

A NEW ISOLATED SUBSPECIES OF *ALOPIA LIVIDA* (MENKE, 1828) (GASTROPODA: PULMONATA: CLAUSILIIDAE) FROM THE FĂGĂRAȘ MOUNTAINS, ROMANIA

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ABSTRACT: *Alopiia livida* (Menke) is one of the widest distributed species of its primarily limestone-dwelling genus that is native to the Romanian Carpathians. Its discontinuous range includes large parts of the Bucegi Mts and a few scattered occurrences westward to the Apuseni mountain complex. Here we provide description of *A. livida vargabandii* Fehér et Szekeres n. ssp. from the Făgăraș Mts, a mountain range of primarily carbonate-free bedrock from where earlier only two insular populations of other *Alopiia* species were known. The relationship of *A. livida* to other species in the genus, as well as relations between the subspecies of *A. livida*, are addressed by means of phylogenetic analysis using mitochondrial *COI* sequences. Zoogeographical aspects and taxonomic problems of these taxa are also discussed.

KEY WORDS: Alopiniinae, endemism, zoogeography, Carpathians

INTRODUCTION

Obligate rock-dwelling door snails of the subfamily Alopiniinae substantially contribute to the species diversity of the limestone regions in southern Europe. Alopiniine genera comprise several narrow-range taxa of insular distribution. The geographic isolation and the resulting genetic drift without niche differentiation play a primary role in the early phase of their speciation (FEHÉR et al. 2018). Among the genera of this subfamily *Alopiia* Adams et Adams, 1855 has one of the northernmost distribution areas. Except for a single subspecies in Slovakia, it is endemic to the Romanian Carpathians. In the eastern part of the Southern Carpathians, its centre of diversity, the genus is represented by numerous, often polytypic species of considerable morpholog-

ical variation (SOÓS 1928, NORDSIECK 2008, FEHÉR et al. 2013). Species of *Alopiia* show strong preference for carbonate-rich, mostly limestone habitats, therefore they are conspicuously absent in mostly non-carbonaceous mountain ranges. Such is the case in the Făgăraș Mts, a roughly 70 km long part of the main Carpathian range, from where only two *Alopiia* records have been reported so far. Uniquely in the genus, these locally isolated and much confined populations of *A. pomatias* (Pfeiffer, 1868) and *A. mafteiana mafteiana* Grossu, 1967 inhabit slate cliffs (AGÓCSY & PÓCS 1961, GROSSU 1967). Therefore, the recent discovery by the second author of an additional *Alopiia* on a small marble outcrop in this mountain range was unexpected.

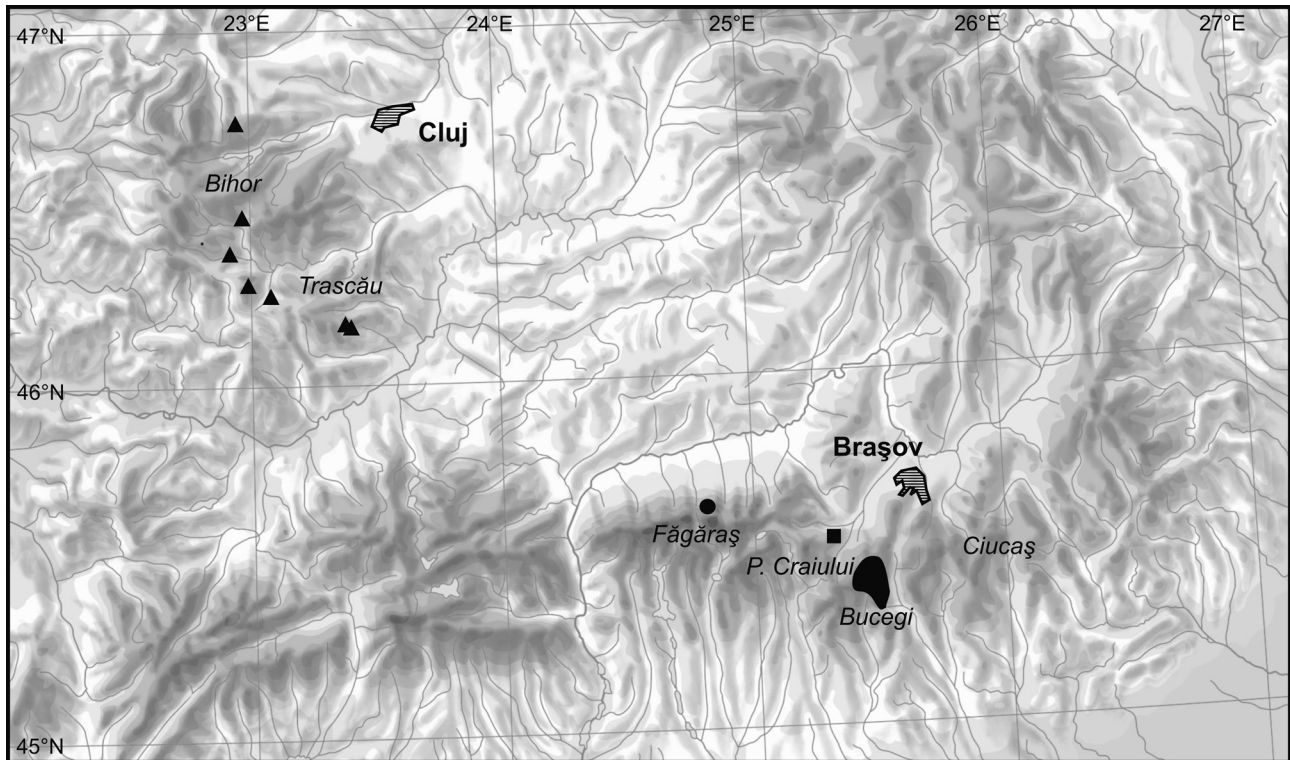


Fig. 1. Distribution of *A. livida* in the Romanian Carpathians. Symbols show localities of *A. livida livida* and *A. livida bipalatalis* (blotch), *A. livida julii* (triangles), *A. livida deaniana* (square), and *A. livida vargabandii* n. ssp. (circle). Names of mountains are in italics

The population occurring in the upper part of the Sâmbăta Valley represents a new subspecies of *A. livida* (Menke, 1828), a widely distributed member of the genus (Fig. 1). Whereas its nominotypical form and *A. livida bipalatalis* (Kimakowicz, 1883) have relatively large, practically continuous ranges in the Bucegi Mts, another two subspecies occur in scattered localities which are remote from that area:

A. livida deaniana Cooke, 1922 inhabits a small part of the Măgura Range, flanked by two other species of *Alopi*a, in the northern part of the Piatra Craiului Mts, and *A. livida julii* Wagner, 1914 is found in a few isolated sites of the predominantly limestone Tascău and Bihor Mts. The new subspecies from the Făgăraș Mts is described below.

MATERIALS AND METHODS

Live snails were collected from cliff surfaces and crevices. Specimens for molecular analyses were stored in 96% ethanol.

DNA samples were isolated from foot tissues of three ethanol-preserved paratypes using DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany). A 655 base pair coding segment of the mitochondrial cytochrome oxidase subunit I gene (*COI*) was then PCR-amplified from each of the samples using the PF372 and PR373 primers of FEHÉR et al. (2013) and the procedure described in PÁLL-GERGELY et al. (2019). Purification and bidirectional sequencing of the PCR products were performed by LGC Genomics (Berlin, Germany). The determined sequences, identical in all samples, were deposited in GenBank under accession numbers MK434162 to MK434164.

Phylogenetic analyses of the obtained sequences were done in relation to *A. livida COI* sequences published by FEHÉR et al. (2013) and KOCH et al. (2017), as well as those of the morphologically most similar taxa of *Alopi*a belonging to *COI* clade D1 in FEHÉR et al. (2013), namely *A. canescens canescens* (Charpentier, 1852), *A. canescens haueri* (Bielz, 1859), *A. canescens striaticollis* (Kimakowicz, 1894), *A. nefasta nefasta* (Kimakowicz, 1894), *A. nefasta helenae* Kimakowicz, 1928, *A. nefasta mauritii* Kimakowicz, 1928, and *A. nefasta zagani* Szekeres, 1969 (FEHÉR et al. 2013). Sequences of the taxa from D2 sister clade, *A. glorifica intercedens* (Schmidt, 1857), *A. glorifica magnifica* Kimakowicz, 1962, *A. mariae hildegardae* Kimakowicz, 1931, and *A. mariae soosi* Brandt, 1931, were included as outgroups. The DNA sequences used in this study are listed in Table 1.

The sequences were aligned manually. The optimum partitioning scheme and best-fit model of sequence evolution were selected using the ModelFinder function (KALYAANAMOORTHY et al. 2017) in IQ-Tree 1.6.9 (NGUYEN et al. 2015) applying Bayesian Information Criterion (BIC): 1st codon position: TNe+1; 2nd codon position: F81+F; 3rd codon position: TIM2+F+G4.

Phylogenetic relationships were estimated with a Maximum Likelihood-based (ML) tree reconstruction by IQ-TREE. Nodal supports were estimated by SH-aLRT test and approximate Bayes test (ANISIMOVA et al. 2011), as well as by 1,000 ultra-fast bootstrap repeats (HOANG et al. 2017). All analyses, including model test, tree reconstruction and bootstrapping, were run on the W-IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at>, TRIFINOPOULOS et al. 2016). To infer and visualise genealogical relationships among the haplotypes a statistical parsimony

network was constructed with TCS (CLEMENT et al. 2002) as implemented in PopART 1.7 (LEIGH & BRYANT 2015).

The type material of the new subspecies is deposited in the mollusc collections of the Field Museum of Natural History, Chicago (FMNH), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF), Grigore Antipa National Natural History Museum, Bucharest (MNINGA), Hungarian Natural History Museum, Budapest (HNHM), Musée National d'Histoire Naturelle, Paris (MNHN), Natural History Museum, London (NHMUK), Natural History Museum, Sibiu (MINS), Natural History Museum of the University of Florida, Gainesville (UF), Naturhistorisches Museum, Vienna (NHMW), Zoological Institute of the Polish Academy of Sciences, Warsaw (IZPAN), as well as the private collections of MIKLÓS SZEKERES, Budapest (SZ) and ANDRÁS VARGA, Gyöngyös (VA).

Table 1. *COI* gene sequences used in this study

Taxon	Locality	GenBank accession number
<i>A. canescens canescens</i>	Ciucaş Mts, Vârful Ciucaş (45°31'16"N, 25°55'20"E), 1,850 m	JQ911791 ^a
<i>A. canescens haueri</i>	Ciucaş Mts, Mt. Dungu (45°33'13"N, 25°54'00"E), 1,240 m	JQ911792 ^a
<i>A. canescens striaticollis</i>	Ciucaş Mts, Mt. Tesla (45°29'26"N, 25°53'22"E), 1,340 m	JQ911793 ^a
<i>A. glorifica intercedens</i>	Piatra Craiului Mts, Valea Dâmboviței (45°25'31"N, 25°11'28"E), 810 m	JQ911801 ^a
<i>A. glorifica magnifica</i>	Piatra Craiului Mts, Podu Dâmbovicioarei (45°26'35"N, 25°23'20"E), 920 m	JQ911799 ^a
<i>A. livida bipalatalis</i>	Bucegi Mts, Valea Gaura (45°26'25"N, 25°25'27"E), 1,900 m	JQ911812 ^a
<i>A. livida deaniana</i>	Piatra Craiului Mts, Măgura Mică (45°31'41"N, 25°18'47"E), 1,290 m	JQ911813 ^a
<i>A. livida julii</i>	Bihor Mts, Valea Ordâncușa (46°27'55"N, 22°50'14"E), 820 m	JQ911814 ^a
<i>A. livida livida</i>	Bucegi Mts, Mt. Țiganest – Velican, (45°28'37"N, 25°26'02"E), 1,950 m	KY801962 ^b , KY801963 ^b
<i>A. livida livida</i>	Bucegi Mts, Valea Velican, (45°28'31"N, 25°26'12"E), 1,870 m	KY801957 ^b
<i>A. livida livida</i>	Bucegi Mts, Valea Obârșia Ialomiței (45°25'00"N, 25°26'45"E), 1,860 m	KY801945 ^b , KY801946 ^b
<i>A. livida livida</i>	Bucegi Mts, Cheile Tătarului (45°21'48"N, 25°26'00"E), 1,470 m	KY801947 ^b , KY801948 ^b
<i>A. livida livida</i>	Bucegi Mts, Valea Ialomiței (45°21'44"N, 25°25'44"E), 1,490 m	JQ911815 ^a
<i>A. livida livida</i>	Bucegi Mts, Valea Peleş (45°21'21"N, 25°32'02"E), 1,020 m	JQ911816 ^a
<i>A. livida vargabandii</i> n. ssp.	Făgăraş Mts, Piatra Caprei (45°37'54"N, 24°48'14"E), 1,710 m	MK434162– MK434164
<i>A. mariae hildegardae</i>	Căpățâna Mts, Mt. Buila (45°14'19"N, 24°06'27"E), 1,350 m	JQ911821 ^a
<i>A. mariae soosi</i>	Căpățâna Mts, Valea Oltețului (45°12'03"N, 23°47'00"E), 670 m	JQ911823 ^a
<i>A. nefasta helenae</i>	Ciucaş Mts, Valea Gropșoarei (45°28'56"N, 25°57'50"E), 1,280 m	JQ911827 ^a
<i>A. nefasta mauritii</i>	Ciucaş Mts, Valea Gropșoarei (45°29'43"N, 25°57'34"E), 1,550 m	JQ911828 ^a
<i>A. nefasta nefasta</i>	Ciucaş Mts, Mt. Bratocea (45°29'46"N, 25°53'52"E), 1,660 m	JQ911829 ^a
<i>A. nefasta zagani</i>	Ciucaş Mts, Valea Gropșoarei (45°28'57"N, 25°57'56"E), 1,320 m	JQ911830 ^a

^aFEHÉR et al. (2013), ^bKOCH et al. (2017).



RESULTS AND DISCUSSION

Genus *Alopia* Adams et Adams, 1855

Type species: *Clausilia bielzii* Pfeiffer, 1849

Alopia livida (Menke, 1828)*Alopia livida vargabandii* Fehér et Szekeres n. ssp.

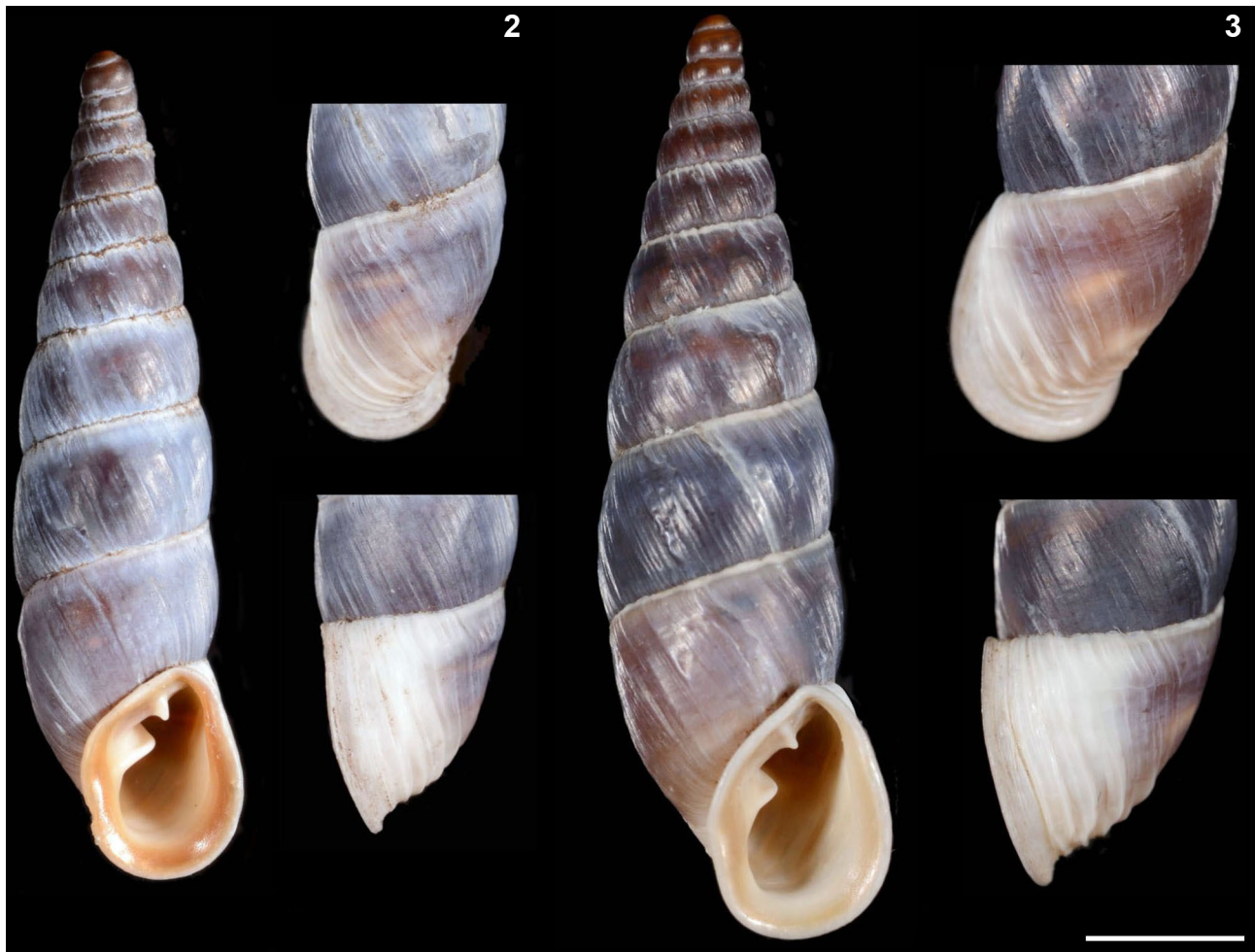
Fig. 2

Type material. Holotype: Romania, Făgăraş Mts, Piatra Caprei over Valea Sâmbăta (45°37'53.5"N, 24°48'14.1"E), 1,710 m a.s.l., leg. M. SZEKERES and A. VARGA 24.07.2017 (HNHM-MOL-102507). Paratypes: same locality and collection data (FMNH/2, HNHM-MOL-101041/2 and HNHM-CGR-21605 to -21607 in 96% ethanol, IZPAN 5/2019/2, MINS-Mollusca 209.732/2, MNHN-IM-2012-27282/2, MNINGA-GST

7002/2, NHMUK 20190580/2, NHMW 113105/2, SMF 356928/2, UF/2, SZ/54, VA/142).

Differential diagnosis. Differs from all other subspecies of *A. livida* in the frequent presence of rudimentary plica principalis and clausilium.

Description. The dextral, elongate conical shell consists of $8\frac{2}{3}$ to $9\frac{3}{4}$ whorls. Its dark purple-brown shell appears bluish because of the white surface layer of the teleoconch. The surface of the whorls is wrinkled at the apical part, smooth at the centre, and then turns strongly costate over the whitish neck. At the rather rounded basis a weak crest is recognisable. The large, ovoid aperture has a wide, brownish, detached margin. The lamella superior is short, weakly emerged. In about 20% of the specimens a weak or rudimentary lamella spiralis is also present much deeper than the inner end of the lamella superior (Figs 4–5). The lamella inferior is strong. The lamella subcolumellaris is mostly missing but rarely its much reduced remnants are recognisable. Most



Figs 2–3. *Alopia livida*: 2 – *Alopia livida vargabandii* n. ssp., holotype, HNHM-MOL-102507; 3 – *Alopia livida bipalatalis*, Bucegi Mts, Valea Mălaeşti, 1,700 m. Scale bar 3 mm



Figs 4–5. Opened last whorl of *Alopia livida vargabandii* n. ssp. with variably developed clausiliar apparatus: 4 – specimen with rudimentary lamella spiralis and clausilium plate; 5 – specimen lacking these structures. Scale bar 1 mm

of the specimens have only two diffuse dorsal plicae that correspond to the superior and basalis (Fig. 6B). Less frequently a short and sharp plica principalis can also be observed (Fig. 6A), or all of the plicae are absent (Fig. 6C). Near the columella a much reduced clausilium with small and narrow plate is present in roughly 10% of the studied shells (Fig. 4), whereas others entirely lack this structure (Fig. 5).

Measurements. Holotype: shell height 16.2 mm, whorl width 4.0 mm, aperture height 4.2 mm, aperture width 3.2 mm; paratypes: shell height 15.4–18.1 mm, whorl width 3.9–4.6 mm, aperture height 4.1–4.4 mm, aperture width 3.0–3.5 mm.

Habitat. *Alopia livida vargabandii* n. ssp. inhabits a small, roughly 0.5 km² outcrop of Buda-Mușeteica-type marble (TÎRLĂ et al. 2016) emerging from the slate and gneiss surroundings of the Sâmbăta Ridge (Fig. 7). Live specimens were found mostly in shaded parts and shallow crevices of the eroded rock surfaces (Fig. 8), which they shared with *Bulgarica cana* (Held, 1836). Although the area of occupancy is very narrow, in the near future it will be granted protection as part of the planned Făgăraș National Park. Due to the obligate rock-dwelling nature of the new

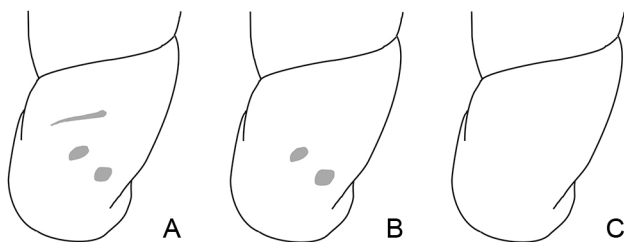


Fig. 6. Variably developed palatal plicae in *Alopia livida vargabandii* n. ssp. Weak plica principalis with residual plicae superior and basalis (A), only residual plicae superior and basalis present (B), plicae absent (C)

subspecies the extent or quality of its habitat are not exposed to immediate threats, the overall population does not seem to face decline or extreme size fluctuations.

Etymology. The new subspecies is named in honour of András (Bandi) Varga, a dedicated malacologist and friend of the authors.

Remarks. Morphologically *A. livida vargabandii* n. ssp. is closest to *A. livida bipalatalis* (Fig. 3) which also has a strong neck sculpture and two lump-like palatal plicae, but differs from it in the frequent presence of a rudimentary principal plica and clausilium. Other subspecies of *A. livida* with fine neck sculpture are completely devoid of clausilium, and mostly also of any palatal plicae. Very rarely a weak remnant of a principal plica is present in *A. livida julii* Wagner, 1914 and *A. livida deaniana* Cooke, 1922, but the lower two plicae are always absent. *Alopia livida livida* always lacks plicae.

In order to find out how the mitochondrial *COI* sequence of the new subspecies relates to those of taxa in clade D1 (that includes *A. livida*) and its sister clade D2 of FEHÉR et al. (2013) we constructed an ML tree (not shown). Whereas these clades had high confidence levels (SH-aLRT >95%, approximate Bayes support >0.95, ultrafast bootstrap support >95%) (FEHÉR et al. 2013), within clade D1 only a few subclade nodes (e.g. those of the *A. nefasta* or *A. canescens* subspecies) were strongly supported. To test the reliability of the inferred dichotomous tree, as well as to visualise alternative relationships within our dataset, we also generated a statistical parsimony network (Fig. 9). This revealed a predominantly non-treelike, reticulate topology, which is consistent with the weak support of some branches in the ML tree. Remarkably, well separated groups in the TCS network proved to be the same as those also hav-

ing strong node support in the tree. Therefore the network, properly exposing relationships of closely related haplotypes (POSADA & CRANDALL 2001), seemed well suited for presenting the intricate phylogenetic affiliations in these clades. The COI network (Fig. 9) placed *A. livida vargabandii* n. ssp. near subspecies of *A. livida*, *A. canescens* and *A. nefasta*, but at a clearly distinct position. This is consistent with its belonging to the same clade and representing a valid new taxon.

According to the TCS network *A. livida* is a paraphyletic taxon, ancestral to *A. canescens*, *A. nefasta* and *A. nixa*. Whereas morphologically the new subspecies apparently belongs to *A. livida*, the COI sequence data show it just as closely related to *A. canescens* and *A. nefasta*, two species of the Ciucaș Mts with distinct characters and ranges. Whereas all subspecies of *A. canescens* are sinistral and lack clausilium, those of *A. nefasta* include both sinistral and dextral taxa of widely varying degree of reduction of the clausiliar apparatus. We tentatively classify the new subspecies within *A. livida* because of its shell morphology, very similar to that of *A. livida bipalatalis*, and because both *A. canescens* and *A. nefasta* are narrow-range species that seem to have evolved locally in the Ciucaș Mts.

The nominotypical form of *A. livida* and *A. livida bipalatalis* have separate but largely continuous dis-

tribution areas in the Bucegi Mts, where occasionally they can hybridise with other species (KOCH et al. 2017). By contrast, *A. livida deaniana* inhabits only a small part of the Măgura Ridge in the Pietra Craiului Mts, and *A. livida julii* occurs at multiple isolated localities in the Bihor and Trascău Mts (Fig. 1). Such sporadic occurrence of the latter subspecies is intriguing because their populations are separated by vast limestone areas that seem to offer equally suitable habitats for this clausiliid. Despite such disjunct distribution of the species, which is not unique in its genus (FEHÉR et al. 2013), the discovery of *A. livida vargabandii* n. ssp. in the Făgăraș Mts is somewhat surprising. So far this is the only *Alopi*a that lives on marble, a re-crystallised form of limestone. The possibility of its relict status here seems to be supported by the presence on the same cliffs of *Silene zawadzki* Herbich, 1835, a flowering plant that has its closest other occurrences in the northernmost mountains of the Eastern Carpathians (BARTÓK et al. 2016).

The classification of the considerably varied *A. livida* populations in the Bucegi Mts is ambiguous. No verifiable original material is available for the typical form for which the brief description by MENKE (1828) tentatively gives former Hungary as locality. In an assessment of the concepts of this species, NORDSIECK



Figs 7–8. Habitat of *Alopi*a *livida vargabandii* n. ssp.: 7 – Pietra Caprei in the Făgăraș Mts; 8 – individuals of the new subspecies attached to a marble cliff

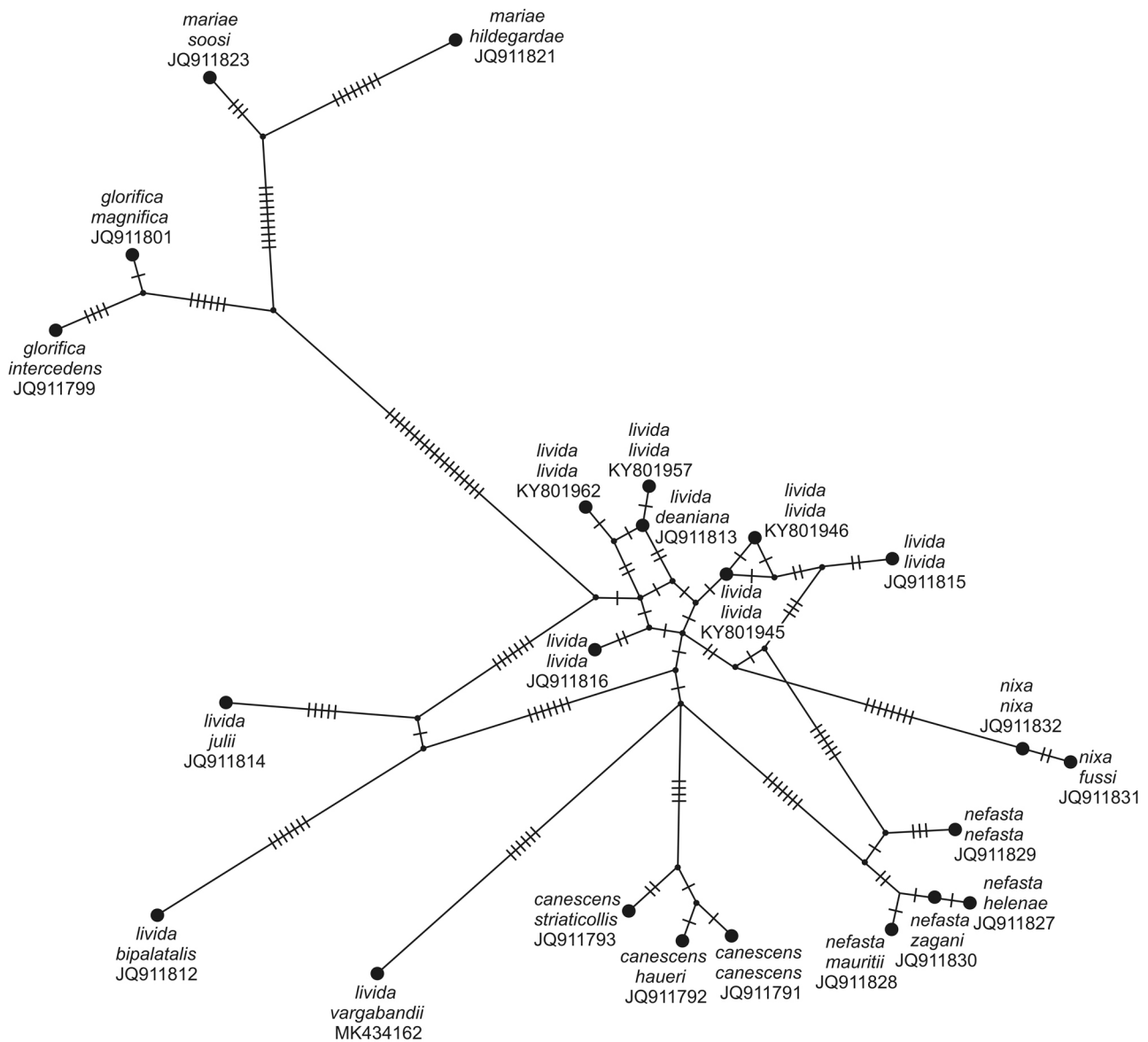


Fig. 9. Statistical parsimony network reconstructed from *COI* haplotypes of the clade comprising *A. canescens*, *A. livida*, *A. nefasta* and *A. nixa*, as well as of the closest sister clade including subspecies of *A. glorifica* (Charpentier, 1852) and *A. mariae* (Kimakowicz, 1931). Sequences are identified with names of the subspecies and GenBank accession numbers. Hatchmarks show the number of nucleotide substitutions between haplotypes

(2015) convincingly argues that MENKE'S (1828) material must have originated from the northern slopes of this mountain. The literature of the past century mostly distinguished *A. livida bipalatalis* and *A. livida livida* as the subspecies with or without palatal folds, respectively (WAGNER 1914, SOÓS 1928, GROSSU 1967, NORDSIECK 2015). However, this easily recognisable trait varies much in the degree to which it is pronounced and its taxonomic significance is questionable. Furthermore, our phylogenetic analysis shows that, despite the morphological similarity, the examined populations of *A. livida livida* are not closely related within the species (Fig. 9). Elucidating the relationships between the Bucegi populations will

require more detailed molecular studies, which also rely on further, fast evolving DNA markers that can provide sufficient phylogenetic information. Its results could answer the question how diverse and distinct the *Alopi* forms of the Bucegi Mts are and how their subspecific classification is feasible.

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