ISIMEROPÉ, A NEW GENUS OF HYDROBIIDAE (CAENOCASTROPODA: RISSOIDEA) FROM GREECE

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ABSTRACT

Isimerope semele n. gen. and n. sp., a valvatiform hydrobiid from southern continental Greece, is described based on morphological and molecular data. Isimerope is distinguished from other European and circum-Mediterranean valvatiform hydrobiid genera by a unique combination of morphological characters, including distinctive male and female genitalia. Isimerope is differentiated from morphologically similar Graecoarganiella, which is also endemic to Greece, by a 10.15% mean COI sequence divergence. Isimerope semele is composed of three small populations living in disturbed habitats, including springs and a river.

INTRODUCTION

The hydrobiid fauna of Europe is particularly rich in valvatiform species (Bodon, Manganelli & Giusti, 2001), but their anatomical study is challenging because of their minute size (Arconada & Ramos, 2006). During the last few decades many new valvatiform taxa have been described from the Mediterranean region, including France (e.g. Bodon et al., 2001), Italy (e.g. Bodon & Giusti, 1986; Bodon et al., 1995; Manganelli et al., 1998), Spain (e.g. Ramos et al., 2000; Arconada & Ramos, 2001, 2002, 2006, 2007; Arconada et al., 2007), Israel (e.g. Schütz, 1991), Turkey (e.g. Schütz & Şeng, 1989) and the Balkan Peninsula (e.g. Radoman, 1966, 1983).

Seven valvatiform or valvatiform-planispiral genera (Daphniola Radoman, 1973, Fissuria Boeters, 1981, Graecoarganiella Falniowski & Szarowska, 2011a, Hauffenia Pollonera, 1898, Islamia Radoman, 1973, Prespolitorea Radoman, 1983 and Pseudoslania Radoman, 1979) and thirteen species have been recorded so far from Greece (Reischuëtz, 1988; Reischuëtz & Reischuëtz, 2004; Bank, 2006; Radea, 2011; Falniowski & Szarowska, 2011a). Most of these taxa are crenobionts and a high percentage (42.8% of the genera, 92.3% of the species) is endemic to this country (Gittenberger, 1982; Radoman, 1985; Reischuëtz, 1988; Falniowski & Szarowska, 2000, 2011a, 2011b; Reischuëtz & Reischuëtz, 2004; Radea, 2011).

In 2012, we surveyed 25 localities across Greece for hydrobiids, within the framework of the research project ‘Species on the brink of extinction’, which was designed to assess the conservation status of hydrobiids that were classified as threatened in Greece (IUCN, 2012). Here we describe a new genus and a new species of a valvatiform hydrobiid gastropod that was collected from three localities in south continental Greece during the course of this survey.

MATERIAL AND METHODS

Specimens of the new taxon were collected from Megali Vrysi (stream), ‘Second Spring’ (spring) and Piana (river) in Peloponnësos (Fig. 1). Snails were collected by hand from stones, gravel and dead leaves and transported alive to the laboratory.

For each population two specimens of each sex were dissected and studied anatomically. Before dissection, the shell of each specimen was removed by soaking in Perenny solution. External morphology was photographed using a Canon EOS 1000D camera attached to a stereomicroscope (Stemi 2000-C, Zeiss, Germany). Radulae and opercula were cleaned with KOH solution (5 g/l) at room temperature, rinsed in distilled water and air-dried before being mounted on stubs and spray-coated in gold–palladium. The protoconch, operculum and radula were studied using scanning electron microscopy (SEM; JEOL JSM–35 operating at 25 kV). Morphological terminology follows that of Hershler & Ponder (1998).

Only a few specimens were collected from each locality (i.e. 9 specimens from Megali Vrysi, 12 from ‘Second Spring’ and 10 from Piana) owing to the small size of the populations. The
collected material was deposited in the Zoological Museum of the University of Athens (ZMUA) and the personal collection of C. Radea.

DNA extraction, amplification and sequencing

The entire animal was used for genomic DNA isolation. Details of the specimens used in the molecular analyses are provided in Table 1. DNA was extracted using the PureLink Genomic DNA mini kit (Invitrogen) following the manufacturers’ protocol. A fragment of the mitochondrial gene cytochrome oxidase subunit I (COI) was amplified from each specimen using the universal primers LCO1490 and HCO2198 (Folmer et al., 1994). PCR was performed in a 25 μl volume, in which 1–2 μl of template DNA was mixed with 0.2 mM dNTPs, 0.4 mM of each primer and 0.5 units of Taq polymerase. The concentration of the MgCl₂ was 3.5 mM. Thermocycling was performed in a MyCycler (Biorad) thermocycler. The cycle program comprised an initial denaturation step at 95°C for 3 min, followed by 40 cycles of 15 s at 95°C, 1 min at 42°C, and 1.5 min at 72°C. The cycling was ended with 10 min extension at 72°C.

Sequence alignment and genetic data analysis

The newly generated sequences were viewed and edited using CodonCode Aligner v. 2.06 (GeneCodes Corporation). The authenticity of the mtDNA sequences and the homology with the targeted mitochondrial gene were evaluated by a BLAST search in the NCBI genetic database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The genetic distances separating individual or grouped sequences were calculated using MEGA5 (Tamura et al., 2011) implementing the Kimura 2-parameter (K2P) model (Kimura, 1980) of nucleotide substitution. We chose this model because it is one of the most frequently used in pairwise comparisons of taxa. Variable and parsimony-informative sites were estimated with MEGA5. We also included in our analyses COI sequences from other valvatiform genera. Sequences were aligned with CodonCode Aligner v. 2.06. Bayesian phylogenetic analysis was performed using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003). Bythinella australis was used as the outgroup. Modeltest v. 3.7 (Posada & Crandall, 1998) and the Akaike Information Criterion (Akaike, 1974) were used to select the appropriate substitution model. During the MrBayes analysis model, parameter values were treated as unknown and were estimated during the run. The number of generations was set to 2 × 10⁶ and two independent runs were performed simultaneously. In each run four chains were involved. The average standard deviation of split frequencies of the two simultaneous and independent runs was used to determine the stationarity point of likelihoods (see MrBayes v. 3.1.2 manual). According to this index, stationarity in the analyses was achieved well before 0.25 × 10⁶ generations. A tree was sampled every 100th generation and, consequently, the summary of the Bayesian analysis relied on 4 × 10⁵ samples (sum of two runs). From each run 15001 samples were used, while 4999 were discarded as burn-in. From the remaining 30002 trees (sum of two runs), a 50% majority-rule consensus tree was constructed. Support for the nodes was assessed by posterior probabilities.

We also compared the COI sequences of the new taxon with those of hydrobiid species deposited in GenBank that exhibited high levels of similarity based on a blast homology search.

SYSTEMATIC DESCRIPTION

Family HYDROBIIDAE Troschel, 1857

Isimerope Radea & Parmakelis, new genus

Type species: Isimerope semele new species, by original designation.

Etymology: The generic name was derived from Greek mythology: the first element Ισί (Ιση in Greek), is an adjective meaning ‘equivalent’, and the second, Μερόπη (Μερόπη in Greek), is the name of one of the seven Pleiades, daughters of Atlas and Pleione. Gender feminine.

Diagnosis: Shell minute (maximum height 1.55 mm, maximum width 2.00 mm), dextral, valvatiform; operculum without peg; central tooth trapezoidal with one basal cusp on each side; ctenidium absent; penis with narrow lobe along inner edge (at 2/5 of its length), distal section swollen, pigmented black; bursa copulatrix pyriform, positioned posterior to albumen gland; renal oviduct well-developed and coiled in an M shape; seminal receptacle absent.

Referred species: Isimerope semele n. sp., described below.

Isimerope semele Radea & Parmakelis, new species

(Figs 2–7)

Table 1. Species, families (according to Wilke et al., 2013), locality details, GenBank accession numbers and publication references for COI sequences used in the phylogenetic analysis of this study.

<table>
<thead>
<tr>
<th>Species, families</th>
<th>Country</th>
<th>Sampling locality</th>
<th>GenBank accession number</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bythinella austriaca (Frauenfeld, 1857)</td>
<td>Poland</td>
<td>Mlynik spring, Ojców National Park</td>
<td>FJ545132</td>
<td>Falniowski, Szarowska &amp; Sirbu (2009)</td>
</tr>
<tr>
<td>Daphniola exigua (A. Schmidt, 1856)</td>
<td>Greece</td>
<td>Two springs close to the railway station Ag. Paraskevi</td>
<td>EU047765</td>
<td>Falniowski, Szarowska &amp; Grzmił (2007)</td>
</tr>
<tr>
<td>Daphniola graeca Radoman, 1973</td>
<td>Greece</td>
<td>Daphne spring about 30 km north of Larissa</td>
<td>EU047763</td>
<td>Falniowski et al. (2007)</td>
</tr>
<tr>
<td>Graecoarganiella parmatisiana Falniowski &amp; Szarowska, 2011</td>
<td>Greece</td>
<td>Mainalo Mt., WSW of Piana, NW of Tripolis, Peloponnisos, cistem and spring</td>
<td>JN202348-52</td>
<td>Falniowski &amp; Szarowska (2011a)</td>
</tr>
<tr>
<td>Graecoarganiella sp.</td>
<td>Greece</td>
<td>Mainalo Mt., WSW of Piana, NW of Tripolis, Peloponnisos, cistem and spring</td>
<td>JN202353-54</td>
<td>Falniowski &amp; Szarowska (2011a)</td>
</tr>
<tr>
<td>Hauffenia sp.</td>
<td>Slovakia</td>
<td>Patřovická spring, Gemesna Hôrka</td>
<td>EF070614</td>
<td>Szarowska (2006)</td>
</tr>
<tr>
<td>Hauffenia sp. 1</td>
<td>Slovakia</td>
<td>Kunova Teplica</td>
<td>JF313940</td>
<td>Štefek et al. (2011)</td>
</tr>
<tr>
<td>Hauffenia tellinii Pollonera, 1898</td>
<td>Italy</td>
<td>Friuli, Venetia Julia, Gorizia, Isonzo River, near Sagrado, spring</td>
<td>AF387640</td>
<td>Wilke et al. (2001)</td>
</tr>
<tr>
<td>Horatia strumi</td>
<td>Spain</td>
<td>Cadiz province, Zahara, Puente de Los Palominos Creek (1487)</td>
<td>AF213345</td>
<td>Wilke, Rolián &amp; Davis (2000)</td>
</tr>
<tr>
<td>Hydrobia acuta acuta (Draparnaud, 1805)</td>
<td>France</td>
<td>Hérault, Etang du Prévost</td>
<td>AF278808</td>
<td>Wilke et al. (2000)</td>
</tr>
<tr>
<td>Hydrobia ventrosa (Montagu, 1803)</td>
<td>United Kingdom</td>
<td>North Sea, Snettisham lagoon</td>
<td>AF118335</td>
<td>Wilke &amp; Davis (2000)</td>
</tr>
<tr>
<td>Isimerope semele n. sp.</td>
<td>Greece</td>
<td>Megali Vrisi, Pharmakas Mt., Argolida</td>
<td>KC841149</td>
<td>Present study</td>
</tr>
<tr>
<td>Isimerope semele n. sp.</td>
<td>Greece</td>
<td>Second Spring, Pharmakas Mt., Argolida</td>
<td>KC841150</td>
<td>Present study</td>
</tr>
<tr>
<td>Pseudamnicola lucensis (Issel, 1866)</td>
<td>Italy</td>
<td>Tuscany, Lucca, Bagni di Luca, Bagni Caldi, thermal spring</td>
<td>AF387651</td>
<td>Wilke et al. (2001)</td>
</tr>
</tbody>
</table>

Referred material: ZMUA 4094; a small spring, just a few kilometres away from the type locality, "Second Spring", Pharmakas Mt., Argolida, Peloponnisos, 37.6389°N, 22.5125°E, 1230 m a.s.l., leg. C. Radea and Th. Constantinidis, 3 April 2012. ZMUA 4095; Piana, Elissonas river, Mainalo Mt., Arkadia, Peloponnisos, 37.57611°N, 22.23917°E, 1010 m a.s.l., leg. C. Radea and A. Marmari, 23 June 2012.

Etymology: The specific name (in apposition) was derived from Greek mythology: Semele, (Σεμέλη in Greek), was the mortal mother, by Zeus, of Dionysus, god of wine, vineyards, pleasure, ritual madness and ecstasy.

Diagnosis: As for genus.

Shell: (Figs 2A–E, 3A): Colourless, valvataform, with up to 3.5 whorls, thin, transparent when fresh; spire depressed, blunt; whorls rounded, with shallow sutures. Measurements: Table 2. Periostracum pale corneous; columella thick (Fig. 2A–E); umbilicus open, deep, not very wide, in some specimens partially covered by reflected colunmellar margin (Fig. 2B); aperture subcircular to ovate, inner lip adnate, outer lip prosocline (Fig. 2C–D); peristome continuous, thickened at colunmellar margin, reflected at columellar and slightly at lower margin, outer margin simple. Protoconch sculptured with dense net of irregularly shaped depressions (Fig. 3A–C).

Operculum: (Fig. 3D): Ovate, thin, corneous, paucispiral; dark orange, darker at nucleus; inner side weakly convex; nucleus subcentral; muscle attachment area ovate.

Radula: (Fig. 4A): Central tooth trapezoidal, dorsal edge strongly concave (Fig. 4B, C), one pair of medium-sized basal cusps (bc2), basal tongue broadly V-shaped and about equal to lateral margin; median cusp blunt, broader and longer than laterals, five lateral cusps on each side of median cusp, the outer three not well defined; at the edges of radula, median cusp short and square, lateral cusps poorly delineated. Lateral tooth face taller than wide (Fig. 4C), basal tongue well developed; outer wing moderately flexed; cutting edge much shorter than outer wing; central cusp longer than lateral cusps, 6 lateral cusps on outer side, 4–5 on inner side usually shorter than outer ones or not well defined. Inner marginal teeth with ca. 22–24 long equal-sized cusps (Fig. 4D). Outer marginal teeth with ca. 12–15 cusps (Fig. 4E).

Non-genital anatomy: In living specimens, mantle grey-black with white border, the colour being visible under the transparent shell; snout grey-black, longer than wide, parallel-sided with strong distal lobation; eye spots present; tentacles rather wide with a median longitudinal black stripe up to the half of their length; soft body pigmentation variable. Ctenidium absent. U-shaped rectum containing ovate, orange-yellow, longitudinally packed faecal pellets. Nervous system (Fig. 5):
cerebral ganglia similarly sized, light grey; supraoesophageal and suboesophageal ganglia white; supraoesophageal connective longer than suboesophageal connective.

Female reproductive system (Fig. 6A): Pallial oviduct glands with straight border, capsule gland comprising about 2/3 of pallial oviduct; bursa copulatrix medium-sized, pyriform, positioned posterior to albumen gland; renal oviduct unpigmented, well-developed, coiled tightly in an M shape; seminal receptacle absent; coiled oviduct somewhat widened near bursa copulatrix, partly overlapping bursa copulatrix, having a pink pearly sheen.

Egg capsule (Fig. 2E): An egg capsule (containing a single egg) was found inside the umbilicus of several specimens.
Distribution and habitat: *Isimerope semele* appears to be restricted to Peloponnios. At the type locality it was found on stones, gravel and dead leaves of *Juglans regia* in a spring brook together with numerous *Bythinella* sp. In the ‘Second Spring’, specimens were found on stones in a spring with *Juncus* sp. In Piana, the snails were found on stones along the bank of the Elissonas River.

Remarks: The shells of the specimens from Megali Vrisi and ‘Second Spring’ were heavily encrusted with epibionts, the diatom *Cocconeis* sp. being the most numerous, whereas the specimens from Piana did not bear any epibionts.

Sequence data and phylogenetic analysis

The lengths of the COI fragments obtained from the three specimens were 615, 618 and 643 bp (Table 2). After alignment with sequences retrieved from GenBank the dataset consisted of 664 bp, of which 247 sites were variable and 201 were parsimony informative. Of the newly sequenced specimens, 20 sites were variable and none were parsimony informative. The mean sequence divergence (K2P distance) among the newly sequenced specimens was 2.3%. The Bayesian tree (Fig. 8) is only moderately well resolved, as expected since only a single mtDNA gene was used. Nonetheless, the placement of the new taxon within the clade composed of *Graecorganiella* specimens is well supported.

The specimen from Piana was clustered (with strong support) with two specimens identified as ‘*Graecorganiella* sp.’ by Falniowski & Szarowska (2011a) from nearby localities, while the two specimens from Argolida (Megali Vrisi and ‘Second Spring’) grouped together. All five of these individuals formed a well-supported clade. The sequence divergence between the three newly-sequenced individuals and other hydrobiid genera, apart from *Graecorganiella*, was greater than 15%.

### Table 2. Shell morphometry of *Isimerope semele* n. sp. Measurements are in mm.

<table>
<thead>
<tr>
<th>Locality</th>
<th>sh</th>
<th>sw</th>
<th>ah</th>
<th>aw</th>
<th>sh/sw</th>
<th>ah/aw</th>
<th>sh/ah</th>
<th>sw/aw</th>
</tr>
</thead>
<tbody>
<tr>
<td>Megali Vrisi</td>
<td>Min</td>
<td>0.80</td>
<td>1.55</td>
<td>0.75</td>
<td>0.65</td>
<td>0.60</td>
<td>1.12</td>
<td>0.94</td>
</tr>
<tr>
<td>x</td>
<td>0.91</td>
<td>1.66</td>
<td>0.87</td>
<td>0.73</td>
<td>0.91</td>
<td>1.19</td>
<td>1.04</td>
<td>2.26</td>
</tr>
<tr>
<td>SD</td>
<td>0.10</td>
<td>0.08</td>
<td>0.06</td>
<td>0.07</td>
<td>0.10</td>
<td>0.11</td>
<td>0.11</td>
<td>0.19</td>
</tr>
<tr>
<td>CV*</td>
<td>0.11</td>
<td>0.07</td>
<td>0.07</td>
<td>0.09</td>
<td>0.11</td>
<td>0.09</td>
<td>0.11</td>
<td>0.09</td>
</tr>
<tr>
<td>Min</td>
<td>0.95</td>
<td>1.30</td>
<td>0.60</td>
<td>0.70</td>
<td>0.58</td>
<td>1.00</td>
<td>1.10</td>
<td>1.86</td>
</tr>
<tr>
<td>x</td>
<td>1.05</td>
<td>1.65</td>
<td>0.87</td>
<td>0.76</td>
<td>0.64</td>
<td>1.14</td>
<td>1.21</td>
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<tr>
<td>SD</td>
<td>0.06</td>
<td>0.16</td>
<td>0.13</td>
<td>0.06</td>
<td>0.36</td>
<td>0.17</td>
<td>0.43</td>
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<tr>
<td>CV*</td>
<td>0.11</td>
<td>0.10</td>
<td>0.16</td>
<td>0.09</td>
<td>0.57</td>
<td>0.15</td>
<td>0.36</td>
<td>0.10</td>
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<tr>
<td>Piana</td>
<td>Min</td>
<td>1.10</td>
<td>1.60</td>
<td>0.80</td>
<td>0.70</td>
<td>0.67</td>
<td>1.00</td>
<td>1.29</td>
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<tr>
<td>x</td>
<td>1.26</td>
<td>1.72</td>
<td>0.85</td>
<td>0.81</td>
<td>0.73</td>
<td>0.97</td>
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<td>2.14</td>
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<tr>
<td>SD</td>
<td>0.13</td>
<td>0.14</td>
<td>0.05</td>
<td>0.08</td>
<td>0.06</td>
<td>0.08</td>
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</tr>
<tr>
<td>CV*</td>
<td>0.10</td>
<td>0.08</td>
<td>0.06</td>
<td>0.10</td>
<td>0.08</td>
<td>0.09</td>
<td>0.09</td>
<td>0.06</td>
</tr>
</tbody>
</table>

### Abbreviations: sh, shell height; sw, shell width; ah, aperture height; aw, aperture width; CV* = (1 + 1/n)*SD/x, (coefficient of variation corrected for sample size, Sokal & Rohlf, 1995); Max, maximum; Min, minimum; n, number of specimens; SD, standard deviation; x, mean.

DISCUSSION

Following Bodon et al. (2001) and Arconada & Ramos (2001, 2006, 2007), the genera of Hydrobiidae are distinguished by the combination of features from both male and female genitalia. *Isimerope* is differentiated from *Tarraconia* Ramos & Arconada, 2000 (type species *Hauffenia* (Neohoratia) *gasulli* Boeters, in Gasull, 1981), the only known valvatiform genus with two specimens identified as ‘*Graecorganiella* sp.’ by Falniowski & Szarowska (2011a) from nearby localities, while the two specimens from Argolida (Megali Vrisi and ‘Second Spring’) grouped together. All five of these individuals formed a well-supported clade. The sequence divergence between the three newly-sequenced individuals and other hydrobiid genera, apart from *Graecorganiella*, was greater than 15%.
the outer margin of the peristome (Ramos et al., 2000). Besides
the similarity in the female genitalia, Isirome resembles Tarraconia in carrying an egg capsule inside the umbilicus and having eye spots, a U-shaped rectum and an operculum without a peg.


The new genus is also anatomically differentiated from another valvatiform hydrobiid genus that was recently described from Greece, Graecoarganiella Falniowski & Szarowska, 2011 (type

Figure 8. Bayesian phylogeny of selected Hydrobiidae. The dashed outline encompasses the three investigated Isirome semen specimens and the similar ‘Graecoarganiella sp.’ sequences of Falniowski & Szarowska (2011a). Numbers on nodes are posterior probabilities (only values above 0.5 are shown). The species/subspecies names are given as registered in GenBank and followed by their GenBank accession numbers (see Table 1). According to Arconada & Ramos (2001), Horatia sturmi is a composite of two species, Boetersiella sturmi and Chondrobasis levantina. Unfortunately we cannot determine to which of these two species the sequence with accession number AF213345 belongs.
species *G. parnassiana* by original designation) (Falniowski & Szarowska, 2011a). *Graecoarganiella* has two seminal receptacles, an elongated black-pigmented penis with a simple or double lobe near its basal area and 5–6 well-defined lateral cusps on each side of the central tooth of radula (Falniowski & Szarowska, 2011a: 195, Fig. 8C). The type species of *Graecoarganiella* was collected on Parnassos Mountain and, according to the authors, another species of the same genus, ‘*Graecoarganiella* sp.’, was collected from Piana on Mainalo Mountain, in a locality very close to that of our third *Isimerope semele* population. Falniowski & Szarowska (2011a) suggested that the populations from Parnassos and Piana are two congeneric species based on genetic data alone, without anatomical evidence.

*Isimerope* is well differentiated from non-valvatiform hydrobiids both morphologically and genetically (COI sequence divergence >15%). The new genus, apart from anatomical features, is further differentiated from the morphologically similar *Graecoarganiella parnassiana* by mean COI sequence divergence of 10.15%. This level of genetic divergence falls within the range of values recorded for closely related hydrobiid genera (e.g. *Andriohydrobia*, *Hydrobia*, *Pergia*, *Ventrosia* vs *Salenthydrobia* 10.38–14.83%, Wilke, 2003; *Floridobia* vs *Nymphophilus* 10.0–10.9%, *Floridobia* vs *Pyrguloopsis* 8.1–12.9%, Liu & Hershler, 2005; *Grossiana* vs *Daphniola* 10.2–12.3%, Falniowski et al., 2007) and other rissoidean genera (e.g. *Charobius* and *Minckleyella* vs morphologically similar genera 8.6–13.6% and 5.2–13.5% respectively, Hershler, Liu & Landye, 2011).

Based on the phylogenetic tree (Fig. 8), it is evident that *Graecoarganiella parnassiana* forms a clade well separated from the clade of *‘Graecoarganiella* sp.’ and *I. semele*. ‘*Graecoarganiella* sp.’ is almost identical (0.7% sequence divergence) in its COI sequence with our specimen from Piana, which has a quite different anatomy from *G. parnassiana*. The similarity in external morphology between *I. semele* and ‘*Graecoarganiella* sp.’ (Falniowski & Szarowska 2011a: 192, fig. 4G–I), the closely proximal collection sites, and the results of our molecular analysis suggest that ‘*Graecoarganiella* sp.’ from Piana should be assigned to *I. semele*.

The phylogenetic clade comprising the three investigated specimens of the present study and the sequences of ‘*Graecoarganiella* sp.’ from Piana exhibits some internal topological structure, with the two subclades corresponding to the

### Table 3. *Isimerope* compared morphologically with 31 other valvatiform genera distributed in the Balkan Peninsula and Mediterranean areas.

<table>
<thead>
<tr>
<th>Character states:</th>
<th>Bursa copulatrix</th>
<th>Seminal receptacle(s)</th>
<th>Penis</th>
<th>Penial lobe(s)</th>
<th>Ctenidium</th>
<th>Eyes</th>
<th>Operculum</th>
<th>Umbilicus</th>
<th>Rectum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Isimerope</em> new genus</td>
<td>1 0 1 3 0 1 0 1 2</td>
<td>(U)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Argangiella</em></td>
<td>1 1 0 0 1 0 0 2</td>
<td>(U) or (S)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Boetersiella</em></td>
<td>1 1 0 0 1 0 2</td>
<td>(U)</td>
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<td><em>Bracenica</em></td>
<td>1 3 1 2 – 0 1</td>
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<td><em>Chondrobasia</em></td>
<td>1 1 1 0 1 0 2</td>
<td>(U)</td>
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<tr>
<td><em>Dabriansa</em></td>
<td>1 1 0 0 1 0 –</td>
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<tr>
<td><em>Daphniola</em></td>
<td>1 3 1 2 1 1 0 0</td>
<td>–</td>
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<tr>
<td><em>Fissuria</em></td>
<td>1 3 3 1 0 0 0 1 2</td>
<td>(S)</td>
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<tr>
<td><em>Gocea</em></td>
<td>1 3 1 0 4 – 1 1 2</td>
<td>(Z) or (?)</td>
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<tr>
<td><em>Graecoarganiella</em></td>
<td>1 3 1 1 0 1 2 1</td>
<td>(U) or (V)</td>
<td></td>
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<tr>
<td><em>Hauffenia</em></td>
<td>1 2 0 0 1 0 1 0 2</td>
<td>(Z) or (S)</td>
<td></td>
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<tr>
<td><em>Herautella</em></td>
<td>1 1 0 0 1 0 2</td>
<td>(U) or (S)</td>
<td></td>
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<tr>
<td><em>Horatia</em></td>
<td>1 3 1 2 3 1 1 0 1</td>
<td>(S)</td>
<td></td>
<td></td>
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<tr>
<td><em>Iberoratia</em></td>
<td>1 3 1 2 1 1 0 2</td>
<td>(U) or (S)</td>
<td></td>
<td></td>
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<tr>
<td><em>Islamia</em></td>
<td>0 3 1 4 1 1 0 0</td>
<td>(U)</td>
<td></td>
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<tr>
<td><em>Josefus</em></td>
<td>0 3 1 4 0 1 0 1</td>
<td>(U)</td>
<td></td>
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<tr>
<td><em>Karevia</em></td>
<td>1 3 1 3 – 1 0* 3 3</td>
<td>–</td>
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<tr>
<td><em>Kerkia</em></td>
<td>1 3 1 1 3 1 0 1 2</td>
<td>(S)</td>
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<tr>
<td><em>Lyhniida</em></td>
<td>1 2 0 1 4 – 1 0 0</td>
<td>–</td>
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<tr>
<td><em>Milesiana</em></td>
<td>0 3 1 2 1 1 0 2</td>
<td>(U)</td>
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<tr>
<td><em>Ohrdocaulifera</em></td>
<td>1 3 1 3 – 1 0 1</td>
<td>–</td>
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<tr>
<td><em>Ohrigoea</em></td>
<td>1 3 1 3 – 1 0 2</td>
<td>–</td>
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<tr>
<td><em>Pezzola</em></td>
<td>0,1 3 0 0 0 0 0 2 2</td>
<td>(S)</td>
<td></td>
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<tr>
<td><em>Prespolitorea</em></td>
<td>1 3 1 3 – 1 0* 1 1</td>
<td>–</td>
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<tr>
<td><em>Pseudohoratia</em></td>
<td>1 2 1 3 1 1 1 0 2</td>
<td>(O)</td>
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<tr>
<td><em>Pseudoislamia</em></td>
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<tr>
<td><em>Sardhoratia</em></td>
<td>1 3 0 0 0 0 0 0 0</td>
<td>(S)</td>
<td></td>
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<tr>
<td><em>Sheltanok</em></td>
<td>1 1 0 0 1* 1 0* 3 3</td>
<td>–</td>
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<tr>
<td><em>Spathogyne</em></td>
<td>1 3 1 2 1 1 0* 2</td>
<td>(V)</td>
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<tr>
<td><em>Strugia</em></td>
<td>1 2 1 3 – 1 0 2</td>
<td>–</td>
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<tr>
<td><em>Tarraconia</em></td>
<td>1 0 1 2 1 1 0 3</td>
<td>(U)</td>
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<tr>
<td><em>Zaumia</em></td>
<td>1 2 1* 4* – 0 0 1 1</td>
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</table>

Character states: bursa copulatrix: absent (0), present (1); seminal receptacle: absent (0), distal seminal receptacle (1), proximal seminal receptacle (2), distal and proximal seminal receptacle (3); penis: simple (0), with one lobe (1), with two lobes (2), with more than two lobes (3); penial lobe(s): absent (0), basal lobe (1), medial lobe (2), lobe at 2/3 of penis length (3), apical lobe (4); ctenidium: absent (0), present (1); eyes: absent (0), present (1); operculum: simple (0), peg-bearing (1); umbilicus: narrow (0), medium (1), wide (2), very wide (3); rectum: without or almost without bend (0), Z-like (Z), U-like (U), S-like (S), V-like (V), ?-like (?); *: deduced by Bodon et al. (2001); **: Schütt & Søessen, 1989: 117, fig. 2B; –: no data. Sources: Arconada & Ramos, 2001, 2006, 2007; Bodon & Giusti, 1986; Bodon et al., 1995, 2001; Manganelli et al., 1998; Radoman, 1966, 1983; Ramos et al., 2000; Schütt, 1991; Schütt & Søessen, 1989.
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