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Morphological and molecular characterization of the *Colomerus vitis* erineum strain (Trombidiformes: Eriophyidae) from grapevine erinea and buds

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Abstract

The grapevine erineum mite strain (GEM) of *Colomerus vitis* (Pagenstecher) has spread throughout the main viticultural areas worldwide and was recently demonstrated to be a vector of *Grapevine pinot gris virus* (GPGV) and *Grapevine inner necrosis virus* (GINV). Its females mainly overwinter under the outer bud scales as winter morphs (deutogynes). Goals of this study were to characterize the morphology of protogynes (spring–summer morphs) and deutogynes

(winter morphs), to confirm their genetic similarity, and to establish the seasonal period of the deutogyne occurrence. Buds or leaves from a single vineyard (cv. Luisa), Bari area, Apulia, Italy, infested with GEM were sampled 6 × from December 2015 to January 2017. Sixty-six traits commonly used for taxonomic identification were analysed on females. The length of the tibial setae *l′* on leg I and the tarsal setae *ft′* on leg II, as well as the number of smooth dorsal semiannuli differed significantly between protogynes and deutogynes, and were easier to detect than other significantly distinctive traits. ITS1 was investigated in individuals collected from buds and erinea, and the sequences confirmed that these two morphs have identical ITS1 fragments. The 1-year study demonstrated the simultaneous presence of protogynes and deutogynes in July and September 2016, whereas only protogynes were found in April and May 2016, and only deutogynes in December 2015 and January 2017.

AQ1

Keywords

Morphological examination
Protogynes
Deutogynes
ITS1
Biology

Introduction

Colomerus vitis (Acari: Eriophyidae) was named and very briefly described by Pagenstecher (1857); more details were given by Nalepa (1890) and Canestrini (1892) (as *Phytoptus vitis* (Landois) by the latter author). Later, Keifer (1944) and Manson (1984) provided a more accurate morphological description of females but they did not morphologically separate protogynes (i.e. spring–summer morph) from deutogynes (i.e. overwintering morph). Short descriptions were given also by Boczek (1960), Ryke and Meyer (1960), Mathez (1965) and Petanović (1988). Only Bagdasarian (1981) described the two female morphs. These descriptions do not characterize well the species and leave some doubts.

Colomerus vitis is fairly common on grapevine and three strains were distinguished based only on induced symptoms (Smith and Stafford 1948): bud gall, leaf erineum (with the acronym GEM, i.e. grape erineum mite) and leaf curl. No morphological differences between these three strains have been recorded, leading to the hypothesis that they may belong to a cryptic species complex (Craemer and Saccaggi 2013). Distinction of the bud strain from the GEM strain was provided by restriction fragment length polymorphism (RFLP) applied to the ITS1 region and by microsatellite markers (Carew et al. 2004), but any sequence has been published up to now and more data appear necessary to characterize each single strain of this mite. The GEM strain is much more frequently and widely recorded than the other strains. It induces the development of conspicuous felty erinea on the concave surfaces of blister-like swellings, on the lower and upper leaf surfaces, respectively. It can affect plant growth, influence the yield and quality of berries and was associated with the transmission of viruses (Duso and de Lillo 1996; Avgin and Bahadiroğlu 2004; Javadi Khederi et al. 2014, 2018a, b; Malagnini et al. 2016). After bud opening, deutogynes colonise the unfolding new leaves and cause erinea in which populations of protogynes and males develop, passing gradually to new young leaves. From late summer onwards, the new deutogynes appear and migrate to their overwintering sites, mainly under the outer bud scales (Duso and de Lillo 1996).

The morphological studies published until now on the GEM strain do not clearly separate protogynes from deutogynes, and the seasonal appearance of the overwintering morph has not been carefully studied. The morphology of the same species may vary over the seasons as consequence of interactions between the mite and the plant genotype, as well as due to environmental influences (Manson and Oldfield 1996; Javadi Khederi et al. 2014; Druciarek et al. 2016; Laska et al. 2019). Therefore, the study planned on the erineum strain of *C. vitis* was carried out in the same vineyard by sampling it 6 × over 13 months, covering more generations and more than an annual cycle of the mite. The same cultivar was preferred in order to avoid the influence of the plant defence mechanisms exerted by different cultivars against GEM (Javadi Khederi et al. 2018c, d). The same location was chosen with the purpose that weather conditions could have identical influence on mite biology and physiology. Therefore, it was expected to point out the most relevant morphological differences between protogynes and deutogynes, confirming their genetic similarity, and establishing the seasonal occurrence of the deutogynes.

Materials and methods

Colomerus vitis sampling and collection

Leaf erinea and buds were collected from three randomly selected plants in a vineyard of table grape cv. 'Luisa' located in the Noicattaro countryside (Bari area, Apulia, Italy; GPS: 40°0500′460″N, 16°9832′399″E, 75 m above sea level). Only a single vineyard was chosen to be studied owing to the approximation of the known descriptions of protogynes and deutogynes, and the potential risk that there were not enough morphological differences to justify the observations on a larger number of vineyards. The sampling was done 6 × from December 2015 to January 2017 (Table 1) in order to have buds as first and last sampled organs, and to have leaf erinea samplings for 41–59 days each from the other. Eriophyids were removed from the plant organs by direct inspection under a dissecting stereomicroscope. When mites were deeply sheltered into the erinea, they were extracted by applying the washing and sieving method described by Monfreda et al. (2007). In this case, they were concentrated on a cellulose filter after the extraction. Only live specimens were collected (from the erinea or buds as well as from the dried cellulose filter), slide mounted and used for DNA extraction. These procedures avoided influences on the morphology of the mites and did not interfere with the DNA analysis as previously carried out by Bouneb et al. (2014).

Table 1

Samplings of *Colomerus vitis* collected from erinea and buds and used for morphometric and genetic analysis

Sampling date	Plant organs	Morphological analysis (no. measured females)	ITS1 sequences (no. assayed adults)	GenBank accession number
4 December 2015	Buds	19	10	MH578265 to MH578274
12 April 2016	Leaf erinea	20	5	MH578284 to MH578288
30 May 2016	Leaf erinea	21	10	MH578289 to MH578298
29 July 2016	Leaf erinea	20	5	MH578299 to MH578303
9 September 2016	Leaf erinea	20	8	MH578304 to MH578311

Sampling date	Plant organs	Morphological analysis (no. measured females)	ITS1 sequences (no. assayed adults)	GenBank accession number
13 January 2017	Buds	19	10	MH578275 to MH578283
Total		119	48	

Light microscopy morphometric study

The morphological study was carried out on mites clarified and slide-mounted in Keifer's medium (Amrine and Manson 1996). From 90 to 110 specimens per sampling were slide-mounted. Kapok fibres were added to the mounting medium and placed between the slide and the cover slip to allow specimens to turn around their longitudinal axis (de Lillo et al. 2010), taking measurements of all the traits for each mite. The morphological terminology and setal notation follow that of Lindquist (1996). Measurements were made with a scale and drawing tube, using a phase-contrast Olympus BX50 microscope (Shinjuku, Tokyo, Japan), of 19–21 females in good shape for each sampling (Table 1). Measurements were made according to Amrine and Manson (1996), as modified by de Lillo et al. (2010). They are given in µm and represent the length of the traits, unless otherwise stated. The following clarifications should be noted: dorsal semiannuli were counted from the first semiannulus behind the rear margin of the prodorsal shield, ventral semiannuli were counted from the first complete annulus after coxae II, and coxigenital semiannuli were counted medially from the coxal region to the anterior margin of the external genitalia and were not included in the ventral semiannuli count. The 66 morphological traits, most commonly used in the species descriptions (see as example Denizhan et al. 2008), were measured and compared among the six samplings (Table 2).

Table 2 With respect to the pdf of this article:

please start Table 2 on page +1. It will then fall WITHIN the RESULTS section

Mean (± SD) values of 66 traits of *Colomerus vitis* collected from December 2015 to January 2017 from the sa differences among samplings and between protogynes and deutogynes

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		P
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		F
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
Traits (µm)								
Body	141 ± 11.2	220.5 ± 22.5	201 ± 32.6	186.1 ± 30.3	200.8 ± 22.2	151.6 ± 18.3	(5)	2 3
Body width	36.9 ± 2.7	43 ± 4	39.7 ± 3.5	36.3 ± 3.1	40.8 ± 2.2	39.6 ± 1.7	(16)	3

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see 'Analysis of morphometric data') divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, '1' is the lowest; all $P < 0.01$)

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		F
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		F
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
Palp	14.5 ± 1.1	16.6 ± 1.6	14.3 ± 0.8	14.2 ± 1	14.1 ± 0.8	14.2 ± 0.8	(18)	1
Palp coxa setae (*ep*)	3 ± 0	2.8 ± 0.6	2.9 ± 0.3	3 ± 0	2.9 ± 0.2	3 ± 0		2
Palp genual setae (*d*)	2 ± 0	2.5 ± 0.7	2 ± 0.3	2 ± 0	2 ± 0	2 ± 0	(19)	2
Chelicerae	11.7 ± 0.8	11.8 ± 0.8	11.2 ± 0.8	11.2 ± 0.8	11.1 ± 0.8	11 ± 0.8		1
Prodorsal shield	27.2 ± 3.5	26.9 ± 2.3	28 ± 2.3	27 ± 2	27.6 ± 2.7	26.3 ± 2.4		2
Prodorsal shield width	30.2 ± 1.4	32.6 ± 2.7	31.5 ± 2.7	29.6 ± 2.1	32.2 ± 1.8	31.1 ± 1.8	(32)	3
Frontal lobe	3 ± 0	2.9 ± 0.2	2.6 ± 0.4	2.8 ± 0.4	3 ± 0.2	3 ± 0	(35)	2
Distance between tubercles of scapular setae (*sc*)	14.3 ± 1.1	16 ± 1.5	16.1 ± 1.1	16.3 ± 1.3	15.5 ± 0.7	15.2 ± 1	(21)	1
Scapular setae (*sc*)	19.2 ± 1.8	19.4 ± 1.8	19.5 ± 1.4	17.6 ± 1.8	19.9 ± 1.6	17.6 ± 0.7	(22)	1
Foreleg (from base of trochanter)	27.2 ± 1.3	30.3 ± 2	26.9 ± 1.1	27.5 ± 1.3	26.8 ± 1.2	25.5 ± 1.2	(9)	2
Foreleg: femur	10 ± 0	10.2 ± 0.5	10 ± 0	10 ± 0	10 ± 0	9.8 ± 0.4		1
Foreleg: femur setae (*bv*)	10.5 ± 0.7	10.2 ± 0.9	9.9 ± 0.3	10 ± 0.3	10.2 ± 0.5	10 ± 0		1
Foreleg: genu	5 ± 0	5 ± 0	4.9 ± 0.3	5 ± 0	5 ± 0	4 ± 0	(4)	4
Foreleg: genua setae (*l″*)	19.4 ± 1.6	19.8 ± 1.9	20.1 ± 0.8	18.2 ± 1.6	19.3 ± 1.2	18.6 ± 1.7		1
Foreleg: tibia	5 ± 0	5.8 ± 0.6	5.1 ± 0.6	4.7 ± 0.4	4.8 ± 0.3	4.5 ± 0.5	(11)	5
Foreleg: tibial setae (*l′*)	3.1 ± 0.6	5.1 ± 0.7	5.5 ± 0.6	4.4 ± 0.8	3.3 ± 0.4	3 ± 0	(3)	5
Foreleg: tarsus	6 ± 0.2	6.1 ± 0.3	6 ± 0	5.8 ± 0.3	6 ± 0	5.1 ± 0.6	(7)	6

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see ‘Analysis of morphometric data’) divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, ‘1’ is the lowest; all $P < 0.01$)

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		F
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		F
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
Foreleg: paraxial tarsal setae (*ft′*)	10.5 ± 1.1	11.3 ± 1.4	10.7 ± 0.9	10.7 ± 0.9	10.3 ± 0.7	10.8 ± 0.9		1
Foreleg: antiaxial tarsal setae (*ft″*)	21.5 ± 2.5	20.8 ± 1.3	20.2 ± 1.5	19.2 ± 1.3	19.9 ± 1.2	18.8 ± 1.4	(27)	2
Foreleg: solenidion (*ω*)	7.1 ± 0.3	7.2 ± 0.4	7 ± 0	7 ± 0	7 ± 0	6.7 ± 0.4	(28)	7
Foreleg: empodium	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0		5
Foreleg: empodium rays	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0		5
Hindleg (from base of trochanter)	24.4 ± 1.2	25.9 ± 1.3	25 ± 1.1	24.7 ± 1.1	24.9 ± 1.1	22.9 ± 1.2	(17)	2
Hindleg: femur	10.1 ± 0.4	9.7 ± 0.4	9.9 ± 0.2	9.8 ± 0.4	9.9 ± 0.2	9.8 ± 0.5		9
Hindleg: femur setae (*bv*)	9.8 ± 0.5	9.7 ± 0.6	10 ± 0	9.7 ± 0.4	10 ± 0	10 ± 0		9
Hindleg: genu	4.9 ± 0.2	4.8 ± 0.3	4.6 ± 0.4	4.5 ± 0.5	5 ± 0	4.1 ± 0.3	(10)	4
Hindleg: genua setae (*l″*)	10.2 ± 1.4	10.4 ± 1.2	11.5 ± 0.9	10.2 ± 0.5	10.6 ± 0.5	7.4 ± 0.9	(6)	1
Hindleg: tibia	4.1 ± 0.3	4.4 ± 0.5	4.1 ± 0.3	4.6 ± 0.5	4.5 ± 0.5	4.3 ± 0.4		4
Hindleg: tarsus	5.1 ± 0.4	5.6 ± 0.6	5.5 ± 0.5	5.2 ± 0.4	5.7 ± 0.4	5.1 ± 0.5	(26)	5
Hindleg: paraxial tarsal setae (*ft′*)	3.1 ± 0.4	5.6 ± 0.6	5.6 ± 0.5	4.8 ± 0.8	3.4 ± 0.5	3.1 ± 0.3	(2)	5
Hindleg: antiaxial tarsal setae (*ft″*)	22.2 ± 2.2	22 ± 1.9	20.9 ± 1.4	19.6 ± 1.6	21.2 ± 1.9	20.5 ± 1.1	(24)	2
Hindleg: solenidion (*ω*)	9.9 ± 0.2	9.5 ± 0.5	9.8 ± 0.3	9.2 ± 0.7	10 ± 0	10 ± 0	(15)	9
Hindleg: empodium	5 ± 0	5 ± 0.2	5 ± 0	5 ± 0	5 ± 0	5 ± 0		5

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see ‘Analysis of morphometric data’) divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, ‘1’ is the lowest; all $P < 0.01$)

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		F
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		F
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
Hindleg: empodium rays	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0	5 ± 0		5
Distance between tubercles of setae *1b*	6.6 ± 0.4	6.9 ± 0.7	6.6 ± 0.6	6.8 ± 0.6	7.3 ± 0.4	6.6 ± 0.4		6
Distance between tubercles of setae *1a*	8.5 ± 0.7	8.9 ± 0.6	9 ± 0.8	9 ± 0.6	8.5 ± 0.6	8.1 ± 0.5	(29)	9
Distance between tubercles of setae *1b* and *1a*	3 ± 0	3.1 ± 0.4	3 ± 0.2	3.1 ± 0.3	3 ± 0.2	3 ± 0		3
Distance between tubercles of setae *2a*	17.8 ± 1.4	18.8 ± 1.3	19 ± 1.2	18.5 ± 1.1	18.5 ± 1	17 ± 0.9	(23)	1
Distance between tubercles of setae *1a* and *2a*	4.5 ± 0.5	4.9 ± 0.6	5.2 ± 0.9	5 ± 0	5 ± 0	4.9 ± 0.2		5
Coxal setae *1b*	4.7 ± 0.4	5.3 ± 0.5	5.1 ± 0.5	5 ± 0.3	4.7 ± 0.5	5 ± 0	(33)	5
Coxal setae *1a*	18.5 ± 4.5	21 ± 2.9	21.2 ± 3.3	19.5 ± 2.9	21.4 ± 2.9	18 ± 2.7		2
Coxal setae *2a*	32.2 ± 6.6	29.1 ± 4.2	29.1 ± 3.8	31.4 ± 4.8	33.2 ± 4.5	29.7 ± 5.1		2
Sternal line	5 ± 0	5 ± 0.2	5 ± 0	5 ± 0	5.2 ± 0.4	5 ± 0		5
No. dorsal semiannuli	72.3 ± 6.1	81.9 ± 7.4	82.6 ± 6.3	79 ± 5.6	73.1 ± 3.5	83.9 ± 6.5	(13)	8
No. ventral semiannuli	69.6 ± 4	77.6 ± 4.2	76.8 ± 4.5	74.4 ± 4	70.5 ± 2.3	73.1 ± 5	(14)	7
Semiannulus number between coxae and genital region	5 ± 0	4.3 ± 0.4	5 ± 0	5 ± 0	4.9 ± 0.3	5 ± 0	(8)	4
Lateral setae *c2*	16.1 ± 1.4	17.6 ± 1.7	16.3 ± 1.1	15.7 ± 1.2	16.4 ± 1.2	16.7 ± 0.9		1

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see ‘Analysis of morphometric data’) divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, ‘1’ is the lowest; all $P < 0.01$)

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		F
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		F
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
On semiannulus	9.5 ± 1	7.4 ± 1	7.9 ± 1.4	7.6 ± 0.8	8 ± 0.7	7.8 ± 1	(20)	7
I ventral setae *d*	41.4 ± 5.7	42.5 ± 6.6	43.3 ± 4.4	36.9 ± 5	39.8 ± 3.9	39.5 ± 4.7		4
On semiannulus	26.2 ± 6.7	24.1 ± 1.4	23.5 ± 2.1	23 ± 1.7	23.1 ± 1.7	21.6 ± 2.4		2
II ventral setae *e*	47.5 ± 7.8	50.2 ± 7.5	43 ± 10.5	45.8 ± 6.1	48.9 ± 5	43.6 ± 7		4
On semiannulus	41.6 ± 3	44.9 ± 2.3	44 ± 3.3	42.6 ± 2.9	42.3 ± 4.2	41 ± 3.6	(34)	4
III ventral setae *f*	13.5 ± 1.5	14 ± 1.2	13.6 ± 1.1	12.9 ± 0.9	12.8 ± 0.7	12.5 ± 0.7	(31)	1
On semiannulus	65 ± 4	73.9 ± 4.3	72.7 ± 4.5	70.3 ± 3.9	66.4 ± 2.3	69 ± 5	(12)	7
No. annuli before *f* and the anal lobe	4.1 ± 0.3	4 ± 0	4 ± 0	4 ± 0	4 ± 0	4 ± 0.2		4
No. last annuli with elongated tubercles	4.2 ± 0.4	4 ± 0	4 ± 0	4 ± 0	4 ± 0	4 ± 0.2		4
Caudal setae *h2*	54.8 ± 6.9	55.4 ± 5.9	51.2 ± 5.9	50.4 ± 7.5	57.6 ± 5.9	48.2 ± 4.5	(30)	5
Coverflap	10.5 ± 0.9	10.8 ± 1.5	10.8 ± 1.3	10.7 ± 1	10.1 ± 0.5	10 ± 0		1
Coverflap width	17.3 ± 2.1	19.1 ± 0.7	18.8 ± 1.1	18.6 ± 1.3	18.6 ± 0.9	19.1 ± 1.4		1
No. coverflap striae in the distal row	12 ± 1.3	11.5 ± 1.5	12 ± 2.5	12.2 ± 1.9	13.3 ± 1.4	12.7 ± 1.1		1
No. coverflap striae in the proximal row	12.8 ± 0.8	13 ± 1.1	12 ± 1.3	12.5 ± 1.3	12.6 ± 1	10.7 ± 2.1	(25)	1
Genital setae *3a*	16.6 ± 1.3	15 ± 1.8	15.6 ± 1.7	16.2 ± 1.1	17 ± 1.5	15.2 ± 1.6		1
Distance between tubercles of genital setae *3a*	13.8 ± 1.4	13.6 ± 1.1	13.9 ± 0.9	14.1 ± 0.6	14 ± 0.6	14.5 ± 0.6		1

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see ‘Analysis of morphometric data’) divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, ‘1’ is the lowest; all $P < 0.01$)

Sampling date	2015	2016				2017	Sampling variability Kruskal–Wallis test	F
	4 Dec	12 Apr	30 May	29 Jul	9 Sep	13 Jan		A 2 2
Morph	**Deutogyne**	**Protogyne**	**Protogyne**	**Both**	**Deutogyne**	**Deutogyne**		**P**
Plant organ	**Buds**	**Erinea**	**Erinea**	**Erinea**	**Erinea**	**Buds**		**P**
No. females	**19**	**20**	**21**	**20**	**20**	**19**		5
No. last dorsal semiannuli without microtubercles	10 ± 0	0 ± 0	0 ± 0	2 ± 4.1	8 ± 2	10 ± 0	(1)	0

Data refer to length unless otherwise stated. Kruskal–Wallis test was applied on the six groups separated by s was applied on the rearranged data (see 'Analysis of morphometric data') divided into deutogynes and protog are rank numbers based on the P-values (from lowest to highest, '1' is the lowest; all $P < 0.01$)

AQ2

Only the morphological traits which pointed out the most significant differences between the specimens grouped per sampling (see 'Analysis of morphometric data') were used to record the percentages of deutogynes and protogynes during the samplings on 29 July and 16 September. In these cases, additional females previously mounted (45 on 29 July, 16 on 16 September) were measured only for these distinctive morphological traits separating deutogynes from protogynes.

Analysis of morphometric data

The measurements of each morphological trait were examined for normality of distribution with skewness and kurtosis statistics, and as the distributions were non-normal, trait data were analysed among all samplings by non-parametric Kruskal–Wallis tests. Traits displaying the highest significant differences were subsequently used for rearranging the dataset, to separate specimens into two groups: protogynes and deutogynes. Data analyses were repeated between deutogynes and protogynes considering all measured traits using Mann–Whitney *U* tests. Data management and analysis were performed using SPSS v.20 (IBM SPSS Statistics for Windows, Armonk, NY, USA).

ITS1 study

Live mites were placed in centrifuge tubes (one mite per tube) with an eyelash tool or an Austerlitz pin (0.1 mm diameter, about 12 mm long) mounted on a wood dowel, centrifuged in a microcentrifuge at 10,000 rpm for 10 min at 4 °C and stored at − 20 °C until DNA extraction. Total genomic DNA was extracted from single specimens. Aliquots of 100 µl of Chelex suspension (10% in water) (InstaGene matrix™, BioRad) and 5 µl of proteinase-K (20 mg/µl) (Qiagen) were added to each tube. DNA extraction was performed using a thermal cycle of 50 °C for 50–60 min in a water-bath and 100 °C for 10 min in a tube-heater block. The tubes were immediately centrifuged after the thermal cycle for 10 min at 4 °C and 10,000 rpm. The supernatant was used as a DNA template for PCR or was stored at − 20 °C.

ITS1 sequencing was chosen to be studied based on previous studies separating bud from erineum strains (Carew et al. 2004). ITS1 fragments were obtained using the primers 18S 5′ AGA GGA AGT AAA AGT CGT AAC AAG 3′ (forward) and 5.8S 5′ GCT GCG TTC TTC ATC GAT ACT CG 3′ (reverse) (Navajas et al. 1999). The sequences were amplified with PCR in 20 µl final

volume containing 10 µl of GoTaq® Green Master Mix 2X (Promega), 1 µl for each primer 10 µM, 3 µl of water and 5 µl of DNA template. The reactions were conducted according to Carew et al. (2004) with a touch-down thermal cycle consisting of initial denaturation of 2 min at 93 °C, followed by 12 touch-down cycles (20 s at 93 °C, 30 s at 55 °C, decreasing by 1 °C each cycle until 43 °C, 1 min at 72 °C), followed by 25 cycles of 20 s at 93 °C, 30 s at 43 °C and 1 min at 72 °C (increasing elongation by 10 s each cycle). The PCR products were separated with electrophoresis through 1.5% agarose gels in TBE buffer. Five µl of amplicons were purified using Illustra™ ExoProStar™ (GE Healthcare Life Sciences) according to the manufacturer's instructions and sequenced in both senses on a Sanger automated equipment 96-capillary 3730xl DNA analyzer.

The consensus sequences were aligned with Mega7 software (Clustal W algorithm) and the phylogeny distance tree was inferred using the Maximum Likelihood method. *Colomerus vitis* sequences were trimmed and compared with a corresponding sequence of *Phyllocoptes fructiphilus* Keifer available in the NCBI database (GenBank ~~a~~Accession ~~N~~number AJ251692.1).

Results

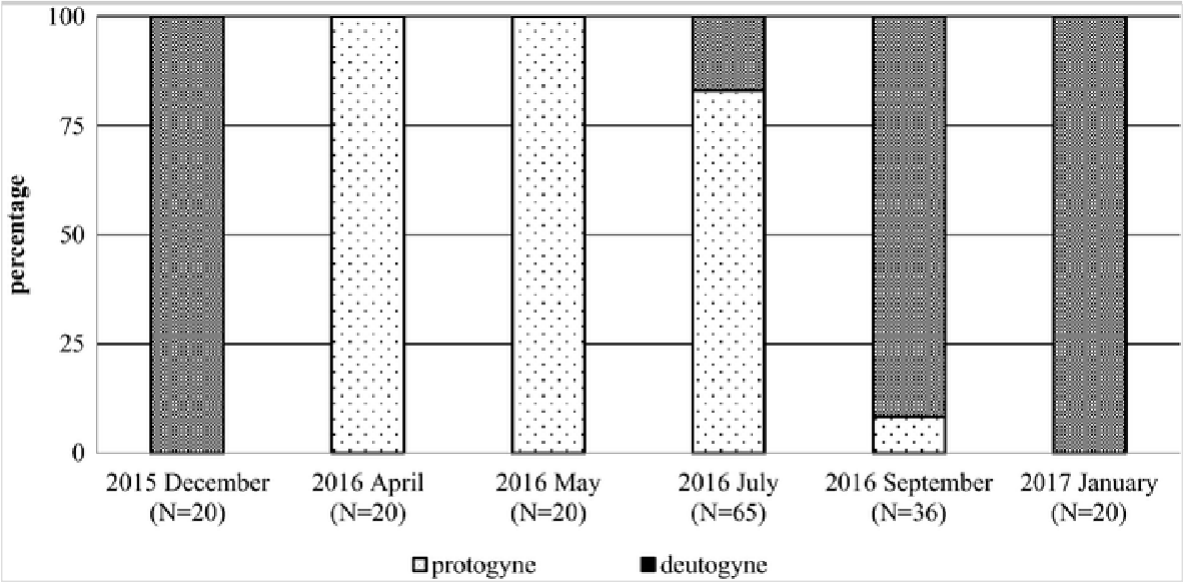
Light microscopy morphometric study

About half of the analysed traits (35 out of 66) showed significant variation in their morphology among the specimens within the six samplings (Table 2). Number of last semiannuli without microtubercles, *ft′* seta length on leg II, *l′* seta and genu length on leg I, and body length appeared to be the most significant traits. Based on these results, the dataset was re-arranged in two groups (one for the deutogynes and one for the protogynes) and analysed again, which resulted in 24 distinctly different traits (Table 2). Three of those were easy to detect and well separated deutogynes from protogynes. Relative to the protogynes, the deutogynes were characterized by the absence of microtubercles on the last 8–10 dorsal semiannuli, shorter tibial setae *l′* on leg I and shorter tarsal setae *ft′* on leg II. The test revealed further minor distinctive traits: deutogynes showed closer opisthosomal seta *f* to the coxigenital region, fewer ventral semiannuli, shorter body, longer solenidion on leg II, shorter genual seta *l″* of leg II, and shorter reciprocal distance between the tubercles of scapular setae *sc* and coxal setae *1a*.

The main distinctive characters were used for checking the percentage of protogynes and deutogynes in a larger sample of specimens collected from erinea in July (49 specimens) and September (16 specimens). Protogynes prevailed in July (83.1% of total females) and almost only deutogynes (91.6% of total females) were found in September (Fig. 1).

Fig. 1

Population composition (% of protogynes and deutogynes) of *Colomerus vitis* samples collected between December 2015 and January 2017

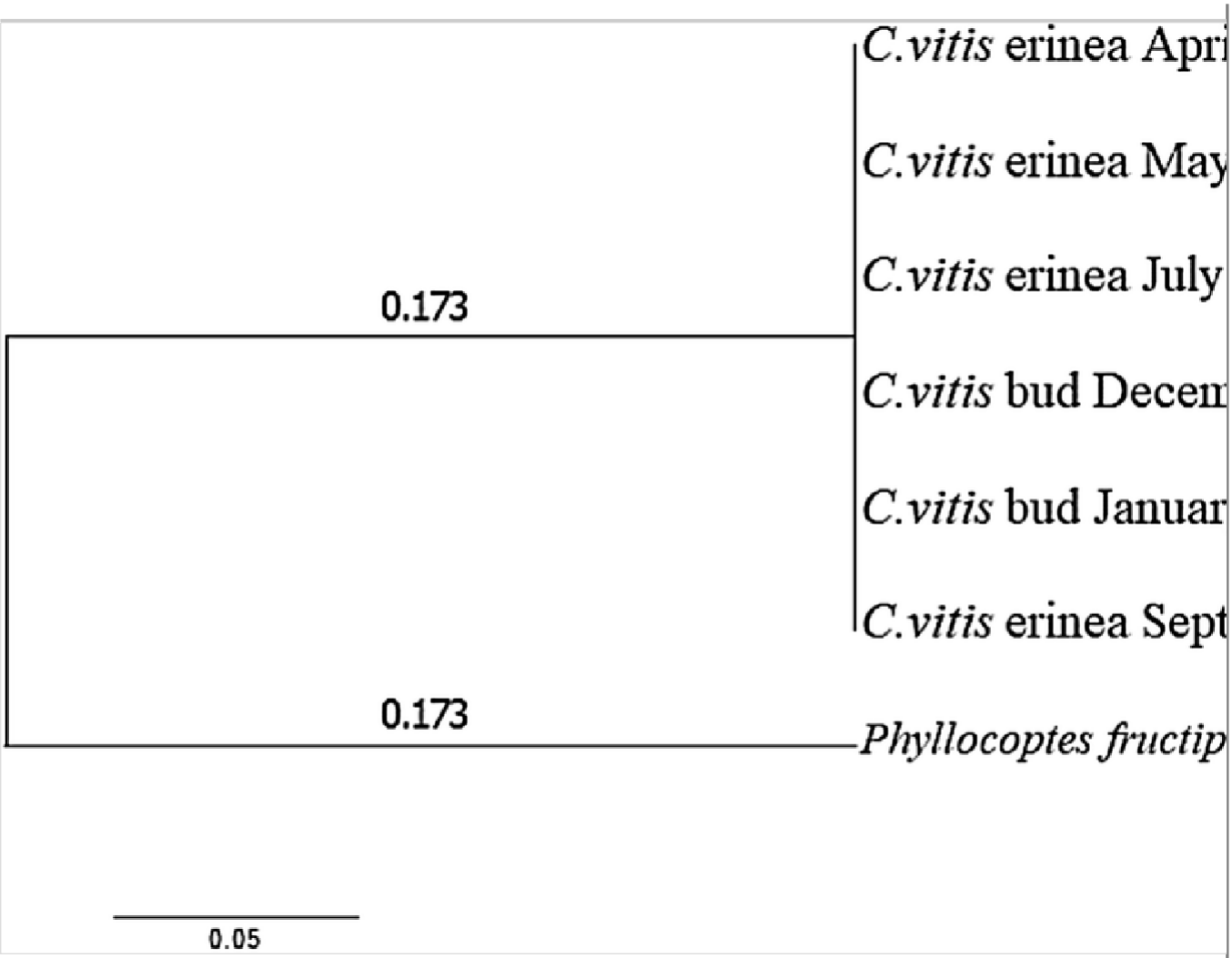


ITS1 study

The ITS1 sequences obtained from individual mites (n = 48) collected from erinea and buds during various samplings were composed constantly of 628 bp, with a nucleotide content percentage of T = 25.2, C = 21.8, A = 29.3 and G = 23.7. The sequences were identical for all tested individuals and no punctiform difference was detected among them (Fig. 2). Specimens collected from buds in December 2015 and January 2017 were all deutogynes, whereas those collected in April and May 2016 were all protogynes; mixed morphs might have been present in the specimens collected in July and September 2016 (Fig. 1). The 48 sequences were deposited in the GenBank (NCBI) as single accessions, with numbers from MH578265 to MH578311 (Table 1).

Fig. 2

Molecular phylogenetic unrooted tree built with ITS1 sequences from *Colomerus vitis* individuals collected from buds and leaf erinea between December 2015 and January 2017 in a single vineyard. Outgroup: *Phyllocoptes fructiphilus* (GenBank: AJ251692.1). Analysis with Maximum Likelihood method, Kimura's 2-parameter model; tree with the highest log likelihood (− 756.0240)



Discussion

Specimens of *C. vitis* collected from the same vineyard in different periods of the year were compared by applying a morphological and genetic approach. Morphological analysis identified three traits highly significant and convenient for separating deutogyne from protogyne females on buds and erinea, as they are easily detected and measured: compared to protogynes, deutogynes lack microtubercles on the last 8–10 dorsal semiannuli, have shorter tibial setae *l′* on leg I and shorter tarsal setae *ft′* on leg II. Genetic analysis established the similarity of the ITS1 region in protogynes and deutogynes and confirmed that the studied specimens belonged to the same species. These are the first sequences deposited in GenBank for GEM.

The previous descriptions (Table 3) of GEM given by Keifer (1944), Bagdasarian (1981) and Manson (1984) were in accordance with the usage at the time in which the descriptions were made, but are not exhaustive in terms of current standards of dataset collection (de Lillo and Skoracka 2010; de Lillo et al. 2010). Except in the case of Keifer (1944), fibres were probably not placed between cover slip and slide, and mounted specimens could not be turned when they were measured. This also implies that mites were occasionally flattened, which could make comparison of some measurements in the old descriptions with the current ones difficult (e.g. body width, distance between setal tubercles and a few others). Bagdasarian (1981) described protogynes separately from deutogynes, but no mention was made of the population studied in order to obtain the data (i.e. whether it was collected from the same vineyard and location, following periodic sample collection, from erinea or from buds). The protogyne described by Bagdasarian (1981) had a 5-rayed empodium whereas the deutogyne had a 4-rayed one, and this was the main difference.

Protogynes also had a longer body and longer *sc*, *c2* and *3a* setae than deutogynes (Table 3). The size of all the other traits in these descriptions of one morph overlapped or formed a continuum with those of the other morph (Table 3). Our measurements are largely in accordance with those of Bagdasarian (1981), apart from the number of rays on the empodium of the deutogyne (five~~5~~ in this study) and the presence of smooth dorsal semiannuli in the posterior part of the opisthosoma (not described by Bagdasarian). The other traits used in this study to separate protogynes from deutogynes were not published by the Armenian author. Some differences can be noted in the descriptions given by Keifer (1944) (who reported longer gnathosoma, foreleg tibia and tarsus, and tarsus of leg II) and by Manson (1984) (who reported longer and larger prodorsal shield), but these authors did not specify the studied morph (Table 3). Only Manson (1984) reported the absence of microtubercles on the last six dorsal semiannuli of the opisthosoma, but he did not realise that it could be a trait of the deutogyne. The differences between the current and previous (not stated protogynes and deutogynes) descriptions, including the brief descriptions by Canestrini (1892), Boczek (1960), Mathez (1965) and Petanović (1988), might be due to different rules followed by the authors for the measurements, the influence of plant genotype and physiology on mite morphology (Javadi Khederi et al. 2014) and the quality of slide mounting and microscopy (de Lillo et al. 2010). And it cannot be excluded that previous authors 'mixed' up the trait sizes of both protogynes and deutogynes because they did not establish which morph they were describing, apart from Bagdasarian (1981).

Table 3

Morphometric data from previous descriptions of *Colomerus vitis* females. Data refer to length unless otherwise stated. Manson (1984) did not state the measured morph. *Colomerus vitis* deutogyne was not described yet at Keifer's time (1944)

Traits (µm)	**Keifer (1944)**	**Bagdasarian (1981)**		**Manson (1984)**
		Protogyne	**Deutogyne**	
Body	160–200	180–220	140–180	147–201
Body width		50–60	40–60	35–37
Palp	21	15–16	15–16	12–14
Palp genual setae (*d*)				2–3
Chelicerae		12–13	12–13	
Prodorsal shield	27	23–26	25–27	29
Prodorsal shield width	32	28–30	30–32	38
Frontal lobe		5	5	5
Distance between tubercles of scapular setae (*sc*)	15	15–16	14–15	18
Scapular setae (*sc*)	18	20–22	16–19	19–24
Foreleg	30	26–27	26–27	21–29
Foreleg: tibia	7	5–6	5–6	4–7
Foreleg: tibial setae (*l′*)				5–6
Foreleg: tarsus	8	6–6,5	6–6,5	5–8
Foreleg: solenidion (*ω*)	8	6–6,5	6–6,5	6–8
Empodium rays	5	5	4	5
Hindleg	26	23–24	23–24	20–26

Traits (µm)	Keifer (1944)	Bagdasarian (1981)		Manson (1984)
		Protogyne	Deutogyne	
Hindleg: tibia	4	4–5	4–4,5	4–5
Hindleg: tarsus	7	5–6	5–6	5–6
Hindleg: solenidion (ω)	10–5	9–10	8–9	9
Coxal setae *1b*		8–10		4–6
Coxal setae *1a*		25		
Coxal setae *2a*		30		
Semiannulus number between coxae and genital region		3–4	3	
No. annuli	65–70			76–89
No. last dorsal semiannuli without microtubercles				Last 6
No. dorsal semiannuli		69–85 (tergites)	65–70 (tergites)	
No. ventral semiannuli		64–77 (sternites)	63–67 (sternites)	
Lateral setae *c2*	19	16–18	14	10–19
On semiannulus	7	8–9	8–9	7
I ventral setae *d*	38	35	35–40	40–46
On semiannulus	22			24
Semiannuli between *c2* and *d*		14–15	12–13	
II ventral setae *e*	42	40–45	40–45	38–60
On semiannulus	40			44
Semiannuli between *d* and *e*		16–22	16–17	
III ventral setae *f*	15–5	12–14	13–15	12–13
Semiannuli between *e* and *f*		20–28	22–25	
No. annuli before *f* and the anal lobe		5	5	
Caudal setae *h1*	Absent			Absent
Caudal setae *h2*		65–70	60–70	
Coverflap	10			11–15
Coverflap width	20			16–21
No. coverflap striae	≥ 16	11		
Genital setae *3a*	14	16–17	12–15	15–19
Distance between tubercles of genital setae *3a*		14–15	13–14	

Amplifications of ITS1 in this study produced sequences with 628 bp and they are the first deposited in GenBank for this species. They are quite similar in length to the PCR products found by Carew et al. (2004) in Australian populations, which were composed of 660 bp including primers. Unfortunately, it can be surmised that the ITS1 of Australian populations was never

sequenced but its RFLP was used for separating the bud strain from the erineum strain (Carew et al. 2004).

In our observations, in early September, erinea largely hosted deutogynes on the youngest leaves, which are usually produced with summer regrowth of the main and lateral shoots. Deutogynes migrate to the overwintering sites, largely consisting of dormant buds, and their development might be triggered by leaf hardening and thermo- and/or photoperiod (Sapozhnikova 1982). The first deutogynes were already found in the erinea from mid-summer (July) onwards. Assessment of off-host survival of GEM at low temperatures, without food and with a paucity of oxygen, confirmed the expected higher rate and longer survival of deutogynes as compared to protogynes (Valenzano et al. 2019). This result is undoubtedly related to the physiological adaptation to overwintering. Based on the higher resistance of deutogynes to stressful environmental conditions, involvement of this morph in wind dispersal before their introduction into the overwintering sites (during summer and early autumn migration), over long distances by means of clouds may be surmised, whereas protogynes, with very poor resistance to stressful environmental conditions, may only be involved in wind dispersal over shorter distances. The hypothesis that deutogynes contribute also to dispersal is supported by previous reports. Deutogynes of *Trisetacus kirghisorum* Shevtchenko and *Aceria inusitata* Britto & Navia were suggested to be dispersal morphs (Shevtchenko and DeMillo 1968; Britto et al. 2008). Considering the relevance of *C. vitis* for the transmission of viruses and the apparently greater efficiency of deutogynes in this action (Malagnini et al. 2016), the role of deutogynes in dispersal may be of important epidemiological significance in terms of the timing of control strategies. Confirmation of the dispersal of deutogynes could come from a fast morphological study (it can take a couple of hours by an expert operator) of mites trapped by means of water pans located at a distance from the vineyards, beginning with observations in July (preliminary positive data are available; D. Valenzano & E. de Lillo, unpubl.).

Finally, the current morphological description of GEM is the first that relates the mite to the seasons and to the ITS1 fragments, and it could be used as a standard. We suggest the extension of a morphological-genetic study of *C. vitis* on other grapevine cultivars located in different geographical areas for several consecutive years, also using other genetic markers (*e.g.* COI), which could provide much greater support for the seasonal occurrence of the deutogynes. In addition, this survey could help in looking for the strain presence of *C. vitis* and better clarify the taxonomical position of the co-generic *Colomerus oculivitis* (Attiah), morphologically close to *C. vitis* and currently restricted only to Egypt and Saudi Arabia – its separation from *C. vitis* is quite poorly demonstrated (Attiah 1967).

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