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New taxonomical, distributional, and ecological data on the Helicodontidae (Gastropoda, Eupulmonata) of Crete (Greece)

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Abstract. Until now, the family Helicodontidae has been represented in Crete by two genera, *Lindholmiola* Hesse, 1931 and *Helicodonta* A. Férussac, 1821, with one species each, *H. wilhelminae* Maassen, 1991 and *L. barbata* (A. Férussac, 1821). We studied for the first time the reproductive system of *H. wilhelminae* and reclassify this species as *Lindholmiola wilhelminae* comb. nov. We present further details on its distribution and ecology and discuss the observed differences between recent and old shells. Based on the rich alcohol and shell materials in the Natural History Museum of Crete, we observed an impressive inter- and intra-population variability within *L. barbata*. The shells vary in form and size; small shells are associated with ecological factors and large shells with the northern part of Lefka Ori, the high mountains in western Crete. The reproductive system variation exceeds the limits of *L. barbata* species and confuses the species-specific characters of the genus, indicating the need for a new revision.

Key words. *Lindholmiola*, *Helicodonta*, intraspecific variability, genitalia, systematics

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Introduction

The family Helicodontidae is currently represented in Crete by two genera, each with one species: *Lindholmiola* P. Hesse, 1931, by *L. barbata* (A. Férussac, 1821) (Vardinoyannis 1994; Welter-Schultes 2012; Subai & Neubert 2014) and *Helicodonta* A. Férussac 1821, by *H. wilhelminae* Maassen, 1991 (Maassen 1991; Welter-Schultes 2012; Subai & Neubert 2014). Both species are endemic to Crete.

The genus *Helicodonta* is mainly distributed in Central and Southern Europe (Schileyko 2005; Welter-Schultes 2012). It prefers humid, mountain forests where it lives in leaf litter, rock crevices, and among stones (Welter-Schultes 2012). In contrast, *Lindholmiola* displays greater diversity and is primarily found in the Balkan Peninsula and Asia Minor, with limited populations in eastern Italy and southern Moldavia (Subai & Neubert 2014). *Lindholmiola* exhibits a wide spectrum of habitats, inhabiting forests, shrublands, and cultivated areas, and has an altitudinal range extending from lowlands to 2000 m a.s.l. (Subai & Neubert 2014).

Subai & Neubert (2014) revised the genus *Lindholmiola* and documented the distribution of *L. barbata* on Crete based on institutional and private Central European collections. They also presented its shell characteristics and genitalia, noting that in size and shell shape, *L. barbata* does not vary considerably, and no local forms are known. This species is widespread in central and western Crete but absent from the eastern part.

Maassen (1991) described a new subspecies of *H. gyria* (J.R. Roth, 1839), *H. g. wilhelminae*, from the western slopes of Mount Dikti in central Crete. Until then, *H. gyria* was known only from SW Turkey. Both the Turkish and Cretan taxa were known only from their shells. Subai & Neubert (2014) examined the genitalia of an adult specimen of *H. gyria* collected by Subai in 1999 from south-western Turkey. They concluded that the species should be placed in the genus *Lindholmiola*. However, the taxon from Crete remained in *Helicodonta* as *H. wilhelminae* (Welter-Schultes 2012; Subai & Neubert 2014). The Cretan taxon represents the southernmost occurrence of the genus.

Based on the extensive alcohol-preserved and shell materials in the collections of the Natural History Museum of Crete, we aim to re-evaluate the taxonomy of *H. wilhelminae* and provide expanded distributional data for this species and *L. barbata*. Additionally, we explore the variability of these species' shells and genitalia and their ecological requirements.

Materials and Methods

The malacological collections of the Natural History Museum of Crete (NHMC) comprise more than 278 lots of Helicodontidae—166 lots of shells and 112 lots in alcohol—which were collected from 181 sites on Crete and adjacent islands. Based on the existing taxonomy (Subai & Neubert 2014), this material was identified as *L. barbata* (158 lots of shell and 109 lots in alcohol) and *H. wilhelminae* (8 lots of shells and 3 lots in alcohol). Most of the samples were collected by Dr K. Vardinoyannis, during her Ph.D. research on the malacofauna of Crete (Vardinoyannis 1994), with additional contributions from other scientists and amateurs over the last 30 years.

We measured all the adult shells ($n = 588$) for shell height (SH), shell diameter (SD), and the number of whorls (W). For *L. barbata*, we also recorded the form of the umbilicus: entirely closed (C), almost closed (AC), or open (O). Measurements were carried out with a digital vernier caliper. Whorls were counted following Kerney & Cameron (1979). We studied the genitalia of more than 50 specimens of *L. barbata*, taking care to include representatives from across the species' shell variability and geographic distribution. Seasonal samples from Theriso Gorge and the north part of Omalos Plateau were studied to assess the variability or stability of the external or internal characters of the genitalia.

Moreover, for *H. wilhelminae* we measured the width of the ultimate (WLW) and penultimate whorls (WPW) and the width of the umbilicus (WU). Five specimens were dissected from the two populations of *H. wilhelminae.*

To check for size differences between recent and old shells, we classified as recent all specimens from alcohol-preserved material or dry shells with a vivid colour. Old shells were defined as those from subfossil populations, very old specimens from locations without living populations, and those found deep in the soil. To compare differences between older and recent shells of *H. wilhelminae*, we performed *t*-tests for each measurement of SH and SD. To test whether altitude has a significant impact in shell size differences of *L. barbata* (SH and SD), we initially categorized the data into five altitudinal intervals (0–400 m, 400–800 m, 800–1200 m, 1200–1600 m, and 1600–2000 m) and subsequently conducted an analysis of variance (ANOVA) followed by a Tukey test to assess the mean differences among these categories. The altitudinal zones were divided according to the ecosystem zones of Crete, which include: Mediterranean (0–800 m), mountainous (800–1600 m), and subalpine (1600 m and above).

All the examined material is presented alphabetically by Regional Unit and locality.

Results and Systematics

Family Helicodontidae Kobelt, 1904

Genus *Lindholmiola* P. Hesse, 1931

Type species. *Helix* (*Helicigona*) *lens* A. Férussac, 1832.

***Lindholmiola wilhelminae* (Maassen, 1991)**
Figures 1–5

Material examined. Irakleio regional unit: Agia Foteini cave around, above Avdou 30.x.1994, 35.211°N 025.423

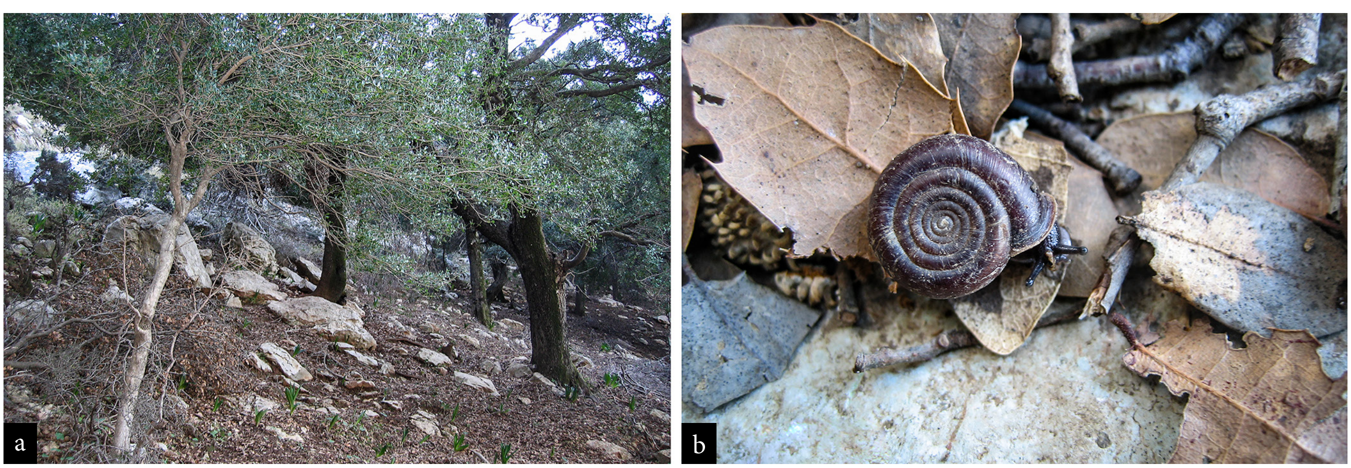

Figure 1. Habitat of *Lindholmiola wilhelminae* (**b**) and a live individual (**b**).

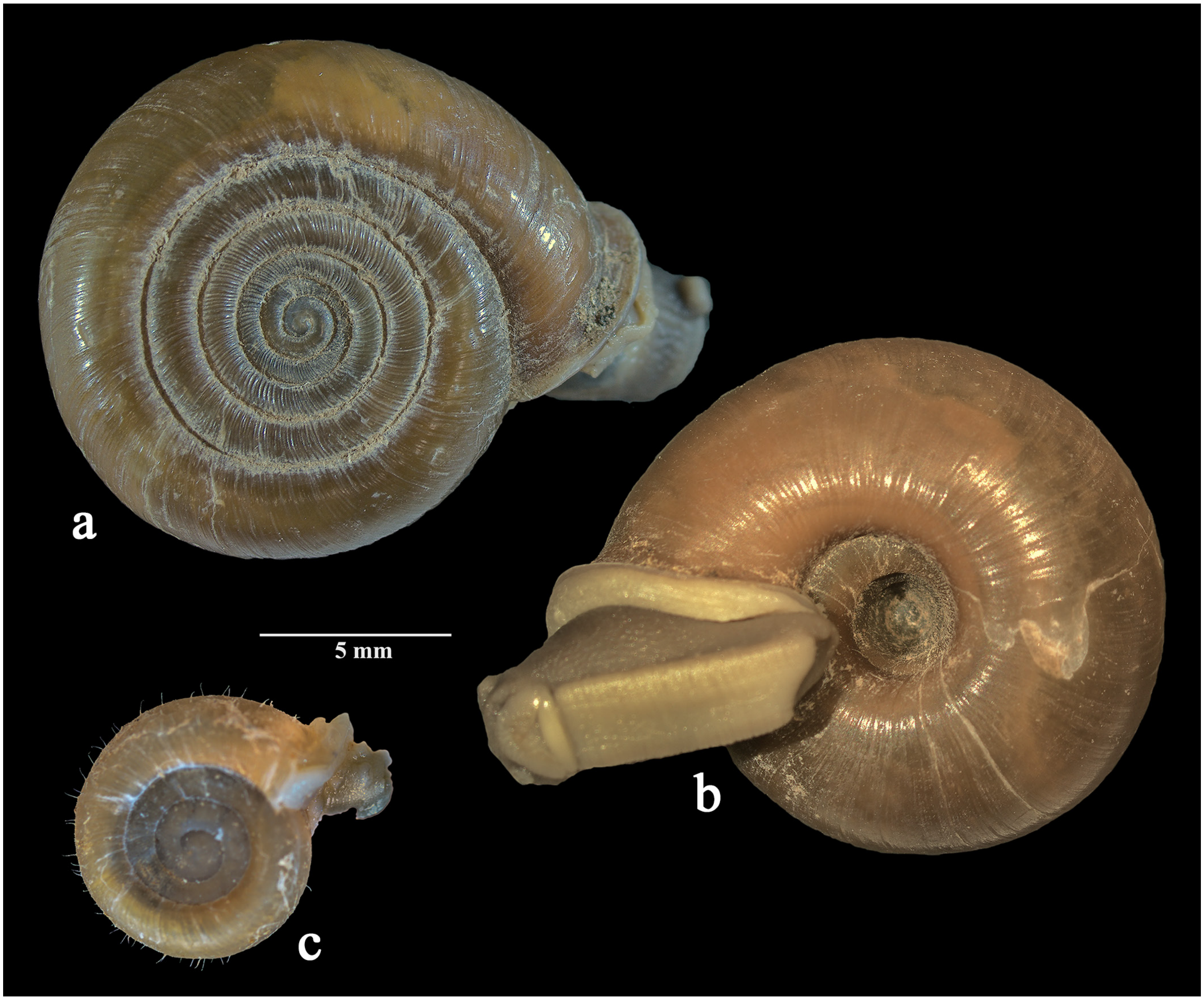

Figure 2. Adult (**a, b**) and juvenile (**c**) specimens of *Lindholmiola wilhelminae* preserved in alcohol. Scale is the same for all individuals.

°E, leg. MM, NHMC50.33402 shells: 2 ind. (all old); same locality, 2.iv.1995, leg. MM, NHMC50.33603 shells: 3 ind. (all old), alcohol: 1 ind.; Agia Foteini, a little below the cave in *Quercus* forest, 19.iii.1999, 35.2121°N 025.4238°E, leg. KV, NHMC50.34155 shells: 11 ind. (6 recent, 5 old), alcohol: 3 ind.; same locality 22.iv.2004 leg. KV, NHMC50.27833 shells: 1 ind. (old); same locality 5.xi.2017 leg. Bitzilekis NHMC50.46482 shells: 1 ind. (recent), alcohol: 3 ind.; Kato Karouzana 31.iii.1991, 35.2283 °N 025.3567°E, leg. KV, NHMC50.8388 shells: 1 ind. (subfossil); Krasi forest 19.iii.1999, 35.2325°N 025.4828°E, leg. MM, NHMC50.6801 shells: 5 ind. (all recent).

LASITHI REGIONAL UNIT: Kato Metochi, 9.iv.1991, 35.1832°N 025.4318°E, leg. KV, NHMC50.14247 shells: 1 juv. (subfossil).

Diagnosis. Shell depressed; first three whorls slightly sunken; whorls densely and regularly coiled. Genitalia with glandular tissue at distal end of epiphallus. Penis almost globular or tubular; bursa copulatrix long and clavate.

Shell characteristics and measurements. Thirty-one adult shells were measured (19 recent and 12 old) (Table 1). Shell depressed, with rounded periphery; first three whorls slightly immersed, the rest at same level; last whorl descending before aperture, at the maximum, ⅓ of the penultimate whorl; protoconch smooth; radial stripes appear after the first 1½ whorls, which gradually become more regular, until penultimate whorl; penultimate whorl with irregular radial stripes; last whorl smooth; suture deep; hairs present, only in juveniles not more than 3½ whorls (Fig. 2c); umbilicus broad and conical (Fig. 2b); shell colour light brown; aper-

Table 1. Measurements of *Lindholmiola wilhelminae* shells. SH: Shell height, SD: shell diameter, WLW: width of ultimate whorl, WPW: width of penultimate whorl, WU: width of umbilicus.

	All (*n* =31) Mean (min–max) in mm	Recent shells (*n* =19) Mean (min–max) in mm	Old shells (*n* =12) Mean (min–max) in mm
SH	6.84 (5.50–7.80)	7.70 (6.30–7.80)	6.47 (5.55–7.00)
SD	15.36 (12.75–17.00)	15.80 (14.60–17.00)	14.67 (12.75–15.90)
WLW	2.83 (2.45–3.20)	2.90 (2.45–3.20)	2.72 (2.45–3.10)
WPW	1.57 (1.25–2.30)	1.62 (1.35–2.30)	1.47 (1.25–1.60)
WU	3.85 (2.95–4.60)	4.07 (3.50–4.60)	3.51 (2.95–4.10)
Whorls	5.90 (5.4–6.3)	6.10 (5.7–6.3)	5.71 (5.4–6.1)

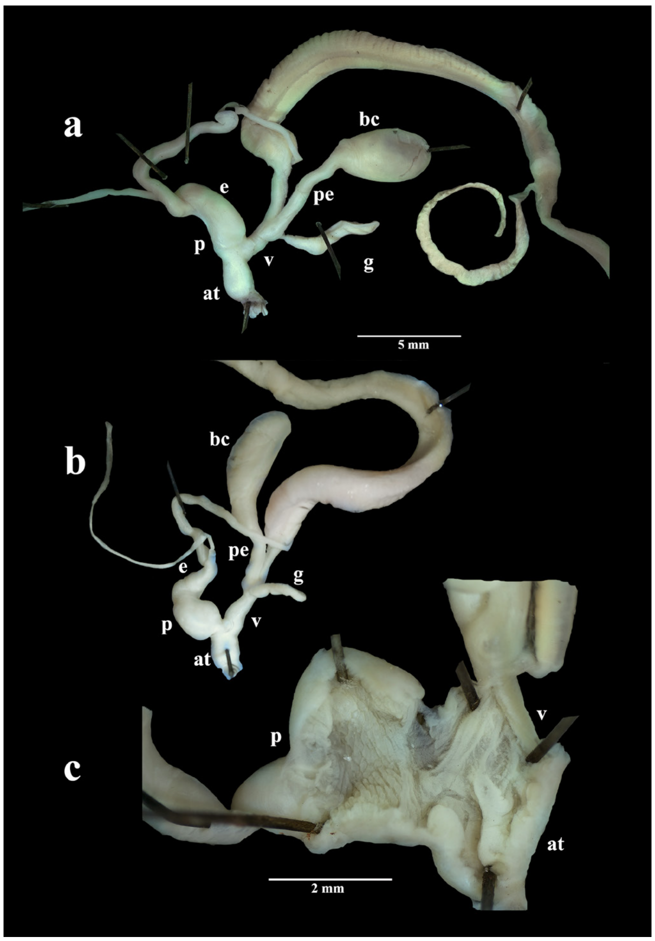

Figure 3. Genitalia of *Lindholmiola wilhelminae* from Agia Foteini. **a**, collected 15.xi.2017. **b**, collected 2.iv.1995. **c**, internal structure of penis. at: atrium, bc: bursa copulatrix, e: epiphallus, g: glandula, p: penis, pe: pedunculus, v: vagina. Scale is the same, 5 mm, for a and b.

tural lip reflected; aperture whitish.

Genitalia (Fig. 3). Penis variable, globular to tubular; penial lumen without obvious penial pilaster (Fig. 3c); length of vagina shorter than or equal to free oviduct; atrium well developed, in length and diameter equal to or larger than vagina, filled with 3 or 4 pilasters; 1 or 2 of which continue in vagina; glandula tubular, with a short stalk, variable in length, diameter at base equal or slightly larger than pedunculus; bursa copulatrix long and clavate, 1–3 times length of glandula, equal or twice the length of pedunculus.

Ecology and distribution (Figs 1, 4). Living specimens were found in close to piles of stones in shaded places or small openings of *Quercus* forests on the western slopes of Mount Dikti above Krasi and Avdou villages. Subfossil shells were discovered in alluvial sediments over a broader area, extending from the western foothills of Mount Dikti to an altitude of 800 m, where the predominant vegetation consists of phrygana and maquis.

Remarks. We observed statistically significant differences between recent and old shells for all measured shell characters. Recent shells are significantly larger in terms of shell diameter, height, number of whorls, width of the umbilicus, and the width of the last and penultimate whorls (Fig. 5).

Maassen (1991) distinguished *H. g. wilhelminae* from the nominal *H. gyria* based on its fewer whorls (6.2 compared to 6.5–7.2, respectively) and a more than twofold difference in the width of the last whorl compared to the penultimate whorl. However, our measurements, taken from 31 shells of *L. wilhelminae* (including 19 recent shells), expand the range of the measurements reported by Maassen (1991). Consequently, we found no significant differences in the number of whorls or the width of the last two whorls between the two taxa. Study of the reproductive systems of *L. gyria* (one specimen from Phaselis, Antalya, Turkey) by Subai & Neubert (2014) and *L. wilhelminae* (five specimens from two populations in our study), leaves no doubt that, despite their conchological similarity to other *Helicodonta* species, both should be placed within the genus *Lindholmiola* based on taxonomic characters presented by Schileyko (2005) and Subai & Neubert (2014). This classification is supported by the presence of a single glandula and glandular tissue at the

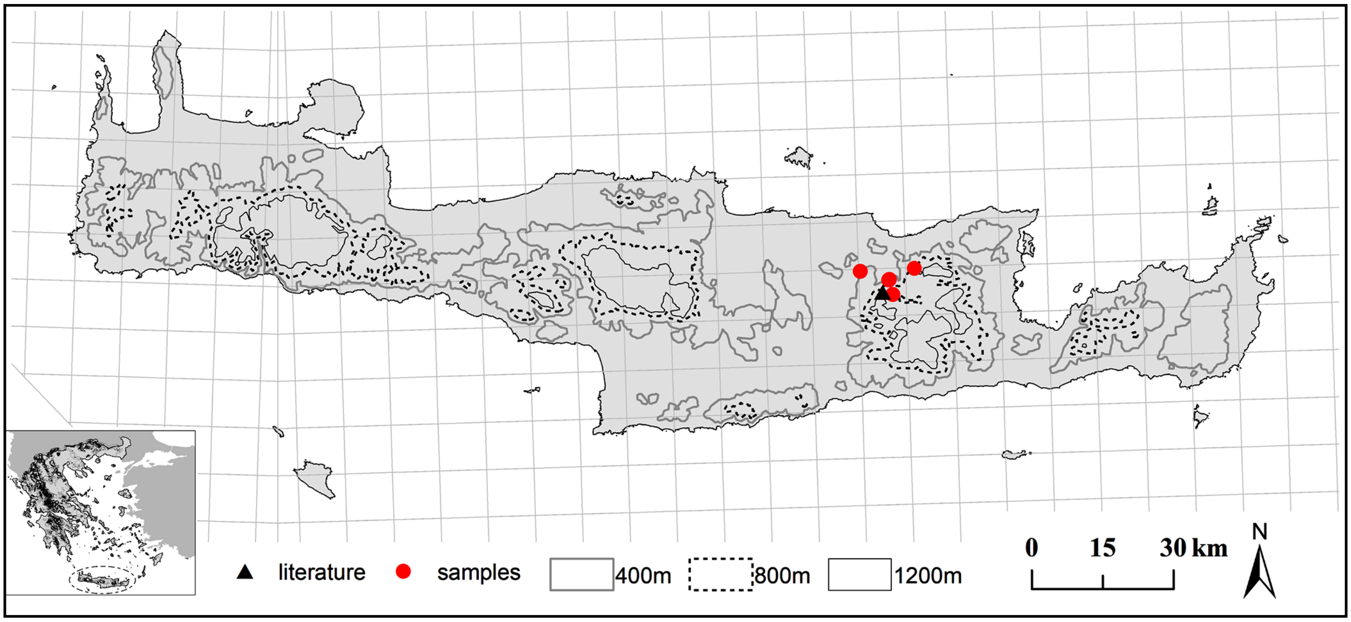

Figure 4. Geographic distribution of *Lindholmiola wilhelminae*. Bibliographic data are by Maassen (1991) and are presented in 10 × 10 km UTM squares.

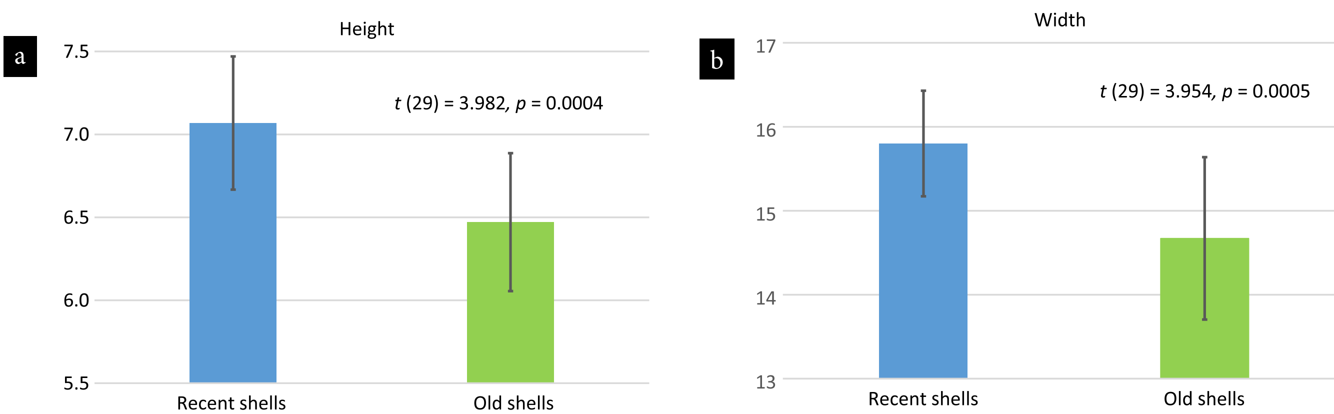

Figure 5. Differences of shell height (**a**) and shell diameter (**b**) among recent and old shells of *Lindholmiola wilhelminae*.

distal end of the epiphallus, distinguishing these two *Lindholmiola* species from the genus *Helicodonta*, which has two fork-like glandulae, a long vagina, and no glandular tissue at the distal end of the epiphallus (Schileyko 2005).

Lindholmiola wilhelminae should be regarded as a distinct species and not a subspecies of *L. gyria* due to several conchological and anatomical differences. *Lindholmiola wilhelminae* has a broader (2.95–4.6 mm) and more conical umbilicus, compared to the cylindrical umbilicus (2.8–3.3 mm in diameter) of *L. gyria*. Moreover, the two species differ in their reproductive systems: *L. wilhelminae* has a penis which varies from spherical to tubular; the glandula is very long and as thick as the pedunculus; there is a clavate rather than tubular bursa copulatrix; and the penial lumen is without obvious pilasters. However, we note that the variability of the genitalia in *L. gyria* is not yet fully recorded and understood.

Lindholmiola barbata (A. Férussac, 1821)

Figures 6–9

Material examined. CHANIA REGIONAL UNIT: Afrata, 30.i.1987, 35.5741°N 023.7757°E, leg. KV, NHMC50.9191 shells: 4 ind., alcohol: 3 ind.; Agia Eirini gorge, 28.x.1989, 35.3354°N 023.836°E, leg. KV, NHMC50.5091 shells: 2 ind.; Agia Eirini gorge, exit in the south, 18.i.2014, 35.2859°N 023.823°E, leg. KV, NHMC50.41180 shells: 1 ind., alcohol: 13 ind.; Agia Marina, 8.ii.1987, 35.5171°N 023.93°E, leg. KV, NHMC50.5072 shells: 6 ind., alcohol: 6 ind.; Anopoli, at Agia Aikaterini church, 17.xi.2014, 35.2124°N 024.0882°E, leg. KV, NHMC50.43020 shells: 1

ind.; Aradaina gorge 20.viii.2015, 35.2251°N 024.0653°E, leg. KV, NHMC50.43562 shells: 3 ind.; Asfendou 18. xii.1987, 35.2408°N 024.2142°E, leg. KV, NHMC50.9238 shells: 1 ind.; Asfendou - Kallikratis 18.xii.1987, 35.242°N 024.2253°E, leg. KV, NHMC50.35859 alcohol: juv.; Askyfou, opposite Ammoudari, 16.xi1987, 35.2917°N 024.1719 °E, leg. KV, NHMC50.5074 alcohol: juv.; Balos, 21.iv.1996, 35.5778°N 023.5858°E, leg. MM, NHMC50.24471 shells: 1 ind.; Bapiolos – Manoliopoulo, 8.ii.1987, 35.4693°N 023.863°E, leg. KV, NHMC50.9210 shells: 4 ind., alcohol: 3 ind.; Chliaro, 26.ii.1991, 35.4181°N 023.9143°E, leg. KV, NHMC50.9214 shells: juv.; Deres – Papadiana, 26.ii.1991, 35.4321°N 023.8446°E, leg. KV, NHMC50.9220 shells: juv. alcohol: 3 ind.; Elafonisos, at the west end of the beach, end of the road 30.iv.1996, 35.2716°N 023.5407°E, leg. Hadjicharalambous, NHMC50.24696 shells: 1 ind.; Falasarna, 24. iv.1990, 35.509°N 023.577°E, leg. KV, NHMC50.14835 shells: 5 ind.; Foinikas to Livaniana, 16.xi.2014, 35.2037°N 024.0642°E, leg. KV, NHMC50.43000 shells: 13 ind.; Mount Fterolakkos, 11.v.1987, 35.2885°N 024.3221°E, leg. KV, NHMC50.5073 shells: 2 ind., alcohol: juv.; Georgioupoli, 10.xi.1996, 35.3631°N 024.2594°E, leg. Hadjicharalambous, NHMC50.22004 alcohol: 1 ind.; Glistridi, 4.ii.1987, 35.5728°N 023.7327°E, leg. KV, NHMC50.9213 shells: juv.; Gramvousa peninsula north to the spring 13.i.1988, 35.5637°N 023.6042°E, leg. KV, NHMC50.9239 shells: 1 ind.; Iligkas gorge, 2.vi.2015, 35.2053°N 024.1256°E, leg. MM, NHMC50.43569 shells: juv.; Kalamitsi Amygdali – Exopoli, 15.xi.1990, 35.3769°N 024.2394°E, leg. KV, NHMC50.5087 shells: 11 ind., alcohol: juv.; Kallikratis - Patsiano, 5 km north of Patsianos, 175 m alt., 18.xi.2000, 35.2088°N 024.2332°E, leg. Stathi NHMC50.21999 alcohol: 1 ind.; Kampoi, 27.ii.1991, 35.4181°N 024.0689°E, leg. KV, NHMC50.14947 shells: 2 ind., alcohol: juv.; Katholiko, Achyrospilios cave, 23.xii.2007, 35.591°N 024.1447°E, leg. Georgiakakis NHMC50.44745 shells: juv.; Kato Stalos 8/2/1987,35.5113°N023.9461°E,leg.KV,NHMC50.14969 shells: 1 ind., alcohol: 3 ind.; Katochori – Kampoi, 27. ii.1991, 35.4278°N 024.0543°E, leg. KV, NHMC50.5086 shells: 3 ind.; Kefalas, 15.xi.1990, 35.4061°N 024.2504°E, leg. KV, NHMC50.5126 shells: 6 ind., alcohol: 3 ind.; Kladou gorge, 15.vii.1994, 35.2404°N 023.9286°E, leg. MM, NHMC50.24697 shells: 2 ind.; Kolymvari, 8.iv.1995, 35.5416°N 023.7778°E, leg. KV, NHMC50.23694 alcohol: juv.; Kontopoula to Kamateri Kefala peak, 7.v.1987, 35.4459°N 024.048°E, leg. KV, NHMC50.14970 alcohol: 1 ind.; Kounoupidiana – Agios Onoufrios, 17.iii.1990, 35.5429°N 024.0661°E, leg. KV, NHMC50.9250 shells: juv., alcohol: 2 ind.; Kourna lake, 1.v.1985, 35.3269°N 024.279°E, leg. Kollaros NHMC50.24473 shells: 3 ind.; same locality 10/11/1996 leg. Hadjicharalambous, NHMC 50.24472 shells: 1 ind.; same locality 14/3/1997 leg. Lymberakis, NHMC50.22008 alcohol: juv.; Kourna lake, *Quercus* forest at the south side of the lake, 30.x.1996, 35.3265°N 024.2783°E, leg. Lymberakis NHMC50.43714 alcohol: 1 ind.; same locality 29.xii.1996, leg. Lymberakis, NHMC 50.22005 alcohol: 1 juv.; same locality 24.i.1997, leg. Stathi NHMC50.23714 shells: 2 ind., alcohol: 5 ind.; same locality, 10.v.1997, leg. Lymberakis, NHMC50.22006 alcohol: 1 ind.; same locality, 10.vii.1997, leg. Lymberakis, NHMC 50.43943 alcohol: juv.; Kouroupitos XYTA, 17.v.2009, 35.5382°N 024.1947°E, leg. Georgantis, NHMC50.34231 shells: 1 ind.; Kouroupitos XYTA (inside the area), 14. xii.2009, 35.5382°N 024.1947°E, leg. Giannakakis, NHMC 50.34337 alcohol: 2 ind.; Koustogerako south at Mount Chondroi Volakoi, 18.i.2014, 35.2565°N 023.823°E, leg. KV, NHMC50.41175 alcohol: 5 ind.; Koustogerako, at Agia Aikaterini church, 850 m alt., 18.i.2014, 35.2746°N 023.8485°E, leg. KV, NHMC50.41103 shells: 2 ind., alcohol: juv.; Krapi in *Quercus coccifera* forest, 28.iv.2002, 35.3162°N 024.2096°E, leg. Roditakis, NHMC50.43103 alcohol: juv.; same locality, leg. Roditakis, NHMC50.43114 alcohol: 1 ind.; Krapi SW slopes, 27.iv./1988, 35.314°N 024.1819°E, leg. KV, NHMC50.9232 shells: 1 ind.; Lefka Ori mountains, 1400 m alt., 3.vi.1988, 35.26°N 024.0998°E, leg. KV, NHMC50.9122 alcohol: juv.; Lefka Ori mountains, 1600 m alt., 3.vi.1988, 35.3011°N 024.1303°E, leg. KV, NHMC50.14371 shells: 1 ind.; Lefka Ori mountains, 2 km south of Kares, 30.i.2014, 35.3767°N 024.0797°E, leg. KV, NHMC50.41210 shells: 2 ind.; Lefka Ori mountains, 4 km south of Kares, 30.i.2014, 35.3664°N 024.076°E, leg. KV, NHMC50.41199 shells: 2 ind.; Lefka Ori mountains, 800 m ascending from Anopoli in a pinewood, 8.vi.1991, 35.2422°N 024.0844°E, leg. KV, NHMC50.14401 shells: 2 ind.; Lefka Ori mountains, Athymolakkos stream, south of Agios Modestos church, 1150 m alt., 26.ii.2014, 35.3806°N 024.0433°E, leg. KV, NHMC50.41315 shells: 2 ind.; Lefka Ori mountains, Athymolakkos stream, south of Agios Modestos church, 1350 m alt., 26.ii.2014, 35.3737°N 024.0365°E, leg. KV, NHMC50.41236 shells: 4 ind., alcohol: 1 ind.; Lefka Ori mountains, before Omalos plateau on the way to antennas, 1200 m alt., 9.viii.2008, 35.3544°N 023.9072°E, leg. Georgantis, NHMC50.33451 shells: juv.; same locality 5.ix.2008 leg. Georgantis, NHMC50.33284 shells: 1 ind.; same locality 6.x.2008, leg. Georgantis, NHMC50.32993 shells: 2 ind.; same locality 2.xii.2008 leg. Georgantis, NHMC50.32921 shells: 1 ind.; same locality, 15.i.2009, leg. Georgantis, NHMC50.32740 alcohol: juv.;

same locality 11.ii.2009, leg. Georgantis, NHMC50.32723 shells: 3 ind.; same locality, 10.iii.2009, leg. Georgantis, NHMC50.32309 shells: 2 ind., alcohol: 2 ind.; same locality, 3.iv.2009, leg. Georgantis, NHMC50.32698 alcohol: juv.; same locality, 15.v.2009, leg. Georgantis, NHMC 50.32774 alcohol: 2 ind.; same locality, 7.vi.2009, leg. Georgantis, NHMC50.32905 shells: 2 ind., alcohol: juv.; Lefka Ori mountains, below Melindaou peak (site 1), 24.iv.2004, 35.3299°N 023.9803°E, leg. MM, NHMC50.23633 shells: juv., alcohol: 1 ind.; Lefka Ori mountains, Fournoti, 18.viii.1996, 35.2232°N 023.922°E, leg. MM, NHMC50.34004 shells: 15 ind.; Lefka Ori mountains, from Greleska halfway to Agioi Theodoroi, 30.v.2015, 35.3126°N 023.8557°E, leg. KV, NHMC50.43564 shells: juv.; Lefka Ori mountains, Gournes at Agios Pavlos, south of Kares, 30.i.2014, 35.3598°N 024.0741°E, leg. KV, NHMC50.43561 shells: 6 ind.; Lefka Ori mountains, Gournes south of Kares, 30.i.2014, 35.362°N 024.0808°E, leg. KV, NHMC50.41201 shells: 10 ind.; Lefka Ori mountains, Kallergi hut on the way to Melindaou peak, 9.v.2004, 35.3326°N 023.974°E, leg. MM, NHMC50.7077 shells: 2 ind., alcohol: 4 ind.; Lefka Ori mountains, Melindaou peak, north of mountain (site 4), 9.v.2004, 35.3289°N 023.9846°E, leg. MM, NHMC 50.43715 alcohol: 2 ind.; Lefka Ori mountains, Melindaou peak, 2000 m alt., 1.vii.1994, 35.3305°N 023.9812°E, leg. MM, NHMC50.20560 shells: 2 ind.; Lefka Ori mountains, Melissitis stream at 1000 m alt., below Bimpo peak, 30.v.2015, 35.3479°N 023.9328°E, leg. KV, NHMC50.43565 shells: 1 ind.; Lefka Ori mountains, Melissitis stream at 800 m alt., west of Vothonas peak, 30.v.2015, 35.3584°N 023.928°E, leg. KV, NHMC50.43566 shells: 1 ind.; Lefka Ori mountains, Psari, Varathro 20/7/2008, 35.3811°N 024.0336°E, leg. Kardamaki, NHMC50.41248 shells: juv.; Lefka Ori mountains, Tsichlopigado halfway to Agios Modestos church, 830 m alt., 26.ii.2014, 35.3979°N 024.0446°E, leg. KV, NHMC50.41292 shells: 1 ind.; Lefka Ori mountains, west side at Greleska, 19.i.2014, 35.3105°N 023.8482°E, leg. KV, NHMC50.41193 shells: 1 ind.; Lissos, 28.x.1989, 35.2432°N 023.7843°E, leg. KV, NHMC50.9245 shells: 2 ind.; Livaniana, 300 m before village, 16.xi.2014, 35.208°N 024.0637°E, leg. KV, NHMC50.42923 shells: juv., alcohol: juv.; Machairoi – Ramni, 13.i.1991, 35.4063°N 024.1169°E, leg. KV, NHMC50.14944 shells: 6 ind.; Machairoi gorge, 13.i.1991, 35.4147°N 024.1274°E, leg. KV, NHMC50.14943 shells: 2 ind., alcohol: juv.; Marathi, 19.vii.1999, 35.5061°N 024.1775°E, leg. Lymberakis, NHMC 50.23701 shells: 8 ind., alcohol: 1 ind.; Megala Chorafia, 13.i.1991, 35.4632°N 024.118°E, leg. KV, NHMC50.5162 shells: 2 ind., alcohol: juv.; Melidoni, 23.xi.1989, 35.3865°N 024.1107°E, leg. KV, NHMC50.9246 shells: 2 ind.; Melidoni to Lefka Ori mountains, Mavri peak, 1000 m a.s.l., 23.xi.1989, 35.3527°N 024.1002°E, leg. KV, NHMC 50.14924 shells: 11 ind.; Melidoni to Lefka Ori mountains, Mavri peak, 1000 m alt., 6.i.2021, 35.351°N 024.0991°E, leg. KV, NHMC50.48965 shells: 5 ind.; Melidoni to Lefka Ori mountains, Mavri peak, 650 m a.s.l., 6/1/2021, 35.351°N 024.0991°E, leg. KV, NHMC50.48975 shells: 2 ind.; Moni Chrysoskalitissas – Livadia, 18.iii.1990 leg. KV, NHMC50.5083 shells: 10 ind.; Moni Chrysoskalitissas – Pervolia, 2 km before quarry 29.iii.1991, 35.3355°N 023.5454°E, leg. KV, NHMC50.24469 shells: 1 ind.; Moni Chrysoskalitissas in a stream by road, 29.iii.1991, 35.3295°N 023.5567°E, leg. KV, NHMC50.5139 shells: 1 ind.; Moni Gkouvernetou, 8.iii.1997, 35.5852°N 024.1404°E, leg. KV, NHMC50.21942 shells: 6 ind., alcohol: 1 ind.; Moni Gkouvernetou – Moni Katholikou, 17.xi.1988, 35.5899°N 024.1467°E, leg. KV, NHMC50.5076 shells: 1 ind., alcohol: 1 ind.; Moni Gkouvernetou, Strongylo Kefali, 9.iii.1997, 35.5925°N 024.1355°E, leg. KV, NHMC50.21945 shells: 6 ind., alcohol: 1 ind.; Myloniana, 26.ii.1991, 35.4609°N 023.9514°E, leg. KV, NHMC50.18513 alcohol: juv.; Nopigia, 6.ii.1987, 35.5088°N 023.7231°E, leg. KV, NHMC 50.9242 shells: 1 ind.; Omalos plateau, south side, on scree, 29.v.2015, 35.323°N 023.8923°E, leg. KV, NHMC50.43563 shells: 2 ind., alcohol: juv.; Omalos plateau, 2 km north, 28.x.1989, 35.3662°N 023.9126°E, leg. KV, NHMC50.24698 shells: juv.; Palaia Agia Roumeli to Agia Paraskevi church, 1.vi.2015, 35.2414°N 023.9625°E, leg. MM, NHMC 50.43568 shells: 3 ind.; Palailoni, 15.xi.1990, 35.4274°N 024.2482°E, leg. KV, NHMC50.38484 alcohol: 5 ind.; Plaka – Almyrida, 25.xi.1990, 35.4529°N 024.2065°E, leg. KV, NHMC50.9224 shells: juv., alcohol: juv.; Platanos – Sfinari, 25.ii.1991, 35.4478°N 023.5833°E, leg. KV, NHMC50.9216 shells: 2 ind., alcohol: 2 ind.; Samaria gorge, after Vrysi spring by river at 470 m alt., 1.vi.2015, 35.2996°N 023.9482°E, leg. KV, NHMC50.43567 shells: juv.; Samaria gorge, just after Sideroportes, 31.v.2014, 35.2574°N 023.9672°E, leg. MM, NHMC50.41983 shells: 1 ind., alcohol: juv.; Samaria gorge, old village Samaria. 31.v.2014, 35.2905°N 023.959°E, leg. MM, NHMC50.41995 shells: 1 ind.; Saridantoni base, 21.v.2013, 35.3579°N 023.9152°E, leg. KV, NHMC50.40265 shells: 3 ind.; Mount Skloka, 27.x.1989, 35.5475°N 024.1774°E, leg. KV, NHMC50.18546 shells: 3 ind.; Mount Skloka, 29.iv.1993, 35.5559°N 024.1640°E, leg. KV, NHMC50.21030 shells: 2 ind., alcohol: 1 ind.; Sougia, 5.xi.1994, 35.2506°N 023.8087°E, leg. KV, NHMC50.28119 shells juv.; Sougia – Lissos, 29.x.1989, 35.2432°N 023.7843°E, leg. KV, NHMC50.5080 shells: 9

ind.; Tavronitis, 7.v.1987, 35.532°N 023.8255°E, leg. KV, NHMC50.9235 shells: juv., alcohol: 7 ind.; Theriso gorge, 300 m alt., 8.viii.2008, 35.4374°N 023.9933°E, leg. Georgantis, NHMC50.32269 shells: 2 ind.; Theriso gorge, 400 m alt., 8.viii.2008, 35.4406°N 023.9885°E, leg. Georgantis, NHMC50.33483 shells: 5 ind.; same locality 7.ix.2008 leg. Georgantis, NHMC50.33301 shells: 5 ind.; same locality, 7.x.2008, leg. Georgantis, NHMC50.32914 shells: 1 ind., alcohol: 1 ind.; same locality, 3.xi.2008, leg. Georgantis, NHMC50.33512 shells: 2 ind., alcohol: juv.; same locality, 8.xii.2008, leg. Georgantis, NHMC50.32807 alcohol: 3 ind.; same locality, 14.i.2009, leg. Georgantis, NHMC 50.32737 shells: 1 ind., alcohol: 2 ind.; same locality, 13. ii.2009, leg. Georgantis, NHMC50.32235 shells: 16 ind., alcohol: 4 ind.; same locality, 11.iii.2009, leg. Georgantis, NHMC50.32276 shells: 1 ind., alcohol: 1 ind.; same locality, 4.iv.2009, leg. Georgantis, NHMC50.32665 shells: 2 ind., alcohol: juv.; same locality, 14.v.2009, leg. Georgantis, NHMC50.32783 shells: 1 ind.; same locality, 8.vi.2009, leg. Georgantis, NHMC50.33513 shells: juv.; Theriso to Mount Kaloros, at Kakoperato mitato, 1400 m alt., 22.v.2013, 35.3552°N 023.9962°E, leg. KV, NHMC50.40275 shells: juv.; Theriso to Mount Kaloros, at Kakoperato mitato, 1400 m alt., 2.iii.2014, 35.3546°N 023.9972°E, leg. KV, NHMC50.41299 shells: juv.; Tigani, 17.iv.1996, 35.6078°N 023.6031°E, leg. KV, NHMC50.7361 shells: 1 ind., alcohol: juv.; Tigani cape, 28.ix.1985, 35.5876°N 023.5981°E, leg. KV, NHMC50.24470 shells: 1 ind.; Topolia, 18.iii.1990, 35.4274°N 023.6863°E, leg. KV, NHMC50.5084 shells: 3 ind.; Tzani Spilios cave entrance, 24.x.2005, 35.3492°N 023.9078°E, leg. KV, NHMC50.25736 alcohol: 2 ind.; Tzitzifes - Fres 9/5/1987, 35.3719°N 024.1465°E, leg. KV, NHMC50.5075 shells: 7 ind., alcohol: 2 ind.; Vafes, Kryonerida gorge, 15.iii.2014, 35.3596°N 024.1724°E, leg. MM, NHMC50.41348 shells: 2 ind., alcohol: 4 ind.; Vamos, 1.xii.1984, 35.4065°N 024.1985°E, leg. MM, NHMC50.22007 shells: 1 ind., alcohol: 2 ind.; Varypetro, 26.ii.1991, 35.463°N 023.9695°E, leg. KV, NHMC50.18500 shells: juv.; alcohol: juv.

ISLANDS OF CHANIA: Agioi Theodoroi isl., 31.iii.2018, 35.5357°N 023.9299°E, leg. Bitzilekis, NHMC50.47134 shells: 3 ind.; Agios Nikolaos isl., 14.vii.1997, 35.4887°N 024.1507°E, leg. Lymberakis NHMC50.40155 shells: 3 ind.; Gavdos isl., Karave – Alyki, 31.v.1987, 34.8154°N 024.1124°E, leg. KV, NHMC50.9183 alcohol: 1 ind.; Karave – Kastri, 24.iii.1991, 34.8406°N 024.1029°E, leg. KV, NHMC50.9119 shells: 1 ind.; Kastri to Sarakiniko, below water reservoir, 9.xi.1996, 34.8488°N 024.0874°E, leg. KV, NHMC50.40521 shells: 2 ind., alcohol: juv.; same locality, 16.iii.1997 leg. Paragamian, NHMC50.40507 alcohol: 3 ind.; same locality 12.vi.1997, leg. Paragamian, NHMC50.40494 alcohol: 2 ind.; Karga isl., 25.xi.1995 leg. KV, NHMC50.41859 shells: 1 ind.

IRAKLEIO REGIONAL UNIT: Agia Eirini, 23.iv.1988, 35.2823°N 025.1654°E, leg. MM, NHMC50.34116 alcohol: 1 ind.; Agia Eirini, Spilia, 24.v.2001, 35.2823°N 025.1654°E, leg. Georgiakakis, NHMC50.43058 shells: juv., alcohol: juv.; Agios Thomas, 13.xi.1990, 35.1467°N 025.0342°E, leg. KV, NHMC50.18502 shells: juv.; Fodele, 2.ii.1986, 35.3816°N 024.9579°E, leg. Legakis, NHMC50.33658 shells: juv.; Fodele, 16.iii.1990, 35.3878°N 024.9541°E, leg. KV, NHMC50.9248 shells: 2 ind.; Giouchtaki, 2 19.xii.1995, 35.2393°N 025.1319°E, leg. Iliopoulos NHMC50.33637 shells: juv.; Giouchtas Mt. 7.xii.1994, 35.25°N 025.15°E, leg. Iliopoulos, NHMC50.33121 shells: 8 ind.; Gonies 1 km to Astyraki, 8.iv.1991, 35.2942°N 024.9262°E, leg. KV, NHMC50.14936 shells: 4 ind., alcohol: juv.; Irakleio – Moires, 1.5 km after Macro (rural 2), 25.iii.2010, 35.2979°N 025.0864°E, leg. Georgopoulou, NHMC50.37310 alcohol: 1 ind.; Kainourgio Chorio, 10.i.1991, 35.2845°N 025.2622°E, leg. KV, NHMC50.5148 shells: 1 ind., alcohol: 2 ind.; Linoperamata, 25.i.1989, 35.344°N 025.047°E, leg. KV, NHMC50.5069 shells: 1 ind.; same locality, 24.xi.1989 leg. KV, NHMC50.33164 shells: 1 ind.; Linoperamata gorge, 24.xi.1989, 35.344°N 025.047°E, leg. KV, NHMC50.34077 alcohol: 3 ind.; Palaiokastro castle, 2.v.1999, 35.3655°N 025.0395°E, leg. MM, NHMC50.2504 shells: 1 ind.; Palaiokastro, Rodia, west slope, 2.v.1999, 35.3606°N 025.0307°E, leg. MM, NHMC50.33428 shells: 3 ind.; Pano Gouves W, 9.iii.2019, 35.3124°N 025.3105°E, leg. Bitzilekis, NHMC50.48097 shells: 3 ind.; Prinias, 13.xi.1990, 35.1698°N 025.0013°E, leg. KV, NHMC50.5082 shells: juv.; Mount Stroumpoulas, 31.iii.1995, 35.3433°N 024.9705°E, leg. MM, NHMC50.33378 shells: 2 ind., alcohol: 2 ind.; Tylissos, 11.i.1991, 35.297°N 025.0158°E, leg. KV, NHMC50.5145 alcohol: juv.; Voroi 1.iv.1991, 35.0685°N 024.8104°E, leg. KV, NHMC50.5088 shells: 1 ind.

RETHYMNO REGIONAL UNIT: Agia Galini, 20.iii.1990, 35.0972°N 024.6855°E, leg. KV, NHMC50.14929 shells: 1 ind.; Agia to Mount Kouloukonas, 18.xi.1990, 35.3692°N 024.7746°E, leg. KV, NHMC50.9231 shells: juv.; Aloides – Sisses, 20.xi.1990, 35.3734°N 024.8724°E, leg. KV, NHMC50.9226 shells: 5 ind., alcohol: 1 ind.; Asomatos – Mariou, 31.i.1988, 35.1913°N 024.4516°E, leg. KV, NHMC50.5077 alcohol: 6 ind.; Atsipades, 28.ii.1991, 35.2239°N 024.4502°E, leg. KV, NHMC50.14931 shells: juv.; Atsipopoulo, 14.xi.1990, 35.3633°N 024.4386°E, leg. KV, NHMC50.18518 shells: 1 ind.; Bali 16.iii.1990, 35.4073°N 024.7959°E, leg. KV, NHMC50.14937 shells: juv.; Chamalevri, 15.iii.1990, 35.3727°N 024.597°E, leg. KV, NHMC50.14926 alcohol: 1 ind.; Chonos, 20.xi.1990, 35.3381°N 024.886°E, leg. KV, NHMC50.9227 shells: 1 ind., alcohol: 2 ind.; Drimiskos, 2 km to Gianniou, 24.i.1989, 35.1702°N 024.4932°E, leg. KV, NHMC50.31925 shells: 2 ind., alcohol: 1 ind.; Drimiskos, 4 km to Gianniou, 24.i.1989, 35.1711°N 024.4788°E, leg. KV, NHMC50.6537 shells: 1 ind., alcohol: 7 ind.; Drosia – Damasta, 14.i.1991, 35.3487°N 024.9105°E, leg. KV, NHMC50.18527 shells: 7 ind.; Eleftherna – Arkadi, 19.xi.1990, 35.3257°N 024.6447 °E, leg. KV, NHMC50.5143 shells: 2 ind., alcohol: juv.; Elenes – Meronas, 28.ii.1991, 35.23°N 024.6148°E, leg. KV, NHMC50.9215 shells: 2 ind.; Gallos, 26.iv.1988, 35.3569°N 024.4529°E, leg. KV, NHMC50.9241 shells: 1 ind., alcohol: 1 ind.; Garazo, 22.iv.1999, 35.3497°N 024.7844°E, leg. Papadimitrakis, NHMC50.31914 alcohol: 2 ind.; same locality, 20.vii.1999, leg. Nikolakakis, NHMC50.46233 alcohol: juv.; same locality, 29.ix.1999, leg. Nikolakakis, NHMC50.39264 alcohol: 2 ind.; same locality, 8.ii.2000, leg. Nikolakakis, NHMC50.46348 alcohol: 1 ind.; Kardaki, 21.vii.1999, 35.2076°N 024.624°E, leg. Nikolakakis, NHMC50.1894 alcohol: juv.; Kare – Oros, 18.i.1991, 35.2891°N 024.495°E, leg. KV, NHMC50.11794 shells: 5 ind., alcohol: 2 ind.; Karoti, 8.v.1987, 35.3339°N 024.349°E, leg. KV, NHMC50.35886 shells: 1 ind., alcohol: juv.; Kissos, 28.ii.1991, 35.1968°N 024.5615°E, leg. KV, NHMC50.5085 shells: juv.; Kynigiana, 1.iv.1995, 35.3236°N 024.687°E, leg. KV, NHMC50.11653 shells: 5 ind., alcohol: 1 ind.; 1 km before Kynigiana, 10.xi.1994, 35.3211°N 024.6886°E, leg. MM, NHMC50.39268 shells: 1 ind., alcohol: 3 ind.; Makrygianni, 18.xi.1990, 35.3489°N 024.8506°E, leg. KV, NHMC50.5141 shells: 1 ind., alcohol: 1 ind.; Margarites – Kynigiana, 19.xi.1990, 35.3326°N 024.6881°E, leg. KV, NHMC50.5144 alcohol: 2 ind.; Melidoni, around cave, 18.i.1991, 35.3846°N 024.7275°E, leg. KV, NHMC50.5142 shells: 1 ind.; Moni Arkadiou 19.xi.1990, 35.3073°N 024.6289°E, leg. KV, NHMC50.14941 alcohol: 4 ind.; Moni Preveli, by stream, 30.xii.1996, 35.1518°N 024.4725°E, leg. Lymberakis, NHMC50.35885 shells: 3 ind.; Moni Preveli, river, 12.v.1997, 35.1518°N 024.4725°E, leg. Lymberakis, NHMC50.46243 alcohol: juv.; Moni Vosakou, 3.ii.2000, 35.3857°N 024.8418°E, leg. KV, NHMC50.13759 shells: 9 ind.; Patsos to Soros peak, 18.i.1991, 35.2373°N 024.5664°E, leg. KV, NHMC50.14946 shells: juv.; Perama at Geropotamos river, at km 52 from Rethymno to Irakleio, 17.xi.1990, 35.3615°N 024.763°E, leg. KV, NHMC50.14949 shells: 4 ind., alcohol: 2 ind.; Petres river, near national road, 8.v.1987, 35.3518°N 024.3572°E, leg. KV, NHMC50.18557 shells: 9 ind., alcohol: juv.; Plakias, 31.i.1988, 35.1918°N 024.3929°E, leg. KV, NHMC50.18544 alcohol: juv.; Potamon dam Amari, site A, 8.vi.2017, 35.2757°N 024.5815°E, leg. Amyntas, NHMC50.46367 alcohol: juv.; Rethymno, 14.xi.1990, 35.3713°N 024.4715°E, leg. KV, NHMC50.35846 shells: juv., alcohol: juv.; Sisses, 2.v.1988, 35.3932°N 024.8896°E, leg. KV, NHMC50.9243 shells: juv.; Sisses – Aloides, 4–5 km, 14.i.1991, 35.3757°N 024.8764°E, leg. KV, NHMC50.5146 shells: juv., alcohol: juv.; Skaleta, 16.iii.1990, 35.3918°N 024.6142°E, leg. KV, NHMC50.9247 shells: 8 ind., alcohol: juv.; Theodora crossroad, 18.xi.1990, 35.3426°N 024.8673°E, leg. KV, NHMC50.14938 shells: 1 ind.; Tsachiana – Doxaro, 18.xi.1990, 35.3403°N 024.843°E, leg. KV, NHMC50.11645 shells: juv., alcohol: 3 ind.

Shell characteristics and genitalia. Characteristics of the shell and the genitalia of the species have been previously described by Subai & Neubert (2014), who remarked that both size and shell shape in *L. barbata* does not considerably vary and that no local forms are known.

However, based on the study of the rich material held in the NHMC (177 populations, including 557 specimens for shell characters (Table 2) and 50 specimens from 32 populations for the genitalia), we observed a remarkable variation in most of characters studied. Among shell measurements, shell diameter varied most strikingly, ranging from 9.05 mm to 18.05 mm (mean 12.02 mm). In contrast, Subai & Neubert (2014) reported a narrower range for shell diameter, 9.7–14.4 mm. Moreover, we found the character of the umbilicus to vary significantly. An umbilicus partly covered by the columellar reflection of the peristome

Table 2. Shell measurements of adult *Lindholmiola barbata.*

	All (n = 557) Mean (min–max) in mm	Recent shells (n = 174) Mean (min–max) in mm	Old shells (n = 383) Mean (min–max) in mm
SH	5.32 (3.90–7.65)	5.24 (4.40–7.20)	5.36 (3.90–7.65)
SW	12.02 (9.05–18.05)	11.75 (9.50–15.25)	12.21 (9.05–18.05)
Whorls	6.1 (5.2–7.4)	6.0 (5.2–6.9)	6.1 (5.3–7.4)

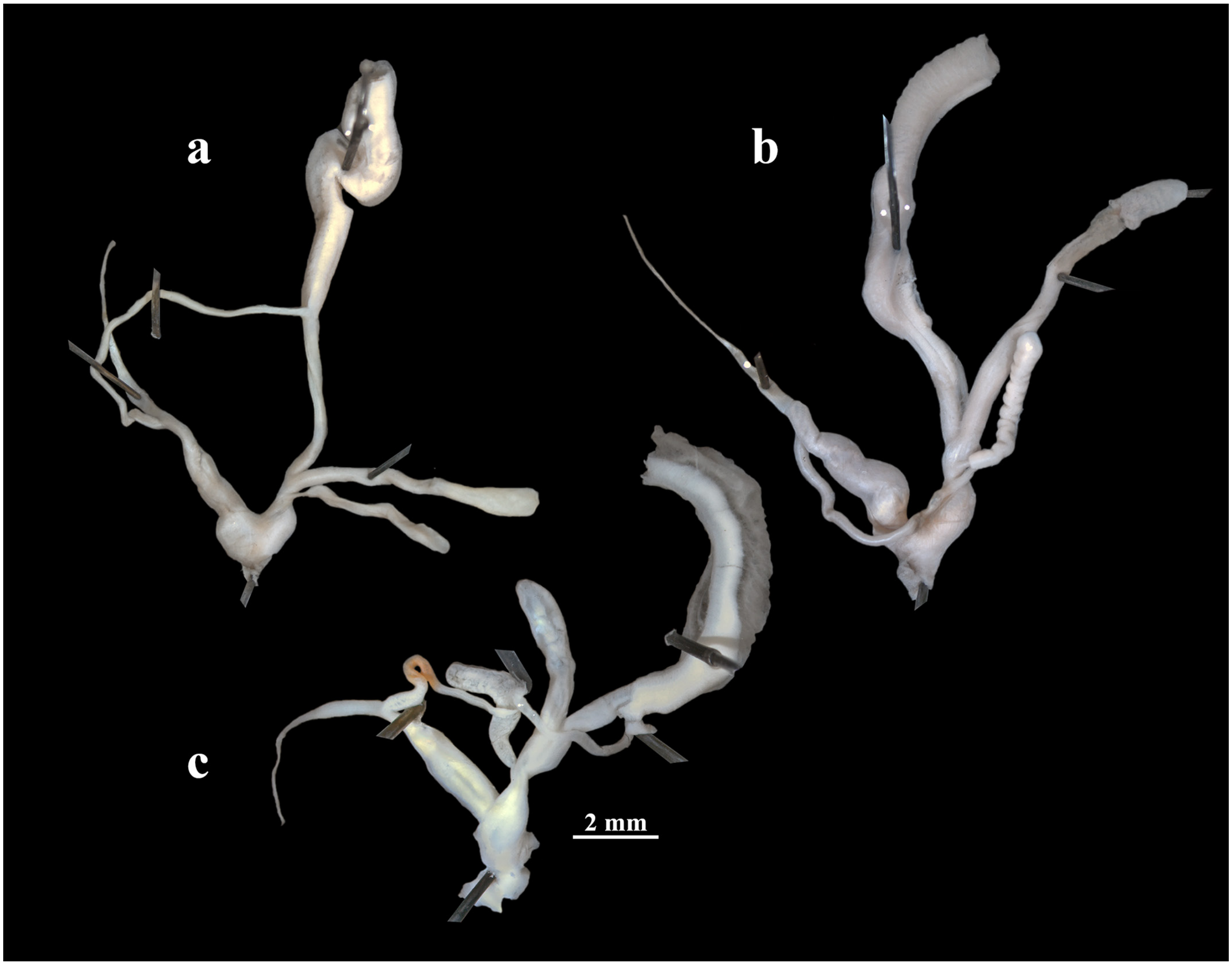

Figure 6. Interpopulation variability of the reproductive system of *Lindholmiola barbata*. **a**, from Vafes, Kryonerida gorge, collected 15.iii.2014. **b**, from Theriso gorge, collected 8.xii.2008. **c**, from Topolia, collected 18.iii.1990. All to same scale.

had been considered as one of the main diagnostic features of *L. barbata*, but in over 25% of our studied populations, the umbilicus was entirely closed, while in others, it was completely open.

We also observed considerable variability in the genitalia among populations and at various times of the year within the same population. In Figure 6 we present three characteristic variations of the genitalia. Differences in the form and relative length of the atrium, vagina, and penis are evident; however, the most striking variability is the form and the relative length of the glandula compared to the bursa copulatrix, which Subai & Neubert (2014) identified as a species-specific character. In the Theriso gorge population (sampled on 8.xii.2008), the glandula was less than half the length of the bursa copulatrix, while in the Vafes Kryonerida gorge population, it was more than two-thirds, and in the Topolia populations it was nearly equal (Fig. 6).

The form of the glandula varies from tubular to clavate, with or without crossing furrows. The Theriso Gorge individuals collected on 8.xii.2008 differed from those collected on 13.ii.2009 (Fig. 7a, b) in the form of the penis (clavate vs tubular), the length of the vagina, and the relative lengths of the glandula and bursa copulatrix. Also, specimens from the population north of Omalos plateau sampled on 10.iii.2009 differed from those of 15.v.2009 (Fig. 7c, d) in the length of the vagina and the form of the glandula.

Furthermore, the internal pilasters and folds of the penis varied significantly between populations and in different months, exceeding the species-specific characteristics reported by Subai & Neubert (2014) for *L. barbata* and overlapping with those of congeneric species. Whereas Subai & Neubert (2014) described *L. barbata* as having

Figure 7. Intrapopulation seasonal variability of the reproductive system of *Lindholmiola barbata*. **a**, **b**, from Theriso gorge, collected 8.xii.2008 and 13.ii.2009, respectively. **c**, **d**, from north of Omalos plateau, collected 10.iii.2009 and 15.v.2009, respectively. All to same scale.

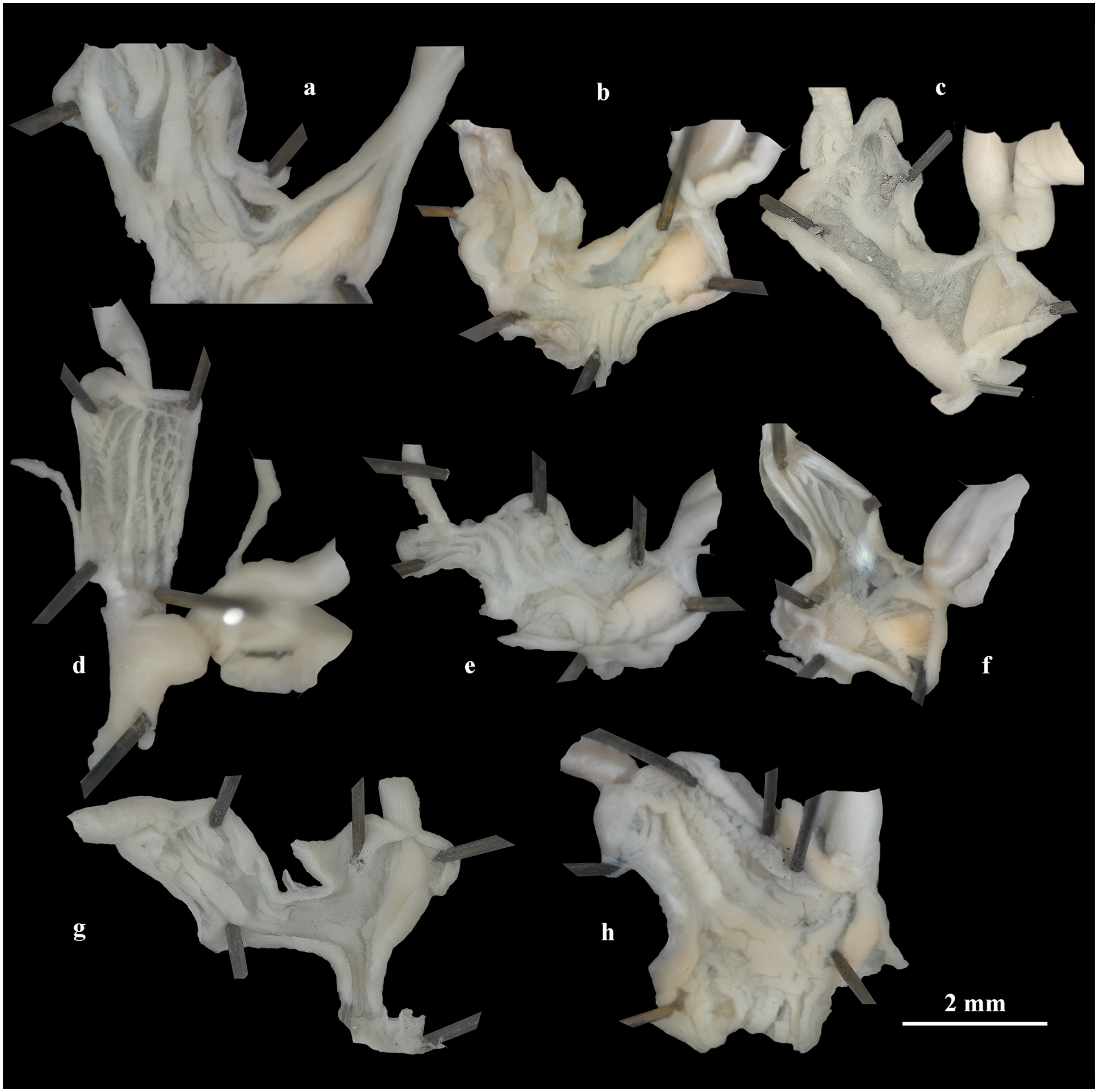

Figure 8. Variability of inter- and intrapopulation of penis, atrium, and vagina of *Lindholmiola barbata*. **a**, from Theriso gorge, collected 13.ii.2009. **b**, from Theriso gorge, collected 8.xii.2008. **c**, **d**, from north of Omalos plateau, collected 15.v.2009 and 10.iii.2009, respectively. **e**, from Vafes, Kryonerida gorge, collected 15.iii.2014. **f**, from Asomatos – Mariou, collected 31.i.1988. **g**, from Linoperamata gorge, collected 24.xi.1989. **h**, from Tzitzifes – Fres, collected 9.v.1987. All to same scale.

two penial pilasters, we found a range of configurations, including longitudinal folds and 1–3 or more longitudinal, V-shaped penial pilasters (Fig. 8).

Ecology and distribution. *Lindholmiola barbata* prefers calcareous substrates rich in organic material. It lives under stones, decaying tree trunks, and leaf litter, from sea level to 2000 m a.s.l. Dense populations are found in shady areas with lowland shrubs, in forests, and in cultivated areas. This species is distributed in western and central Crete (Fig. 9) and occurs on the adjacent islands.

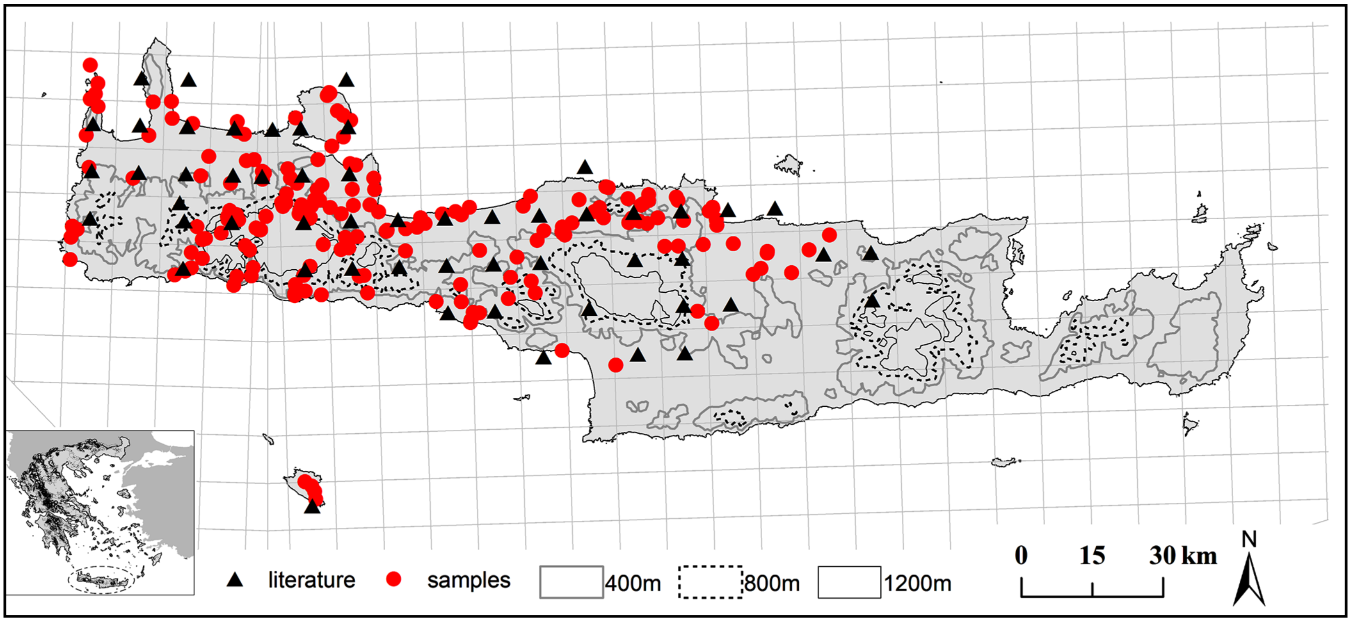

Figure 9. Distribution of *Lindholmiola barbata*. Bibliographic data are presented in 10 × 10 km UTM squares based on Subai & Neubert (2014) for Crete and on Welter-Schultes (1998) for Gavdos.

Shell height, diameter, and the number of whorls increase notably from sea level to 1200 m a.s.l. Above this altitude they show a tendency to stabilise at larger sizes (Fig. 10), which is not statistically significant due to the very small number of specimens. Populations with larger shells exceeding 14 mm in SD are found in the northern Lefka Ori mountains, at around 1000 m in altitude. In the same area, most of the populations having entirely closed umbilici are also observed. On the contrary, smaller shells less than 11 mm SD are typically found in alluvial soils in cultivated areas and on islands, including Gavdos. The distinct geographical concentration of populations with larger shells suggests that they could possibly be designated as a separate subspecies. In contrast, the variation observed among populations with smaller shells seems to be primarily driven by ecological factors, likely related to high population densities and diverse habitat types.

DISCUSSION

The presence of *Lindholmiola wilhelminae* in Crete has been previously regarded as the southernmost geographic

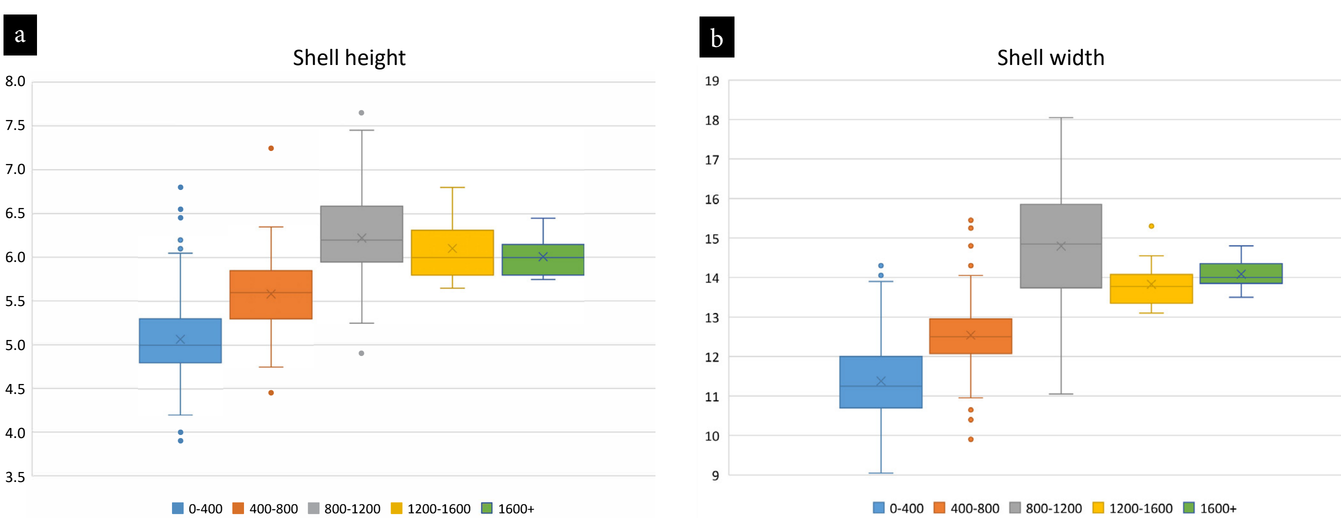

Figure 10. Altitudinal variation of shell height (**a**) and shell diameter (**b**) of *Lindholmiola barbata*.

limit of the genus *Helicodonta*, with the species potentially representing a relictual element in the Cretan fauna (Welter-Schultes 2012). However, our examination of the reproductive system of *L. wilheminae* leaves no doubt that the species should be reclassified as *Lindholmiola*, similar to the reclassification of *L. gyria* in south-western Turkey (Subai & Neubert 2014). Despite differences in shell and genital characters between the two species, they share one of the most fundamental characteristics of the genus *Helicodonta*: the immersion of the first whorls in relation to the last. This characteristic is not observed in any other species of *Lindholmiola*. We propose that this feature does not necessarily indicate a closer phylogenetic relationship between *L. gyria* and *L. wilhelminae*, but may instead result from convergent evolution, given their limited areas of geographic distribution without paleogeographic affinities. The former occurs in the south-eastern limits of the genus *Lindholmiola* in south-western Turkey, while the latter is at the south-eastern limits of the genus in Greece. Research using molecular data is necessary to confirm this hypothesis.

It is particularly noteworthy that there is a statistically significant difference in shell characteristics between recent and older (primarily subfossil) shells of *L. wilhelminae.* It is well documented that a species' population may exhibit smaller shells when population density is high or when under unfavourable environmental conditions (Goodfriend 1986). This phenomenon was also observed in *L. barbata*, where smaller shells were found in dense populations. We hypothesize that the larger recent shells of *L. wilhelminae* may be associated with a contemporary reduction in population density, as both populations with living specimens are very sparse. The species is listed as Endangered on the International Union for the Conservation of Nature (IUCN) Red List (Vardinoyannis & Triantis 2011). We attribute the decline in populations to the destruction of habitat, which is humid maquis, primarily due to the expansion of olive cultivations into formerly maquis-covered areas.

While Subai & Neubert (2014) argued that significant variations or local forms were not found in *L. barbata*, our data reveal that the variation in shells and genitalia variation exceeds the specific characters of this species, complicating the taxonomical revision of the genus *Lindholmiola* (Subai & Neubert 2014). In particular, species like *L. lens* and *L. corcyrensis*, which are conchologically closer to *L. barbata*, overlap in shell height, shell diameter, and number of whorls. Moreover, the columellar reflection of the peristome, which partly covers the umbilicus and was previously considered to be a species-specific character of *L. barbata*, was found to be absent in some populations or extended so much that it completely covers the umbilicus in others. In the reproductive system, the observed variation in the form and relative length of the glandula in relation to the bursa copulatrix, as well as the different forms of penial papillae (also previously assumed as species-specific characters of the genus), diminishes their taxonomic value; this necessitates additional investigation for new informative characters.

The seasonal variability observed in the genitalia of *L. barbata*, including variations in form, relative lengths, and penial pilasters, which were characters considered by Subai & Neubert 2014 as species-specific, not only challenges these authors' proposed revision of the genus *Lindholmiola*, but also raises questions about many other cases of classifications based on small differences, such as relative length, without considering intra- or interpopulation or seasonal variability.

The existing data on the relation between shell size and altitude, for species with a wide altitudinal range, are controversial: most studies support a negative relation (Goodfriend 1986 and references therein; Gospodinova *et al.* 2015), a few support a positive relation (Engelhard & Slik 1994), and others find no relation (Kempermann 1992). In Crete, Welter-Schultes (2000) found a non-linear relationship, in contrast to Engelhard & Slik (1994). In our study, we found that *L. barbata* exhibits a significant increase in shell height and width up to 1200 m a.s.l.; beyond that, there is a stabilisation in size with a slight, though not statistically significant, tendency to decrease. This pattern is also consistent with that proposed by Welter-Schultes (2000) for *Albinaria idaea* L. Pfeiffer, 1850. We believe that this pattern in *L. barbata* results from the observed phenotypic plasticity of this species and the complex ecological parameters of the Cretan environment, such as variation in rainfall and temperature, as well as human impacts, especially its mountainous areas.

As earlier found by Triantis *et al.* (2008), Mylonas & Vardinoyannis (2022), and Maroulis *et al.* (2024), it becomes increasingly apparent that accurately refining the taxonomy of land-snail species in isolated, ecologically complex regions like the Aegean archipelago requires ample material of both shells and live-collected specimens. This is crucial for gaining a comprehensive understanding of such species, by integrating a broad range of information, including population diversity, ecology, and biology, in our taxonomic process.

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REFERENCES

ENGELHARD GH, SLIK JWF. 1994. On altitude dependent characters in *Albinaria idaea* (L. Pfeiffer, 1849), with a revision of the species (Gastropoda Pulmonata: Clausiliidae). *Zoologische Mededelingen* **68**: 21–38.

GOODFRIEND GA. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology* **35**: 204–223. doi: 10.1093/sysbio/35.2.204

GOSPODINOVA AZ, GEORGIEV DG, MOLLOV IA. 2015. Preliminary data of the shell morphometry of populations of *Zebrina detrita* (Mollusca: Gastropoda: Pulmonata) from Bulgaria. *Ecologia Balkanica* **7**: 79–83.

KEMPERMAN TCM. 1992. Systematics and evolutionary history of the *Albinaria* species from the Ionian islands of Kephallinia and Ithaka (Gastropoda Pulmonata: Clausiliidae). Ph.D. thesis, Leiden University, 251 pp.

KERNEY MP, CAMERON RAD. 1979. *A Field Guide to the Land Snails of Britain and North-west Europe* Collins, London, 288 pp.

MAASSEN WJM. 1991. *Helicodonta gyria wilhelminae* nom.subspec. von der griechischen Insel Kreta (Gastropoda Pulmonata: Helicidae). *Basteria* **55**: 123–126.

MAROULIS L, KARAKASI D, BITZILEKIS E, DALIAS P, MYLONAS M, VARDINOYANNIS K. 2024. The terrestrial gastropods in three Dodecanese islands, Rhodes, Symi, Chalki (Aegean Sea, Greece). *Folia Malacologica* **32**: 1–18. doi: 10.12657/folmal.032.001

MYLONAS M, VARDINOYANNIS K. 2022. The terrestrial malacofauna of the southeast-central Aegean islets. *Journal of Conchology* **44**: 317–334.

SCHILEYKO AA. 2005. Treatise on Recent pulmonate molluscs. Part 14. Helicodontidae, Ciliellidae, Hygromiidae. *Ruthenica* Supplement **2**: 1907–2047.

SUBAI P, NEUBERT E. 2014. Revision of the genus *Lindholmiola* Hesse, 1931 (Gastropoda: Pulmonata: Helicodontidae). *Contributions to Natural History* **23**: 1–94.

TRIANTIS KA, VARDINOYANNIS K, MYLONAS M. 2008. Biogeography, land snails and incomplete data sets: the case of three island groups in the Aegean Sea. *Journal of Natural History* **42**: 467–490. https://doi.org/10.1080/00222930701835431

VARDINOYANNIS K. 1994. *Biogeography of Land Snails in the Southern Aegean Islands.* Ph.D. thesis, Department of Biology, University of Athens, 330 pp. [In Greek.]

VARDINOYANNIS K, TRIANTIS K. 2011. *Helicodonta wilhelminae. The IUCN Red List of Threatened Species* 2011: e.T156846A5006552. doi: 10.2305/iucn.uk.2011-1.rlts.t156846a5006552.en

WELTER-SCHULTES FW. 1998. Die Landschnecken der griechischen Insel Gavdos, der südlichsten Insel Europas. *Schriften zur Malakozoologie aus dem Haus der Natur – Cismar* **12**: 1–120.

WELTER-SCHULTES F. 2012. *European Non-marine Molluscs, a Guide for Species Identification.* Planet Poster Editions, Göttingen, 760 pp.

WELTER-SCHULTES FW. 2000. The pattern of geographical and altitudinal variation in the land snail *Albinaria idaea* from Crete (Gastropoda: Clausiliidae). *Biological Journal of the Linnean Society* **71**: 237–250. doi: 10.1111/j.1095-8312.2000.tb01256.x