°56'56.0" E 22°10'00.8", 222 masl.

Description: slightly conical ovate shell with small apex, 4.5-5 slightly convex whorls with clear suture; body whorl about 0.75 of shell height; aperture ovate, slightly angled at the top, peristome sharp; umbilicus closed. H = 2.7-3.0 mm, W = 1.7-1.8 mm.

Anatomy: unknown.

Distribution: known only from type locality on the western slope of the Taygetos Mountains.

***Bythinella kastaliae* Glöer & Hirschfelder, 2020 – Fig. 3.14**

2020 *Bythinella kastaliae* Glöer & Hirschfelder, p. 63, fig. 2.2 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Phocis, Delphi, Kastalia Spring, N 38°28'58.8" / E 22°30'19.1", 530 masl.

Description: ovate cylindrical shell with small and flat apex; 4.5-5 convex whorls with deep suture; body whorl about 0.7 of shell height; ovate aperture slightly angled at the top; peristome sharp, somewhat thickened at the columella; umbilicus closed. H = 2.5-2.8 mm, W = 1.6-1.7 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella kastanolongosensis* Glöer & Pešić, 2020 – Figs 3.15, 4.15**

2020 *Bythinella kastanolongosensis* Glöer & Pešić, p. 2, figs 6-8 [*Ecol. Montenegrina* 36: 1-5].

Type locality: "Greece, Evia Island, the region of Mount Ochi, Kastanolongos, helocrenic spring, 38°3'8.72"N, 24°28'15.83"E.

Description: shell cylindrical with 4.5 slightly convex whorls with a deep suture; body whorl with straight vertical tangent line; ovate aperture slightly angled at the top; peristome sharp with brown periostracum; umbilicus closed. H = 2.8-3.1 mm, W = 1.8-1.9 mm.

Anatomy: the penis is much shorter than the penial appendix, tubular gland thin at proximal end, broader at distal part, with four half-loops.

Distribution: Greece; only known from the type locality in the southern part of the island of Evia.

***Bythinella kithiraensis* Glöer & Hirschfelder, 2020 – Fig. 3.16**

2020 *Bythinella kithiraensis* Glöer & Hirschfelder, p. 65, fig. 2.8 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Kithira Island, Mylopotamos, "Valley of the Mills", tiny spring beside the big waterfall, N 36°14'38.8" / E 22°56'42.0", 275 masl.

Description: cylindrical shell with small and broad flat apex, 4.5-5 convex whorls with deep suture; body whorl about 0.6 of shell height; aperture ovate with sharp peristome; umbilicus closed. H = 2.2-2.5 mm, W = 1.3-1.4 mm.

Anatomy: unknown.

Distribution: known only from type locality.

Remarks: this species was not found in the big spring in the center of Mylopotamos.

***Bythinella klimaensis* Glöer & Reuselaars, 2020 – Fig. 3.17**

2020 *Bythinella klimaensis* Glöer & Reuselaars, p. 26, fig. 2.4 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring in Klima, Aetolia, south of lake Trichonida, Greece at 625 masl, 38° 28' 09.57291" N 21° 28' 54.52199" E.

Description: shell elongated ovate with 4.5-5 slightly convex whorls with deep suture, apex oblique; aperture ovate, slightly angled at the top; peristome broadened at the columella; umbilicus closed; body whorl 0.7 of shell height. H = 2.6-3.4 mm, W = 1.7-1.9 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella konstadinensis* Glöer & Reuselaars, 2020 – Fig. 3.18**

2020 *Bythinella konstadinensis* Glöer & Reuselaars, p. 29, fig. 2.10 [*Ecol. Montenegrina* 29: 20-33].

Type locality: Monia Konstadinou en Elenis, 2 km E of Kosmadei, Samos Isl., Greece at 313 masl (Figure 11), 37° 45.76320' N 26° 40.93519' E.

Description: ovate shell with 4.5-5 slightly convex whorls, separated by deep suture; aperture ovate, slightly angled at the top; peristome sharp; umbilicus closed; body whorl 0.8 of shell height. H = 2.5-2.7 mm, W = 1.7-1.9 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella kosensis* Schütt, 1980 – Fig. 3.19**

1889 *Hydrobia* (*Bythinella*) sp. – Martens, [*Arch. Naturgesch.*, 55: 200]

1980 *Bythinella kosensis* Schütt, p. 131, pl. 10, fig. 28 [*Arch. Moll.* 110: 115-149]

Type locality: „Insel Kos, Quellrinnal oberhalb Agios Dimitrios, 400 m NN, 14.6°C“

Description: shell yellowish, cylindrical conical with slightly convex whorls separated by a deep suture; apex small and blunt;

aperture ovate, somewhat reflexed at the columella; umbilicus closed; the shell is 2.3 mm high and 1.5 mm broad.

Anatomy: unknown.

Distribution: Kos, Chios, Ikaria (Nikaria), Petroupolis (Schütt 1980).

***Bythinella kwanti* Glöer & Reuselaars, 2020 – Fig. 3.20**

2020 *Bythinella kwanti* Glöer & Reuselaars, p. 27, fig. 2.7 [*Ecol. Montenegrina* 29: 20-33].

Type locality: Planitero, south of Kalavrita, NW Peloponnese, Greece at 495 masl altitude, 37° 55' 59.61717" N 22° 09' 45.61220" E.

Description: ovate shell with 4.5-5 slightly convex whorls with a deep suture; aperture ovate, slightly angled at the top; peristome broadened at the columella; umbilicus slit-like; body whorl 0.76 of shell height. H = 2.6-2.9 mm, W = 1.7-1.8 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella kyriaki* Glöer & Reuselaars, 2020 – Fig. 3.21**

2020 *Bythinella kyriaki* Glöer & Reuselaars, p. 21, fig. 2.1 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring 2 km of monastery Kapina, Epirus, Greece at 620 masl, 39° 34' 01.13475" N 21° 07' 19.90862" E

Description: shell ovate with 4-4.5 slightly convex whorls with deep suture; aperture broad ovate to circular angled at the top; peristome slightly reflexed at the columella; umbilicus closed; body whorl 0.7 of shell height, H = 2.2-2.3 mm, W = 1.4-1.5 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella liandinaensis* Glöer & Reuselaars, 2020 – Fig. 3.22**

2020 *Bythinella liandinaensis* Glöer & Reuselaars, p. 28, fig. 2.9 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring between Liandina and Vasiliki, Peloponnese, Greece, at 70 masl, 36° 54' 42.86614" N 22° 26' 33.74825" E.

Description: shell elongated ovate, 4.5-5 slightly convex whorls separated by a deep suture; ovate aperture slightly angled at the top, peristome sharp; umbilicus slit-like; body whorl 0.67 of shell height. H = 2.4-3.0 mm, W = 1.4-1.6 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella olymbosensis* Glöer & Reuselaars, 2020 – Fig. 3.23**

2020 *Bythinella olymbosensis* Glöer & Reuselaars, p. 29, fig. 2.11 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring at Olymbos mountain, about 3 km before the top, south Lesvos island, Greece at 804 masl, 39° 04.15127' N 26° 21.01430' E.

Description: ovate conical shell with 4.5-5 slightly convex whorls with a clear suture; aperture ovate slightly angled at the top, peristome thickened at the columella; umbilicus closed. H = 2.1-2.6 mm, W = 1.4-1.7 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella perivoliensis* Glöer & Reuselaars, 2020 – Fig. 3.24**

2020 *Bythinella radomani* Glöer & Reuselaars (homonym) [*Ecol. Montenegrina* 29: 20-33].

2020 *Bythinella perivoliensis* Glöer & Reuselaars, p. 27, fig. 2.6 [*Ecol. Montenegrina* 31: 45].

Type locality: spring between Kokinochori and Perivoli, Fokidha, Greece at 785 masl, 38° 30' 24.98346" N 22° 01' 16.56789" E.

Description: shell slim ovate with 4.5-5 convex whorls with a deep suture; aperture ovate slightly angled at the top, peristome broadened at the columella; umbilicus closed; body whorl 0.7 of shell height. H = 2.5-2.8 mm, W = 1.5-1.7 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella pesici* Glöer & Reuselaars, 2020 – Fig. 3.25**

2020 *Bythinella pesici* Glöer & Reuselaars, p. 26, fig. 2.3 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring north of Klima, Aetolia, Greece (south of lake Trichonida) at 660 masl.

Description: ovate shell with 4-4.5 convex whorls with deep suture; aperture ovate, peristome somewhat broadened at the columella; umbilicus closed; body whorl 0.75 of shell height. H = 2.3-2.8 mm, W = 1.5-1.7 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella petrosensis* Glöer & Reuselaars, 2020 – Fig. 3.26**

2020 *Bythinella petrosensis* Glöer & Reuselaars, p. 28, fig. 2.8 [*Ecol. Montenegrina* 29: 20-33].

Type locality: spring 5-6 km SE of Aghios Petros, Parnon mountains, Peloponnese, Greece at 1,105 masl, 37° 17' 36.115787" N 22° 35' 30.35337" E.

Description: shell elongated ovate with 3-4.5 convex whorls with a deep suture; aperture ovate, peristome thickened at the columella; umbilicus closed; body whorl 0.8 of shell height. H = 2.0-2.2 mm, W = 1.3 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella rachonica* Georgiev & Glöer, 2020 – Figs 3.27, 4.27**

2020 *Bythinella rachonica* Georgiev & Glöer, p. 135, figs 2, 22-25. [*Ecol. Montenegrina* 35: 129-137].

Type locality: "Greece, Thassos Island, North Aegean, a big spring in the yard of the church of Rachoni village, N40 45 29.6 E24 38 17.3, 107 masl".

Description: cylindrical shell with 4.5 slightly convex whorls with a deep suture; apex obtuse; aperture ovate, peristome sharply angled at the top; umbilicus closed. H = 2.9-3.1 mm, W = 1.8 mm.

Anatomy: penial appendix twice longer than the penis, tubular gland medium-sized, with 5 half loops, tapering from distal to proximal part.

Distribution: only known from type locality.

***Bythinella reischuetzi* Georgiev & Glöer, 2020 – Fig. 3.28**

2020 *Bythinella reischuetzi* Georgiev & Glöer, p. 134, Figs. 2, 18-21 [*Ecol. Montenegrina* 35: 129-137].

Type locality: "Greece, Párnis (Mountain) in Parnitha National Park"

Description: shell ovate, thick-walled with 4-4.5 slightly convex whorls, with clear suture, first whorl in a plane; aperture ovate with a slight angle at the top, peristome thickened at the columella; umbilicus closed. H = 2.5 mm, W = 1.7 mm.

Anatomy: unknown.

Distribution: only known from type locality.

***Bythinella rethymnonensis* Glöer & Hirschfelder, 2020 – Figs 3.29, 4.29**

2020 *Bythinella rethymnonensis* Glöer & Hirschfelder, p. 7 [*Ecol. Montenegrina* 28: 7].

2019 *Bythinella magdalenae* Glöer & Hirschfelder (preocc.), p. 16, figs 20-24 [*Ecologica Montenegrina* 20: 10-23].

Type locality: "Crete, Nómoos Réthymnon, Argiróupoli (14 km SW of Réthymnon), captured spring below the "Church of the Holy Five Virgins", 35°17'35.2" N, 24°20'33.0" E, alt. 195 masl".

Description: shell cylindrical with a small apex, 4-4.5 slightly convex whorls with a deep suture; aperture ovate narrowed at the top, peristome sharp; umbilicus slit-like. H = 2.7-2.9 mm, W = 1.7-1.8 mm.

Anatomy: the penis as long as the penial appendix. The tubular gland has the same width over the full length.

Distribution: central part of Crete.

***Bythinella reuselaarsi* Glöer & Pešić, 2020 – Figs 3. 30, 4.30**
2020 *Bythinella reuselaarsi* Glöer & Pešić, p. 4, figs 9-10 [*Ecol. Montenegrina* 36: 1-5].

Type locality: “Greece, Evia Island, the region of Mount Ochi, limnocrone spring within Platanus grove along the road, near Melissonas village, 38°5’26.43”N, 24°23’54.97”E”.

Description: shell elongated ovate-cylindrical with 4.5 slightly convex whorls with a deep suture; aperture ovate somewhat oblique, peristome sharp; umbilicus closed. H = 3.1 mm, W = 1.9 mm.

Anatomy: penis is much shorter than the penial appendix. The tubular gland is thin at the proximal end and broad at the distal end, with six half-loops.

Distribution: only known from type locality.

***Bythinella righaensis* Glöer & Reuselaars, 2020 – Fig. 3.31**
2020 *Bythinella righaensis* Glöer & Reuselaars, p. 27, fig. 2.5 [*Ecol. Montenegrina* 29: 20-33].

Type locality: Spring in Righani, north of Nafpaktos, Aetolia, Greece at 565 masl, 38° 28’ 56.07778” N 21° 46’ 05.08430” E.

Description: elongated ovate shell with 4.5-5 convex whorls with deep suture; aperture ovate, peristome somewhat thickened at the columella; umbilicus closed; body whorl 0.7 of shell height. H = 3.1 mm, W = 1.8 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella sitiensis* Glöer & Hirschfelder, 2019 – Figs 3.32, 4.32**

2019 *Bythinella sitiensis* Glöer & Hirschfelder, p. 16, figs 25-28 [*Ecol. Montenegrina* 20: 10-23].

Type locality: “Crete, Nómos Lasíthi, fountain in Zou, 6 km south of Sitía, 35°09’15.7” N, 26°06’31.5” E, alt. 181 masl”.

Description: shell cylindrical with small apex, 4-4.5 whorls slightly convex with a deep suture; aperture is ovate, narrowed at the top, peristome thickened at the columella; umbilicus closed. H = 2.5 mm, W = 1.5-1.7 mm.

Anatomy: penis as long as the penial appendix, tubular gland becomes thicker at the distal end.

Distribution: only known from type locality.

***Bythinella taygetensis* Glöer & Hirschfelder, 2020 – Fig. 3.33**
2020 *Bythinella taygetensis* Glöer & Hirschfelder, p. 63, fig. 2.3 [*Ecol. Montenegrina* 30: 60-67].

Type locality: Greece, Laconia, eastern slope of Taygetos Mountains, Anavriti, spring at the southern edge of the village, N 37°01’48.1” / E 22°22’10.8”, 890 masl.

Description: shell elongated cylindrical, 4.5-5 slightly convex whorls with a clear suture, body whorl about 0.7 of shell height; aperture ovate, angled at the top, peristome sharp with a brown border; umbilicus closed. H = 2.4-2.9 mm, W = 1.4-1.6 mm.

Anatomy: unknown.

Distribution: known only from type locality.

***Bythinella walensae* Falniowski, Hofman & Rysiewska, 2016 – Fig. 3.34**

2016 *Bythinella walensae* Falniowski, Hofman & Rysiewska, p. 186, figs. 2-20, [*Folia Malacol.* 24: 185-192].

Type locality: “spring Aria (Aria Pygi), 37°02’11.1”N, 25°29’37.8”E”

Description: cylindrical shell with 4.5 regularly growing convex whorls with a deep suture, apex small and blunt. H = 3.2 mm, W = 1.6 mm broad.

Anatomy: penis as long as the penial appendix.

Distribution: known only from type locality.

***Bythinella lilaia* n. sp. – Figs 3.35, 4.35 & 5**

Type locality: Spring close to Lilaia (Λιλαία) village, NW foothills of Parnassos mountain / Greece. Coordinates: 8.6407, 22.4922. Collection date; July 3rd, 2021. The spring water covers a relatively big area, forming a small pool where the species is quite abundant.

Type Materials: Holotype: H = 3.3 mm, W = 1.9 mm, ZMH 140899. Paratypes: 3 specimens ZMH 140900, 3 specimens coll. Glöer.

Etymology: named after the village Lilaia, closest to the type locality.

Description: the shell is elongated-ovate with a moderately deep suture. The apex is small. The 4.5 whorls are slightly convex. The aperture is ovate with a rounded angle at the top. The umbilicus is closed. The shell is 3.3 mm high and 1.8 mm broad.

Anatomy: penial appendix twice longer than the penis, tubular gland thin at the proximal end and thickened at the distal end, about 6 half loops.

Distribution: only known from type locality.

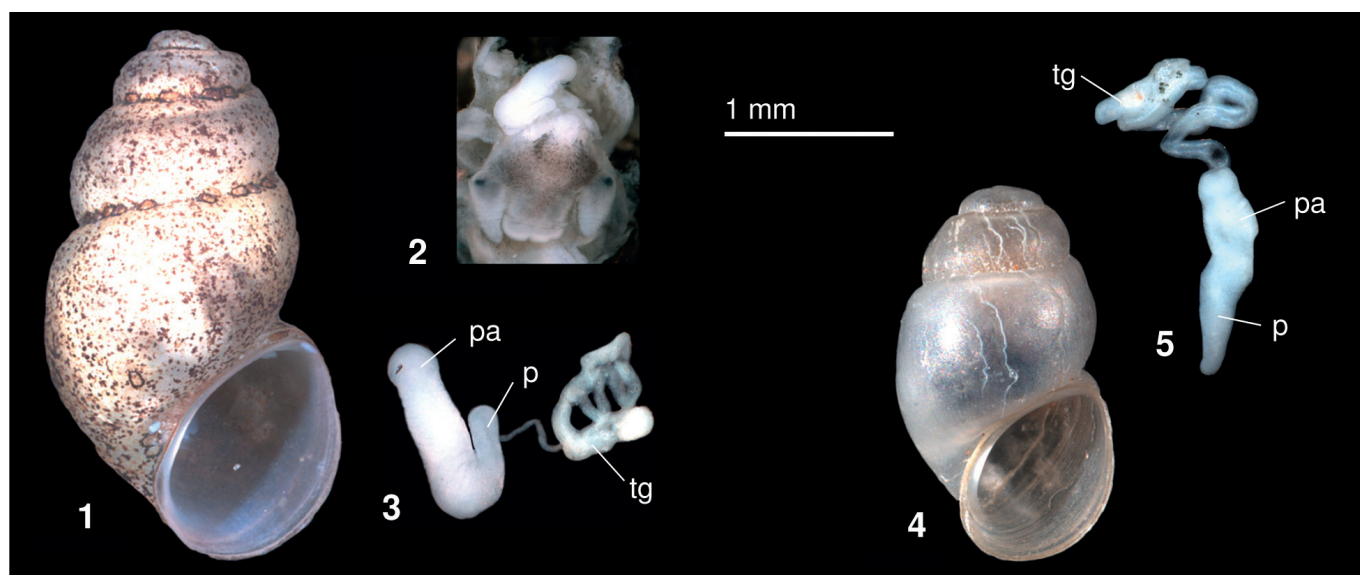


Figure 5. The new species *Bythinella lilaia* n. sp. (5-1 to 5-3) and *Bythinella palmosi* n. sp. (5-4 to 5-5). 1,4: shell; 2: animal; 3,5: male sex tract. *p*: penis; *pa*: penial appendix; *tg*: tubular gland.

***Bythinella palmosi* n. sp.** – Figs 3.36, 4.36, 5

Type locality: Kerasia spring in Syvros village, Lefkada isl. / Greece. Coordinates. 38.6710, 20.6503. Collection date: August 22nd, 2021.

Type Materials: Holotype: H = 2.4 mm, W = 1.5 mm, ZMH 140897. Paratypes: 3 specimens ZMH 140898, 3 specimens coll. Glöer.

Etymology: named after the friend of the second author, George Palmos, who has passed away.

Description: the shell is ovate with a moderately deep suture. The apex is very small and blunt. The 4 whorls are slightly convex. The aperture is ovate with a rounded angle at the top. The umbilicus is closed. The shell is 2.3 mm high and 1.4 mm broad.

Anatomy: penial appendix as long as the penis, tubular gland regularly thick over the full length, with about 5 half loops.

Distribution: only known from type locality, but it is quite likely that the species also occurs in some other springs around Syvros village (apart from Kerasia spring, nine more springs are located in the surrounding area).

Discussion

If we compare neighboring species (e.g. *B. cretensis*/*B. sitiensis* or *B. jozefgregori*/*B. kyraki*) they have a lower similarity (Figure 1), while species which live far away from each other have a higher



Figure 6. Type locality of *Bythinella lilaia* n. sp.



Figure 7. Type locality of *Bythinella palmosi* n. sp.

similarity (e.g. *B. alexpeteri*/*B. atypikos*). This is possibly due to different migration events.

Formerly it was believed that the species diversity of the genus *Bythinella* decreases from west to east in Europe (Glöer & Georgiev, 2011), but at present there are 13 species known from Romania, 23 from Bulgaria, and 35 from Greece (altogether, 71 species in this part of Europe) versus 52 species in France. Thus, such a gradient of species richness is not evident anymore.

While Wilke *et al.* (2010) and Benke *et al.* (2011) could only work with a few species from Greece, Szarowska *et al.* (2016) found by DNA-sequencing (COI) 16 clades, especially on the islands of the Aegean Sea. On mainland Greece and Peloponnese, the clades have a wider distribution. The first clades are about 5 Mya old, and the youngest 1.1 Mya, with colonization and re-colonization events. Spreading has possibly taken place by birds which fly from spring to spring. It is known that gastropods can survive the passage through the digestive track of some animals, but this seems to be irrelevant (Malone, 1965; Leeuwen *et al.*, 2012). It is more plausible a transport of snails which glue on feet or in the feathering of birds. Purchon (1977) reported on birds which actively take snails between their feathers for provisions for journey. Prosobranch snails like *Bythinella* can close their shells with an operculum to hinder desiccation over a longer time than the journey itself. Such transport with birds as vectors works also over long distances (Haase, 2010).

If the number of known *Bythinella* species in the European countries actually reflects its real diversity or if it is a result of thoroughness of investigations, this can still be questioned. Maybe DNA-sequencing of more *Bythinella* species and populations from Greece will give us more insights in this genus, and help reveal their true degree of diversity in this territory.

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