



# What do *Eumerus* Meigen larvae feed on? New immature stages of three species (Diptera: Syrphidae) breeding in different plants

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## Abstract

The genus *Eumerus* Meigen 1822 (Diptera: Syrphidae) is widely distributed in the Old World, though recently introduced into America, and their larvae feed on decaying vegetal material and/or inside underground storage organs of many plants, sometimes generating economic losses as pests. However, little is known about *Eumerus* larval cycles and their interactions with host plants. Here, immatures of three *Eumerus* species from different continents are described, noting their feeding habits and host plants. Larvae of *Eumerus figurans* Walker 1859 were obtained from Hawaiian cultured ginger roots; puparium of *Eumerus alpinus* Rondani 1857 originated from larvae collected in *Asphodelus ramosus* L. in France; puparia of *Eumerus superbus* Shannon 1927 were reared from larvae found in two Zamiaceae species from Australia. Mitochondrial COI sequences served for diagnosing *E. figurans* larvae. Optical and scanning electron microscopy were used to describe body features, head skeletons, anterior spiracles, pupal spiracles, and posterior respiratory processes. Overall, *E. alpinus* resembles *E. nudus* Loew 1848 immatures. *Eumerus superbus* has a remarkable morphology among all described immatures of the genus, being the only *Eumerus* reported from gymnosperms. Head skeleton of *E. figurans* suggests this species is a filtering one. Present findings show that larvae of *Eumerus* can be separated at the species level and that this genus is polyphagous, feeding on a wide range of plant tissues and taxa, including commercial species. This study emphasizes immature stages and breeding sites as important means to understand species life cycles and the interactions with their host plants and ecosystems.

**Keywords** Puparium · Functional morphology · Insect-plant relationship · Geophytes · Phytophagy · Commercial plants

## Introduction

Zoologists and taxonomists have commonly focused their efforts and descriptions on searching for and describing adult insects. However, early stages have particular life cycles and biotic and abiotic requirements, often very different from those of the adults. Studies on Diptera early stages commonly deal with the immatures rearing under laboratory conditions to

get not only the adult stage but also valuable data on the larval microhabitat, feeding habits, and species life cycle (e.g. Ricarte et al. 2015, 2017; Rotheray 2009; Speight and Garrigue 2014). These data also have a bearing on the economic implications of particular species (e.g. Pérez-Bañón et al. 2003). In holometabolous insects, immatures do not share with their adults ecological niches neither feeding habits, and so avoiding competition for the same resources as the adults (e.g. Krivosheina 2018; Ricarte et al. 2008, 2017). For these reasons, many immature insects act as bioaccumulators and biotic indicators (e.g. Katagi and Tanaka 2016; Tollett et al. 2008), agents of forensic science information (e.g. Amendt et al. 2004; Velásquez et al. 2010), indicators of environmental and conservation value (e.g. Chiari et al. 2014; Sánchez-Galván et al. 2014, 2017), agricultural pests (e.g. Assem et al. 1972; Hardy 1964), and natural enemies (e.g. Amorós-Jiménez et al. 2014; Smith et al. 2008), thus having significance in many areas of current concern.

Adult hoverflies often visit flowers searching for nectar and pollen, while larvae have very diverse feeding habits, from

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predatory to saprophagous (Rotheray and Gilbert 1999; Sánchez-Galván et al. 2017). Within hoverflies, the genus *Eumerus* Meigen 1822 (Diptera: Syrphidae) is widely distributed from the Eastern Atlantic region to the far East and Australia, being very diverse in the Mediterranean Basin, where the species richness is the highest (Ricarte et al. 2008). Other centers of diversity are Central Asia and South Africa, while the Oriental region with less than 30 species is less diverse, but also less studied, and the Australian fauna is rather small with about a dozen species, which reach as far east as New Caledonia and Fiji, each with an endemic species. All Northern and Southern American as well as the Hawaiian species are introduced. Worldwide, there are more than 285 valid species of *Eumerus* (Evenhuis and Pape 2019; Hauser, pers. comm.) of which 170 are known from the Palearctic region (Chroni et al. 2018; Grković et al. 2017; Ricarte et al. 2017, 2018; Hauser, pers. comm.). *Eumerus* larvae feed either on decaying plant tissues or as phytophages inside underground storage organs of geophytes (Pérez-Bañón and Marcos-García 1998; Ricarte et al. 2017).

The phylogenetic position of *Eumerus* within the monophyletic Syrphidae family is still unclear. *Eumerus* has for a long time been considered as a member of the subfamily Eristalinae, although some recent studies suggest this subfamily is a group of paraphyletic clades (Rotheray and Gilbert 1999; Skevington and Yeates 2000; Ståhls et al. 2003; Young et al. 2016). Evidences from these authors support the proposition that *Merodon* Meigen 1803 is closely related to *Eumerus*. Whether only larval morphology is used (Rotheray and Gilbert 1999) or larval and adult morphology with DNA sequencing (Ståhls et al. 2003; Young et al. 2016), consensus trees support *Eumerus* and *Merodon* as a monophyletic clade: the Eumerini (Doczkal and Pape 2009; Mengual et al. 2015). In addition, larvae of some *Eumerus* species develop and feed under similar conditions to species of *Merodon* (Ricarte et al. 2008, 2017). In fact, these saprophagous to phytophagous feeding habits of *Eumerus* larvae also support the proximity of this genus to the known phytophagous larvae of *Merodon*, for which head skeleton data exist (Ricarte et al. 2008, 2017; Rotheray and Gilbert 1999).

In a recent paper, Ricarte et al. (2017) reviewed and compiled all information available for *Eumerus* early stages, detailing whether or not they were fully described, and the host plants of these species. It seems that *Eumerus* is, in general, polyphagous and widely saprophagous, being able to live and feed on many different decaying substrates, with a wide range of consistencies (e.g. Efflatoun 1922; Hardy 1964; Ricarte et al. 2008, 2017), in comparison with *Merodon*, which has only been found living inside monocot geophytes, even if they are known for having toxic compounds (e.g. *Drimia maritima* (L.) Stearn, Asparagaceae; Ricarte et al. 2017). In addition, head skeletons of the *Eumerus* larvae so far described show a wide range of degrees of sclerotization and morphologies,

from *Eumerus nudus* Loew 1848—with a strongly sclerotized head skeleton, feeding inside the swollen roots of monocots (Ricarte et al. 2017)—to *Eumerus strigatus* (Fallén, 1817)—with a less sclerotized head skeleton, feeding on rotten bulbs to rotten fruits (Gyulai 1980; Keifer 1930; Ricarte et al. 2017). These data on cephalopharyngeal skeletons support the saprophagous polyphagy and the wide range of microhabitats suitable for *Eumerus* larvae.

Since 2017, some new species of *Eumerus* have been described (Chroni et al. 2018; Ricarte et al. 2018; Grković et al. 2019a, b), not including new descriptions of early stages. Only Piwowarczyk and Mielczarek (2018) reported for the first time an interaction between larvae of *Eumerus mucidus* Bezzi 1921 and the parasitic plant *Cistanche armena* (K. Koch) M.V. Agab. (Orobanchaceae), a very rare species of broomrape that only occurs in Mount Ararat (Ararat Province, Armenia). This new and unique interaction between *Eumerus* and an endemism of Armenia might have conservation implications.

Some *Eumerus* species require to be taken into consideration as pests. Species such as the ginger maggot, *Eumerus figurans* Walker 1859, or the small bulb flies, *Eumerus funeralis* Meigen 1822 and *Eumerus strigatus*, are well known pests, causing biological and economic damage in agriculture and horticulture (Pérez-Bañón and Marcos-García 1998). For example, *Eumerus strigatus* and *Eumerus funeralis* are able to spoil more than 50% of Alliaceae production in Chile (Larraín 2017). Moreover, saprophagous feeding habits allow some species of *Eumerus* to cohabit with other saprophagous species, taking advantage of previously rotten tissues. In this way, *E. figurans* was reported infesting ginger roots up to a 21.42% of larvae abundance alongside other ginger maggot flies belonging to Micropezidae and Platystomatidae families (Sandhya 2015). However, even if it is well known that some *Eumerus* species cause agricultural damage and there is extensive literature on pest control (for example, Assem et al. 1972), there are little scientific or agricultural reports about plant infestation rates and economic losses in crop yields. Further research is needed in order to fulfil these gaps between *Eumerus*, host plants, and society.

The general aim of this study is to increase knowledge of the biology of *Eumerus* species through detailing their early stage morphology and breeding sites. Our main research questions are: (1) do early stages of *Eumerus alpinus* (Rondani 1857), *Eumerus figurans*, and *Eumerus superbus* (Shannon 1927) have distinctive enough morphological traits linked to their feeding habits and breeding sites? And (2) how specialist are the known *Eumerus* early stages in relation to the diversity of their host plants and the plant tissues they feed on? On one hand, *Eumerus* larvae are very similar to each other, commonly not described and unidentifiable morphologically until reared to the adult stage, requiring time and adequate conditions, which is not always possible. For these reasons, some

papers have sought to demonstrate that early stages of *Eumerus* and the closely related genus *Merodon* are distinguishable based on their morphology, relating them to their microhabitat and feeding habit (Pérez-Bañón and Marcos-García 1998; Ricarte et al. 2008, 2017). In this paper, we increase to 13 the number of *Eumerus* species for which the early stages are described within a total count of more than 285 *Eumerus* species worldwide. Recent compilations of host plant data have been very useful to indicate the wide range of host plants on which *Eumerus* can feed, showing that this genus is far more polyphagous than *Merodon* (Ricarte et al. 2008, 2017). In this way, we expect our studied species to show similar morphofunctional traits and feeding regimes among *Eumerus*, with very diverse host plant candidates. In general, we stress the importance of immature stage knowledge to fully understand species biology and the interactions they establish among their host plants and the habitats they live at.

## Materials and methods

### Origin, identification, and study of the described early stages

For the present study, early stage samples from Hawaii (USA), France, and Australia were examined. Labels were checked and origins and plant hosts were noted. Martin Speight reared a larva of *E. alpinus* to adult (female). This larva was collected from swollen roots of *Asphodelus ramosus* L. (Xanthorrhoeaceae) in 2013 from the Oriental Pyrenees, Southern France. Five larvae and an adult male of *E. figurans* were intercepted in California from ginger rhizomes (*Zingiber* sp., Zingiberaceae) coming from Hawaii by the California Department of Food and Agriculture (CDFA, USA). Martin Hauser has on loan four reared adults of *E. superbus* from the Australian National Insect Collection in Canberra, Australia, two males and two females with their puparia, collected as larvae from different places of New South Wales, Australia, between 1965 and 1970. These larvae were found inside female cones of *Lepidozamia peroffskyana* Regel and *Macrozamia communis* L. A. S. Johnson (both Zamiaceae).

The studied female of *E. alpinus* was identified by Speight and Garrigue (2014) as *Eumerus olivaceus* Loew 1848. Grković et al. (2017) established that the valid name for the *E. olivaceus* of authors from mainland Europe is *E. alpinus*, while the name *E. olivaceus* is limited to an endemic species from Sicily, Italy. *Eumerus superbus* adults were identified by Dr. Martin Hauser. Although there are only two species of *Eumerus* introduced to Hawaii, *E. aurifrons* (Wiedemann, 1824) and *E. figurans*, and only the second one is known to attack ginger, to confirm the identity of *E. figurans* specimens,

several larvae were sequenced for the COI barcode gene and compared with sequences of *E. figurans* adults from Thailand, which were a 100% match. The method used is the same described in Rodrigues Júnior et al. (2015).

All the studied 3rd instar larvae (L3) were preserved in 70% ethanol solution. For their examination, puparia samples were soaked 24 h in distilled water to soften. Then, puparia were treated in an ultrasonic bath at 50 Hz for 25 min in periods of 5 min (to avoid any detachment of fragile parts of the puparia). Before observation and description, samples were brushed softly with a fine paint brush to remove any remaining dirt.

Body size of early stages were measured from the anterior margin of the prothorax to the anus, ventrally. Height and width were measured at their maxima. For the posterior respiratory process (PRP), size was expressed as a proportion between the distance from the transverse ridge to the center of the spiracular plate ( $\alpha$ ) and the width of the PRP at the transverse ridge level ( $\beta$ ). Measurements of the specimens were made with a LEICA M205C stereomicroscope and Leica Application Suite v.4.8 software. Microscopic photography and descriptions of the anterior respiratory process (ARP), pupal spiracles (PS), and PRP were taken with a HITACHI S-3000N scanning electron microscope (SEM). Head skeletons were removed with pins from the anteroventral margin of puparia after a 10-min bath in KOH solution. Head skeleton of *E. figurans* was extracted from an L3 instar larva without KOH treatment. All head skeletons were preserved in glycerin and studied with a stereo microscope. Morphological terminology of the early stages of *Eumerus* follows Hartley (1961) and Rotheray (1993). Head skeleton terminology follows Hartley (1963), Roberts (1970), and Rotheray and Gilbert (1999). All botanical terms follow Font Quer (1953). A compilation of abbreviations for both zoological and botanical features used in this paper is shown in Table 1.

Sampled material is deposited in the following collections: CEUA, Entomological Collection of the University of Alicante, CIBIO Research Institute, Spain; CSCA, California State Collection of Arthropods, Department of Food and Agriculture, Plant Pest Diagnostic Branch, Sacramento, USA; ANIC, Australian National Insect Collection, Canberra, Australia.

### Bibliographical analyses of *Eumerus* and their host plants

Adding our new findings to the information gathered by Ricarte et al. (2017), we provide an updated key to early stages of *Eumerus* and graphical representations about historical knowledge on early stages of this genus and the interactions *Eumerus* establish with their host plants. For the historical overview, the first record of each *Eumerus* species early stage

**Table 1** Abbreviations used for morphological features of early stages and plant families

Abbreviations	
Early stage features	
AS	Anterior spiracle
C	Spiracular scar
D	Dorsal cornu
L	Mandibular lobe
M	Mandibular hook
O	Spiracular opening
P	Pharyngeal ridges
PRP	Posterior respiratory process
R	Transverse ridge
S	Spiracular seta
T	Accessory tooth
V	Ventral cornu
Plant families	
ALL	Alliaceae
AMA	Amaryllidaceae
ANN	Annonaceae
API	Apiaceae
ARA	Araceae
ASP	Asparagaceae
AST	Asteraceae
BRA	Brassicaceae
BRO	Bromeliaceae
CAC	Cactaceae
CUC	Cucurbitaceae
EUP	Euphorbiaceae
IRI	Iridaceae
LIL	Liliaceae
LOG	Loganiaceae
ORO	Orobanchaceae
POA	Poaceae
ROS	Rosaceae
SAP	Sapindaceae
SOL	Solanaceae
VIT	Vitaceae
XAN	Xanthorrhoeaceae
ZAM	Zamiaceae
ZIN	Zingiberaceae

found feeding on a plant is stated as the early stage finding year; the first record of each *Eumerus* species early stage described enough to differentiate it from that of another species is stated as the early stage description year.

Additionally, we used “bipartite” package in R software (Dormann 2011) to illustrate the interactions between *Eumerus* early stages and their host plants using presence/

absence data. Interactions could only be depicted opposing plant genera to *Eumerus* species due to a lack of bibliographical accuracy when describing plant hosts, for example, using common or local names. For this reason, if a single *Eumerus* species was able to feed on two different species of the same genus, the interaction was only considered once. Additionally, we consider plant genera of commercial interest as any genus with at least a single species already with an economic interest reported in literature.

Furthermore, using “circlize” package in R software (Gu et al. 2014), we provide another interaction graph between *Eumerus* species and the parts of the plants these species feed on. In this case, abundance data on interactions between *Eumerus* species and parts of the plants of different genera was used. In this case, if a single *Eumerus* species was able to feed on two different plant tissues of the same plant species, the interaction was considered twice. As a rule, we used the term “stem” restricting its sense to aerial stems, above ground. In the same way, “processed material” refers to any plant material cooked or refined as food.

## Results

### Descriptions of new *Eumerus* early stages

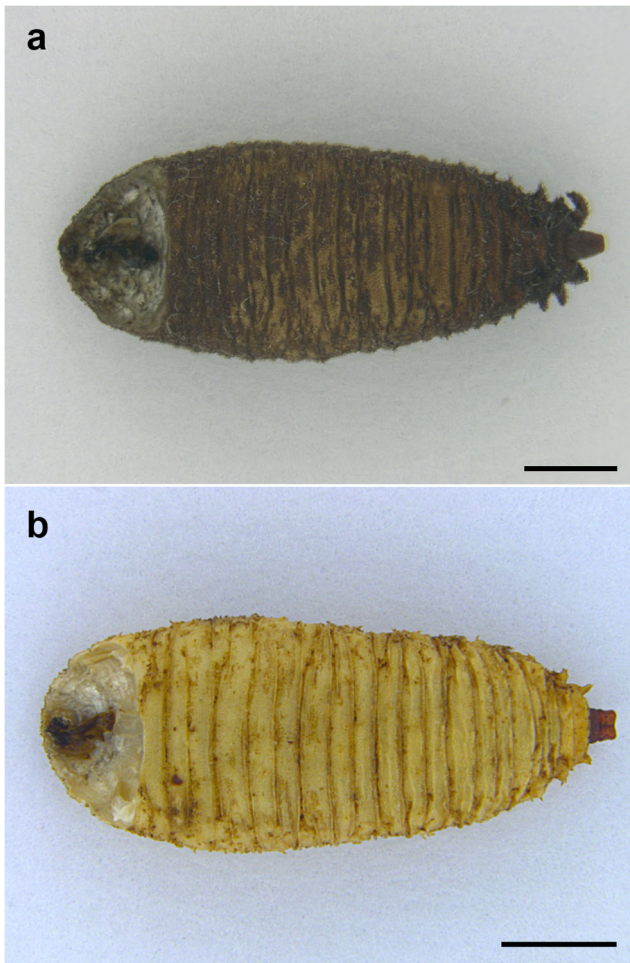
#### *Eumerus alpinus* Rondani 1857

(Figs. 1a; 3a; 4a; 5a, b; 6a, b).

**Shape and size of puparium** (Fig. 1a) Subcylindrical in cross-section, posteriorly tapered, dark brown. Surface of the tegument entirely coated with curved spicules. Mesothoracic prolegs absent. Abdomen with 6 pairs of locomotory organs bearing 1 row of crochets posteriorly curved. Anal segment with three pairs of lappets, middle ones divided in two projections, 3rd pair longer and more curved than the rest. All lappets bearing 2–3 sensilla. Length: 9.37 mm; width: 4.82 mm; height: 4.24 mm ( $n = 1$ ).

**Head skeleton** (Fig. 3a) Mandibular hooks highly sclerotized and mandibular lobes coriaceous, well-developed, fused with the mandibles; dorsal cornu shorter and wider than ventral cornu, dorsal cornu tapering, fin shaped; labrum not prominent, highly sclerotized; pharyngeal sclerite very sclerotized, long, 1/3 the length of the dorsal cornu; tentorial arm sclerotized, wide, ending at mid ventral cornu; tentorial bar heavily sclerotized; mandibular hooks 0.42 mm long, with 2–3 accessory teeth and, in apical view, 21% more separated at the apex than the basal width.

**Anterior spiracles** (Fig. 4a) Cylindrical structures, dark brown and shiny, lightly curved to the tip,  $\approx 101 \mu\text{m}$  long  $\times 56 \mu\text{m}$

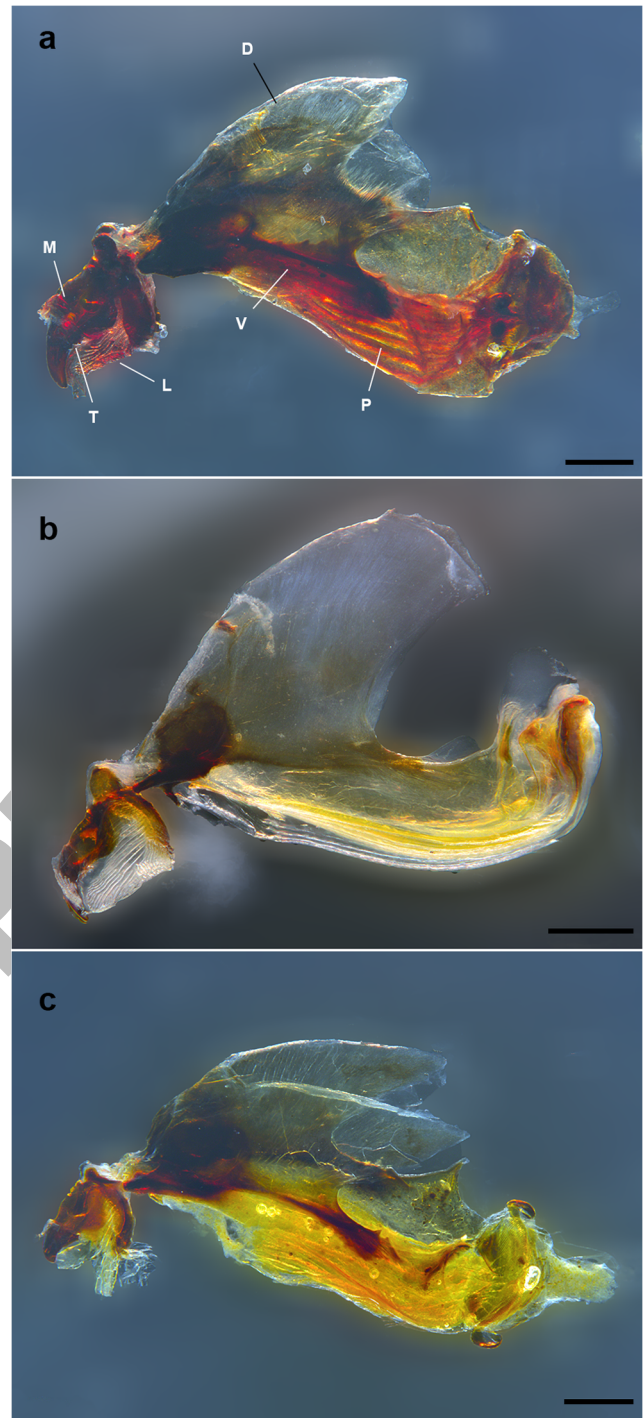


**Fig. 1** General shape of *Eumerus* puparia, dorsal view. **a** *Eumerus alpinus*. **b** *Eumerus superbus*. Scale lines: **a** and **b** = 2 mm

wide, 1.8× longer than broad, with two linear spiracular openings at the apex. Smooth surface without any ornament.

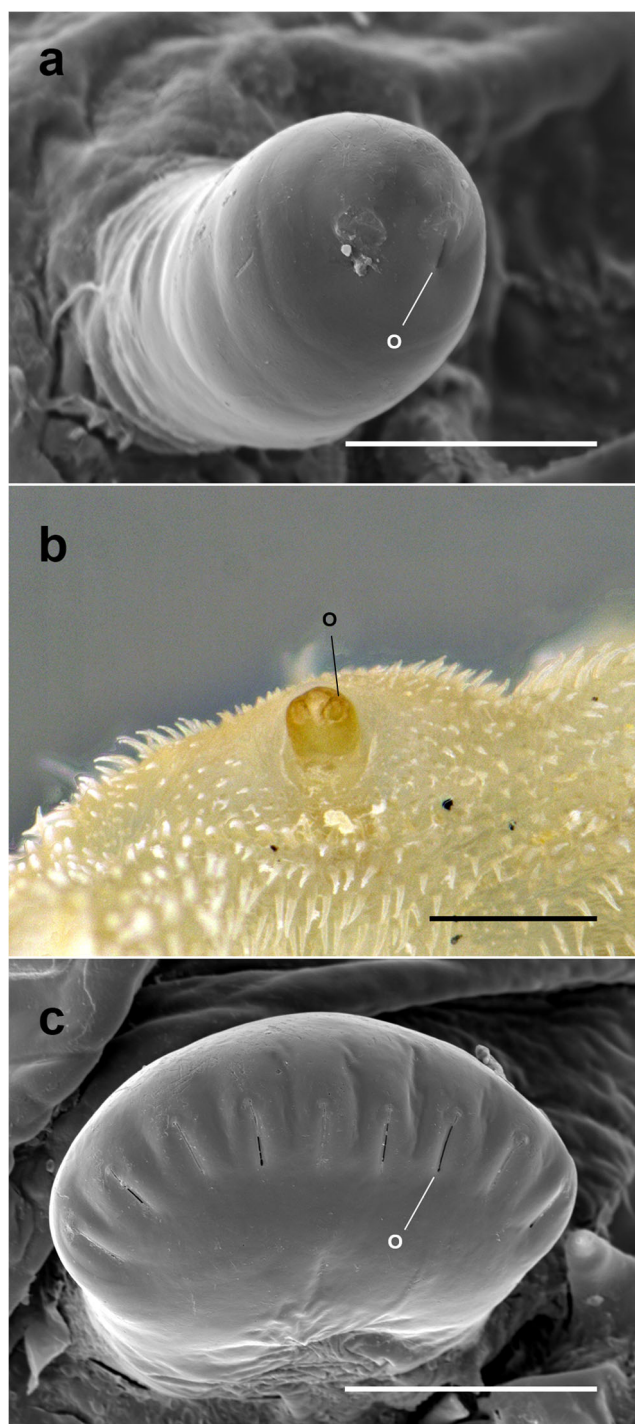


**Fig. 2** General shape of *Eumerus figurans* larva, dorsal view. Scale line = 2 mm



**Fig. 3** Head skeletons of *Eumerus*, lateral view. **a** *Eumerus alpinus*. **b** *Eumerus figurans*. **c** *Eumerus superbus*. D dorsal cornu, L mandibular lobe, M mandibular hook, P pharyngeal ridges, T accessory tooth, V ventral cornu. Scale lines = 250  $\mu$ m

**Pupal spiracles** (Fig. 5a, b) Subconic structures, short and thick, tapering to the tip,  $\approx 306 \mu\text{m}$  long  $\times 192 \mu\text{m}$  wide, 60% longer than broad at the base, separated from each other 5.8 times their length. Smooth surface along the structure except for the granular apex. Regularly spaced round spiracular



**Fig. 4** Anterior spiracles (AS) of *Eumerus* larvae and puparia, apico-ventral view. **a** *Eumerus alpinus*, puparium; SEM. **b** *Eumerus figurans*, larva; stereo microscope. **c** *Eumerus superbus*, puparium; SEM. O spiracular opening. Scale lines: **a** = 50  $\mu$ m; **b** = 200  $\mu$ m; **c** = 100  $\mu$ m

tubercles along the dorsal surface, absent on the ventral surface, bearing 5–7 linear spiracular openings radially arranged.

**PRP** (Fig. 6a, b) Subcylindrical to ovoid tube in cross-section, tapering posteriorly;  $\alpha$  = 387.32  $\mu$ m;  $\beta$  = 570.42;  $\alpha/\beta$  = 0.68.

Below transverse ridge, surface with fine transversal striations with longitudinal wrinkles; immediately above ridge punctured, then granulated towards the apex until almost smooth; 3 pairs of sinuous spiracular openings, with 4 pairs of divided and simply branched setae, not feathery, around the margin of the spiracular plate. Spiracular plate with a light dorsoventral constriction at the center.

**Species distribution** Spain, southern France, Switzerland, Italy (excluding Sicily), parts of the former Yugoslavia, Bulgaria and Romania (Speight 2017).

**Material examined** 1 puparium with emerged female, Madeloc, env. Banyuls-sur-mer, Pyrénées-Orientales, France. Larva ex root of *Asphodelus ramosus* (*Xanthorrhoeaceae*). Leg. M. C. D. Speight. 2013. Deposited at CEUA.

*Eumerus figurans* Walker 1859

(Figs. 2; 3b; 4b; 6c, d).

**Shape and size of third instar (L3) larvae** (Fig. 2) Subcylindrical in cross-section, posteriorly tapered, with anal segment elongated. Length: mean 6.78 mm (range 5.61–7.48); width: mean 2.8 mm (range 2.4–3.22); height: mean 2.19 (range 1.7–3.09) ( $n = 3$ ).

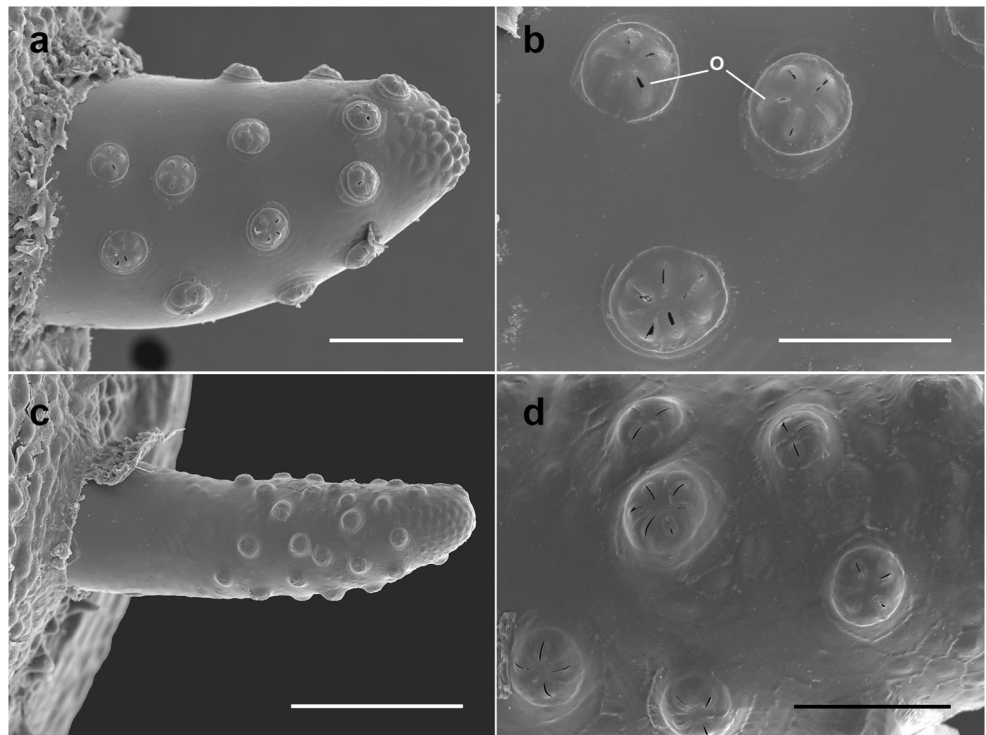
**Head** Antenno-maxillary organs on bulbous and rounded projections with a brown mark on the lateral sides; dorsal lips bearing thin and long clear setae arranged in numerous rows (13–15) and mandibular lobes without setae.

**Head skeleton** (Fig. 3b) Mandibular hooks heavily sclerotized and mandibular lobes fleshy, well-developed, fused with the mandibles; dorsal and ventral cornua almost similar in length, dorsal cornu not tapering, wider than ventral; labrum not prominent, lightly sclerotized; pharyngeal sclerite short, 1/4 the length of the dorsal cornu; tentorial arm lightly sclerotized, diffuse, ending at mid ventral cornu; tentorial bar heavily sclerotized; mandibular hooks 0.36 mm long, without accessory teeth and, in apical view, 23% more separated at the apex than the basal width.

**Thorax** Anterior spiracles oval, pale brown and shiny, flattened to the tip, dome apex with three openings (Fig. 4b). Length: mean 94  $\mu$ m (range 76–112); width: mean 83  $\mu$ m (range 80–87); height: mean 48  $\mu$ m (range 46–50). Mesothoracic prolegs absent.

**Abdomen** Integument villous, covered in long triangular setae and sensilla with 2 to 4 setae each. Locomotory organs on segments 1–6, bearing fine and clear spicules, without

**Fig. 5** Pupal spiracles (PS) of *Eumerus* puparia (left) and details of the tubercles bearing spiracular openings (right). **a, b** *Eumerus alpinus*. **c, d** *Eumerus superbus*. O spiracular opening. Scale lines: **a** = 100  $\mu$ m; **b** and **d** = 50  $\mu$ m; **c** = 250  $\mu$ m



crochets. Anal segment oriented upward, 1.18 mm long (range 0.65–1.45),  $\approx 1.5$  times longer than the 6th segment (mean 0.83, range 0.65–1.03), ventral surface longer than dorsal. Three pairs of lappets present, 1st and 2nd conic, 3rd longer than the others, middle ones divided into two projections. PRP: (Fig. 6c, d) Subcylindrical tube, sometimes not perfectly symmetrical, tapering posteriorly.  $\alpha = 341 \mu\text{m}$ ;  $\beta = 43 \mu\text{m}$ ;  $\alpha/\beta = 0.795$ . Below transverse ridge, surface coarse, with some longitudinal and transversal wrinkles; above ridge, surface punctured to smooth towards the apex; spiracular plate with 3 very sinuous openings, margins with 4 pairs of multi ramous setae.

**Species distribution** Commonly associated to ginger cultures, possibly widespread; from Oriental, Australasian, and Afrotropical bioregions: Bali, Borneo, Celebes, India (Rajasthan), Indonesia (Java, Sulawesi), Japan, Malaysia (Sabah/Borneo), Myanmar, Philippines (Palawan), Sri Lanka, Taiwan, Thailand, Vietnam; USA (Hawaii); Seychelles (Evenhuis and Pape 2019; Hauser, unpublished data).

**Material examined** Three L3 instar larvae. #1: USA: HI, Hawaii Co., Honokaa, ex ginger, 2009, *E. figurans* (immature) PDR#1509453 Det. M. Hauser Dec 2016; #2: USA: HI, Hawaii ex ginger root, 2009, *E. figurans* (immature) PDR#1308785, Det. M. Hauser Dec. 2016; #3: USA, HI, Honolulu Co, Honolulu ex ginger, 2009, 16 V936, *Eumerus marginatus* (immature) PDR# 1308801, Det. M. Hauser Dec. 2016. Deposited at CSCA.

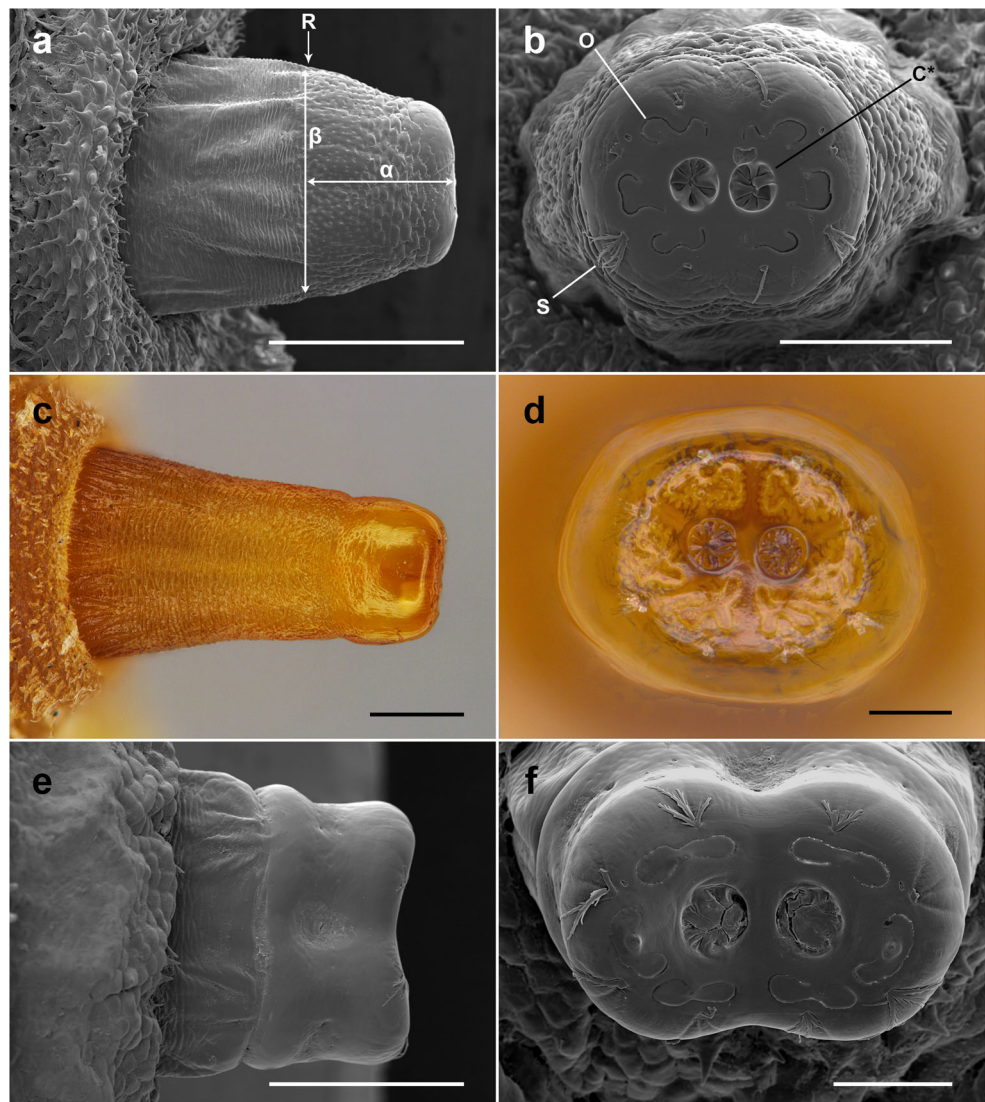
#### *Eumerus superbus* Shannon 1927

(Fig. 1b; 3c; 4c; 5c, d; 6e, f).

**Shape and size of puparium** (Fig. 1b) Subcylindrical in cross-section, posteriorly tapered, pale brown. Surface of the tegument entirely reticulated, as if it had reptilian scales. Mesothoracic prolegs absent. Abdomen with 6 pairs of diffuse locomotory organs, bearing diffuse rows of minimum crochets posteriorly curved, very similar to the surrounding spicules. Anal segment with three pairs of lappets, middle ones divided in two projections, 3rd pair very robust and longer than the rest. All lappets bearing 2–6 sensilla, 3rd one having additional small lateroposterior sensilla. Length: mean 9.58 mm (range 7.71–10.66); width: mean 4.87 mm (range 3.98–5.22); height: mean 4.1 mm (range 3.38–4.38) ( $n = 4$ ).

**Head skeleton** (Fig. 3c) Mandibular hooks highly sclerotized and mandibular lobes fleshy, well-developed, fused with the mandibles; dorsal cornu shorter and wider than ventral cornu, dorsal cornu tapering, fin shaped; final part of the ventral cornu with a dorsal projection facing upwards consisting of a sclerotized fold facing the lumen of the cavity; labrum prominent, sclerotized; pharyngeal sclerite long, 1/3 the length of the dorsal cornu; tentorial arm more sclerotized to the frontal and posterior ends than in the middle, reaching at mid ventral cornu, finished by two sclerotized teeth dorsally facing; tentorial bar heavily sclerotized; mandibular hooks 0.32 mm long, without

**Fig. 6** Posterior respiratory processes (PRP) of *Eumerus* larvae and puparia in dorsal view (left) and polar view (right). **a, b** *Eumerus alpinus*, puparium; SEM. **c, d** *Eumerus figurans*, larva; stereo microscope. **e, f** *Eumerus superbus*, puparium; SEM.  $\alpha$  distance from the transverse ridge to the center of the spiracular plate,  $\beta$  width of the PRP at the transverse ridge level, C\* spiracular scar, O spiracular opening, R transverse ridge, S spiracular seta. Scale lines: **a** and **e** = 500  $\mu\text{m}$ ; **b** and **c** = 250  $\mu\text{m}$ ; **d** = 100  $\mu\text{m}$ ; **f** = 200  $\mu\text{m}$



accessory teeth, apical part of the hooks almost triangular in lateral view and, in apical view, 14% more separated at the apex than the basal width.

**Anterior spiracles** (Fig. 4c) Spatula shaped structures, light brown and shiny, dorsoventrally flattened, narrow at the base, wider to the apex,  $\approx 198 \mu\text{m}$  long  $\times$   $184 \mu\text{m}$  wide at the base, 16% wider to the apex at their maxima, almost equally longer than broad. Nine linear spiracular openings on a single row along the arched apex. Smooth surface with some wrinkles towards the base.

**Pupal spiracles** (Fig. 5c, d) Cylindrical structures, tapering to the tip,  $\approx 574 \mu\text{m}$  long  $\times$   $188 \mu\text{m}$  wide, 3 $\times$  longer than broad at the base. Smooth surface, lightly granulated and reticulated along the structure, apex more granulated and reticulated than the rest of the PS. Irregularly spaced round spiracular tubercles along the distal half of the dorsal

surface, absent on the ventral surface, bearing 3–6 linear spiracular openings radially arranged.

**PRP** (Fig. 6e, f) Dorsoventrally flattened tube in cross-section;  $\alpha = 366.2 \mu\text{m}$ ;  $\beta = 704.23$ ;  $\alpha/\beta = 0.52$ . Below transverse ridge, surface with fine transversal striations with longitudinal and diagonal wrinkles; above ridge smooth, with a constriction forming a subtle transversal groove, half distance from the transverse ridge to the spiracular plate, lightly punctured; 3 pairs of sinuous spiracular openings, curved to themselves, with 4 pairs of divided and simply branched setae, not feathery, around the margin of the spiracular plate. Spiracular plate with an evident dorsoventral constriction at the center.

**Species distribution** Only known to Australia (Evenhuis and Pape 2019).



**Material examined** 4 puparia. 2 males and 1 female bred from *Lepidozamia peroffskyana* seed cones, Leg. C. Burgess, 1970; 1 female bred from *Macrozamia communis*, Leg. M. S. Upton, 1965. All known specimens of this species are reared and no adult has yet been caught in the wild (Hauser, pers. comm.) Deposited at ANIC.

**Key to *Eumerus* early stages (L3 larvae and puparia)**

This key includes all known larvae/puparia of *Eumerus*, following the previous key of Ricarte et al. (2017).

- 1a. Mesothoracic prolegs present .....2
- 1b. Mesothoracic prolegs absent .....3
- 2a. Head skeleton: mandibular hook serrated apically; dorsal cornu rounded. Pupal spiracles bearing tubercles with 6–10 spiracular openings. PRP with inconspicuous vestiture .....*E. etnensis*
- 2b. Head skeleton: mandibular hook not serrated; dorsal cornu pointed. Pupal spiracles bearing tubercles with 5–7 spiracular openings. PRP with conspicuous vestiture .....*E. obliquus*
- 3a. Anal segment contracted, as long as broad or broader; only first pair of lappets well developed; PRP short, barely visible or not visible with larva/puparium in lateral view .....4
- 3b. Anal segment elongated to varying degrees; all three pairs of lappets developed or third pair more developed than the other pairs; PRP long, clearly visible with larva/puparium in lateral view .....5
- 4a. Tentorial arm heavily sclerotized; dorsal cornu shorter than ventral cornu (host plants: *Tragopogon* spp.) .....*E. tricolor*
- 4b. Tentorial arm slightly sclerotized; dorsal cornu longer than ventral cornu (host plant: *Cistanche phelypaea*) .....*E. compertus*
- 5a. PRP conspicuously asymmetric above transverse ridge, specially near the apex .....*E. hungaricus*
- 5b. PRP symmetrical (Fig. 6a–e) .....6
- 6a. Mandibular hooks without accessory teeth; anterior part of the hooks triangular shaped in lateral view (Fig. 3c); AS spatula shaped, with numerous linear openings along the apex (Fig. 4c); final part of the PRP with a prominent dorsoventral constriction (Australian species reared from Zamiaceae plants) (Fig. 6e, f) .....*E. superbus*
- 6b. Mandibular hooks with prominent accessory teeth, eroded or not to different degrees; anterior part of the hooks with the typical curved shape; AS sub-oval to cylindrical with 2–4 spiracular openings at the apex; final part of the PRP without prominent constriction (Fig. 6b, d) .....7
- 7a. AS oval (Fig. 4b), with 3 openings; head skeleton with wide cornua; dorsal cornu not fin shaped, rounded

- and wide (pest of *Zingiber* sp., known as ginger maggot) (Fig. 3b) .....*E. figurans*
- 7b. AS subcylindrical to cylindrical, with or without a different number of openings; head skeleton with narrower cornua, dorsal cornu usually fin shaped, acute at the apex .....8
- 8a. Mandibular hook with a single accessory tooth; PRP with spicules basally .....*E. pulchellus*
- 8b. Mandibular hook with more than one accessory tooth. PRP without spicules .....9
- 9a. Head skeleton with large mandibular hooks, apically curved for about half of their total length; PRP with spiracular openings very sinuous, clearly ω-shaped .....10
- 9b. Head skeleton with smaller mandibular hooks, bar-shaped, apically curved for less than half of their total length; PRP with spiracular openings U-shaped or slightly sinuous .....11
- 10a. Pupal spiracles separated approx. 6× the length of the PS; surface of the pupal spiracles only granulated at the apex (Fig. 5a); PS tubercles with 5–7 radial openings (Fig. 5b); spiracular plate of the PRP almost round; interspiracular setae with 3–5 branches (Fig. 6b) .....*E. alpinus*
- 10b. Pupal spiracles separated approx. 8× the length of the PS; surface of the pupal spiracles densely granulated towards the apex, least 1/3 of the total length; PS tubercles with 3–5 radial openings; spiracular plate of the PRP less rounded (wider than height); interspiracular setae with 3–8 branches .....*E. nudus*
- 11a. Mandibular hook with 4 accessory teeth; PRP below transverse ridge with conspicuous transverse striations all over .....*E. pusillus*
- 11b. Mandibular hook with more than 4 accessory teeth; PRP below transverse ridge with different vestiture .....12
- 12a. Antenno-maxillary organs of larva separated by an inconspicuous groove or without groove; mandibular hook usually with seven accessory teeth, rarely six; PRP below transverse ridge with coarse diagonal wrinkles, faintly striated transversally .....*E. strigatus*
- 12b. Antenno-maxillary organs of larva separated by a conspicuous groove; mandibular hook usually with five accessory teeth, rarely six; vestiture of PRP undescribed .....*E. funeralis*

**Additions to the available data on the *Eumerus* early stages worldwide and their host plant relationships**

As shown in Table 2, new information on *Eumerus* larvae with their host plants is provided in this paper, increasing the data on the revision by Ricarte et al. (2017). As far as we know, early stages of *E. cistanchei* Efflatoun 1926 and *E. mucidus* have not been described yet (Table 2). Although

**Table 2** Food plants and early stages of *Eumerus* species

Species	Host plants <sup>a</sup>	Morphology <sup>b</sup>
<i>Eumerus</i> Meigen 1822		
<i>E. ammophilus</i> Paramonov, 1927	Larvae found in stems of <i>Cistanche</i> Hoffmanns. ex Link (Orobanchaceae) and adults feeding on the flowers of the same plant (Stackelberg 1961).	Undescribed
<i>E. arnoldii</i> Stackelberg, 1952	Larvae found in “gigantic” broomrape ( <i>Cistanche</i> sp.) (Stackelberg 1961).	Undescribed
<i>E. cistanchei</i> Efflatoun, 1926	Reared from <i>Cistanche lutea</i> Wight, cohabiting with larvae of <i>E. mucidus</i> (Efflatoun 1926).	Undescribed
<i>E. figurans</i> Walker, 1859	Found damaging “lily bulbs” ( <i>Lilium</i> , Liliaceae), <i>Narcissus</i> L. (Amaryllidaceae) and ginger ( <i>Zingiber</i> sp., Zingiberaceae) (Hardy 1964). Found in pineapple stumps (Carter 1968). Feeding inside rotten corms of <i>Colocassia esculenta</i> (L.) Schott (Araceae) (Miyasaka et al. 2003). Reared from ginger rhizomes.	Present paper
<i>E. mucidus</i> Bezzi, 1921	Reared from <i>Cistanche phelypaea</i> (L.) Cout. in Egypt (Shaumar and Kamal 1978) and from stems and tubers of endemic <i>C. armena</i> (K.Koch) M. V. Agab. (Piwowarczyk and Mielczarek 2018).	Undescribed
<i>E. alpinus</i> Rondani, 1857	Reared from <i>Asphodelus ramosus</i> (Speight and Garrigue 2014).	General description of overall shape and morphology (Speight and Garrigue 2014). Detailed descriptions and microstructures in present paper
<i>E. superbus</i> Shannon, 1927	Reared from cones of <i>Lepidozamia peroffskyana</i> and <i>Macrozamia communis</i> (Zamiaceae).	Present paper
<i>E. turcmenorum</i> Paramonov, 1927	Larvae found in stems of “gigantic” broomrape ( <i>Cistanche</i> sp.) (Stackelberg 1961).	Undescribed
<i>E. vestitus</i> Bezzi, 1912	From different crops: potatoes and tomatoes (Solanaceae), watermelon (Cucurbitaceae), grapes (Vitaceae), and peach (Rosaceae), (Shaumar and Kamal 1978).	Undescribed

<sup>a</sup> This includes information on actual and/or potential host plants of each species larva

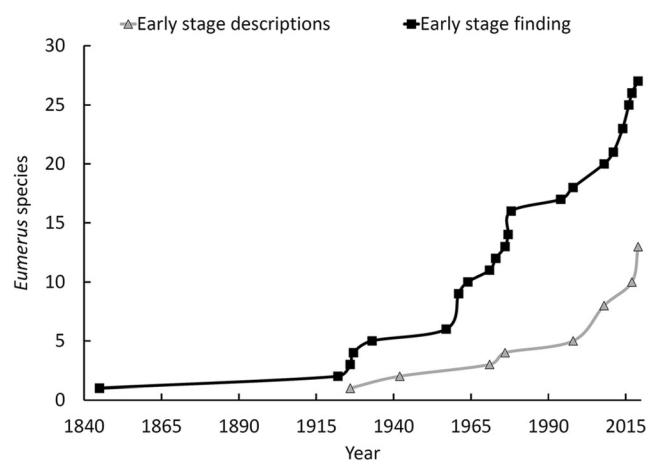
<sup>b</sup> Current state of the descriptions of the early stages of each species

Efflatoun wrote in the same paper where he described *E. cistanchei* for the first time (1926) that he would be describing larvae and puparia of these two species in a next publication, he never published it. For records of *E. figurans* (as *E. marginatus*) feeding on lily bulbs from Hardy (1964), we assume genus *Lilium* L. (Liliaceae).

### Early stage descriptions, a recent trend

There are less described early stages than discovered ones. In Fig. 7, we show trends for both early stage finding and early stage descriptions, both increasing during the twentieth century. More than 60% of the descriptions of *Eumerus* have been achieved during the last decade. However, only a third of the known life cycles of *Eumerus* have been discovered during the same period. New host plants associations have been a slower but continuous process in comparison with the descriptions of the found specimens. The oldest record for early stage discoveries we found belongs to Dufour (1845), a paper in which he described how larvae of *E. strigatus* fed inside onion

bulbs. It took until 1926 for the second immature publication, when Wilcox described the egg, larva, and puparium of



**Fig. 7** Total count of described early stages of *Eumerus* (triangles) and total count of known life cycles of early stages of *Eumerus* species (squares) by the first time a host-plant interaction was reported. X-axis shows years. Y-axis, number of *Eumerus* species

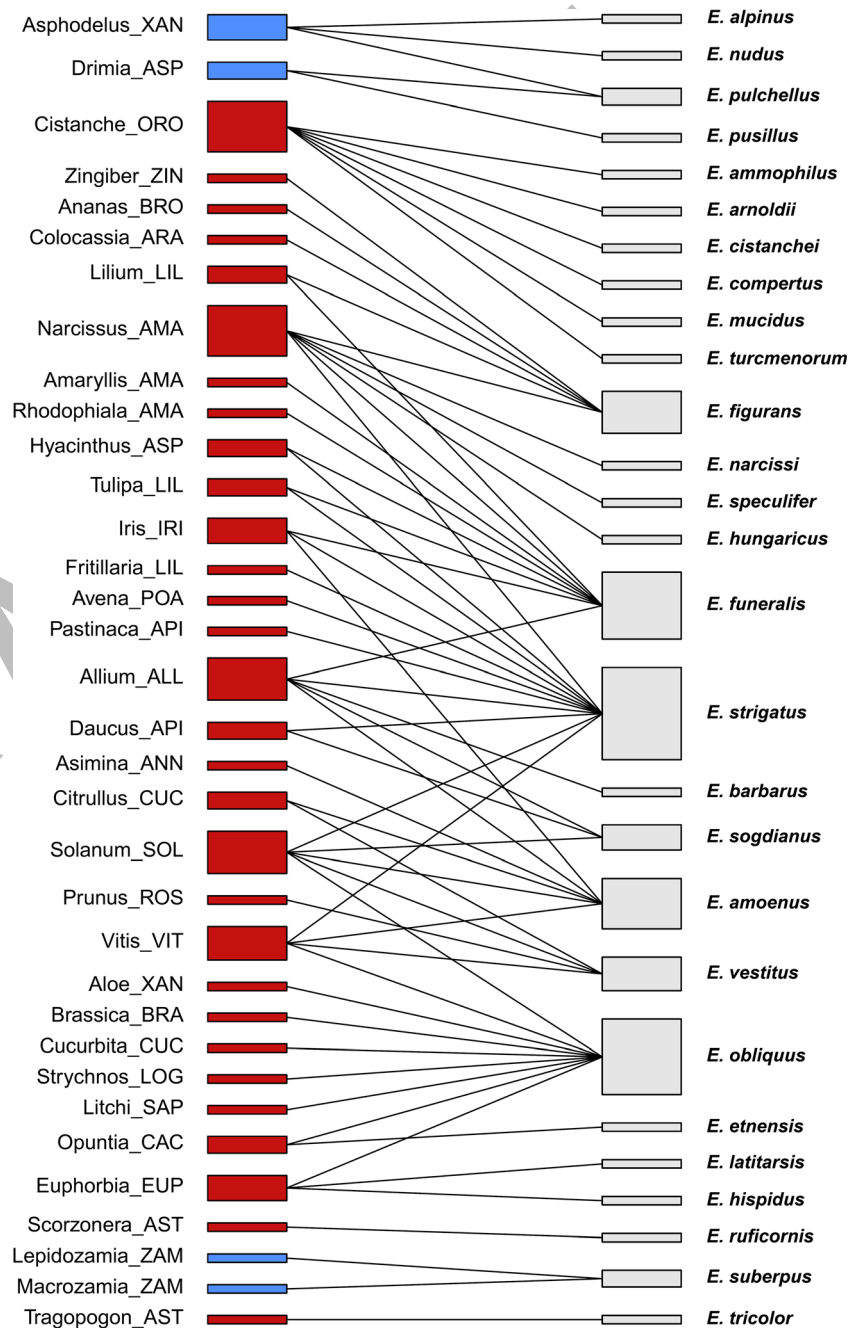
*E. strigatus*. The total count of described early stages of *Eumerus* is now 13 (including this study).

***Eumerus* hoverflies feed on a wide range of plants, many with commercial interest**

Some species of *Eumerus* show very polyphagous ranges of host plants for their larvae (Fig. 8). That is the case of *E. strigatus*, which, according to published records, has been reported from at least 11 different genera of plants. The same occurs for the subsequent most polyphagous

species, *E. obliquus* (Fabricius 1805), *E. funeralis*, and *E. amoenus*, respectively, reported from nine, eight, and six different plant genera. All four species feed on plants with commercial interest, and some of them are known to be pests of these plants. There are many species of *Eumerus* reported from single host genera as in the cases of *E. alpinus* and *E. nudus*, which only feed on *Asphodelus* (Xanthorrhoeaceae), *E. ruficornis* Meigen 1822, which is the only known *Eumerus* species that feed on *Scorzonera* L. (Asteraceae) and *E. tricolor* (Fabricius 1798), only known from two species of *Tragopogon* L. (Asteraceae).

**Fig. 8** “Bipartite” network between *Eumerus* species (right) and the genera of host plants (left). Length of the boxes show the number of interactions. Colors of the plant boxes: in red (dark color), genera with at least one species with economic value; in blue (light color), without economic value. Plant genera followed by plant family abbreviations as in Table 1



In the case of *E. superbus*, it was only reported from two species of Zamiaceae plants, thus being the first records of *Eumerus* for gymnosperms.

Additionally, some plant genera are reported as host plants for different *Eumerus* species. This is the case of *Cistanche* and *Narcissus*, with six *Eumerus* species each, and *Allium* L. and *Solanum* L., with five species each. However, *Eumerus* species feeding on *Cistanche*, are not known to feed on any other plant genera. Conversely, *Allium*, *Narcissus*, and *Solanum* are host plants for some *Eumerus* species able to feed on more than one plant genus. Only three *Eumerus* species are able to feed on all cited genera of some plant families: *E. funeralis* in Amaryllidaceae, *E. strigatus* in Apiaceae, and *E. superbus* in Zamiaceae.

Among all 34 studied plant taxa, only 4 genera were considered as without current commercial value. Therefore, *Eumerus* feeds on a higher number of plants with commercial interest rather than without it (Fig. 8).

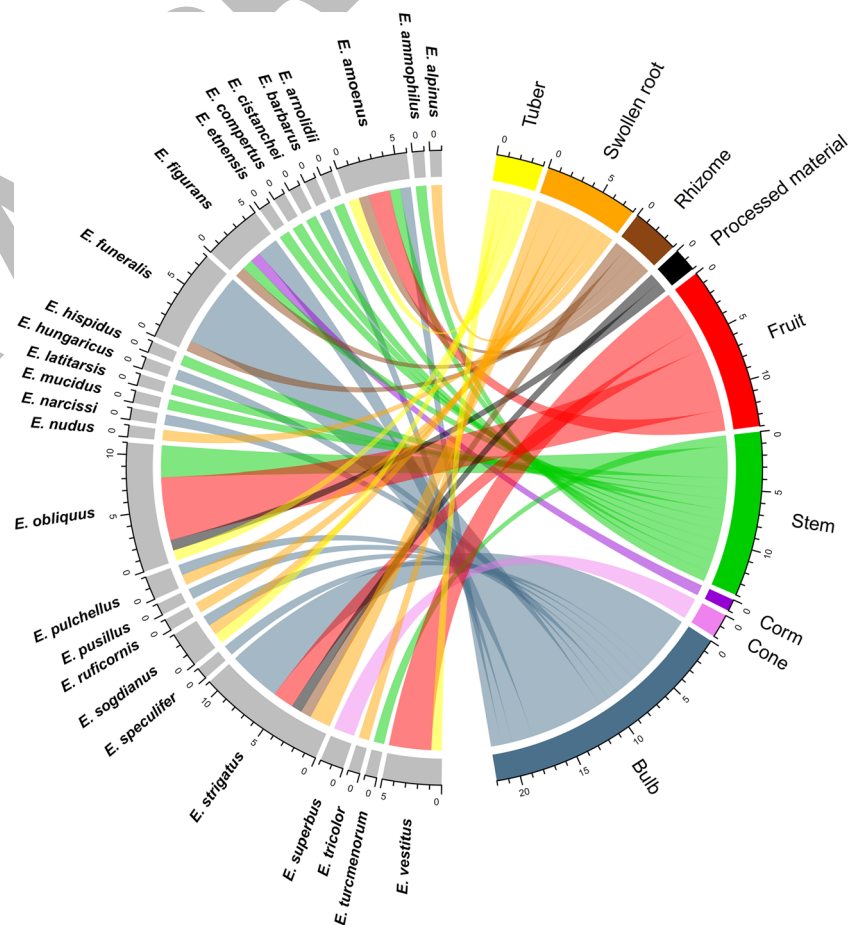
### ***Eumerus* hoverflies feed on a wide range of plant tissues, not only bulbs**

The variety of suitable plant tissues immature *Eumerus* are able to feed on also explains their polyphagy. *Eumerus* early

stages interact with many different plant tissues, being bulbs, fruits, stems, and swollen roots the most common interactions (Fig. 9). Species like *E. amoenus* and *E. strigatus* are the most diverse ones, feeding on five different types of plant tissues. While *E. amoenus* interactions with plant tissues are almost equally balanced, *E. strigatus* was more commonly related to bulbs rather than to other types of tissues. Almost an alike situation affects *E. figurans* and *E. obliquus*, the first one having almost equal interactions with four types of plant tissues and the second one attacking more fruits and aerial stems than tubers or processed materials. Some *Eumerus* species were only reported from single plant tissues, being the stem the most repeated one in these cases (nine species), followed by bulbs (five species) and swollen roots (four species). At the other end, we find that none *Eumerus* species has been reported to exclusively feed on tubers, rhizomes, fruits, or processed plant materials. Some special cases are those of *E. figurans* and *E. superbus*. *E. figurans* was the only species ever reported from corms, a special type of underground storage organ, midway between bulbs and tubers; *E. superbus* was the only species ever reported from gymnosperm cones.

Even though our findings appreciate that many types of bulbous plants are hosts for *Eumerus*, underground organs are, in general, suitable habitats for their larvae. However,

**Fig. 9** Feeding network between larvae of *Eumerus* species (left, in gray) and plant tissues they feed on (right, colored) based on the interactions historically reported in bibliography for different genera of plants. Links between sides indicate relationships. Scales on each segment show the number of interactions established with the counter side. Plant tissue color palette as follows: tuber (yellow), swollen root (orange), rhizome (brown), processed material (black), fruits (red), stem (light green), corm (purple), cone (pink), and bulb (blue). Picture made using “circlize” package for R software



bulbs and stems are equally reported as host tissues for 11 species of *Eumerus* larvae. In fact, if we consider all stems botanically, the addition of underground stems with structural function (rhizomes) and storage function (tubers and corms) to aerial stems (in green) conform the largest group of stem feeding *Eumerus* species. We do not include bulbs in this group because their stems are reduced to a minimum disc and it is covered by many layers of leaves with storage functions. These leaves are what *Eumerus* larvae mainly attack and dig through when entering a bulb, and, therefore, stems are not the majority of the biomass in these cases.

## Discussion

In this paper, the main objective was to study *Eumerus* biology through the morphology of their early stages and host plants. According to our results, these larvae described here are well differentiated from all previously described immature stages of *Eumerus*, including in particular morphological traits related to their feeding regimes. *E. alpinus* is very alike to *E. nudus*, both species having strong grazing-like mandibles, while *E. figurans* has a typical filtering mandible, with well-developed mandibular lobes. Historically, many authors have recorded host plants for *Eumerus*, the majority of them of commercial interest, but descriptions of immature stages seem a rather recent trend. Taking at face value the identifications of species recorded in the literature, most known immature stages of *Eumerus* can feed on a wide range of plant species and plant tissues, even if some species are apparently monophagous (e.g. *Cistanche*).

## Early stage morphology

All species described in this study have sclerotized mandibular hooks to different degrees, those of *E. alpinus* being the largest (Fig. 3). Only *E. alpinus* presented well-developed secondary teeth, although some small protuberances were found in *E. figurans* and *E. superbus* that might indicate high deterioration of these structures after scraping plant tissues. While extracting head skeletons of *E. alpinus* and *E. superbus*, some clusters of scraped and decomposed plant material were obtained from inside their mouths. This suggests the ability of at least these two species to generate their own decaying feeding material and microhabitats. All three species have pharyngeal ridges (Fig. 3) that may help them feed on microorganisms present in fluids from decaying plant tissues, as the larvae of saprophagous hoverflies do (Sánchez-Galván et al. 2017). These conclusions support the apparently wide range of feeding strategies of *Eumerus*, from saprophagy to phytophagy, as suggested many authors (e.g. Ricarte et al. 2017; Rotheray and Gilbert 1999). In this way, it is remarkable how alike head skeletons of *E. alpinus* and *E. nudus* are in size, shape, and

ornamentation. In general, *E. alpinus* has a slightly bigger head skeleton than *E. nudus*. Width of the dorsal cornu and length of the pharyngeal ridges of *E. nudus* are the only measurements surpassing those of *E. alpinus*. Mouth hooks of *E. nudus* are smaller than stated by Ricarte et al. (2017), being almost equal to those of *E. alpinus*. Despite both species having well-developed mouth parts, a smaller head skeleton and a shorter pharyngeal surface through which *E. nudus* may be able to filtrate food perhaps indicates a slightly more saprophagous feeding habit in this species compared with *E. alpinus*. In any case, these two species must have a close phylogenetic relationship as they feed on two similar *Asphodelus* species (Ricarte et al. 2017; Speight and Garrigue 2014) and both species have very alike larvae and adult forms.

The three studied species have very different AS structures. *E. alpinus* has very similar AS to those of *E. nudus*, almost equal in shape and size (*E. alpinus* 1.8 times longer than broad; *E. nudus* 1.6 times longer than broad). *Eumerus superbus* has the most distinctive AS compared with other *Eumerus* species. The high number of spiracular openings *E. superbus* (Fig. 4c) might suggest either a higher oxygen requirement of the larva or a particular need of more efficient AS. On one hand, *E. superbus* has big sized puparia, along with *E. alpinus*, *E. nudus*, and *E. obliquus* (Ricarte et al. 2008, 2017), which metabolically might have higher requirements of oxygen and, therefore, more spiracular openings on the AS. On the other hand, cycads are commonly known to have mucilage (Langenheim 2003), a substance that may plug the openings of the AS; thus, *E. superbus* might have adapted to this viscous substance developing more spiracular openings while damaging plant tissue.

Pupal spiracles were described only for *E. alpinus* and *E. superbus*. *Eumerus superbus* PS are almost twice the length of those of *E. alpinus* (Fig. 5). Although both species lack pupal tubercles on the dorsal surface of the PS, they reach the base of the PS in *E. alpinus*, but in *E. superbus*, they only reach half of the length of the PS. Moreover, the surface of *E. superbus* is more granulated than the surface of *E. alpinus*. Comparing these species to previously described ones, PS of *E. alpinus* are very alike to those of *E. nudus* in overall shape and dimensions, but it is possible to differentiate them. In *E. alpinus*, PS are separated approx. 6× the length of the PS, pupal tubercles bear 5–7 openings, and the surface of the structure is only granulated at the apex; in *E. nudus*, PS are more separated, 8× the length of the PS, pupal tubercles bear 3–5 openings, and the surface of the PS is granulated towards the apex at least 1/3 of the total length.

Locomotory organs of our three species seem very alike. *Eumerus alpinus* is the only one having a well-developed line of crochets although sometimes difficult to see. The very similar *E. nudus* has 2 rows of well-developed crochets (Ricarte et al. 2017). Additionally, none of the studied species have mesothoracic prolegs, *E. etnensis* van der Goot 1964 and

*E. obliquus* being the only currently described species with these organs (Pérez-Bañón and Marcos-García 1998; Ricarte et al. 2008).

PRP structures of the studied species show numerous differences (Fig. 6). *E. alpinus* has a PRP almost identical to *E. nudus* in shape, surface, measurements, and ornamentation (Ricarte et al. 2017). However, *E. alpinus* has a rounder spiracular plate than *E. nudus*, which is more oval. Moreover, *E. alpinus* has less divided setae on the spiracular plate than *E. nudus*. *E. superbus* has the most particular PRP, with a prominent dorsoventral constriction towards the apex, slightly present at the spiracular plate of *E. alpinus*, *E. nudus*, and *E. pulchellus* Loew 1848 (Ricarte et al. 2008, 2017). This constriction is absent in *E. figurans*.

### Host plant interaction analyses

Although a large number of *Eumerus* species have been described in their adult form, information about their developmental stages has been almost nonexistent until recently. Both, morphological descriptions and host plant-related papers seem a rather recent trend, with the majority of studies published during the last part of the twentieth century or later (Hartley 1961, 1963; Pérez-Bañón and Marcos-García 1998; Ricarte et al. 2008, 2017; Rotheray and Gilbert 1999). This increasing interest in early stages of *Eumerus* has allowed researchers to analyze previously known immature stages that were, or not, sufficiently described. This is the case of *E. figurans*, whose larval interactions with ginger and other plant species have been known for a long time (Hardy 1964). This knowledge gap on life cycles of *Eumerus* and closely related genera still remains, especially among *Eumerus* species of no known commercial significance, in part because it is very difficult to find early stages in nonagricultural situations (Ricarte et al. 2017; Speight 2016). However, observing both adult behavior and plant species screening based on previous records of host plants and plant tissues is essential for finding new host plants and early stages.

*Eumerus* is commonly known to associate with geophytes (Piwowarczyk and Mielczarek 2018; Rotheray and Gilbert 1999; Speight et al. 2013). However, the literature record shows that some *Eumerus* species are very polyphagous, feeding inside a wide range of plants and tissues, not only underground ones, and some others have a more restricted and specific list of host plants. *Eumerus* larvae then, feed on single plant species belonging to very different plant genera and families. Some *Eumerus* species feed on various plant tissues, coinciding or not with the same plant genera. These data allow us to differentiate *Eumerus* between polyphagous or generalist species and monophagous or specialist species, as reported for the genus *Cheilisia* (Diptera, Syrphidae) (Stuke 2000) and many other herbivorous insects (Schoonhoven et al. 2005). The best example of this would be the generalist and

polyphagous pest *E. obliquus*, able to feed on nine different genera of plants but having up to 11 interactions among different plant tissues (Figs. 8 and 9). This is because *E. obliquus* larvae feed on two different species of *Solanum*, potato and tomato, attacking tubers and fruits, respectively (de Moor 1973), and they are also able to attack fruits and stems of *Opuntia maxima* Mill. (Ricarte et al. 2008). In fact, *E. obliquus* along with other widespread and generalist species like *E. amoenus*, *E. figurans*, *E. funeralis*, and *E. strigatus* may be taking advantage of their wide range of host plant spectrum to travel worldwide as larvae inside plant structures (e.g. de Moor 1973; Morales and Marinoni 2007; Speight et al. 2013). Moreover, many *Eumerus* immatures are nearly exclusively found on plants of diverse origins, meaning that the host plant of the native distribution is still unknown (Hauser, pers. comm.). However, the ability of *Eumerus* to colonize this high variety of plants and tissues might be related to its trophic habit, previously reported as micophagous (Creager and Spruijt 1935; Rotheray and Gilbert 1999) and latterly saprophagous (Rotheray 2009; Rotheray and Gilbert 2011). It is feasible that many *Eumerus* larvae reported in this study were able to live within decaying plant tissues because of organic debris and associated microbiota, as some other studies have suggested within *Copestylum* Macquart, 1846 (Diptera: Syrphidae), among many tropical plants and tissues (Rotheray 2009; Rotheray et al. 2007). In fact, generalist *Eumerus* may be generating their own decaying microhabitat within host plants by penetrating plant tissues and allowing microbiota to flourish because of larvae presence and movement (Rotheray et al. 2007) rather than having specific relationships within any plant taxa.

On the contrary, many species of *Eumerus* seem to be more specialist than generalist, as in the cases of *E. ruficornis* and *E. tricolor*, both currently found feeding only on *Scorzonera* and *Tragopogon* swollen roots (both Asteraceae). An interesting case is that of *Cistanche*, (Orobanchaceae), which commonly parasitizes roots of Chenopodiaceae (Piwowarczyk et al. 2019), where larvae of *E. ammophilus*, *E. arnoldii*, *E. cistanchei*, *E. compertus* Villeneuve in Villeneuve and Gauthier, 1924, *E. mucidus*, and *E. turcmenorum* were uniquely reported. It is surprising how this arid and semiarid habitat related plant genus (Moreno Moral et al. 2018) is of such importance in dry environments to many *Eumerus* species, feeding inside their soft and swollen-to-various-degrees parenchymatous stems. *E. mucidus* was only reported from *C. phelypaea* from Egypt and Israel (Kaplan 1974; Shaumar and Kamal 1978) until 2018, when it was reared from the endemic *C. armena* (Mt. Ararat, Armenia, Piwowarczyk and Mielczarek 2018). As *C. phelypaea* is not present in Armenia (Piwowarczyk et al. 2019), it is possible that the vicariant *C. armena* might be the only suitable host in that country for *E. mucidus*.

Plant tissues *Eumerus* larvae are able to feed on are of major importance for both generalist and specialist species. Different parts of the plant have different cellular structures and chemical compositions (Schoonhoven et al. 2005) that may determine the optimal conditions for microbiota and survival by *Eumerus* larvae. For this reason, we considered specialized botanical terminology for all reported plant tissues (Font Quer 1953). In the case of specialist species, plant tissues *Eumerus* larvae feed on are even more interesting as these data may show their preferences when attacking their host plants. *Eumerus* and *Merodon* are able to live inside living plant tissue known to have toxic compounds (Ricarte et al. 2017). These toxins should impede herbivory, thus making some tissues less suitable as microhabitat candidates for both genera. However, the metabolic mechanisms that allow *Eumerus* and *Merodon* to bear, or not, these toxicities are still unknown. The extent to which the decaying plant tissues ingested by saprophagous *Eumerus* larvae retain their toxicity is unclear. But, in principle, the wide taxonomic range of plants hosting some of the saprophagous *Eumerus* species, e.g. *Eumerus strigatus*, could be a reflection of the greater significance of whether an appropriate combination of yeasts and microbes is generated by the decay of the plant tissues than whether the living plant's tissues would be toxic. A further issue is the extent to which saprophagous *Eumerus* larvae depend upon phytophagous larvae of other insects to initiate decay in bulbs in order to provide the *Eumerus* larvae with appropriate living conditions. This was alluded to by Ricarte et al. (2008) and Speight and Garrigue (2014), observing that the saprophagous larvae of *Eumerus pusillus* Loew 1848 and *Eumerus pulchellus*, for instance, are normally found in decaying bulbs or tubers with phytophagous *Merodon* or *Eumerus* larvae.

It seems logical that generalist *Eumerus* may have weaker and unspecific relationships among their respective host plants than have specialist *Eumerus*. In fact, a more phytophagous feeding habit rather than a filtering one of some *Eumerus* species and closely related *Merodon* (Ricarte et al. 2008, 2017) may be related to the degree of specialization between these hoverflies and their host plants. As examples, the early stages of *E. alpinus* and *E. nudus* live only in alike microhabitats inside very similar *Asphodelus* species, and their morphologies are close to each other. In the case of *E. superbis*, which has the most particular ensemble of morphological traits among other *Eumerus* early stages, its unique habitat inside reproductive cones of Zamiaceae might have had morphofunctional implications over this species. However, after comparing our compiled data on host plants with the molecular ones of (Chroni et al. 2017) *Eumerus*, species of the same molecular clade do not feed on the same plant families. But this lack of association is not as yet well supported by molecular results. As Chroni et al. (2017) pointed out, more specimens per taxa should be included in molecular analyses to better resolve the phylogenetic tree of *Eumerus*.

Additionally, *E. superbis* is one of few *Eumerus* species known to Australia, the rest of them being clearly unrelated to *E. superbis* (Hauser, pers. comm.). This continent, a long time isolated biogeographical region with very particular flora, might have also contributed to the morphological features of the early stages of *E. superbis*. Population analyses with biogeographical approaches may highlight the importance of geographical isolation in this species, within genus *Eumerus* (Chroni et al. 2017) as well as in other Diptera (Kočiš Tubiĉ et al. 2018; Pramual et al. 2012; Vujić et al. 2012).

The majority of the documented interactions established by *Eumerus* larvae with plants are for plants with commercial value in different parts of the world. These include daffodils, hyacinths, onion, and garlic or ginger (Assem et al. 1972; Creager and Spruijt 1935; Hodson 1927; Ricarte et al. 2017). For this reason, some species like *E. figurans*, *E. funeralis*, *E. obliquus*, or *E. strigatus* are considered as pests for plants with agricultural or horticultural value in many countries (Pérez-Bañón and Marcos-García 1998; USDA 2016). Commercial plants are of major interest and are relatively easy to find and grow for experimental purposes, thus interactions of *Eumerus* larvae with these plants may be more visible in the literature than interactions with wild plants. Moreover, it is very difficult to find *Eumerus* early stages in the wild (Ricarte et al. 2017), a fact that may be contributing to the low number of *Eumerus* immatures currently described.

## Conclusion

In our study, only a few genera of host plants were considered without commercial value, but they may remain as potential banks for horticultural or pharmacological purposes in the future. In the case of *Macrozamia* Miq. and *Lepidozamia* Regel, two host genera for *E. superbis* in Australia, both were considered as without commercial value. However, these plants might be of potential food and garden use (Whitelock 2002) as some other plants of the Zamiaceae family already are (Mayett Moreno et al. 2014). This may be relevant for the conservation of *E. superbis* as the massive devastation of late 2019 and early 2020 fires in Australia has destroyed the collection sites and host plants of some of our specimens from New South Wales and surrounding areas (Landgate 2020). The capability to fly away from burnt areas of adults of *E. superbis* is unknown but having more host plants anywhere else would potentially help this species survival. On the contrary, the parasitic genus *Cistanche*, which is considered a wild taxon in western countries, was assigned to commercial value taxa as it is a well-known group of plants in traditional Chinese medicine (e.g. Gu et al. 2016; Li et al. 2018). One of the *Cistanche* species could even be of significant economic importance in conservation and governmental purposes as it is endemic to a very restricted area of Armenia and *E. mucidus* feeds inside this unique

plant, compromising its performance and survival in the wild (Piwowarczyk et al. 2019; Piwowarczyk and Mielczarek 2018). Even though many of the *Eumerus* species lack of a well-known life cycle, the implications of the interactions they establish may be of major relevance.

In conclusion, the three species we describe can be easily distinguishable among immature stages of other *Eumerus* due to their distinctive morphological and functional features and the relationships they establish with the host plants they feed on. Our findings fit within the general descriptions of larvae of the genus, even if the larvae of only small portion of the global count of *Eumerus* species is yet described. However, *Eumerus* has proved to be a very polyphagous and generalist genus, with a wide range of suitable plant microhabitats where their immature stages can develop. In this paper, we highlight the importance of relating *Eumerus* immature stages to a proper plant tissue as these data may provide information on what their feeding habits are. Proofs on whether *Eumerus* species are saprophagous and/or phytophagous should be a major priority as knowing what they feed on, finding, sampling, and pest control difficulties might be eased.

Overall, there are still many uncertainties about the life cycle of *Eumerus* immatures that should be addressed in the future. Moreover, it would be interesting to assess if the evolution of *Eumerus* may have been influenced by host plants and geographical isolation as well. Insect early stages and the interactions they establish with other living beings are, in general, poorly known, and similar studies could be undertaken within other groups with alike contexts.

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**Research data policy** All data generated and analyzed in this study are included within this published article.

**Author contributions** M<sup>a</sup> Ángeles Marcos-García and Antonio Ricarte contributed to the study conception and design of this paper. Material preparation and data collection and analysis were performed by Gabriel J. Souba-Dols. The first draft of the manuscript was written by Gabriel J. Souba-Dols, and all authors commented on previous versions of the manuscript. All authors added relevant information and read, discussed, and approved the final manuscript.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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