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Review

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How to escape from insect egg parasitoids: a review of potential factors explaining parasitoid absence across the Insecta

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The egg is the first life stage directly exposed to the environment in oviparous animals, including many vertebrates and most arthropods. Eggs are vulnerable and prone to mortality risks. In arthropods, one of the most common egg mortality factors is attack from parasitoids. Yet, parasitoids that attack the egg stage are absent in more than half of all insect (sub)orders. In this review, we explore possible causes explaining why eggs of some insect taxa are not parasitized. Many insect (sub)orders that are not attacked by egg parasitoids lack herbivorous species, with some notable exceptions. Factors we consider to have led to escape from egg parasitism are parental egg care, rapid egg development, small egg size, hiding eggs, by e.g. placing them into the soil, applying egg coatings or having thick chorions preventing egg penetration, eusociality, and egg cannibalism. A quantitative network analysis of host–parasitoid associations shows that the five most-speciose genera of egg parasitoids display patterns of specificity with respect to certain insect orders, especially Lepidoptera and Hemiptera, largely including herbivorous species that deposit their eggs on plants. Finally, we discuss the many counteradaptations that particularly herbivorous species have developed to lower the risk of attack by egg parasitoids.

1. Introduction

Egg laying by animals, including insects, frees the female from hosting and nourishing the developing embryo inside her body [1]. Nevertheless, the highly vulnerable egg stage needs to be protected from mortality risks, to ensure successful development. While eggs of a number of taxa of six-legged arthropods (Hexapoda) are attacked by parasitoids, eggs of many others seem to completely escape from attack by parasitoids, which, surprisingly, has only been mentioned once in the vast amount of literature about egg parasitoids [2].

Egg parasitoids are specialized to attack eggs of many arthropod species belonging to the Hexapoda but also spiders (Araneae). During oviposition, the embryo is killed and the immature wasp feeds on it until completion of its development. In comparison with parasitoids of other life stages, egg parasitoids face challenges, such as the quick location of hidden/ protected host eggs during their vulnerable phase of development, and the dealing with a fast-developing host [3]. Egg parasitoids have been shown to play an important role in biological control of pest insects [4]. The use of arthropod eggs as hosts by parasitoids has evolved in the Hymenoptera in at least 18 independent lineages [5], (AP, unpublished observations). It has been suggested that egg parasitoids are associated with hosts belonging to 15 out of the 32 insect orders, though without providing order names [2]. A major caveat in attempting to quantify the occurrence and avoidance of egg parasitoids across all insects is the obvious non-equivalence of

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[†]Deceased.

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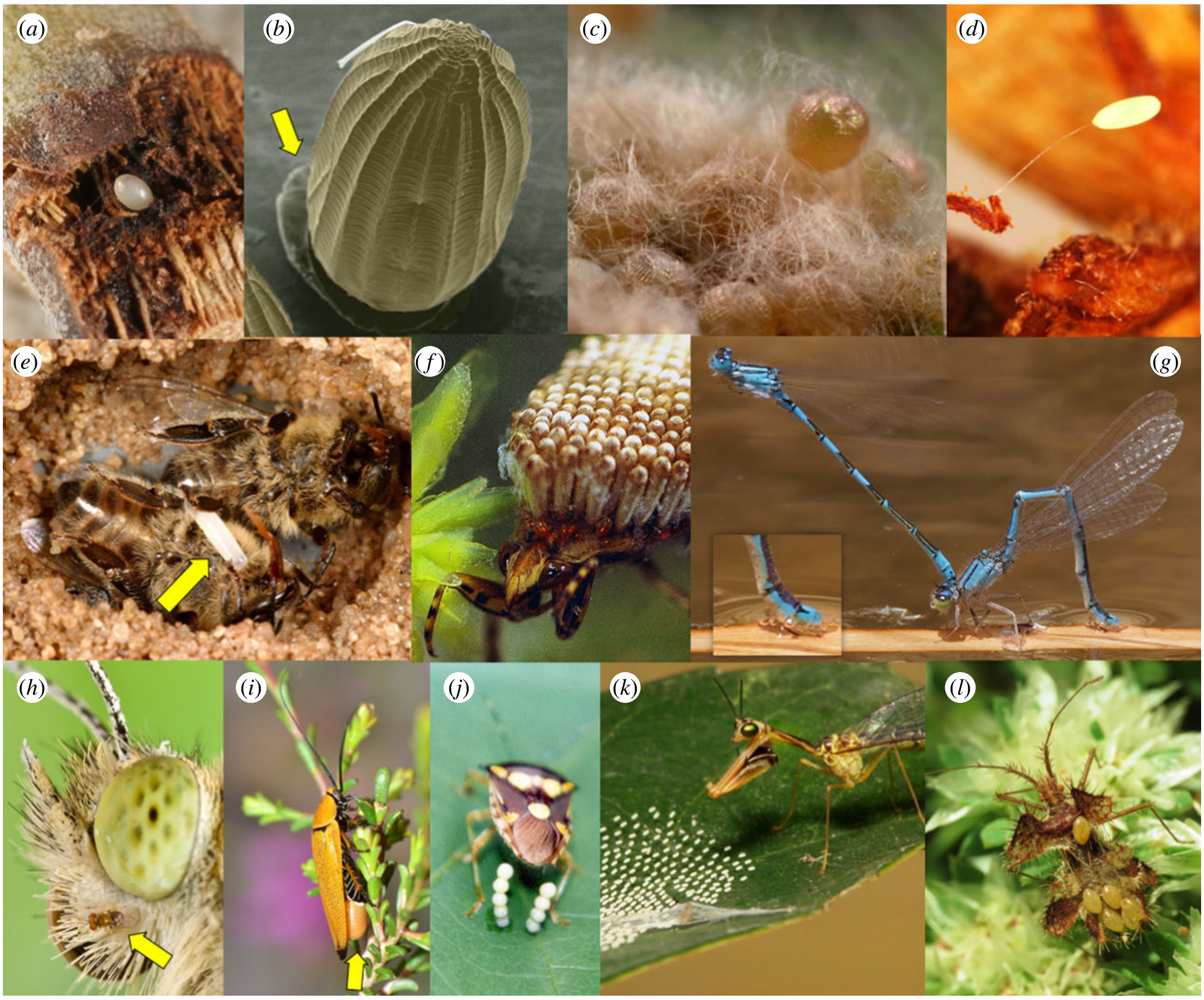

Figure 1. Examples of oviposition sites, parental care, egg-laying modes, and possible factors driving the evolution of egg parasitism. (*a*) Curculionid beetle egg laid inside a twig (credit: Bruno de Medeiros), (*b*) scanning electron microscopy (SEM) picture of a *Pieris brassicae* butterfly egg; yellow arrow points to egg glue made of accessory reproductive gland (ARG) secretion (credit: Nina E. Fatouros), (*c*) *Spodoptera frugiperda* moth egg clutch with hairs deposited for protection (credit: Ted C. MacRae), (*d*) Chrysopid lacewing egg placed onto the tip of a stalk (credit: Nina E. Fatouros), (*e*) European beewolf (*Philanthus trialgulum*) egg (yellow arrow) laid onto paralysed honeybees and protected by nitric oxide against mould fungi (credit: Gudrun Herzner), (*f*) giant water bug male with egg clutch on his back (credit: Tom Schultz), (*g*) *Coenagrion caerulescens* damselfly ovipositing onto twig in water while being in a tandem (credit: Antoine van der Heijden), (*h*) Phoretic *Trichogramma evanescens* wasp below eye of *P. brassicae* butterfly female (yellow arrow pointing to) (credit: Nina E. Fatouros), (*i*) cockroach *(Ellipsidion humerale)* with ootheca (yellow arrow pointing to it) (credit: Jean and Fred) (*j*) *Platynopiellusseptum decemmaculata* bug depositing eggs in an 'arche-like' structure (credit: Andrew Polaszek), (*k*) egg-guarding mantisfly (credit: John Horstman), (*l*) Golden egg bug (Phyllomorpha laciniata) carrying eggs (credit: Simon Oliver).

'Linnean'-derived hierarchies above the species level, and arguably even at species level. While remaining useful constructs for grouping organisms sharing common ancestry, many traditionally accepted higher categories have been shown—especially in the light of molecular studies—not to be monophyletic. The currently accepted orders and suborders of insects do, however, approximate to major lineages of evolutionary descent and consequently often shared biology, and therefore, in our opinion, serve as useful proxies for monophyletic lineages. Where we refer to 'orders' and 'suborders' below, these should be interpreted as 'major evolutionary lineages' [6].

Insect taxonomy and systematics have undergone a number of changes during the past decades. In this paper, we will use the system proposed by Misof *et al.* [7], who divides the Superclass of Hexapoda into 32 orders. Termites (Isoptera) are since recently nested into cockroaches forming together the clade Blattodea [8]; thus, the insect phylogenetic tree now consists of 31 orders. As stated above, we need to bear in mind the artificiality of these categories, which are heterogeneous in terms of their composition, even where they constitute monophyletic evolutionary lineages.

In this review paper, we will first provide information on the biology of insect eggs, the ways they can be protected (§2, figure 1; electronic supplementary material, table S1) and the challenges egg parasitoids face in finding host eggs (electronic supplementary material, S1). We discuss the factors that might have led to the escape from egg parasitoids in some orders and visualize it in an insect phylogenetic tree including the diet of the host, its oviposition site, the occurrence of parental care, (ovo)vivipary, and eusociality (§3, figure 2; electronic supplementary material table S1). Finally, we present the results of a quantitative network analysis of host–parasitoid associations. This analysis addresses the question whether the large genera of hymenopteran egg parasitoids co-diversified with certain insect orders (§4, figure 3; electronic supplementary material, S1 and electronic supplementary material table S2). Again, with genus comparisons, we clearly face the question of artificiality and

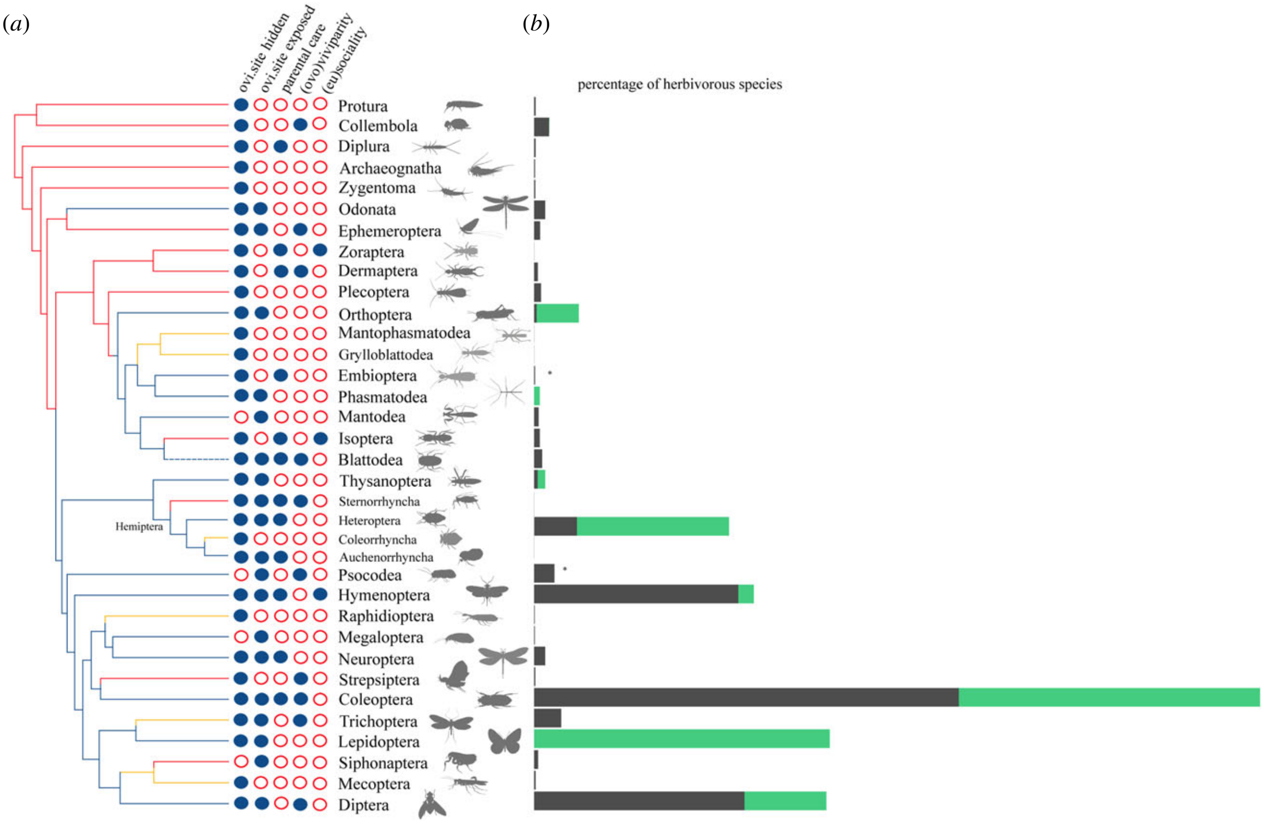

Figure 2. Phylogenetic tree of the Hexapoda with factors that might contribute to the escape from egg parasitism and prevalence of herbivory per order. (*a*) Phylogeny is adapted from Misof *et al*. [7] and Beutel *et al*. [9] and factors contributing to escape from egg parasitism (oviposition site hidden/ exposed, parental care, ovoviviparity, eusociality) presented by blue circles for presence, red empty circles for absence or not known. Egg parasitoid presence/absence is mapped on the tree: blue lines mean egg parasitoid presence, red lines mean egg parasitoid absence, yellow lines mean egg parasitoid presence to be expected. Dashed line means that Blattodea now incl. Isoptera [6] (*b*) percentage of herbivorous species (green bars) and non-herbivorous species (dark grey bars) per order according to Wiens *et al*. [10] and McKenna *et al*. [11], species numbers per order according to Stork *et al*. [12]. Asterisks indicate orders including species feeding on lower plants and occasionally dead plant tissue (Embioptera and Psocodea) and thus not falling under the definition of herbivorous—primary feeding on living plant tissue during one or more life stages—according to Wiens *et al*. [10]. For the Hemiptera, the percentage of herbivorous/non-herbivorous species is shown for the whole order.

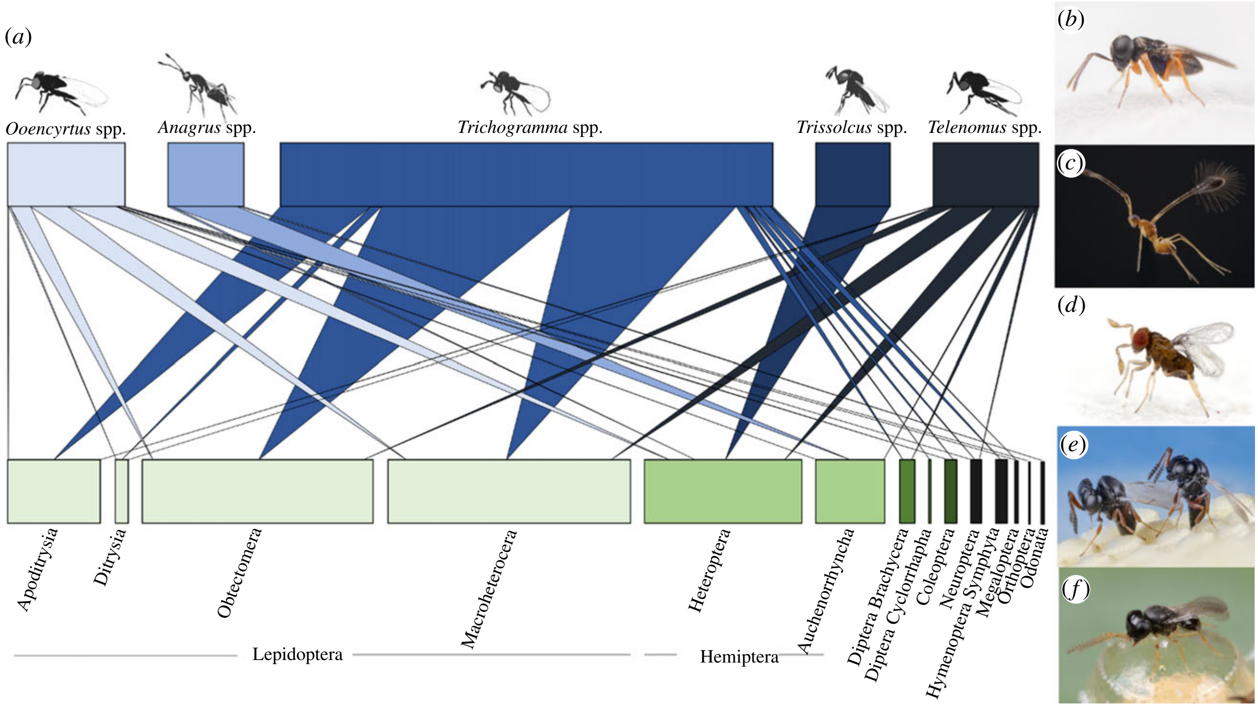

Figure 3. Quantitative network of host–parasitoid associations from the five largest genera of egg parasitoids *Ooencyrtus*, *Anagrus*, *Trichogramma*, *Trissolcus*, and *Telenomus*. (*a*) Network of the egg parasitoid genus coevolving with certain insect orders and/or suborders/clades, (*b*) *Ooencyrtus* species (credit: Jitte Groothuis), (*c*) *Myrmar* species resembling *Anagrus* (credit: Ross Piper), (*d*) *Trichogramma evanescens*, (*e*) *Trissolcus basalis* (credit: Hans M. Smid), (*f*) *Telenomus* sp. (credit: Ross Piper).

non-equivalence, so we can best consider these genera as in the above cases megadiverse species radiations about which useful generalizations can be made.

2. Protection of insect eggs

(a) Egg shell (chorion), egg size, and oviposition site

An insect egg consists of an oocyte provisioned with a nutritive substance surrounded by an epithelial layer of somatically derived follicle cells; in some cases, the oocyte is associated with nutritive cells [13]. Different insect orders have egg shells of widely different composition and structure. An evolutionary novelty of insect eggs is the serosa, an extra-embryonic membrane that envelops the embryo and yolk. The serosa protects the embryo from desiccation and enables arthropods to occupy terrestrial habitats [14]. In primarily unwinged insects, the serosa does not completely envelop the embryo, and, therefore most live in leaf litter, under bark and in other places with high humidity. The serosa has also been shown to provide immunity to the insect egg [15] and eggs may exhibit immunological activity in response to egg parasitoids [16,17].

Insect egg sizes and shapes are extremely diverse [18]. They vary from 0.02 mm (the parasitoid *Platygaster vernalis* [Hymenoptera: Platygastridae]) to more than 10 mm in length (the bush cricket *Saga pedo* [Orthoptera: Tettigoniidae], the carpenter bee *Xylocopa auripennis* [Hymenoptera: Apidae], and the coleopteran *Bolboleaus hiaticollis* [Coleoptera: Geotrupidae]) [19]. The morphological diversity of insect eggs is best explained by ecological differences, apart from correlation with adult body size. A recent study has shown that oviposition shifts to new environments such as aquatic habitats or inside hosts, explaining the evolution of smaller eggs; some of the smallest eggs are from parasitoid wasps (*P. vernalis*) that develop polyembrionically [18].

Insect eggs cannot defend themselves against attack by actively escaping from predators or parasitoids. However, they can escape from attack by being laid inconspicuously by their mothers through the choice of a safe oviposition site. Many insects place their eggs into plant or animal tissue or in small crevices in the soil, under stones or at other concealed locations (figure 1*a*). Recognition of eggs by natural enemies may be hindered by coverings resemblance to plant structures or water droplets or by disruptive colouration [13].

(b) Egg secretions

The egg-laying female uses secretions from the oviduct and the accessory reproductive glands (ARGs). The egg-associated secretion has many functions, among others supporting the egg to glide through the oviduct to the outside, attachment, and protection of eggs. Coating eggs with secretions can protect them against predators, parasitoids, and pathogens. The coatings range from a jelly-like material (egg parasitoids are stuck in it) to hard dry foam (mantids) or a thin-walled hard case (cockroaches) [13]. However, in the case of mantids such oothecae remain vulnerable as the foam of mantid egg masses appears to attract Podagrion and other egg parasitoids [20]: also cockroach oothecae are attacked by a range of egg parasitoid taxa including Evaniidae, *Blaticidella* (Encyrtidae), and *Eutrichosomella* spp. (Aphelinidae) [21]. ARGs may also produce silk to protect eggs (egg cocoons). (Semi-)aquatic species of the Plecoptera, Odonata, Ephemeroptera, Chironomidae (Diptera), Trichoptera, and Coleoptera coat their eggs with a gelatinous secretion called spumaline produced by ARG. This material swells in contact with water which is needed to place eggs under water. The alder leaf beetle *Agelastica alni* (Coleoptera: Chrysomelidae) has its eggs covered with the same material (though the eggs are not laid under water but on alder leaves) and it protects the eggs by sticking on the mouthparts or legs of natural enemies [13]. In some insect orders, ARGs also produce cement for attaching eggs to each other and to the substrate (figure 1*b*). Whether or not spumaline has been a deterrent to ooparasitism by the independent lineages of parasitoids that successfully attack submerged insect eggs (see below) remains to be demonstrated.

Secretions of ARGs from some herbivorous insects have been shown to contain elicitors that induce egg-killing plant responses [22]. Chemical cues released by egg-laying females of both herbivorous and carnivorous insects are produced by ARGs [13]. For example, females of the desert locusts (*Schistocerca gregaria*) release an oviposition pheromone from the egg-pod froth produced by the glands; the pheromone attracts conspecific gravid females ensuring temporal and spatial cohesiveness of the offspring population [23]. On the contrary, host-marking pheromones are typically used by herbivorous insects and parasitoids to avoid deposition of eggs on previously exploited host resources. Although there is evidence of host-marking pheromones in many families within the orders Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Neuroptera, information about the chemistry involved [24] and possible egg parasitoid species being attracted to them (see below) is scarce.

(c) Egg defences

In addition to egg secretions, numerous natural products, which are highly reactive or present as pro-toxins, are known from insect eggs as defensive materials against natural enemies. In some cases, the female may protect the eggs with natural products, which are biosynthesized *de novo*, and in others they are of dietary origin [13]. Moreover, many insects cover eggs with fecal matter, hairs, or scales, secretions from glands, providing a physical barrier to natural enemies. Here, chemical protection is also used, such as toxic hair coverings which occur in Lepidoptera: adults of a few taxa take up poisonous larval hairs and cover their eggs with them (figure 1*c*). Still, unrelated taxa that cover their egg masses in hairs or scales are attacked by egg parasitoids, e.g. *Scirpophaga* and *Spodoptera* moths by *Telenomus* wasps [25].

Eggs of Chrysopidae and Mantispidae (both Neuroptera) are placed onto the tip of a stalk, which serves as protection against predation and also cannibalism [13] (figure 1*d*). The egg stalk of the chrysopid *Ceraeochysa smithi* is coated by a protective secretion that repels ants [26]. However, at least one and possibly more lineages of *Telenomus* are specialist egg parasitoids of stalked eggs of berothid and chrysopid lacewings [27]. Defensive egg chemicals produced *de novo* by the insects are known from species of Lepidoptera, Diptera, Neuroptera, Coleoptera, and Hymenoptera [13]. Chemical barriers (sticky fluids with repellent chemicals), alarm pheromones, chemical weapons, and defence secretions are used to defend eggs against predators and pathogens. For example, a recent study discovered that eggs of the European beewolf, *Philanthus triangulum* (Hymenoptera: Crabronidae) emit a strong antifungal agent, a gaseous radical nitric oxide, which protects themselves and the beewolf's provisions (paralysed honeybees) against fungi [28] (figure 1*e*). Apparently, most of the known defensive chemicals do not provide complete protection against egg parasitoids.

Autogenously produced defensive components within eggs that are of anti-microbial activity are known from many Coleopteran species, e.g. cantharidin produced by blister beetles (Meloidae) or anthraquinones produced by leaf beetles (Chrysomelidae) [13,29]. The effect of many autogenously produced defensive components within insect eggs on egg parasitoids has apparently seldom been studied. Anthraquinones are present in eggs of Galerucini (Chrysomelidae) [30]. They are obviously in part metabolized and in part excreted unchanged by the egg parasitoids; anthraquinones were detected in the fecal pellets released by the egg parasitoids prior to pupation inside the host; adult parasitoids host-feeding upon Galerucini eggs do not contain any anthraquinones, suggesting that the adult parasitoids completely metabolize and degrade these compounds (M. Hilker, personal communication). Eggs of several ladybird species produce alkaloids [13]. Yet, a number of parasitoids are known from eggs of herbivorous ladybird species [31]. Likewise, the effect of many defensive components of extrinsic origin (often from the host plant) within insect eggs on egg parasitoids has apparently seldom been studied [32].

3. Factors explaining escape from egg parasitism in certain insect orders

(a) General patterns

We conducted a literature review and screened Web of Science, Google scholar, and hymenopteran parasitoid online databases [33,34]. We found no presence of egg parasitoids attacking 17 out of the 31 hexapod orders. Although this is about half of the orders, the orders escaping egg parasitism contain only about 30% of the total number of estimated insect species [12]. Figure 2*a* illustrates which insect orders are parasitized (blue coloured lines mapped on the tree) in the egg stage and which factors (oviposition site, parental care, (ovo)viviparity, (eu)sociality) might be relevant for preventing egg parasitism in insects (for more details see electronic supplementary material, table S1). Moreover, we present the percentage of herbivorous and non-herbivorous (i.e. predatory, parasitoid, detritivorous, omnivorous) species per order (figure 2*b*; electronic supplementary material, table S1).

Orders that include species with a herbivorous life style and exposed oviposition sites on plants appear to have a higher risk of being attacked by egg parasitoids with the major exception of all species in the hemipteran suborder Sternorrhyncha which includes aphids (Aphidoidea), scale insects (Coccoidea), jumping plant lice (Psylloidea), and whiteflies (Aleyrodoidea). In most species, eggs are laid exposed, have a relatively weak chorion and yet escape parasitism. One possible explanation for this may lie in the fact that the subsequent developmental stages of some Sternorrhyncha are also egg-like such as those of the coccoids and whiteflies, in contrast with the mobile nymphs of the remaining Hemiptera. The (post-crawler) nymphs of those families (but also many aphids and psyllids) are, like eggs, sessile 'bags of protein', unable to escape parasitoids physically by running or jumping. Yet unlike eggs, these nymphs are known to have a well-developed immune system with specific cells (haemocytes) described to play a role in encapsulation against parasitoid eggs [35]. Avoidance of, or host-shifting away from, Sternorrhyncha eggs over evolutionary time might have enabled a degree of niche specialization by a diverse array of parasitoids of nymphal Sternorrhyncha. It is possible, even probable, that given the apparent vulnerability of their eggs, egg parasitoids of Sternorrhyncha existed in the past, but may have caused their own extinction in some cases because their host resource was so scarce (aphids), parental care and (ovo)viviparity evolved (scale insects and aphids), and in others due to host-shifting over time towards larval parasitism. Among the remaining Hemiptera, parasitoids of post-egg stages are rare, occurring in a few highly specialized families such as Dryinidae, while egg parasitoids of both Auchenorrhyncha (cicadas, plant-, tree, and leaf hoppers, and spittlebugs) and Heteroptera (true bugs) are spectacularly both diverse and abundant, as this study has revealed.

Species of more than half of the orders, which are parasitized in the egg stage, select oviposition sites mostly on exposed plant tissue, with some important exceptions. The three largest orders that contribute to the majority of herbivorous species, Lepidoptera, Coleoptera, and Hemiptera (about 380 000 of the *ca*. 450 000 described herbivore insect species) [10,11] are heavily parasitized by egg parasitoids (electronic supplementary material, table S2, figure 3). In other words, none of the orders that contain herbivorous species feeding on Angiosperms (see definition for herbivory by Wiens *et al*. [10]) escape from egg parasitism with the major exception of the suborder Sternorrhyncha of the Hemiptera (discussed above) (figure 2). Species from orders feeding on lower plants such as algae and mosses, belonging to Embioptera (webspinners) and Psocodea suborder Psocoptera (barklice, booklice, or barkflies), are also parasitized by egg parasitoids. Only six orders with non-herbivorous species are also attacked by egg parasitoids, i.e. Hemiptera (many Heteroptera), Megaloptera (alderflies, dobsonflies, and fishflies), Mantodea (mantids), Neuroptera (net-winged insects), and Odonata (damsel- and dragonflies), all with predatory life style and the Blattodea (cockroaches) being largely omnivorous (figure 2).

(b) Parental care and sociality

An interesting case of escape from egg parasitoids are the around 1900 species of earwigs (Dermaptera). Most earwig species are omnivorous, but a few species are also known to be herbivorous or predatory. Some species live on decaying material and occasionally on dead insects. Some species are viviparous and give birth to live young. Notably, earwigs are subsocial insect species that show maternal care [36]. The mother will pay close attention to the needs of her eggs, defends them from predators, and continuously cleans the eggs to protect them from fungi [37]. Their primary insect parasitoids are tachinid fly species that parasitize the older earwig stages [38]. Besides maternal care, earwigs often place their eggs in burrows [37], which could give an additional explanation for not being found by parasitoid wasps. Numerous other insects bury their eggs in soil, such as necrophagous beetles of the Scarabaeinae. These beetles eat and breed in decaying organic matter (dung and/or carrion) and show complex nesting behaviour with elaborate parental care, which is seen as an adaptive response to the threats of microbes in these environments [39]. Generally, insects that bury eggs seem to escape from egg parasitism, with some exceptions (see below).

Parasitism pressure has often been considered as an important selective factor for the evolution of parental care and sociality [40]. Social insects physically defend their eggs by placing them in nests of often complex constructions, e.g. with entrance turrets lined with sticky secretions along their inner surface, nest blockage, and plugs of various materials, even body parts [13]. Yet, colonies of social insects should be highly vulnerable to parasitism because of the locally high density of potential hosts. Eusociality is defined by cooperative brood care, overlapping generations, and division of labour and exists in the Hymenoptera suborder Apocrita (ants, bees, wasps) and in the Isoptera (termites). Social insects are attacked by some parasitoids of larvae and adults, but none are known from eggs [41]. This could be the result of the brood care in combination with the use of sheltered nest sites that might impair access to the eggs.

The evolution from phytophagy to parasitism and predation and from solitary to eusocial life might also explain why egg parasitism is less abundant in eusocial and parasitic Hymenoptera than in the herbivorous Symphyta (sawflies, horntails, and wood wasps). The monophyletic ectophytophagous sawflies diverged from all other Hymenoptera around 200 Mya. Recent studies suggest that the most recent common ancestor of Hymenoptera has been ecto- or endophytophagous [5]. Symphyta eggs may suffer from high parasitism rates, such as eggs of the pine sawfly *Diprion pini* (Diprionidae). Egg deposition by *D. pini* induces changes in the volatile pattern of pine trees rendering egg-laden twigs attractive to *Closterocerus ruforum*, an eulophid parasitoid species specialized on pine sawfly eggs [3]. During egg deposition, the sawfly cuts a slit into pine needles and lays her eggs into the needle tissue. The act of oviposition in combination with the applied oviduct secretion induces volatiles that attract the wasps [22] (electronic supplementary material, S1).

Egg protection by parental care can reach rather unusual forms. In the case of the giant water bugs (Hemiptera: Belostomatidae), the eggs are typically laid on the male's wings and carried around until they hatch [40] (figure 1*f*). Males provide for the needs of their eggs by keeping them wet, frequently exposing them to atmospheric air. Eggs removed from the males dry out, indicating that in that case paternal egg care probably did not evolve from egg parasitoid pressure. Generally, carnivorous insects seem to be less susceptible to egg parasitism, with notable exceptions among the Heteroptera. Some parasitoid genera specialized on eggs of predatory species in the orders Odonata (e.g. all *Hydrophylita* spp. (Trichogrammatidae) a few *Anagrus* (Mymaridae) spp.), Mantodea (*Mantibaria* spp.), Megaloptera (*Ooencyrtus* and *Trichogramma* spp.), and Neuroptera (*Ooencyrtus*, *Trichogramma* and *Telenomus* spp.) (electronic supplementary material, table S1; figure 3). Among those egg parasitoid species, some phoretic species are known, e.g. the scelionid *M. manticida* on European mantis *Mantis religiosa* (Mantodea: Mantidae) [42], the trichogrammatid *Hyrdophylita emporos* on the damselfly *Psolodesmus mandarinus mandarinus* (Zygoptera: Calopterygidae) [43], and the scelionid *Telenomus calvus* on the soldier bug *Podisus maculiventris* (Heteroptera: Pentatomidae) [44].

(c) Concealed oviposition

The majority of unwinged insects deposit their eggs into soil, leaf litter, or under stones. Their eggs are also among the smallest, mostly smaller than 1 mm length, not exceeding 2 mm, which makes them less suitable for the development of egg parasitoids [19]. Similarly, eggs of Sternorrhyncha are usually not larger than 1 mm. Yet, egg size must not implicitly be a constrain for the absence of parasitism: eggs of thrips (Thysanoptera) can be small, too, but some trichogrammatid (*Megaphragma*) wasps parasitize thrips eggs [45]. Although some insects that bury their eggs and/or egg masses appear to escape from egg parasitoids by this strategy, a huge percentage in this category are still susceptible to parasitism. The Scelionidae are exclusively egg parasitoids. Many genera successfully parasitize the concealed eggs of (especially) Orthoptera and Coleoptera (e.g. Carabidae). Although many Cicadellidae (Hemiptera: Auchenorrhyncha), Cecidomyiidae (Diptera), and other plant feeders oviposit deeply into plant tissue, their eggs are still successfully attacked by parasitoids (Mymaridae and Platygastridae, respectively) [33,34]. In both families, females of some species have ovipositors up to 3.5 times longer than the metasoma, in order to reach eggs that would otherwise be inaccessible buried in soil [46].

Oviposition into the water does not necessary lead to escape from egg parasitoids. Nymphs of the Palaeoptera orders, Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) are aquatic. Females either drop eggs into the water, lay them on the water surface or as some dragonflies and damselflies do, lay them on or into plant tissue above or below water level [47] (figure 1*g*). While no egg parasitoids are known from mayflies, eggs of some Odonata species are parasitized mainly by mymarid and trichogrammatid species (electronic supplementary material, table S1). Some egg parasitoids use phoresy (figure 1*h*; electronic supplementary material, S1), the transport on adult hosts to oviposition sites [48]. Clausen [48] noted a scelionid species of *Calotelea* to be phoretic on the dragonfly *Boyeria vinosa* (Aeshnidae), observing up to 34 individuals mainly attached to the thorax of a single adult female.

Other insects with an aquatic lifestyle, e.g. water beetles of the family Dytiscidae and water bugs of the family Gerridae are also known to be attacked by egg parasitoids, some parasitoids were even observed to swim [49]. Besides evolving a phoretic lifestyle and swimming capabilities, chemical cues emitted from water plants might help egg parasitoids to locate their host eggs. Although not much information is known about chemical cues playing a role in the aquatic host location by parasitoids, a recent study revealed that host plants of aquatic leaf beetles (Chrysomelidae, Donacinae) emit terpenoids located by the female beetles [50].

(d) Formation of ootheca

Concentrated egg deposition in the form of an ootheca may protect eggs from desiccation, predators, and parasitoids. Ootheca formation is a common feature for Dictyoptera (cockroaches, termites, and praying mantis) but also found in grasshoppers and locusts (Orthoptera: Caelifera), heelwalkers (Mantosphasmatodea), and some chrysomelid beetles (Cassidinae) and stick insects (Phasmatodea) [51,52]. Notably, evolutionary shifts to ootheca formation on an arboreal substrate in stick insects are probably a result of protection against parasitoids and desiccation. Two subgroups of cuckoo wasps (Chrysididae, see below) are obligatory parasitoids of stick insect eggs not laid as ootheca; parasitism rates can rise up to 80% [51].

Except for the cockroaches that carry around their ootheca, most other insects drop and/or disperse their ootheca into the ground or upon certain substrates, e.g. plant parts or rocks underground, and apply a coating during or after egg placement. This makes the ootheca difficult to find and to penetrate. Yet, numerous hymenopteran parasitoids within the Aphelinidae, Evaniidae, Encyrtidae, Eulophidae, Eupelmidae, and Pteromalidae specialized on the ootheca of cockroaches (Blattodea) (figure 1*i*; electronic supplementary material, table S1). All evaniid species known from cockroach oothecae are solitary parasitoids, and the relatively large females drill their ovipositor into the ootheca to deposit their eggs [21].

Cockroach species of the Blaberidae might have evolved a counteradaptation to natural enemies of ootheca as this is the only taxon within the Dictyoptera to have evolved both ovovivipary and carrying around the ootheca [52]. Some egg parasitoids are able to overcome the constraints of the hard-coated and/or dispersed oothecas, as in the case of *Mantibaria manticida* (Scelionidae). This obligatory phoretic wasp removes its wings after finding and being transported upon female European praying mantis (*Mantis religiosa*) in order to reach the frothy host eggs laid inside an ootheca before it hardens [42]. The wasps have even been observed to return to the same transporting host after parasitism [48].

(e) Counteradaptations by herbivorous species to egg parasitism

We show that herbivorous insect orders are the ones that are most attacked by egg parasitoids. Many taxa of egg parasitoids specialized on eggs of herbivorous species within the Lepidoptera, Orthoptera, Thysanoptera, Psocoptera, Phasmatodea, Hemiptera, Hymenoptera, Coleoptera, and Diptera. Note that the majority of species from the first five mentioned (sub)orders contain mostly herbivores (figure 2*b*). Yet, numerous intriguing ways to counteradapt to ooparasitism are known from herbivorous species. For example, some shield bugs (Heteroptera: Acanthosomatidae) deposit their eggs with minimal contact onto the plant surface; this oviposition mode might be a strategy to prevent the induction of plant cues attracting parasitoids (figure 1*j*; electronic supplementary material, S1), while others employ parental care [40]. Both behavioural types could be evolutionary responses to egg predation and/or parasitism.

Besides physical protection by guarding females (figure 1*k*), some insects use an even more refined strategy: the coreid golden egg bug *Phyllomorpha laciniata* (Heteroptera: Coreidae) is a specialist of *Paronychia argentea* plant species but deposits its eggs on other conspecifics, acting as 'mobile nests' (figure 1*l*). Egg-laying behaviour of *P. laciniata* females was investigated in the presence of the scelionid egg parasitoid *Gryon bolivari*. Oviposition rate was lower when parasitoids were around than when they were absent, especially when plants were the only substrate to deposit eggs on. Moreover, females strongly preferred to oviposit on conspecifics rather than on plants. This also indicates that the bugs are able to detect *G. bolivari* wasps and avoid oviposition when parasitoids are present [53]. Also, other specialist herbivores such as chrysomelid beetles show numerous types of egg protection including behavioural. The seed beetle *Mimosestes amicus* covers eggs with additional non-viable eggs as a protection from parasitism by the trichogrammatid *Uscana semifumipennis*. Egg stacking was shown to significantly reduce the mortality of protected eggs [54]. Stem boring Lepidoptera attacking cereals and grasses often lay their eggs between the whorls of unopened leaves. In such cases even highly adapted parasitoids such as *Telenomus busseolae* that are strongly dorso-ventrally flattened to gain access to these eggs, are still only able to parasitize the peripheral ones (AP & FB, personal observations). In this way, the susceptible eggs effectively form a protective barrier for their siblings. The investment in egg protection probably carries substantial costs and females that invest in egg defence may not lay as many eggs as females that do not protect their eggs.

4. Coevolution of common egg parasitoids with certain host insect orders

Within the Hymenoptera, at least 14 families, and 18 independently evolved lineages, include parasitoid wasps of insect eggs. Based upon a recently published and robust phylogeny of the Hymenoptera inferred from substantial phylogenomic data [5], and more detailed analyses of the superfamily Chalcidoidea [55,56], we calculate that the use of arthropod eggs as hosts by parasitoids has evolved in the Hymenoptera in at least 18 independent lineages. Three superfamilies outside of the monophyletic Proctotrupomorpha clade contain egg- or egg-larval parasitoids (Evanioidea, Chrysidoidea, Ichneumonoidea); within Proctotrupomorpha, Scelionidae are exclusively egg parasitoids, with a further 14 lineages of independently evolved egg parasitoids within the Chalcidoidea, and probably many more when chalcid phylogeny is better understood. In one family, Aphelinidae, egg parasitoids have evolved independently in five lineages, at least once in the genera *Centrodora* and *Eutrichosomella*, and at least three times in *Encarsia* [57] (AP 2020, unpublished observations).

Two families, the Trichogrammatidae and Scelionidae, are entirely and one, the Mymaridae, almost entirely (with exception of the genus *Stethynium*) all egg parasitoids [58–60]. The Rotoitidae are probably all egg parasitoids of Coleorrhyncha but this still needs to be confirmed (J Heraty 2019, personal communication). For all the other families, egg parasitoids are scattered over several genera [2]. We made a quantitative network of host–parasitoid associations for the five largest hymenopteran genera all containing ooparasitoid species (figure 3). Details on the analysis and databases used and information on the different genera can be found in the electronic supplementary material (electronic supplementary material, S1, electronic supplementary material table S1).

Anagrus (Hymenoptera: Mymaridae) includes about 101 described species so far [33]. Members of this genus evolved the ability to develop within eggs of leafhoppers (Auchenorrhyncha: Cicadellidae), planthoppers (Auchenorrhyncha: Delphacidae), damselflies and dragonflies (Odonata), all of which are embedded in plant tissue. In our quantitative food web analysis, we found a total of 332 host–parasitoid records with *Anagrus* wasps associated with eggs of Hemiptera (95.48%) and Odonata (4.52%) (figure 3*a*). The genus *Ooencyrtus* (Hymenoptera: Encyrtidae), (figure 3*b*) comprises about 343 described species [33]. Moreover, other species appear to be hyperparasitoids of Dryinidae and Braconidae [61]. We found a total of 534 host–parasitoid records with *Ooencyrtus* wasps largely associated with eggs of Lepidoptera (51.21%) and Hemiptera (42.80%) (figure 3). *Trichogramma* (Hymenoptera: Trichogrammatidae) is the largest and most important genus in the family, with about 241 described species so far [33]. Most species have evolved the ability to exploit eggs of Lepidoptera, with some species also developing in eggs of Coleoptera, Diptera, Hemiptera, Hymenoptera, Neuroptera, and Megaloptera. In our quantitative food webs, we found a total of 2253 host–parasitoid records with *Trichogramma* wasps associated with Lepidopteran eggs in 93.94% of the cases (figure 3*a*).

Trissolcus (Hymenoptera: Scelionidae) (figure 3*e*) comprises about 150 described species [34] and are exclusively egg parasitoids specialized on Hemiptera (figure 3*a*). Similar to *Trichogramma* species, *Telenomus* (Hymenoptera: Scelionidae) (figure 3*f*) wasps are primarily egg parasitoids of Lepidoptera with so far 628 described species [34]. We found a total of 327 host–parasitoid records with *Trissolcus* wasps associated with eggs of Hemiptera (figure 3*a*). In our quantitative network analysis, we found a total of 484 host–parasitoid records with more than 50% of associations between *Telenomus* and Lepidoptera. Yet, host relationships of this genus also extend to other taxa including associations with Hemiptera (32.12%) and Diptera (6.46%) (figure 3). The largest and economically most common families of hosts are stink bugs, particularly the Pentatomidae and Scutelleridae.

Thus, particularly eggs of Lepidoptera and Hemiptera (except Sternorrhyncha) are heavily parasitized by species from the five largest egg parasitoid genera *Ooencyrtus*, *Anagrus*, *Trichogramma*, *Trissolcus*, and *Telenomus*. Besides those large insect orders, eggs of Coleoptera are heavily parasitized but by other families and/or genera (electronic supplementary material, table S1). Beetle eggs of phytophagous families, belonging to the herbivorous Phytophaga clade (incl. Chrysomelidae, Cerambycidae and Curculionidae) and Buprestoidea are parasitized (electronic supplementary material, table S1), as are mainly predatory families such as Carabidae.

5. Conclusion

Our extensive literature and database search reveals that 17 of 32 insect orders appear to escape from egg parasitoids, exceeding the previous estimate of 15 orders by Romani *et al*. [2]. Orders being attacked by egg parasitoids include all orders containing herbivorous species feeding on seed plants (angiosperms and gymnosperms) and algae and mosses. Egg parasitism evolved in the Hymenoptera, and three families (Evaniidae, Mymaridae, Trichogrammatidae) are, with one known exception, entirely composed of egg parasitoid species. A large number of egg parasitoid wasps that include the smallest known insects are not yet described. Thus, we cannot exclude that some species from the 17 insect orders without egg parasitism are in fact attacked by egg parasitoids not described yet. In summary, our analysis of possible factors that lead to escape from egg parasitoids reveals astonishing adaptations of species from these insect orders, whose eggs are heavily parasitized (Lepidoptera, Hemiptera [except in the Sternorrhyncha] and Coleoptera) (electronic supplementary material, table S1; figure 3*a*), such as egg guarding or carrying, avoidance of induction of plant cues, egg deposition into concealed/ hidden places, or physical or chemical protection of eggs.

Contrarily, the evolution of oothecae, parental care, and oviposition into concealed places probably developed among other reasons as an escape from egg parasitism. On the other hand, insects from orders that totally or partially escape from egg parasitism seem to deposit eggs into or onto hosts (parasitic Hymenoptera, Siphonaptera, Strepsiptera, and Phthiraptera), hidden places such as soil, leaf litter, under stone, bark, or water (all Entognatha, Grylloblattodea, Dermaptera, Plecoptera, Ephemeroptera, Raphidioptera, Trichoptera, Mecoptera), or nests with brood care (Aculeata/Hymenoptera and Isoptera/Blattodea). Egg developmental time, egg size, and the structure of the egg shell are probably also constraints.

We hypothesize that host-foraging strategies that (i) make use of plant cues, induced by host egg deposition [3,22]. or (ii) involve phoresy are likely to be more widespread than so far assumed (electronic supplementary material, S1) [62]. Such counteradaptative foraging strategies might have ensured parasitoids locating host eggs deposited in, e.g. concealed places. New studies on the prevalence of such strategies among egg parasitoids and observations on different host–parasitoid associations will further identify patterns and will also contribute to a better understanding on the evolution of egg parasitism.

Data accessibility. Data files are available as supplementary material.

Authors' contributions. J.v.L, F.B. conceived the study; J.v.L. N.E.F., A.C. assembled and processed datasets; N.E.F., J.v.L., and A.C. wrote a first draft of the manuscript. All authors (except for F.B.) interpreted results, drafted, and revised the manuscript.

Competing interests. We declare we have no competing interests.

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