



Research article

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A new species of *Metafruticicola* (Gastropoda, Hygromiidae) from the Aegean Archipelago and new anatomical and distributional data on some congeneric species

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Abstract. *Metafruticicola* is a diverse land snail genus inhabiting the north-eastern Mediterranean region from S Albania to Israel. In this study, we describe *Metafruticicola kavafis* sp. nov., a new species for science from Kasos Island. We also focus on the reproductive system of steno-endemic species and subspecies of the genus from small islands of the Aegean Archipelago, whose anatomy was previously completely unknown. These species are *M. crassicosta*, *M. pieperi*, *M. coartata gemina* and *M. nicosiana conciliatrix*. For the latter subspecies, only the outlines of the genitalia were previously given. Additionally, we investigated in detail for the first time the genital anatomy of *M. nicosiana nicosiana* from Cyprus. Hitherto, information on the genital apparatus of this subspecies was based on sparse data derived from sexually immature specimens. These new anatomical data contribute to a plethora of controversies concerning the subgeneric division of *Metafruticicola*, which was based solely on conchological features and especially the microsculpture of the teleoconch. We suggest that the current subgeneric division of the genus should be abandoned.

Keywords. *Metafruticicola*, distribution, taxonomy, Aegean, Cyprus.

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Introduction

The genus *Metafruticicola* Ihering, 1892 is a species rich genus in the Eastern Mediterranean region, distributed from the Aegean islands to Israel. Knowledge of the reproductive system of several taxa of

Metafruticicola has already been acquired for some time (Hesse 1884, 1931; Fuchs & Käufel 1934, 1936; Hudec 1971; Schileyko 1972; Reischütz 1983, 1986, 1988; Mylonas & Vardinoyannis 1989; Subai 1999). However, much of this knowledge is restricted to descriptive drawings of the external proximal part of the genitalia. Schileyko (1972), Reischütz (1988) and Subai (1999) were the first to give a detailed representation of the anatomy of five species along with the inner structure of the penis, i.e., the penial papilla. These species were *M. pellita* (Férussac, 1832) given by Schileyko (1972) and Reischütz (1988), *M. sublecta* (Maltzan, 1884) given by Schileyko (1972), *M. noverca* (Pfeiffer, 1853) and *M. redtenbacheri* (Pfeiffer, 1856) given by Reischütz (1988), who described the latter species as *M. coartata* (see Bank *et al.* 2013), and *M. occidentalis* Subai, 1999 given by Subai (1999). Welter-Schultes (2012) remarked that *Metafruticicola* is a genus which urgently needs revision. A year later, Bank *et al.* (2013) presented a thorough taxonomical revision based on the microsculpture of the shell. They divided the genus into four subgenera: *Metafruticicola* s. str., *Cretigena* Schileyko, 1972, *Rothifruticicola* Bank, Gittenberger & Neubert, 2013 and *Westerlundia* Kobelt, 1904. In addition, they provided detailed descriptions and illustrations of the genitalia of 11 species and subspecies, as well as data on the ratio between the different parts of the reproductive system. The aforementioned taxa are: *M. pellita*, *M. sublecta*, *M. redtenbacheri*, *M. nicosiana claudia* Bank & Welter-Schultes, 1998, *M. n. freytagi* (Maltzan, 1883), *M. n. maaseni* Bank, Gittenberger & Neubert, 2013, *M. dictaea* (Martens, 1889), *M. zonella* (Pfeiffer, 1865), *M. berytensis* (Pfeiffer, 1841), *M. naxiana* (Férussac, 1832) and *M. noverca*. Bank *et al.* (2013) also gave for those taxa descriptions and illustrations of the inner parts of the reproductive system, mainly of the penis, focusing on the structure of the penial papilla. Although they noticed that there was a lack of uniformity in both the external morphology of the genitalia as well as the form of penial papilla and the inner surface of both the penis and lower part of the duct of the gametolytic gland, they did not use these characters in their taxonomic revision, due to “the dearth of specimens with fully grown genitalia”. Schileyko & Féher (2017) gave detailed anatomical descriptions and illustrations of the genitalia and the structure of the penial papilla, as well as cross-sections through the penis for eight species of *Metafruticicola*, namely *M. pellita*, *M. sublecta*, *M. redtenbacheri*, *M. nicosiana soror* Fuchs & Käufel, 1936, *M. coartata coartata* Fuchs & Käufel, 1936, *M. naxiana*, *M. occidentalis* and *M. andria* (von Martens, 1889) and for two species of the closely related genus *Hiltrudia* Nordsieck, 1993. Schileyko & Féher (2017) primarily focused on the anatomy and the phylogenetic placement of *M. occidentalis* within the genus and placed it in a new subgenus, *Elbasania*. Based on some anatomical similarities, they speculated that *M. andria* also belongs in the new subgenus. The research efforts by Bank *et al.* (2013) and Schileyko & Féher (2017) contributed the most to our knowledge on the anatomy of the reproductive system of *Metafruticicola* and especially the structure of the penial papilla. Schileyko & Féher (2017) also claimed that penial papillae are a good taxonomical indicator distinguishing several taxa within the genus, although due to lack of material they did not proceed to a new revision. Mylonas *et al.* (2019) were the first to thoroughly examine the genitalia of *M. schuberti* (Roth, 1839) and *M. rugosissima* Bank, Gittenberger & Neubert, 2013 from the Kastellorizo island group, while Hausdorf *et al.* (2004) presented the genitalia of the alpine species *Metafruticicola dedegoelensis* Hausdorf, Gümüş & Yıldırım, 2004 and *M. oerstani* Hausdorf, Gümüş & Yıldırım, 2004 from Turkey. Currently 30 extant taxa are recognized. The genital anatomy of 20 of these is well-known, while for 17 the penis papilla has also been described.

The main purpose of this paper is to present, both conchologically and anatomically, a new species of *Metafruticicola* from the island of Kasos (Dodecanese, Greece). Moreover, the genitalia and the penial papilla of *M. crassicosta* Bank, Gittenberger & Neubert, 2013, *M. n. conciliatrix* Fuchs & Käufel, 1936, *M. pieperi* Bank, Gittenberger & Neubert, 2013 and *M. coartata gemina* Fuchs & Käufel, 1936, which are distributed in the Aegean Archipelago, and *M. nicosiana nicosiana* (Mousson, 1854) from Cyprus are described in detail for the first time. We also present new distributional and anatomical data from many islet populations of *M. coartata coartata*.

Material and methods

For the past three years, the first author collected ample material from many islands and islets of the Aegean. Additionally, we studied all the material in the collections of the Natural History Museum of Crete (NHMC), which is the result of an intensive collection effort by the researchers of NHMC over the last 40 years in the eastern Mediterranean region. All of the dissected specimens are preserved in 75% ethanol. The material was identified by the first author. Only fully mature shells and specimens were studied. Shell measurements were taken with a digital vernier caliper and the number of whorls was counted, both following Cameron (2003). Additionally, we counted the prominent shell interruptions, that are considered a pause in shell deposition due to aestivation, following Pollard *et al.* (1977).

Dissections were conducted under a Zeiss Stemi 508 stereo microscope and photos of the shells and anatomies were taken with a Jenoptik ProgRes Gryphax microscope camera mounted on the stereo microscope. Distributional maps were produced with the use of ArcGIS.

Abbreviations

D	=	shell diameter
dg	=	duct of the gametolytic gland
e	=	epiphallus
f	=	flagellum
fo	=	free oviduct
g	=	gametolytic gland.
H	=	shell height
p	=	penis
pp	=	penial papilla
pr	=	penial retractor
v	=	vagina
vd	=	vas deferens
W	=	number of whorls

Results

Class Gastropoda Cuvier, 1795
 Order Stylommatophora A. Schmidt, 1855
 Superfamily Helicoidea Rafinesque, 1815
 Family Hygromiidae Tryon, 1866
 Subfamily Metafruticicolinae Schileyko, 1972
 Genus *Metafruticicola* Ihering, 1892

***Metafruticicola kavafis* sp. nov.**

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Figs 1, 3

Diagnosis

A rather small species of *Metafruticicola* with a globular shell and a narrow umbilicus that may be covered to a small degree by the converging peristome. Shell light brownish with a whitish band on the periphery. Protoconch with regularly spaced axial ribs (Fig. 1A). Penis papilla is very long, curved at the tip and “tongue-shaped”.

Etymology

Named in honor of Konstantinos Kavafis (Constantine P. Cavafy), one of the greatest Greek poets, who lived in late 19th to early 20th century. His most renowned poem is Ithaca.

Material examined

Holotype

GREECE • 1 spec. in 75% alcohol and dissection (dimensions: H 8.69 mm, D 11.85 mm, W $5\frac{2}{8}$); Dodecanese, Kasos Island, Alonaki above Poli; 35.4031° N, 26.9415° E; 25 Nov. 1988; M. Mylonas leg.; NHMC 50.8135.

Paratypes

GREECE • 6 shells, 7 specs in 75% alcohol, 6 dissections; same collection data as for holotype; NHMC 50.51421.

Other material

GREECE • 29 shells, 2 specs in 75% alcohol, 1 dissection; same collection data as for holotype; 22 Mar. 2018; E. Bitzilekis leg.; NHMC 50.47114 • 2 shells; Dodecanese, Kasos Island, Prionas Mt; 35.4107° N, 26.9764° E; 15 Feb. 1992; K. Vardinoyannis leg.; NHMC 50.5650.

Locus typicus

Greece, Dodecanese, Kasos Island, Alonaki east of Poli.

Description (Fig. 1A)

SHELL. Pale brownish with one whitish band on the periphery and one prominent growth interruption. Upper insertion of the aperture is slightly descending. Peristome is slightly reflected with a pale yellowish internal thickening. It bears a narrow umbilicus, which is not or hardly covered by the reflected peristomial edge. Upper and lower insertion of the peristome are hardly converging and are either not connected or connected by a weakly developed callus. Whorls $5\frac{1}{8}$ – $5\frac{6}{8}$. The microsculpture of the protoconch carries regular, narrowly spaced, axial ribs that in some animals seem to transform to elongated pustulation. Teleoconch shiny, with radial growth ridges and without hairs or hair scars.

SHELL DIMENSIONS (n = 37). H 7.39–10.13 mm (mean = 8.71 mm); D 10.41–13.11 mm (mean = 11.81 mm); W $5\frac{1}{8}$ – $5\frac{6}{8}$ (mean = $5\frac{4}{8}$). All shells with one growth interruption.

GENITALIA (Fig. 1B–D). Flagellum long, one and a half times the length of epiphallus. Epiphallus evenly thick. Penial retractor is attached in the middle or upper third of the epiphallus. Penis bulky, thicker and quite distinct in its junction with epiphallus and half the size of the latter. At the junction with the epiphallus a prominent bump is formed. Inside the penis there is a very long tongue-like papilla with many irregular furrows, which folds like a scoop at the edge. Epiphallic pore opens on the top of the longitudinal slit, which runs throughout the whole length of the back of the “tongue”. Inner penial walls are smooth (Fig. 1C). Vas deferens slender. Vagina one third of penis’ length and half its width. The base of the duct of the gametolytic gland is thick-walled and as broad as the penis. Inside the thickened base of this duct there are slender longitudinal ridges (Fig. 1D). Free oviduct slender and at its junction to the duct of the gametolytic gland a bump is formed. Gametolytic gland is oval.

Distribution

Currently, it is only known from the eastern part of Kasos Island, east of the small village of Poli and eastwards till the mountain Prionas, which is the highest peak of the island.

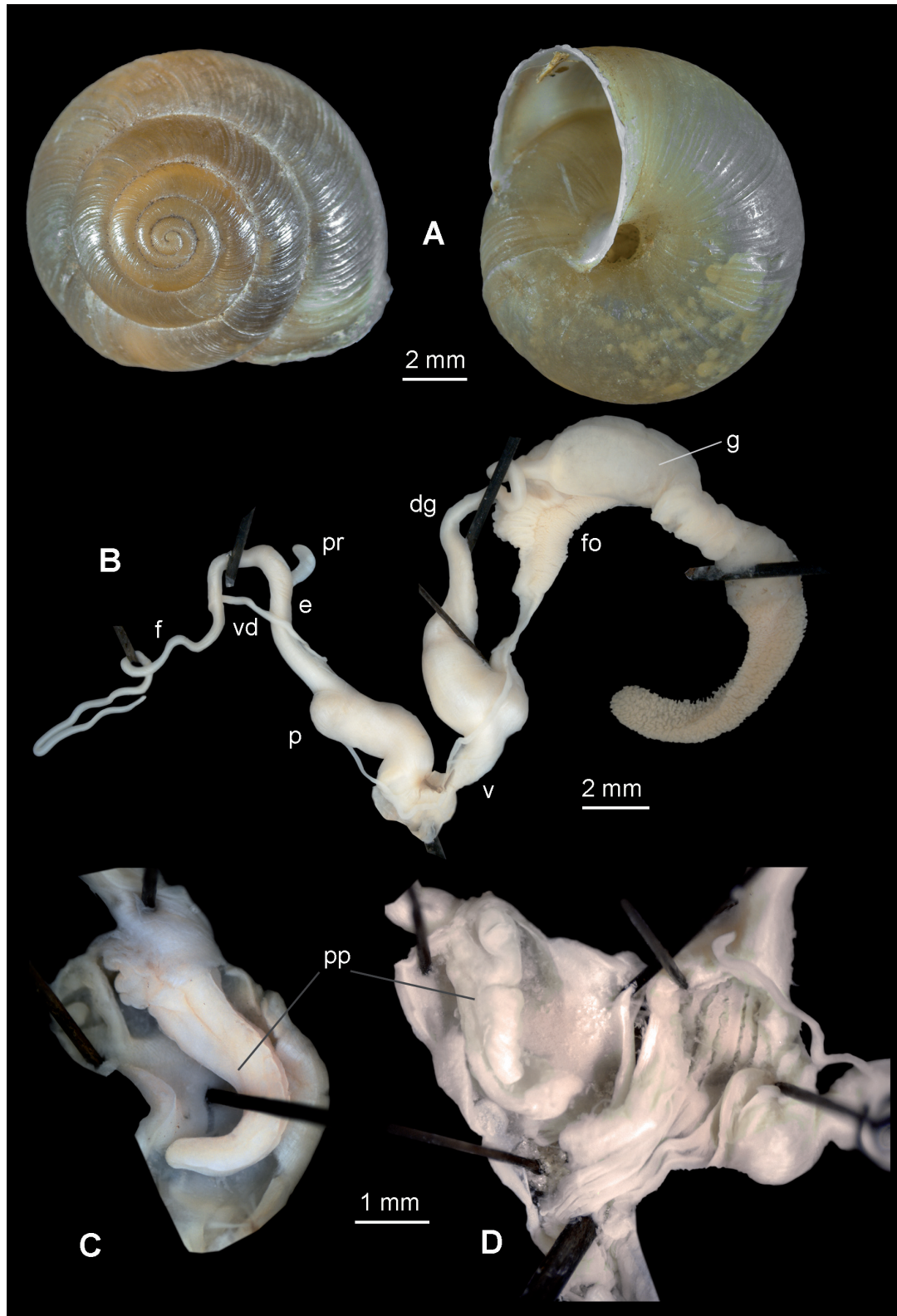


Fig. 1. *Metafruticicola (Rothifruticicola) kavafis* sp. nov., holotype, Greece, Kasos Island, Alonaki above Poli (NHMC 50.8135). **A.** Shell. **B.** General view of genitalia. **C.** Lateral view of penial papilla. **D.** Internal structure of penis, penial papilla and the base of the duct of the gametolytic gland. Abbreviations: see Material and methods.

Remarks

Metafruticicola kavafis sp. nov. can be distinguished from *M. n. conciliatrix* by its generally smaller shell. However, small specimens of *M. n. conciliatrix* are generally darker and less globular than *M. kavafis*. The penial papilla of *M. kavafis* is unique and can hardly be confused with that of any other congeneric species. It lives exclusively in phryganic ecosystems and abandoned cultivations. The species is not common in the area where it was found. Both living specimens and empty shells were found almost exclusively in close affiliation to the shrub *Lithodora hispidula* (Sm.) Griseb. In late March, juveniles and semi-adults were still active either in the litter or on *Lithodora hispidula*, whereas all living adults and some semi-adults that were found had already sealed their aperture with an epiphragm and were aestivating, facing upwards, deep in the litter under the plants. There were no signs of the animals under rock boulders or other phryganic plants like *Thymbra capitata* (L.) Cav. or *Sarcopoterium spinosum* (L.) Spach. *Metafruticicola kavafis* lives sympatrically with *M. pellita*. However, the latter species was found in many habitats, even under *Lithodora hispidula*, though it showed a clear preference for shelters under piles of rocks, where it could be found in very dense populations.

Metafruticicola nicosiana nicosiana (Mousson, 1854)

Fig. 2A, C, E

Material examined

CYPRUS – **Paphos district** • 3 specs in 75% alcohol, 3 dissections; Vouni Panagias; 34.9069° N, 32.6476° E; 23 Dec 2004; M. Mylonas leg.; NHMC 50.22238. – **Limassol district** • 6 shells, 6 specs in 75% alcohol, 6 dissections; Sanctuary of Apollo Hylates; 34.67° N, 32.8612° E; 17 Feb. 2000; K. Vardinoyannis leg.; NHMC 50.21350 • 9 shells, 1 spec. in 75% alcohol, 1 dissection; Agios Georgios Alamanou; 34.7171° N, 33.2303 E; 26 Feb. 2010; K. Vardinoyannis leg.; NHMC 50.35422.

Locus typicus

Cyprus “provenant des monts calcaires entre Cerines et Nicosie”.

Description

SHELL. Description is given by Bank *et al.* (2013: 101).

SHELL DIMENSIONS (n = 15). H 6.69–8.69 mm; D 9.91–12.7 mm; W 5–5⁴/₈.

GENITALIA (Fig. 2C, E). The reproductive system and its inner structures are described here for the first time. Flagellum very long, more than twice the length of epiphallus. Epiphallus evenly thick throughout its length. Penial retractor attached at the proximal third of the epiphallus. Penis bulky, thicker and quite distinct in its junction with epiphallus and less than half the length of the latter. Inside the penis there is a heart-shaped penial papilla, but when viewing it from the rear it appears globular. Specimens from Vouni Panagias show some horizontal ridges on the surface of the penial papilla, while in the animals from the Sanctuary of Apollo Hylates the surface is smooth (Fig. 2E). Epiphallic pore opens in the slit that divides the upper side of the papilla. Inner penial walls with few prominent vertical ridges (Fig. 2E). These ridges were significantly smoother in two out of the five animals. Vas deferens slender. Vagina as thick as the penis and half to one third of its length. The base of the duct of the gametolytic gland is as broad as the penis and is thick-walled. Inside its thickened base there are slender longitudinal ridges (Fig. 2E). Free oviduct around three quarters the length of the penis and half the width of the base of the duct of the gametolytic gland. Gametolytic gland globular to oval-shaped.

Metafruticicola nicosiana conciliatrix Fuchs & Käufel, 1936

Figs 2B, D, F, 3

Material examined

GREECE – **Dodecanese, Karpathos Island** • 44 shells, 8 specs in 75% alcohol; Avlona to Tristomo, Tsouli area at Malo Mt; 35.7997° N, 27.2043° E; alt. 400 m; 22 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39957 • 6 shells, 1 spec. in 75% alcohol; Asia; 35.681° N, 27.1319° E; 20 Dec. 2012; P. Lymberakis leg.; NHMC 50.39804 • 18 shells, 5 specs in 75% alcohol, 2 dissections; Asia; 35.6814° N, 27.1322° E; 24 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39991 • 13 shells, 1 spec. in 75% alcohol; Olympos, ascending to Profitis Ilias Mt east side; 35.7371° N, 27.1804° E; 22 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39973 • 12 shells, 2 specs in 75% alcohol, 2 dissections; Othos to Kali Limni; 35.5531° N, 27.1496° E; 9 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.8139 • 22 shells, 3 specs in 75% alcohol, 1 dissection; Pei; 35.7086° N, 27.1515° E; 24 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39986 •

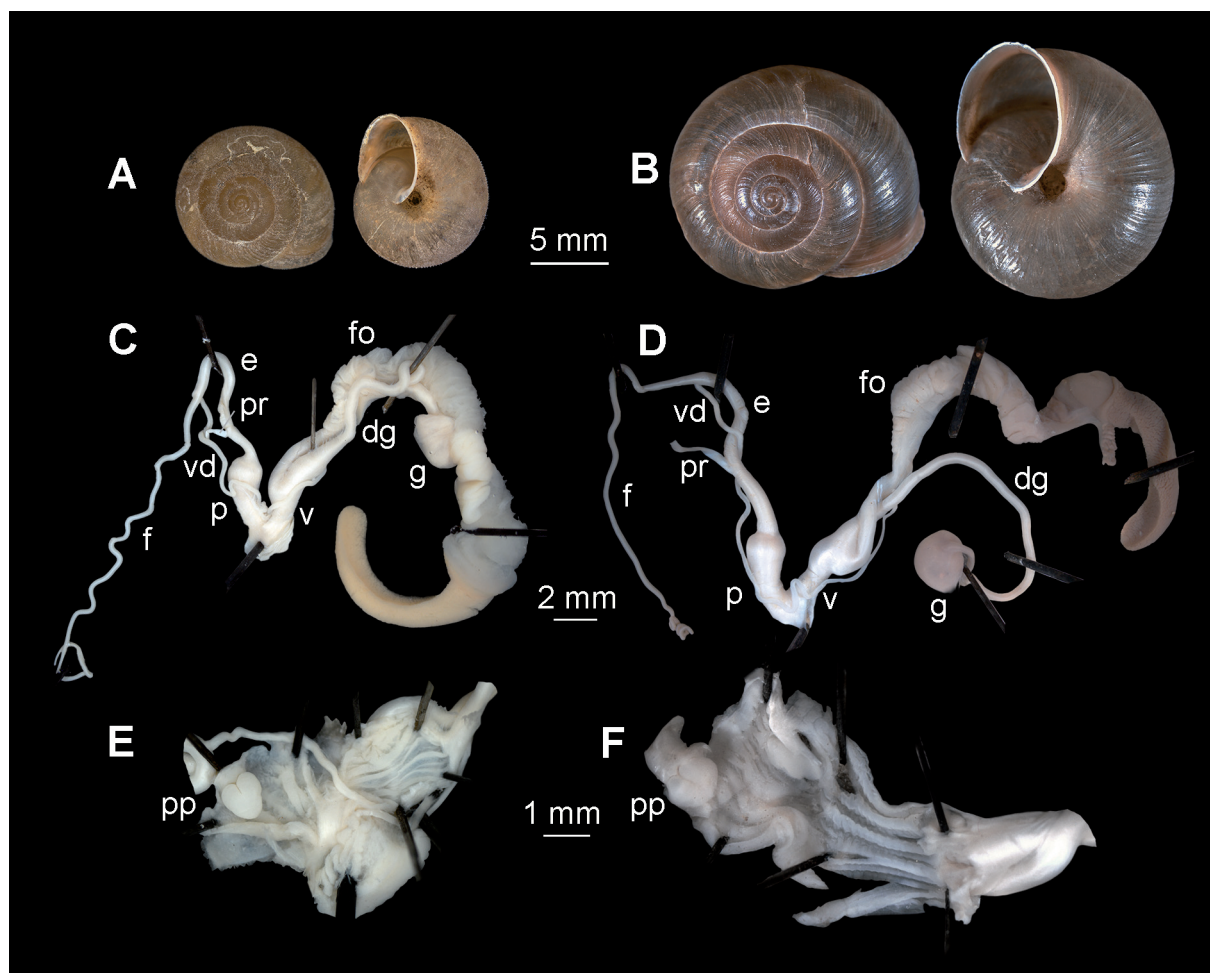


Fig. 2. *Metafruticicola* (*Rothifruticicola*) *nicosiana*. **A, C, E.** *M. (Rothifruticicola) nicosiana nicosiana* (Mousson, 1854), Cyprus, Limassol district, Sanctuary of Apollo Hylates (NHMC 50.21350). **A.** Shell. **C.** General view of genitalia. **E.** Internal structure of penis, penial papilla and the base of the duct of the gametolytic gland. **B, D, F.** *M. (Rothifruticicola) nicosiana conciliatrix* Fuchs & Käufel, 1936, Greece, Karpathos Island, Asia (NHMC 50.39991). **B.** Shell. **D.** General view of genitalia. **F.** Internal structure of penis, penial papilla and the base of the duct of the gametolytic gland. Abbreviations: see Material and methods.

32 shells, 1 spec. in 75% alcohol; Pilai; 35.7711° N, 27.191° E; 21 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39942 • 15 shells; Myrtonas; 35.5786° N, 27.1726° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5647 • 2 shells, 2 specs in 75% alcohol; Myrtonas; 35.5813° N, 27.1666° E; 23 Nov. 1988; M. Mylonas leg.; NHMC 50.8122 • 1 shell; Myrtonas NW; 35.5826° N, 27.1663° E; alt. 300 m; 14 Feb. 2016; M. Mylonas leg.; NHMC 50.45009 • 17 shells; Myrtonas NW; 35.5826° N, 27.1663° E; alt. 300 m; 14 Dec 2017; K. Vardinoyannis leg.; NHMC 50.46675 • 5 shells; Myrtonas at hill south; 35.5772° N, 27.1743° E; 16 Apr. 2015; M. Mylonas leg.; NHMC 50.43301 • 7 shells; Myrtonas to Spoa above Agios Ioannis beach; 35.6183° N, 27.1425° E; 21 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39965 • 9 shells, 1 spec. in 75% alcohol, 1 dissection; Spoa 1–3 km to Myrtonas; 35.6198° N, 27.141° E; 23 Nov. 1988; M. Mylonas leg.; NHMC 50.15320 • 25 shells, 1 spec. in 75% alcohol; Spoa to Mesochori; 35.6256° N, 27.1179° E; 25 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40018 • 2 shells, 1 spec. in 75% alcohol; Spoa to Mesochori; 35.6213° N, 27.1113° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.8029 • 3 shells; Mesochori; 35.628° N, 27.1095° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5611 • 4 shells, 1 spec. in 75% alcohol; Mesochori to Pyles; 35.6251° N, 27.1168° E; 8 Apr. 2000; K. Vardinoyannis leg.; NHMC 50.5800 • 1 spec. in 75% alcohol; Mesochori at Panagia church; 35.6251° N, 27.1168° E; 8 Apr. 2000; K. Vardinoyannis leg.; NHMC 50.2983 • 2 shells, 2 specs in 75% alcohol; Menetes to Kouroi; 35.5056° N, 27.1634° E; 17 Dec. 1989; P. Dalias leg.; NHMC 50.19087 • 4 shells; Lastos plateau; 35.5765° N, 27.1415° E; 9 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.8137 • 3 shells, 3 specs in 75% alcohol; Achordaia; 35.7836° N, 27.1931° E; 4 Apr. 2013; A. Trichas leg.; NHMC 50.41086 • 3 shells; Achordaia; 35.7836° N, 27.1931° E; 17 Dec. 2012; P. Lymberakis leg.; NHMC 50.39821 • 10 shells; Volada to Lastos; 35.5616° N, 27.1533° E; 8 Apr. 2000; A. Parmakelis leg.; NHMC 50.18227 • 6 shells; Aperi 6 km to Myrtonas; 35.5933° N, 27.172° E; 16 Apr. 2015; M. Mylonas leg.; NHMC 50.43545 • 10 shells, 1 spec. in 75% alcohol; Avlona to Olympos at Agios Konstantinos church; 35.761° N, 27.1793° E; 21 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.39949 • 9 shells; Spoa 1–3 km before; 35.6297° N, 27.1371° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5612 • 7 shells, 2 specs in 75% alcohol; Lefkos south at Koumpas Mt; 35.5823° N, 27.0871° E; 25 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40072 • 8 shells, 1 spec. in 75% alcohol; Lastos plateau, pinewood; 35.5757° N, 27.1297° E; alt. 700 m; 17 Apr. 2015; M. Mylonas leg.; NHMC 50.43304 • 11 shells; Kali Limni Mt; 35.5865° N, 27.133° E; alt. 700–950 m; 18 Apr. 2015; M. Mylonas leg.; NHMC 50.43305 • 14 shells, 1 spec. in 75% alcohol; Kali Limni Mt; 35.5816° N, 27.1381° E; 9 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.15318 • 9 shells, 10 specs in 75% alcohol, 2 dissections; Olympos-Monastery-Diafani; 35.7546° N, 27.1911° E; 22 Nov. 1988; M. Mylonas leg.; NHMC 50.15329 • 4 shells; Achamantia; 35.6867° N, 27.1477° E; 20 Dec. 2012; P. Lymberakis leg.; NHMC 50.39808 • 2 shells; Volada to Lastos; 35.5588° N, 27.1419° E; 26 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40112 • 2 shells, 1 spec. in 75% alcohol, 1 dissection; Pigadia south slopes; 35.5028° N, 27.2066° E; 20 Nov. 1988; M. Mylonas leg.; NHMC 50.39425 • 1 spec. in 75% alcohol, 1 dissection; Pigadia; 35.5061° N, 27.2109° E; 20 Nov. 1988; M. Mylonas leg.; NHMC 50.40120 • 5 shells; Pigadia north slopes; 35.5335° N, 27.2004° E; 20 Nov. 1988; M. Mylonas leg.; NHMC 50.15339 • 4 shells, 1 spec. in 75% alcohol; Pigadia SE, pinewood and phrygana; 35.5068° N, 27.2153° E; 7 Apr. 2000; A. Parmakelis leg.; NHMC 50.19088 • 1 shell; Agios Georgios; 35.5023° N, 27.1156° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5651 • 1 shell; Tristomo; 35.821° N, 27.225° E; 11 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.11919 • 3 shells; Avlona to Tristomo; 35.7862° N, 27.1938° E; 11 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5649 • 3 shells, 4 specs in 75% alcohol, 4 dissections; Othos to Stes; 35.5399° N, 27.1444° E; 21 Nov. 1988; M. Mylonas leg.; NHMC 50.19044 • 5 shells, 2 specs in 75% alcohol; Myrtonas to Spoa; 35.6079° N, 27.1454° E; 26 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40004 • 5 shells; Agios Thoros; 35.4486° N, 27.09° E; 8 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.19074 • 5 shells, 1 spec. in 75% alcohol; Lastos plateau to Kali Limni Mt; 35.5814° N, 27.1363° E; 18 Dec. 1989; P. Dalias leg.; NHMC 50.15312 • 5 shells; Pyles to Agia Kyriaki; 35.5445° N, 27.129° E; 19 Dec. 1989; M. Mylonas leg.; NHMC 50.19086 • 15 shells; Volada to Kali Limni Mt; 35.5587° N, 27.1454° E; 9 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.19083 • 8 shells, 1 spec. in 75% alcohol;

Kolla Mt; 35.5743° N, 27.1529° E; alt. 800 m; 17 Apr. 2015; M. Mylonas leg.; NHMC 50.43300 • 33 shells, 5 specs in 75% alcohol, 1 dissection; Kolla Mt; 35.5726° N, 27.1588° E; alt. 910 m; 17 Apr. 2015; M. Mylonas leg.; NHMC 50.43302 • 2 shells, 1 spec. in 75% alcohol; Kolla Mt; 35.5726° N, 27.1588° E; alt. 910 m; 13 Feb. 2016; M. Mylonas leg.; NHMC 50.44007 • 12 shells; Kyra Panagia bay; 35.5861° N, 27.1768° E; 12 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.5638 • 8 shells; Agios Nikolaos at spring; 35.5753° N, 27.1647° E; 18 Apr. 2015; M. Mylonas leg.; NHMC 50.43303 • 9 shells, 2 specs in 75% alcohol, 1 dissection; Lefkos E to Agios Georgios below Kali Limni Mt; 35.5951° N, 27.0995° E; 25 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40026 • 5 specs in 75% alcohol, 1 dissection; Avlona; 35.7693° N, 27.1819° E; 23 Nov. 1988; M. Mylonas leg.; NHMC 50.15330 • 3 specs in 75% alcohol; Avlona; 35.7679° N, 27.1769° E; 4 Apr. 2013; A. Trichas leg.; NHMC 50.41089 • 1 spec. in 75% alcohol, 1 dissection; Volada to Lastos at Agios Rafail; 35.5535° N, 27.1513° E; 26 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40077. – **Dodecanese, Saria Island** • 3 shells; 35.8427° N, 27.2318° E; 10 Apr. 1989; K. Vardinoyannis leg.; NHMC 50.15311 • 6 shells; Giaplos; 35.8413° N, 27.2319° E; 19 Dec. 2012; A. Trichas leg.; NHMC 50.39845 • 20 shells; Palatia to Argos; 35.8867° N, 27.2328° E; 23 Jan. 2013; K. Vardinoyannis leg.; NHMC 50.40091 • 9 shells; Palatia; 35.8877° N, 27.2306° E; 19 Dec. 2012; A. Trichas leg.; NHMC 50.39835.

Locus typicus

Greece, Karpathos island, Kalolimni Mountain (600 to 1000 m alt.)

Description

SHELL. Description is given by Bank *et al.* (2013: 103).

SHELL DIMENSIONS

- Karpathos Island: (n = 465) H 6.05–12.6 mm (mean = 9.86 mm); D 9.22–18.5 mm (mean = 14.52 mm); W $4\frac{5}{8}$ –6 (mean = $5\frac{4}{8}$).
- Saria Island: (n = 38) H 7.65–11.05 mm (mean = 9.43 mm); D 11.94–15.48 mm (mean = 14.04 mm); W 5 – $5\frac{7}{8}$ (mean = $5\frac{4}{8}$).

Most of the shells have one or rarely two growth interruptions.

GENITALIA (Fig. 2D, F). The inner structure of the reproductive system is given here for the first time (Fig. 2F). Flagellum very long, twice the length of epiphallus. Epiphallus becomes thicker closer to the penis. Penial retractor attached in the middle of the epiphallus. Penis less than half the length of the epiphallus, clavate, thicker and quite distinct at its junction with the epiphallus. Inside the penis there is a very short heart-shaped papilla, which seems globular from its rear side. In some specimens, the penial papilla is depressed in the distal edge causing it to be even shorter and less globular. Epiphallic pore starts with a V-shaped slot and opens in the slit that divides the upper side of the papilla. Inner penial walls have some short vertical ridges (Fig. 2F). Vas deferens slender. Vagina as thick as the penis and half to one third of its length. The base of the duct of the gametolytic gland is as broad as the penis and thick-walled and together with the distal part of the vagina they form a bump. Inside the thickened base of the duct there are slender longitudinal ridges (Fig. 2F). Free oviduct as long as the penis and half the width of the base of the duct of the gametolytic gland. At its junction with the duct, it forms a bump. Gametolytic gland globular.

Remarks

The shell measurements provided here have a wider range than those given by Bank *et al.* (2013) and are closer to the actual shell diversity of the subspecies due to the large number of studied specimens. It is the first time that *M. n. conciliatrix* is mentioned from the island of Saria, while Vardinoyannis (1994) was the first to record it from there as *M. nicosiana* (Fig. 3).

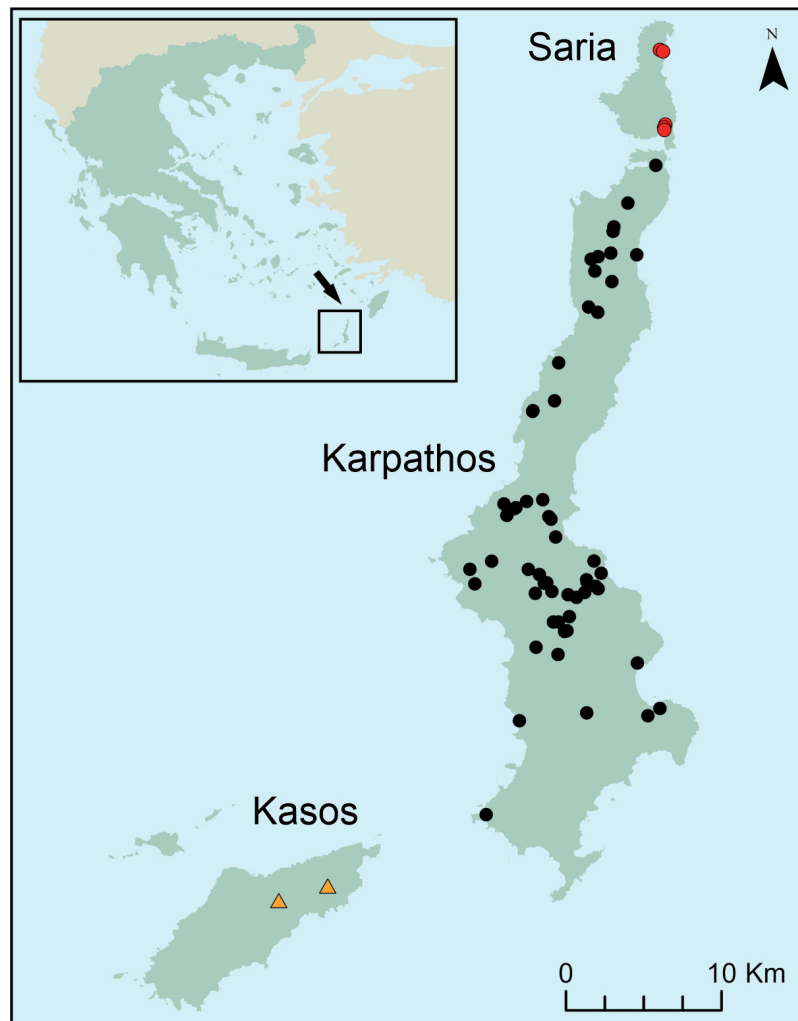


Fig. 3. Distribution of *Metafruticicola* (*Rothifruticicola*) *kavafis* sp. nov. (▲) and *M. (R.) nicosiana conciliatrix* Fuchs & Käufel, 1936 (●). New records of *M. n. conciliatrix* from Saria Island (●).

Our dissections confirm that the two subspecies of *M. nicosiana* also have closely related genital anatomies. In both taxa the anatomy shows that the relative lengths of the different parts of the genitalia are similar and the penial papillae are heart-shaped viewed from the upper side, with a central longitudinal groove in the middle. Even more impressive is the fact that animals from the Sanctuary of Apollo Hylates in Cyprus have more similar papillae to the ones from Karpathos than to the animals from Vouni Panagias from Cyprus, which exhibit some additional circular grooves on the surface of the papilla. However, the main shape of the papilla is similar in all of the animals of the two subspecies.

Metafruticicola pieperi Bank, Gittenberger & Neubert, 2013

Fig. 4

Material examined

GREECE – Crete, Lasithi province • 16 shells, 4 specs in 75% alcohol, 4 dissections; Avgo Islet; 35.6028° N, 25.5769° E; 2 Mar. 1994; M. Mylonas leg.; NHMC 50.40149 • 10 shells; same collection data as for preceding; 27 Apr. 2013; NHMC 50.40340 • 34 shells; same collection data as for preceding; 6 Jun. 2018; NHMC 50.47374 • 13 shells; same collection data as for preceding; 13 Feb. 2020; E. Bitzilekis leg.; NHMC 50.48936.

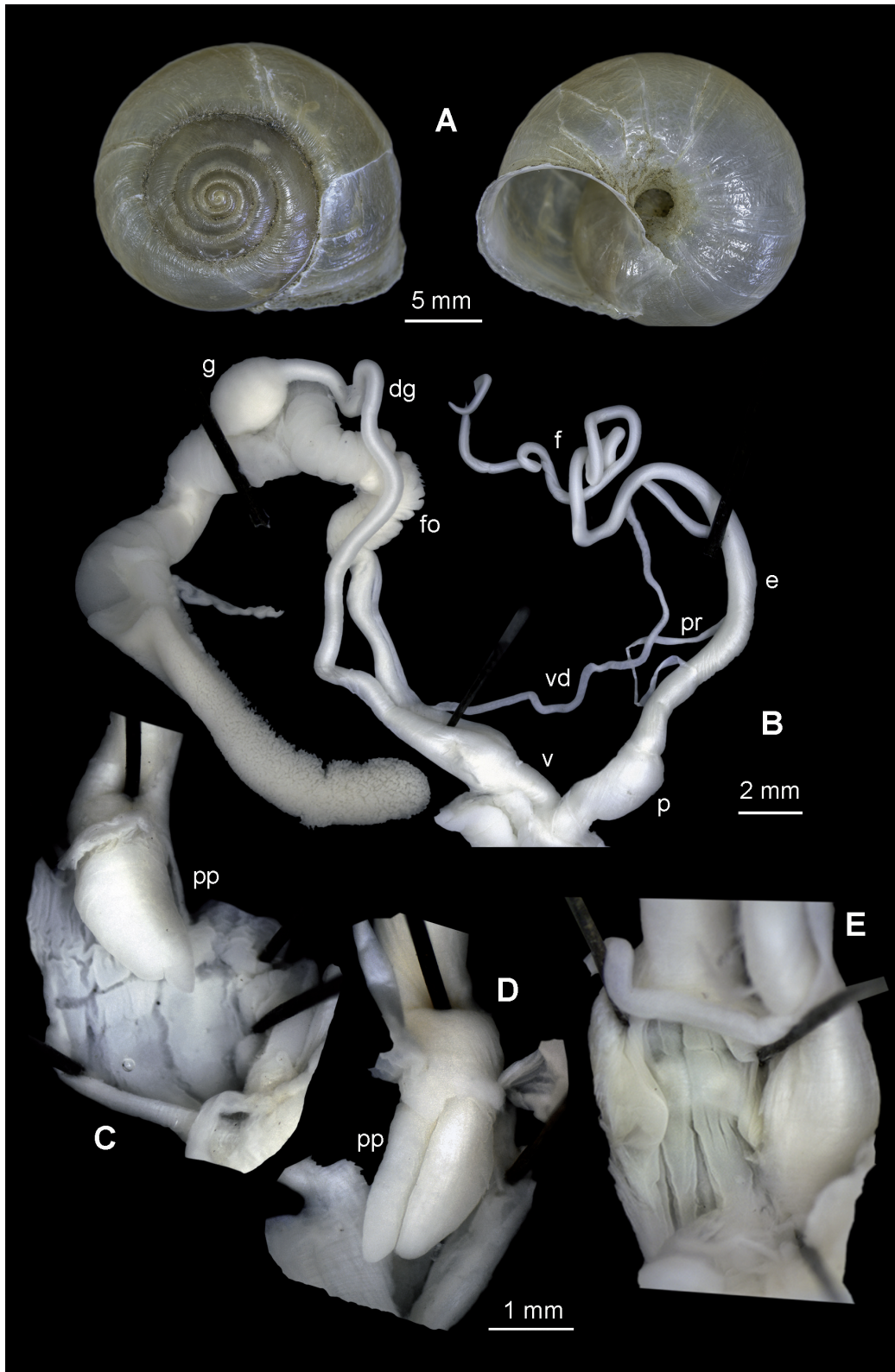


Fig. 4. *Metafruticicola (Rothifruticicola) pieperi* Bank, Gittenberger & Neubert, 2013, Greece, Crete, Lasithi province, Avgo Islet (NHMC 50.40149). **A.** Shell. **B.** General view of genitalia. **C.** Internal structure of penis and rear view of penial papilla. **D.** Front view of penial papilla. **E.** Base of the duct of the gametolytic gland. Abbreviations: see Material and methods.

Locus typicus

Greece, Avgo Islet, Lasithi province, Crete, Greece (40 km NE of Heraklion).

Description

SHELL. Shell description is given by Bank *et al.* (2013: 106).

SHELL DIMENSIONS (n = 73). H 11.82–15.35 mm (mean = 13.62 mm); D 18.45–23.9 mm (mean = 21.04 mm); W $5\frac{5}{8}$ – $6\frac{2}{8}$ (mean = 6). All the shells had one or two prominent growth interruptions.

GENITALIA (Fig. 4B–E). The reproductive system and its inner structures are presented here for the first time. Flagellum very long, three times the length of the epiphallus. Epiphallus evenly thick, but it gets a bit wider near the penis. Penial retractor is attached approximately at the middle of the epiphallus. Penis curved, thicker and distinct at its junction with epiphallus, less than half the size of the epiphallus. Inside the penis there is a triangular two-lobed papilla with rounded tips and in the back side there are some weakly formed circular grooves. One of the lobes is slightly larger than the other. Epiphallic pore starts with a V-shaped slot and opens in the slit dividing the two lobes. From the rear side the two-lobed papilla has a conical shape, revealing that the lobes are not separate. Inner penial walls have a few vertical ridges (Fig. 4C). Vas deferens slender. Vagina thick and around the same length as the penis. The base of the duct of the gametolytic gland is thick-walled and as broad as the penis. Inside its thickened base there are three pilaster-like thickenings and some longitudinal grooves (Fig. 4E). Free oviduct as broad as the duct of the gametolytic gland and twice the length of the penis. Gametolytic gland globular to oval-shaped.

Remarks

Shell measurements have a wider range than those given by Bank *et al.* (2013) and are closer to the actual shell diversity of the species due to the larger number of examined specimens.

At first glance, *Metafruticicola pieperi* seems to have a bilobed papilla which, according to the division of Schileyko & Féher (2017), could be placed alongside *M. redtenbacheri* and *M. nicosiana soror*. This outcome comes in line with Bank *et al.* (2013), since all these taxa belong to the subgenus *Rothifruticicola*. However, looking at the papilla from the back side, it becomes clear that we are rather dealing with a conical papilla with a deep longitudinal groove. Thus, it is closer to the shape of the papilla of *M. coartata* Fuchs & Käufel 1936, especially from the westernmost islands of its distribution (see below and Fig. 6), which however belongs to a different subgenus (*Westerlundia*). Moreover, the presence of “pilaster-like” structures on the inner surface of the thickened base of the duct of the gametolytic sac in *M. pieperi* has been recorded by Bank *et al.* (2013) only in *M. (M.) pellita*, which also belongs to a different subgenus.

Metafruticicola crassicosta Bank, Gittenberger & Neubert, 2013

Fig. 5

Material examined

GREECE – Crete, Chania province • 29 shells, 7 specs in 75% alcohol, 4 dissections; Agioi Theodoroi islet; 35.5357° N, 23.9299° E; 31 Mar. 2018; E. Bitzilekis leg; NHMC 50.43845

Locus typicus

Agioi Theodoroi Islet (Chania, Crete, Greece).

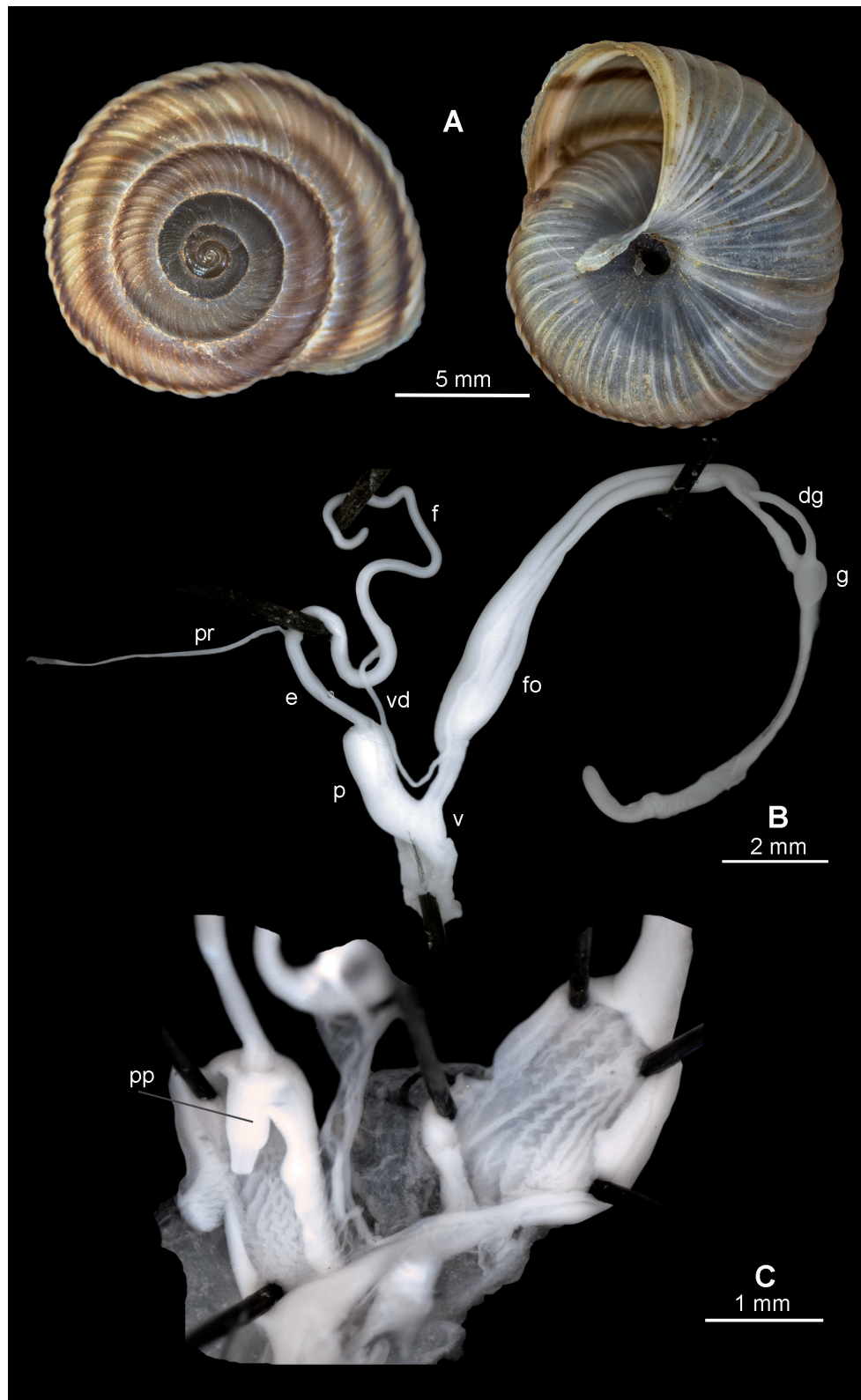


Fig. 5. *Metafruticicola (Cretigena) crassicosta* Bank, Gittenberger & Neubert, 2013, Greece, Crete, Chania province, Agioi Theodoroi Islet (NHMC 50.43845). **A.** Shell. **B.** General view of genitalia. **C.** Internal structure of penis, penial papilla and the base of the duct of the gametolytic gland. Abbreviations: see Material and methods.

Description

SHELL. Shell description is given by Bank *et al.* (2013: 81).

SHELL DIMENSIONS (n = 29). H 7.54–11.70 mm (mean = 9.1 mm); D 11.81–15.60 mm (mean = 13.71 mm); W $4\frac{4}{8}$ – $5\frac{2}{8}$ (mean = $4\frac{7}{8}$).

GENITALIA (Fig. 5B–C). The reproductive system and its inner structures are given here for the first time. Flagellum long, evenly thin, 1.5 times as long as epiphallus. Epiphallus almost as thin as flagellum. Penial retractor attached in the middle of the epiphallus. Penis cylindrical, much thicker and quite distinct from the epiphallus and approximately half the size of epiphallus. Inside the penis there is a smooth conical penial papilla which is thick at the base and thin at the edge. Epiphallic pore opens in the center of the slender edge. Inner penial walls have irregular grooves (Fig. 5C). Vas deferens very slender. Vagina thin and short, half to one third the length of the penis and twice the width of epiphallus. Base of the duct of the gametolytic gland as broad as the penis, thick-walled, and inside its thickened base there are some longitudinal ridges (Fig. 5C). Free oviduct as long as the penis and half the width of the base of the duct of the gametolytic gland. Gametolytic gland oval-shaped.

Remarks

The shell measurements provided here have a wider range than those given by Bank *et al.* (2013) and are closer to the actual shell diversity of the species due to the high number of examined specimens.

The genitalia and penial papilla of *M. crassicosta* are very similar to those of *M. sublecta*. In both species the penial papilla has a conical shape, thicker at the base and thin at the edge. Most differences in the shape of the penial papillae and the inner surface of the penis may be attributed to the fact that the examined specimens of *M. crassicosta* were not fully mature. *M. crassicosta* is endemic to Agioi Theodoroi Islet and lives sympatrically only with *M. noverca*.

Metafruticicola coartata coartata Fuchs & Käufel, 1936
Figs 6, 7A, 8

Material examined

GREECE – **Cyclades** • 7 shells, 19 specs in 75% alcohol, 4 dissections; Askania Islet; 36.2346° N, 25.2135° E; 22 Mar. 1993; M. Mylonas leg.; NHMC 50.4077 • 16 shells, 28 specs in 75% alcohol, 4 dissections; Christiani Islet; 36.2497° N, 25.2038° E; 19 Mar. 1993; M. Mylonas leg.; NHMC 50.3721 • 1 spec. in 95% alcohol; Thirasia Island; 36.4265° N, 25.3423° E; 26 May 2007; K. Vardinoyannis leg.; NHMC 50.42157 • 6 shells; Anafi Island, Moni Zoodochou Pigis to Moni Panagias Kalamiotissas; 36.3583° N, 25.8309° E; 26 Nov. 2021; L. Maroulis leg.; NHMC 50.49858 • 3 shells, 4 specs in 75% alcohol, 2 dissections; Fteno Islet; 36.3111° N, 25.7999° E; 22 Mar. 1993; M. Mylonas leg.; NHMC 50.3726 • 14 shells, 19 specs in 75% alcohol, 2 dissections; Makra Islet; 36.2693° N, 25.8857° E; 21 Mar. 1993; M. Mylonas leg.; NHMC 50.4056 • 8 shells; Pacheia Islet; 36.2737° N, 25.8308° E; 21 Mar. 1993; M. Mylonas leg.; NHMC 50.432. – **Dodecanese** • 46 shells, 3 specs in 75% alcohol, 2 dissections; Sochas Islet; 36.0573° N, 26.4047° E; 18 May 2018; P. Lymberakis leg.; NHMC 50.16877 • 18 shells, 15 specs in 75% alcohol, 3 dissections; Mikri Zafora Islet; 36.0467° N, 26.4096° E; 21 Apr. 1989; M. Mylonas leg.; NHMC 50.9955 • 22 shells; Safonidi Islet; 36.8867° N, 26.9211° E; 30 Mar. 2005; K. Triantis leg.; NHMC 50.26812.

Locus typicus

Greece, “Insel Astropalia” (= Astypalaia).

Description

SHELL. Shell description is given by Bank *et al.* (2013: 117).

SHELL DIMENSIONS (n = 141). H 6.54–12.64 mm; D 11.41–17.52 mm; W $5^{1/8}$ – $5^{7/8}$ whorls.

- Askania Islet (n = 7): H 7.29–12.64 mm (mean = 9.96 mm); D 12.15–16.03 mm (mean = 14.09); W $5^{4/8}$ – $5^{7/8}$ (mean = $5^{5/8}$). All of the shells with one or two prominent growth interruptions.
- Christiani Islet (n = 16): H 6.54–8.6 mm (mean = 7.62 mm); D 11.41–13.39 mm (mean = 12.15 mm); W $5^{1/8}$ – $5^{4/8}$ (mean = $5^{3/8}$). All of the shells with one or two prominent growth interruptions.
- Anafi Island (n = 6): H 7.17–8.43 mm (mean = 7.84 mm); D 11.86–14.75 mm (mean = 13.27 mm); W $5^{1/8}$ – $5^{3/8}$ (mean = $5^{2/8}$). All of the shells with one or two prominent growth interruptions.
- Fteno Islet (n = 3): H 7.72–8.06 mm (mean = 7.89 mm); D 12.3–12.88 mm (mean = 12.59 mm); W $5^{2/8}$ – $5^{4/8}$ (mean = $5^{3/8}$). Shells with one growth interruption.
- Makra Islet (n = 14): H 7.48–9.09 mm (mean = 8.25 mm); D 11.98–14.46 mm (mean = 13.23 mm); W $5^{1/8}$ – $5^{5/8}$ (mean = $5^{3/8}$). Most of the shells with two growth interruptions.
- Pacheia Islet (n = 8): H 7.25–8.28 mm (mean = 7.73 mm); D 11.85–13.72 mm (mean = 12.55 mm); W $5^{1/8}$ – $5^{4/8}$ (mean = $5^{2/8}$). All of the shells with one or two prominent growth interruptions.
- Sochas Islet (n = 46): H 8.7–11.11 mm (mean = 9.98 mm); D 13.68–17.52 mm (mean = 15.68 mm); W $5^{2/8}$ – $5^{7/8}$ (mean = $5^{5/8}$). Shells with one or rarely two interruptions.
- Mikri Zafora Islet (n = 19): H 8.77–11.45 mm (mean = 9.84 mm); D 12.32–16.18 mm (mean = 14.84 mm); W $5^{4/8}$ – $5^{7/8}$ (mean = $5^{5/8}$). Shells with two growth interruptions, several with three.
- Safonidi Islet (n = 22): H 7.53–8.69 mm (mean = 8.06 mm); D 11.08–13.07 mm (mean = 12.10 mm); W $5^{1/8}$ – $5^{4/8}$ (mean = $5^{3/8}$). Shells with one or rarely two interruptions.

GENITALIA (Fig. 6). Flagellum very long, three times the length of the epiphallus. Epiphallus evenly thick. Penial retractor attached in the proximal third of the epiphallus. Penis around three quarters the length of epiphallus in Makra, Mikri Zafora and Askania. In the specimens from Fteno, the penis is around one third the length of epiphallus. In the specimens from Askania and Fteno the penis is clavate, thicker and distinct at its junction with the epiphallus, while from Christiani, Makra, Sochas and Mikri Zafora islets, it is fusiform with less distinct boundaries with the epiphallus. Penial papilla has a smooth surface and a vertical groove in the center; the epiphallic pore lies at its base. In specimens from Sochas and Mikri Zafora the papilla is semi-ellipsoid, whereas in the animals from Christiani, Makra, Askania and Fteno islets the two parts of the papilla are longer, sub-cylindrical, bilobed but not separated, with rounded tips and one of these two parts is bulkier. Inner penial walls have a smooth surface apart from the specimens of Sochas and Mikri Zafora, where some prominent vertical grooves are observed (Fig. 6C), while in Makra these grooves are less prominent (Fig. 6D). Vas deferens slender. In Makra and Mikri Zafora the vagina is short and slender and has distinct boundaries with the thick base of the duct of the gametolytic gland. In Fteno and Askania the vagina is very short and thick and the boundaries with the base of the duct of the gametolytic gland are vague. Inside the thickened base of the duct there are some longitudinal ridges. Free oviduct is a bit longer than the penis and as broad as the duct of the gametolytic gland. Gametolytic gland is ovate.

Remarks

The shell measurements provided here have a wider range than those given by Bank *et al.* (2013), due to the populations of different islets that were examined in this study and the large number of specimens. Part of the material that was examined comes from islands and islets that were, until now, out of the distributional range of *M. c. coartata*, most of which were not previously known to host a species of *Metafruticicola* (Fig. 8).

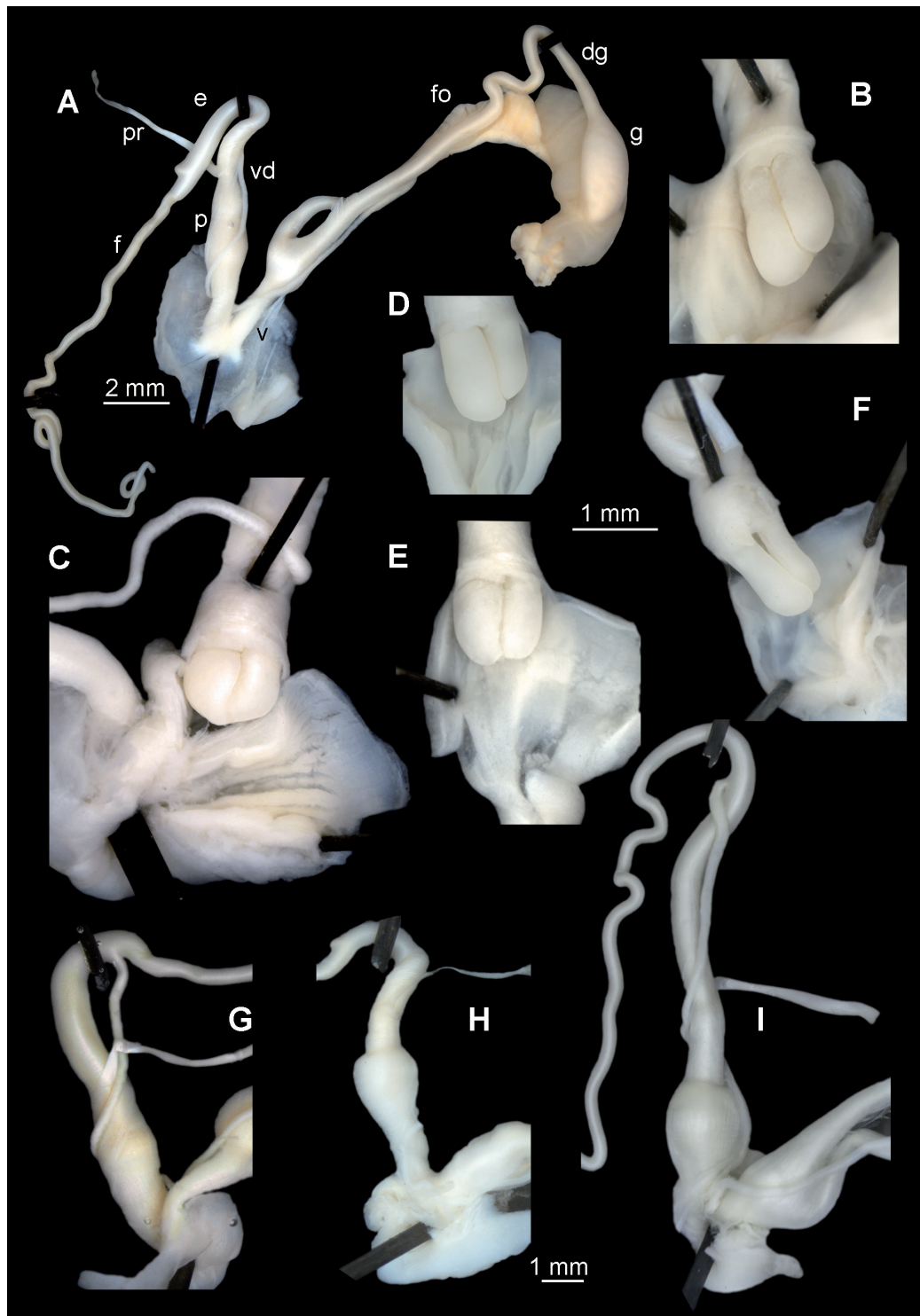


Fig. 6. *Metafruticicola* (*Westerlundia*) *coartata coartata* Fuchs & Käufel, 1936. **A, D.** Greece, Cyclades, Makra Islet (NHMC 50.4056). **B, I.** Greece, Cyclades, Fteno Islet (NHMC 50.3726). **C, G.** Greece, Dodecanese, Zafora Mikri Islet (NHMC 50.9955). **E, H.** Greece, Cyclades, Askania Islet (NHMC 50.4077). **F.** Greece, Cyclades, Christiani Islet (NHMC 50.3721). **A.** General view of genitalia. **B–F.** Diversity in the shape of penial papillae and inner surface of penial walls. **G–I.** Diversity in the shape of penis, vagina and the base of the duct of the gametolytic gland. Abbreviations: see Material and methods.

Metafruticicola coartata gemina Fuchs & Käufel, 1936

Fig 7B–D, 8

Material examined

GREECE – **Dodecanese** • 7 shells, 9 specs in 75% alcohol, 4 dissections; Karavia Nisia, north islet; 36.0006° N, 26.4354° E; 21 Apr. 1989; M. Mylonas leg.; NHMC 50.6805 • 6 shells; same collection data as for preceding; 16 May 2018; P. Lymberakis leg.; NHMC 50.20961.

Locus typicus

Greece, Karavia Nisia, northern larger islet of the two.

Description

SHELL. Shell description is given by Bank *et al.* (2013: 119).

SHELL DIMENSIONS ($n = 13$). H 8.18–9.83 mm (mean = 9.23 mm); D 14.27–15.65 mm (mean = 14.98 mm); W $5\frac{4}{8}$ – $5\frac{6}{8}$ (mean = $5\frac{5}{8}$). All the shells with two growth interruptions.

GENITALIA (Fig. 7C–D). The reproductive system and its inner structures are presented for the first time. Flagellum at least twice the length of the epiphallus. Epiphallus evenly thick. Penial retractor is attached near the junction of the epiphallus with the penis. Penis fusiform, around the same length as the epiphallus and with less distinct boundaries with the latter. Penial papilla semi-ellipsoid with smooth surface and a vertical groove in the center; the epiphallic pore lies at its base. Inner penial surface has some prominent vertical ridges (Fig. 7D). Vas deferens slender. Vagina short and slender with distinct boundaries to the thick base of the duct of the gametolytic gland. Gametolytic gland is ovate.

Remarks

The shell measurements provided here are slightly different than those given by Bank *et al.* (2013). Both subspecies of *M. coartata* share similar genitalia, revealing a close relationship between them. Penial papillae of the animals from Karavi north islet are semi-ellipsoid and almost identical to those of *M. c. coartata* from Sochas and Mikri Zafora islets, even though they belong to different subspecies. All three islets belong to the same island group and are part of the Syrna archipelago. In general, penial papillae of the westernmost islets of *M. coartata*'s distribution (Christiani, Askania, Fteno and Makra) show a more bilobed shape.

Discussion

The plethora of specimens in the collections of NHMC, both dry shells and in 75% ethanol, gave us the opportunity to re-approach and more accurately determine several morphological features, concerning certain taxa of the Aegean Archipelago and Cyprus. These traits are primarily anatomical aspects of the genitalia of the species and subspecies under investigation, that were previously completely unknown or very poorly known and secondly conchological characteristics.

Metafruticicola nicosiana is a polytypic species with seven subspecies, six of which occur in the southern islands of the Aegean (Crete, Gavdos, Karpathos, Rhodes) and the seventh in Cyprus. The four subspecies whose genitalia and the shape of penial papilla were known (Bank *et al.* 2013: 102; Schileiko & Féher 2017: 69) are *M. n. claudia* from Gavdos Isl., *M. n. freytagi* from western Crete, *M. n. maasseni* from eastern Crete and *M. n. soror* from Rhodes Isl. Fuchs & Käufel (1936) gave a vague drawing of the genitalia of *M. n. conciliatrix* from Karpathos with no further written description. They stated that *M. n. conciliatrix* and *M. n. soror* have strong similarities with *M. n. nicosiana*. However, they based their conclusion on sparse anatomical data from sexually immature specimens of an attempt

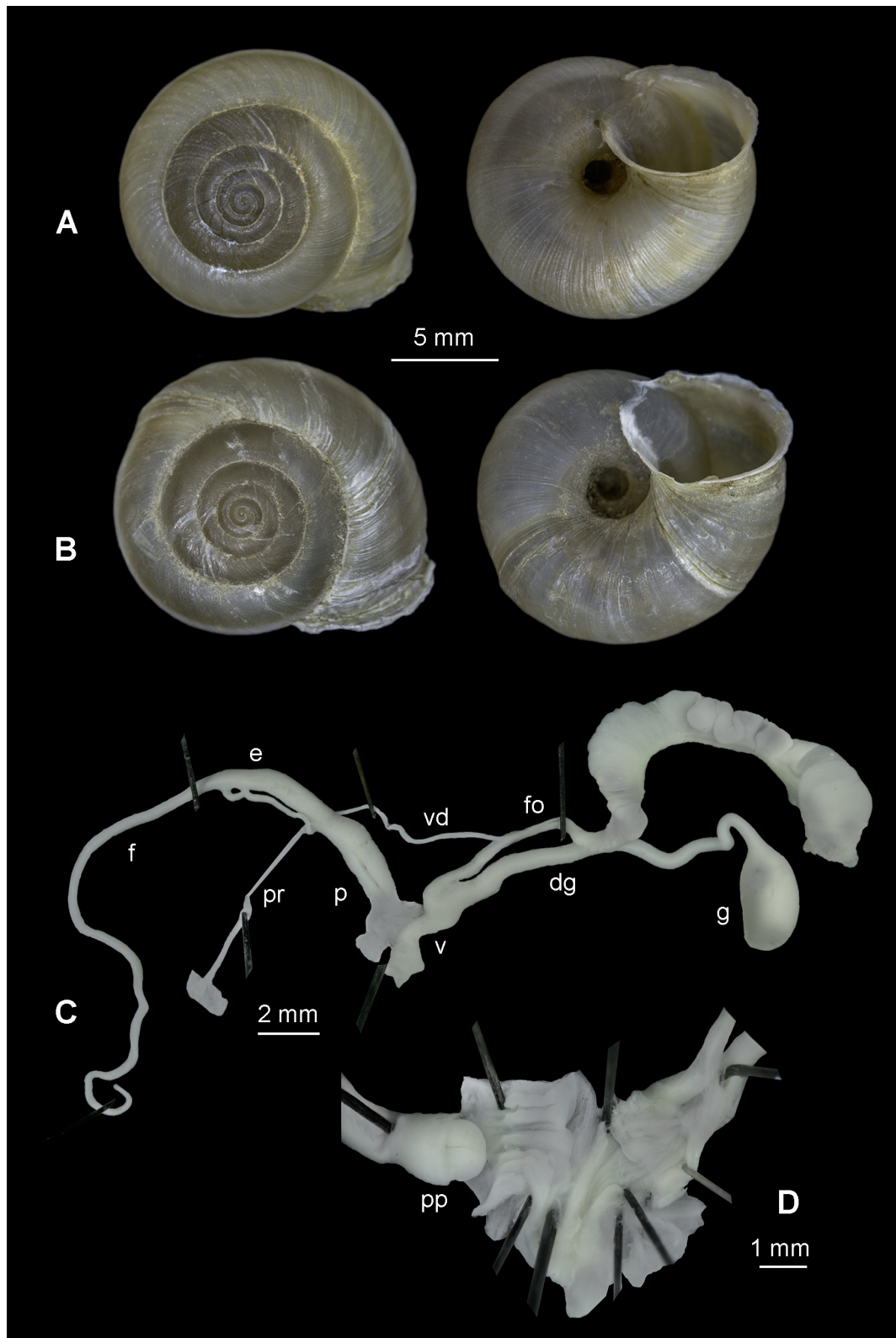


Fig. 7. *Metafruticicola* (*Westerlundia*) *coartata*. **A.** *M. (Westerlundia) c. coartata* Fuchs & Käufel, 1936, Greece, Cyclades, Makra Islet (NHMC 50.4056). Shell. **B–D.** *M. (Westerlundia) c. gemina* Fuchs & Käufel, 1936, Greece, Dodecanese, Karavia Nisia, north Islet (NHMC 50.6805). **B.** Shell. **C.** General view of genitalia. **D.** View of penial papilla. Abbreviations: see Material and methods.

made by Hesse (1931) to study the reproductive system of *M. n. nicosiana*. A comparison between the genitalia of *M. n. soror*, given by Schileyko & Féher (2017), and that of *M. n. nicosiana* and *M. n. conciliatrix* from this study reveal major differences, especially in the shape of penial papillae. It is noteworthy that from all subspecies of *M. nicosiana*, penial papilla of *M. n. conciliatrix* from Karpathos Isl. is closer related in form to that of *M. n. nicosiana*, even though the latter is the most geographically distant of all the other subspecies. Taking into consideration the three main variants of penis papillae proposed by Schileyko & Féher (2017), the polytypic *M. nicosiana* turns out to have representatives in all groups; *M. n. freytagi* has a simple tube with apical pore, *M. n. claudia*, *n. maasseni*, *n. conciliatrix* and *n. nicosiana* share a conical papilla with a vertical furrow, while *M. n. soror* has a bilobed papilla.

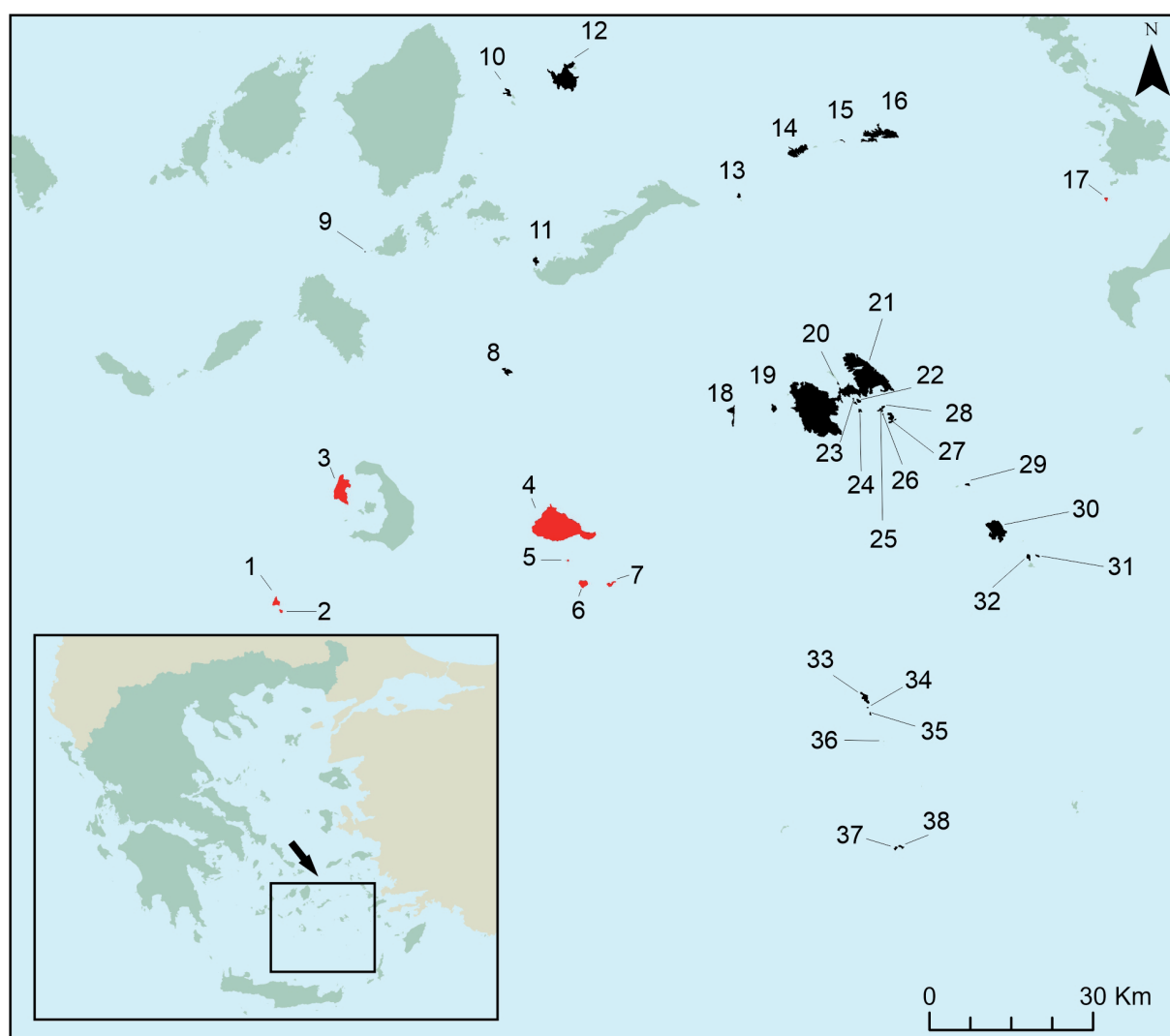


Fig. 8. Distribution of *Metafruticicola (Westerlundia) coartata* Fuchs & Käufel, 1936. Known (black) and new (red) distributional records on the presence of the species in various Aegean islands. — **Greece, Cyclades:** 1. Christiani; 2. Askania; 3. Thirasia; 4. Anafi; 5. Fteno; 6. Pacheia; 7. Makra; 8. Anydros; 9. Mikros Avelas; 10. Machaires; 11. Gramvousa; 12. Donousa; 13. Liadi. — **Greece, Dodecanese:** 14 Kinaros; 15. Megalo & Mikro Mavro; 16. Levitha; 17. Safonidi; 18. Ofidousa; 19. Pontikousa; 20. Fokionisia; 21. Astypalaia; 22. Chondros; 23. Lianos; 24. Agia Kyriaki; 25. Tigani; 26. Fteno; 27. Kounoupoi; 28. Koutsomytis; 29. Mikros & Megalos Aderfos; 30. Syrna; 31. Stefania; 32. Mesonisi; 33. Megali Zafora; 34. Sochas; 35. Mikri Zafora; 36. Karavi North; 37. Ounio West; 38. Ounio East.

As was already mentioned, the two subspecies of *M. coartata* share quite similar genitalia and penis papillae. Nonetheless, there is a noticeable diversity in the shape of both penis and penial papilla in *M. c. coartata*. Similarities in penial papilla show a stronger geographical correlation rather than differentiation at the subspecies level (see description in *M. c. coartata*). Papillae of similar structure to those from Karavi, Sochas and Mikri Zafora are shown also from dissections made by Schileyko & Féher (2017) from Astypalaia island and east Ounio islet. Favoring the view of Schileyko & Féher (2017) on the higher significance of anatomical characters over conchological ones, we suggest that the validity of the subspecific status of *M. c. gemina* should be questioned. Conchologically, the most profound difference between the two subspecies is the wider umbilicus of *M. c. gemina*. However, our samples throughout the distributional range of *M. coartata* reveal that there is a spectrum concerning the broadness of the umbilicus and it is difficult to come to a conclusion where to draw a line between the two subspecies concerning this character. Thus, a plethora of characters in both anatomical and conchological features reveals a significant intraspecific diversity, that cannot however justify a clear subspecific level division.

Metafruticicola coartata mostly lives on small uninhabited islands of the central and southern Aegean Archipelago. It is remarkable that although it is found to thrive in small islets, it has never been found in larger islands with the exception of Astypalaia and Anafi. In Astypalaia it is one of the most common snail species. *Metafruticicola pellita* is the second species of *Metafruticicola* in Astypalaia, although it can only be found in the northeastern part of the island around Vathy bay. These two species have been found sympatrically; however, the density of *Metafruticicola coartata* is lower when *Metafruticicola pellita* is also present. The distribution of *M. c. coartata* has been revised by Bank *et al.* (2013: 118). Our sampling efforts have revealed that the distribution of this species is wider both west- and eastwards of the currently known distribution. It inhabits Anafi and its satellite islets Fteno, Makra and Pacheia, as well as the volcanic islands Thirasia, Christiani and Askania around Santorini. In contrast to Astypalaia, *Metafruticicola coartata* is quite rare in Anafi and it has only been found at one location in the easternmost part of the island. Here we have the complete opposite pattern, where *Metafruticicola pellita* dominates the island. Gambetta (1929) mentioned both species from the island of Astakida. Our intensive sampling efforts revealed no presence of any species of *Metafruticicola* on this small islet (Mylonas & Vardinoyannis 2022). This discrepancy is thus attributed to the fact that the records of Gambetta were most probably based on confusion of localities. *Metafruticicola coartata* is also present in the small islet of Safonidi in the Kalymnos Island group, where it was previously falsely identified by Triantis *et al.* (2008) as *Metafruticicola redtenbacheri*. The presence of *M. coartata* in Safonidi is remarkable, since all other adjacent islands and islets are inside the distributional range of *M. redtenbacheri* alone.

The reproductive system and the form of the penial papilla of *M. crassicosta* are very similar to those of *M. sublecta*. It is safe to assume that any quantitative differences should be attributed to the specimens of *M. crassicosta* not being fully mature. In favor of this view is the fact that the similarities were even more profound with anatomies of *Metafruticicola sublecta* from Ederi hill, 18 km east of Heraklion, that were also not fully mature. These two species also share one distinct shell character among all congeneric species, which is whitish shells with three brown bands on the periphery. Further molecular work, that is in progress, aims to examine the validity of the taxonomic status of *M. crassicosta* at the specific level. Based on the lack of differences in the genitalia, but considering the shell's pronounced ribs that cannot be found in other populations of *M. sublecta* in mainland Crete or adjacent islets, *M. crassicosta* could be downgraded to a subspecies of *M. sublecta*. However, we refrain from such a statement, awaiting the phylogenetic results of the abovementioned ongoing study.

Although *Metafruticicola* is considered a genus with quite well-known representatives in the South Aegean Arc (Bank *et al.* 2013; Neubert & Hirschfelder 2017), the presence of a second species of *Metafruticicola* from Kasos was previously overlooked, whereas Vardinoyannis (1994) mentioned it as

Metafruticicola nicosiana. Even though one could argue that *M. kavafis* sp. nov. exhibits some general shell similarities with *M. n. conciliatrix*, the inner structure of the genitalia, i.e., penis papillae, of these two taxa are utterly different. In fact, the penis papilla of *M. kavafis* is quite bizarre and does not look like any of the currently known forms in *Metafruticicola*. Thus, we refrain from making assumptions about its closest relative based only on these data. Based on conchological characters and due to some similarities to *M. n. conciliatrix* though, one could place *M. kavafis* in subgenus *Rothifruticicola*, concerning the current valid subgeneric division. It is considered to be one of a few species of land snails that is endemic to Kasos, without being present on Karpathos. In addition, ecological observations on the species during sampling efforts revealed for the first time in *Metafruticicola* a potential preference of a snail species of the genus for a particular plant.

The claim of Schileyko & Féher (2017) that *M. pellita* and *M. naxiana* share papillae of similar structure should be approached cautiously. The sample of *M. naxiana* in Schileyko & Féher (2017) is from the islet Gianysada, which belongs to the Dionysades island group in eastern Crete. Welter-Schultes & Wiese (1991) reported the presence of one single species of *Metafruticicola* from Gianysada. According to Triantis *et al.* 2004, the only species of *Metafruticicola* of the island group of Dionysades is *M. pellita*, an identification that was also confirmed by Bank *et al.* (2013: 72), far from *Metafruticicola naxiana*'s distribution (Bank *et al.* 2013: 122). Bank *et al.* (2013) presented two dissections of *M. naxiana*, one from Dia Island and a second one from north-central Crete, a site opposite to Dia Isl. Both dissections display several differences from those of *M. pellita*. Thus, this controversy should be attributed to a misidentification of the specimen from Gianysada (Schileyko & Féher 2017: 71).

The subgeneric division of *Metafruticicola* presented by Bank *et al.* (2013) is questioned by our results. The above anatomical evidence and the study of Schileyko & Féher (2017) reveal several discrepancies between anatomical and conchological traits and this raises doubts concerning the placement of the several species in the existing sub-generic division. Even by examining several conchological features, contradictory results have already been shown (Bitzilekis *et al.* 2017). Scarce molecular data are in concordance with this view, since Neiber *et al.* (2017) and Neiber (2019) have already shown that *M. noverca* and *M. naxiana*, that have been placed in the subgenus *Westerlundia*, do not form a monophyletic group. Therefore, we are in favor of the abolishment of the current subgeneric division in *Metafruticicola*, although a more detailed discussion of the validity of the subgeneric division of the genus will be postponed to the molecular phylogenetic study in preparation.

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