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Polyphagous koinobiosis: The biology and biocontrol potential of a braconid endoparasitoid of exophytic caterpillars

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Abstract Polyphagous koinobiosis might be a novel perspective to help elucidate the evolution of the physiological and ecological traits of parasitoid wasps and determine their use as biocontrol agents. The euphorine braconid *Meteorus pulchricornis* is a polyphagous koinobiont endoparasitoid of exophytic caterpillars from 15 families within 10 lepidopteran superfamilies. Here, the biology of this common but enigmatic parasitoid wasp is reviewed. The unique cocoon suspension system of *M. pulchricornis* protects it against predators during and after cocoon spinning. This structural cocoon protection method, as well as robust immune suppression mechanism, likely enables its very wide host range. In Japan, *M. pulchricornis* can reproduce both sexually and asexually, and the coexistence of sexual and asexual strains might be encouraged by its high polyphagy. In this review, the potential use of *M.*

pulchricornis as a biocontrol agent is also addressed.

Keywords Cocoon suspension • Euphorinae • Host generalist • Lepidoptera • *Meteorus pulchricornis* • Thelytoky

Introduction

Parasitoid wasps of the genus *Meteorus* Haliday (Hymenoptera: Braconidae) are so named because of their spindle-shaped cocoons, each suspended by a silk thread resembling shooting stars or meteors (Fig. 1). This braconid genus comprises more than 300 species distributed across all zoogeographical regions (Huddleston 1980; Muesebeck 1923; Stigenberg and Ronquist 2011; Yu et al. 2012). *Meteorus pulchricornis* (Wesmael) (Fig. 2) is one of the most common *Meteorus* species in the Palearctic region (Chen and Wu 2000; Maeto 1989a; Stigenberg and Shaw 2013). It was accidentally introduced and naturalized in New Zealand (Berry 1997; Berry and Walker 2004; Hartnett et al. 2018) and Australia (Gerard et al. 2011). In East Asia and Australasia, this species is known as a parasitoid of many exophytic pest caterpillars (Table 1).

Meteorus pulchricornis is a solitary koinobiont endoparasitoid of lepidopteran larvae. Its general bionomics (Askari et al. 1977; Fuester et al. 1993; Suzuki and Tanaka 2007; Takashino et al. 2001), adult diet (Wu et al. 2008), circadian activity (Nishimura et al. 2015), courtship and mating behavior (Askari and Coppel 1978), oviposition behavior (Chau and Maeto 2009; Kageyama and Sugiura 2016; Sheng et al. 2015; Yamamoto et al. 2009; Zhou et al. 2017), adaptive melanism (Abe et al. 2013), superparasitism (Chau

and Maeto 2008, 2009; Zhang et al. 2014), immune suppression mechanism (Suzuki and Tanaka 2006; Suzuki et al. 2009), mitochondrial genome (Wei et al. 2010), and modes of reproduction (Tsutsui et al. 2014) have been studied. Some congeneric species have also been studied, albeit less rigorously. These include *Meteorus autographae* Muesebeck (Grant and Shepard 1984), *Meteorus ictericus* (Nees) (Bürgi and Mills 2013), *Meteorus pendulus* (Müller) [= *M. gyrator* (Thunberg)] (Bell et al. 2000, 2003, 2004; Down et al. 2005; Smethurst et al. 2004), and *Meteorus trachynotus* Viereck (Thireau et al. 1990); see also Shaw and Huddleston (1991) and Quicke (2015) for studies on other *Meteorus* species.

Although *M. pulchricornis* is a well-known parasitoid of caterpillars and its biology has been extensively studied, some of its parasitic traits remain unexplained or paradoxical. As it is an endoparasitic koinobiont, its hosts continue to develop in the early phase of parasitism. Therefore, *M. pulchricornis* can be expected to be host-specific and oligophagous (Althoff 2003; Askew and Shaw 1986; Godfray 1994; Quicke 1997, 2015). However, it is in fact highly polyphagous (Table 1).

Most probably because *M. pulchricornis* is a common natural enemy of recently expanding *Spodoptera* and *Helicoverpa* pest species (Lepidoptera: Noctuidae) (e.g., Liu and Li 2006; Takashino et al. 1998) and it was unintendedly introduced into New Zealand late in the last century (Berry 1997), research papers on *M. pulchricornis* and other *Meteorus* species have steadily increased over the last 10 years (Fig. 3). Such accumulated studies now need to be comprehensively examined. Thus, the present paper comprises a review of all aspects of the biology of this common but enigmatic

parasitoid and addresses its applicability in biological control.

First, the nature and benefits of cocoon suspension, which is unique to *M. pulchricornis* and some of its congeners, is presented. Next, its mode of parasitism and how it enables the wide caterpillar host range observed in this wasp is discussed. Third, the sexual and asexual modes of reproduction of *M. pulchricornis* are explained. In all cases, phylogenetic knowledge aids in understanding the evolutionary novelties and constraints of this organism. Finally, the implications of using this parasitoid as a biocontrol agent are presented.

What is the benefit of cocoon suspension?

A mature *M. pulchricornis* larva descends as it spins a silk thread (usually <5 cm in length) attached to a leaf or twig. It then turns downward, hooks itself to the thread by its abdomen, and builds a spindle-shaped cocoon within 1 day (Fig. 1). The cocoon then undergoes tanning for two days (Askari et al. 1977).

Within Braconidae, cocoon suspension is fairly unique to the *M. pulchricornis* species group of the genus *Meteorus*, whose members are endoparasitoids of exophytic lepidopteran larvae (Maeto 1989a, 1990; Stigenberg and Ronquist 2011). Most species of this group are solitary, but some are gregarious and form spherical cocoon masses (Mitamura 2013; Zitani and Shaw 2002) or cocoon clusters (Barrantes et al. 2011; Maeto 1989b; Shaw and Nishida 2005), both suspended from host plants.

Does cocoon suspension offer protection against hyperparasitoids or predators? Several studies have indicated that the suspended cocoons of

Meteorus species are virtually defenseless against hyperparasitoids (Zitani and Shaw 2002). For example, the generalist pupal parasitoid *Gelis aerator* (Panzer) (Hymenoptera: Ichneumonidae) could easily descend a very long cocoon thread for oviposition (Ogura 2017). Harvey et al. (2011) found that *Gelis agilis* (Fabricius) parasitized *M. pulchricornis* in suspended cocoons to about the same extent as it did in cocoons attached to leaves. Moreover, Sobczak et al. (2012) observed that a female wasp of the pteromalid hyperparasitoid *Toxeumella albipes* Girault flew directly into a cocoon mass made by a gregarious *Meteorus* species.

In contrast, cocoon suspension can effectively defend wasps from predators (Zitani and Shaw 2002). In field trials, both suspended and non-suspended *M. pulchricornis* cocoons were placed on foliage where *Crematogaster matsumurai* Forel (Hymenoptera: Formicidae) workers were foraging (Shirai and Maeto 2009). None of the suspended cocoons that were <12 h old at the time of exposure were lost, but >75% of the non-suspended ones were attacked, suggesting that ant predation is more deleterious to non-suspended than to suspended parasitoid larvae.

Mature emerging larvae and pupae of wasps parasitizing caterpillars exposed on a plant surface are vulnerable to predators, against which the parasitoid wasps have evolved various protection systems. For example, *Homolobus* and *Zele* species (Braconidae: Homolobinae and Euphorinae, respectively), as well as certain gregarious *Meteorus* species, construct cocoons within host pupal chambers (Lyle 1914a,b; Stigenberg et al. 2011). *Aleiodes* and *Macrostomion* species (Braconidae: Rogadinae) pupate within mummified host skin attached to the plant surface or placed within host

pupal chambers (Maeto and Arakaki 2005; Marsh 1979; van Achterberg and Shaw 2016). *Cotesia* and *Glyptapanteles* species (Braconidae: Microgastrinae) usually construct a common, large, dense clump of cocoons firmly fixed to host plants (Marsh 1979; Watanabe 1932). *Cotesia*, *Glyptapanteles*, and *Microplitis* species (Microgastrinae) often manipulate host larvae to guard parasitoid cocoons (Grosman et al. 2008; Harvey et al. 2011; Tanaka and Ohsaki 2006) (Table 2). Similar host behavioral manipulation has been observed in koinobiont parasitoids of free-living spiders (Eberhard 2000; Takasuka et al. 2015) and adult ladybirds (Dheilly et al. 2015).

The above-mentioned parasitoids pupating within host pupal chambers must synchronize their development with that of the host larvae, and the parasitoids that manipulate host behavior into guarding them need the appropriate information to control the host's nervous system.

In addition to *Meteorus* species, cocoon suspension has been observed in certain campoplegine species of the Ichneumonidae (Quicke 2015) and in a few species within the braconid genus *Aleiodes* (Quicke et al. 2006). As mentioned earlier, cocoon suspension decreases the risk of cocoon predation and enables advancement into the niche of parasitism on exophytic caterpillars. Cocoon suspension is highly elaborate in structure (Fig. 1), but unlike other defense strategies, it does not require any host-specific information.

How can a koinobiont be highly polyphagous?

Meteorus pulchricornis parasitizes >60 lepidopteran species belonging to 15

families within 10 superfamilies (Table 1). Therefore, this parasitoid is highly polyphagous on exophytic caterpillars. Most of the host caterpillars are leaf-feeding herbivores, but this also successfully parasitizes grain feeders (*Ephestia kuehniella* Zeller) and wax feeders (*Galleria mellonella* (L.)) (Lepidoptera: Pyralidae) in the laboratory (Table 1). Whereas a wide range of host instars are acceptable, intermediate instars seem to be the best suited for parasitism (Barraclough et al. 2014; Fuester et al. 1993; Liu and Li 2006, 2008; Liu et al. 2013; Malcicka and Harvey 2014; Zhang et al. 2014).

A strain originating from *Lymantria dispar* (L.) (Lepidoptera: Erebidae) successfully parasitized *G. mellonella* (Pyralidae) (Askari et al. 1977). In addition, strains from *Spodoptera litura* Fabricius (Noctuidae) successfully parasitized *L. dispar* (Erebidae) (Kageyama and Sugiura 2016) and *E. kuehniella* (Pyralidae) (Nakano et al. 2018) as well as *Mythimna separata* (Walker) (Noctuidae) (Suzuki and Tanaka 2006; Zhou et al. 2017). These indicate that physiological differentiation of host use among strains from different host families will be small, if any.

Three major braconid lineages include koinobiont endoparasitoids of exophytic caterpillars (Table 2). The subfamily Euphorinae, to which the genus *Meteorus* belongs, contains koinobionts on Coleoptera, Lepidoptera, Hemiptera, Hymenoptera, Neuroptera, Psocoptera, and Orthoptera (Shaw 1988; Stigenberg et al. 2015), whereas the subfamilies Microgastrinae and Rogadinae are specialist koinobionts on Lepidoptera (Quicke 2015; Shaw and Huddleston 1991). Thus, the Euphorinae seem to have a phylogenetic potential for koinobiont polyphagy.

Endoparasitic koinobionts must prevent host hemocytes (granulocytes

and plasmatocytes) from encapsulating their eggs and young larvae (Lackie 1988; Norton and Vinson 1977; Quicke 1997). Certain microgastroid braconids and some ophoniform ichneumonids are oligophagous probably because they regulate host-specific immunity with symbiotic polydnviruses (Edson et al. 1981; Pennacchio and Strand 2006; Quicke 2015). In contrast, *M. pulchricornis* causes rapid and extensive apoptosis of host granulocytes by the co-injection of virus-like particles (VLPs) from its venom glands (Suzuki and Tanaka 2006; Suzuki et al. 2008, 2009; Yokoi et al. 2017) (Table 2). This robust and broad-spectrum immune suppression system may at least partly account for the extreme polyphagy of *M. pulchricornis* (Tanaka 2009).

Harvey et al. (2010, 2015) and Nakano et al. (2018) demonstrated that *M. pulchricornis* physiologically adapts to wide interspecific variations in body size, growth rate, and growth potential of its host larvae. Although it remains unconfirmed, enlarged serosal cells called teratocytes, which have trophic functions within the host body (Bell et al. 2004; Suzuki and Tanaka 2007), might play a role in enabling the wide host range of *Meteorus* species.

The first instar larva of *M. pulchricornis* has a pair of sharp mandibles to fight against conspecific competitors (Chau and Maeto 2008). These mandibles may also be used to subdue multiparasitic competitors such as unarmed gregarious parasitoids (Magdaraog et al. 2012). In addition, *M. pulchricornis* VLPs inhibit the development of gregarious competitors (Magdaraog et al. 2016). These competitive traits may further empower this solitary parasitoid to expand its host range.

Moreover, this species has ecological or behavioral traits that might have contributed to the development of its polyphagy (Table 2). Mature parasitoid

larvae emerging from exophytic hosts are fragile and exposed to high predation pressures both during and after cocoon spinning. Therefore, as mentioned earlier, many koinobiont endoparasitoids of caterpillars either manipulate their hosts into guarding their cocoons or wait until host maturation to construct their cocoons within the host pupal chamber. All these physiological defense tactics require host-specific information and could lead to oligophagy. Nevertheless, *M. pulchricornis* and its relatives may evade predation during the critical phase by suspending mature larvae and cocoons until adult emergence (Fig. 1). This structural defense system does not depend on host-specific developmental or behavioral conditions and, therefore, may promote the evolution of polyphagy. In fact, *Meteorus* species capable of producing suspended cocoons, such as *Meteorus colon* (Haliday), *M. pendulus*, *M. pulchricornis*, and *Meteorus versicolor* (Wesmael), have far wider caterpillar host ranges than their congeners without cocoon suspension (Stigenberg and Shaw 2013).

Host-specific parasitoids usually depend on kairomones for host location and acceptance. However, *M. pulchricornis* females pursue hosts and complete oviposition using only visual cues of host movement when they are near host caterpillars (Fig. 2; Supplementary Video 1; Yamamoto et al. 2009). Other euphorine species also use host's movement to locate them (Godfray 1994; Shaw 1988; Shaw and Huddleston 1991). Physical, nonspecific host recognition seems to be compatible with polyphagy on exophytic caterpillars.

The majority of koinobiont parasitic wasps are pro-ovigenic and do not live as long as idiobionts (Quicke 1997). Nevertheless, *M. pulchricornis* is synovigenic, and the females continue laying eggs for >1 month (Fuester et

al. 1993). Therefore, long-lived females may have many opportunities to encounter and use a wide variety of caterpillars for oviposition.

Nocturnal activity of certain parasitic wasps should also be convenient for finding a variety of exophytic caterpillars because many such caterpillars emerge to feed at night (Quicke 2015). Nishimura et al. (2015) demonstrated the crepuscular and nocturnal activity of female *M. pulchricornis* in foraging.

Meteorus pulchricornis is multivoltine, and it overwinters in the larvae of its host (Hondo 1992; Lyle 1914a; Stigenberg and Shaw 2013) or within its suspended cocoon (our unpublished observation). Adults are active in all seasons except winter (Berry and Walker 2004; Stigenberg and Shaw 2013) and, according to Abe et al. (2013), they increase body temperature via melanism, which is induced by low temperatures at the cocoon stage. Such plastic adaptation to seasonal climate change might also contribute to the variety of hosts that *M. pulchricornis* uses throughout the year.

However, *M. pulchricornis* is not a perfect generalist parasitoid of exophytic caterpillars. For example, there are no records of common *Pieris* species (Lepidoptera: Pieridae) being used as hosts despite intensive field collections (Walker et al. 2004) and laboratory trials (our unpublished observation). Also, *Uraba lugens* Walker (Lepidoptera: Nolidae) was proved to be not a suitable host of *M. pulchricornis* (Berndt 2010), which had been occasionally collected from it (Mansfield et al. 2005).

Spodoptera litura, which feed on soybean leaves, is a common host of *M. pulchricornis* (Table 1). However, Li et al. (2016, 2017a,b) showed that both constitutive and induced soybean resistance to *S. litura* significantly reduced the performance of *M. pulchricornis*. Host plant quality seems to influence

the performance and parasitism of this wasp, as demonstrated for other braconid endoparasitoids of caterpillars (Bukovinszky et al. 2009; Kuramitsu et al. 2016; Kuramitsu and Kainoh 2018). Although *M. pulchricornis* is polyphagous, its host acceptance may vary due to physiological and trophic interactions among host plants, hosts, and parasitoids.

Habitat selection also determines the real host range of parasitoids. Twenty years after its first detection in New Zealand, *M. pulchricornis* has been reared from >25 host species collected from various host plants in urban gardens, crop fields, regenerating forests, and native forest remnants (Berry and Walker 2004; Hartnett et al. 2018). In Japan, the habitats of *M. pulchricornis* range from open fields to woodlands, but unlike its congener *Meteorus narangae* Sonan (Maeto 1989a), *M. pulchricornis* is not generally collected in rice paddy fields. Notably, the light-colored thelytokous strains collected in open fields were genetically differentiated from the dark-colored strains found in forests (Abe et al. 2013).

Only a few semiochemical studies have considered habitat use or host location in *Meteorus* species. Magdaraog et al. (2013) showed that *M. pulchricornis* females were repelled by the odor emitted from hosts pre-occupied with competing parasitoid larvae. Recently, Sheng et al. (2017) reported antennal chemosensory genes in *M. pulchricornis*, which are candidates for future chemoecological studies.

Polyphagous koinobiosis of *M. pulchricornis* might be the culmination of the aforementioned physiological and ecological elements interacting with each other and constituting an adaptive suite (Fig. 4). Further comprehensive studies will be necessary to find a more rational explanation for its wide host

range and unique host use.

How do sexual and asexual strains coexist?

Thelytoky, a type of parthenogenesis in which females are produced from unfertilized eggs, occasionally occurs in the Hymenoptera. According to Quicke (2015, Table 7.1), 11 out of 43 incidences of thelytoky in Braconidae and Ichneumonidae are observed in the small subfamily Euphorinae, which includes *M. pulchricornis*. Its congener, *M. ictericus*, also has thelytokous populations (Bürgi and Mills 2013). The Euphorinae seem to have a predisposition for thelytoky, but the study on *M. pulchricornis* by Tsutsui et al. (2014) was the first to conduct cytogenetic research on this subject in the subfamily.

Both thelytokous (= uniparental) and arrhenotokous (= biparental) strains occur in *M. pulchricornis*, although most studies in East Asia and Australasia were conducted on thelytokous strains. Fuester et al. (1993) compared a Korean thelytokous strain with a European arrhenotokous strain and suggested that arrhenotokous strains are also present in the Far East. Tsutsui et al. (2014) identified both thelytokous and arrhenotokous strains in Japan, revealing that the thelytokous strains were truly asexual apomictic clones not induced by symbiotic bacteria. Abe et al. (2013) showed genetic differentiation in polymorphic melanism among thelytokous strains in Japan.

Fuester et al. (1993)'s attempts to hybridize a Korean thelytokous strain with a European arrhenotokous strain were unsuccessful. Still, deuterotoky (females producing parthenogenetic males and females) has been rarely observed and nuclear genome differentiation between sympatric thelytokous

and arrhenotokous strains is not distinct in Japan (our unpublished data), suggesting that gene flow might actually occur between sexual and asexual strains. Sexual–asexual gene flow was recently detected in aphids and thrips (Halkett et al. 2008; Li et al. 2015). Nevertheless, further research is necessary to elucidate the evolution and fate of asexuality in *M. pulchricornis*.

Thelytokous strains have probably been confined to East Asia and only recently introduced, by accident, to Australasia (Berry and Walker 2004). Arrhenotokous strains are widely distributed in Europe and East Asia, and thus, they might have accumulated far more genetic diversity than thelytokous strains. Moreover, recent mitochondrial DNA analyses have suggested the presence of several arrhenotokous, cryptic species in Europe and Turkey (Stigenberg and Shaw 2013), India (Shamim 2012), and Japan (Shunpei Fujie, unpublished data). Further genetic and ecological investigations on the species complex including *M. pulchricornis* are necessary.

There is no causal relationship between polyphagy and the evolution of thelytoky, but local coexistence of thelytokous and arrhenotokous strains in Japan might be encouraged by the high polyphagy of *M. pulchricornis*. Due to the so-called twofold cost of sex, arrhenotokous (sexual) strains will be easily outcompeted by thelytokous (asexual) strains. In fact, the thelytokous strains of oligophagous euphorines such as *Dinocampus coccinellae* (Schränk) and *Microctonus vittatae* Muesebeck (Braconidae) do not coexist with arrhenotokous strains (Balduf 1926; Smith and Peterson 1950). However, polyphagous sexual strains may take temporary host refuge more easily than oligophagous ones in the presence of asexual competitors.

How can *M. pulchricornis* be used in biological control?

The introduction of arrhenotokous *M. pulchricornis* from Europe into North America during the 1970s to control the gypsy moth *L. dispar* was unsuccessful (Fusco 1981). The reason for this failure is unknown. At any rate, no further attempts will be made to import this polyphagous parasitoid for biological control because it can attack non-target insects. However, the conservation of existing populations or their augmentation in enclosed horticultural systems will be considered. Currently, *M. pulchricornis* is being examined as a potential biocontrol agent against vegetable and bean crop pests such as *Helicoverpa* and *Spodoptera* species in East Asia and Australasia (Chen et al. 2011; Chen and Hwang 2015; Liu and Li 2006; Takashino et al. 1998, 2001; Walker et al. 2016). Although this is a koinobiont parasitoid of young or mid-instar host larvae, which are allowed to develop during parasitism, the parasitized host ends feeding within a few days, thereby hindering subsequent feeding damage (Harvey et al. 2010).

Parasitism levels by *M. pulchricornis* are highly variable in the field (Hondo 1992; Mundaca 2011; Schnitzler et al. 2011; Takashino et al. 1998, 2001; Walker et al. 2004, 2005). Even under laboratory conditions, early post-oviposition host mortality is occasionally >50% (our unpublished data). During oviposition, the parasitoid injects VLPs, which cause rapid apoptosis of host immune cells (Suzuki and Tanaka 2006). This may induce infectious diseases in the parasitized hosts under wet and contaminated conditions. Additionally, when female wasps pursue host larvae (Yamamoto et al. 2009), they may drop them, disrupt larval colonies, and increase larval mortality.

Parasitism observed in the field may underestimate the real impact of *M. pulchricornis* on pest populations. Thus, it should be evaluated considering the rate of oviposition and total host mortality associated with wasp activity. Moreover, because *M. pulchricornis* adults require sugar for longevity and optimal progeny reproduction (Harvey et al. 2017; Wu et al. 2008), their performance as natural enemies will also depend on floral plant abundance and diversity around croplands.

Several studies have examined the ability of *M. pulchricornis* to compete with specialist braconid parasitoids of caterpillars. In terms of larval competition, *M. pulchricornis* performed better than *Cotesia kariyai* (Watanabe) and *Cotesia ruficrus* (Haliday), both of which are gregarious specialist endoparasitoids of *M. separata* (Magdaraog et al. 2012). It also outcompeted *Snellenius manilae* (Ashmead), a solitary specialist endoparasitoid of *S. litura*, in larval competition and cage experiments (Chen and Hwang 2015). However, in both laboratory and field trials, *M. pulchricornis* was inferior to *Cotesia urabae* Austin & Allen when competing for the eucalypt defoliator *U. lugens* (Berndt 2010). Walker et al. (2016) showed that, in terms of larval competition, *M. pulchricornis* dominated *Microplitis croceipes* (Cresson) but was inferior to *Cotesia kazak* (Telenga), both of which are solitary specialist endoparasitoids of *H. armigera*. As mentioned by Walker et al. (2016), *M. pulchricornis* might have an advantage over specialists in diverse cropping systems, where it has a variety of alternative hosts to maintain its populations.

In general, *M. pulchricornis* parasitism was not adversely affected by insect pathogenic viruses (Guo et al. 2013; Nguyen et al. 2005), bacteria

(Wang et al. 2013), or *Bacillus thuringiensis* toxin-expressing transgenic host plants (Barraclough et al. 2009). Moreover, Guo et al. (2013) found that *M. pulchricornis* transmitted nuclear polyhedrosis virus to *Spodoptera* larvae.

Arai et al. (2018) identified female *M. pulchricornis* as vectors of ascoviruses, which cause chronic and lethal infections in lepidopterans. Other known vector parasitoids like *Cotesia* and *Microplitis* species are host specialists. In contrast, *M. pulchricornis* is highly polyphagous and, therefore, can be a key agent in spreading ascoviruses among diverse lepidopterans (Arai et al. 2018).

A method of mitigating the damage to vegetables and ornamentals caused by nocturnal moths is to use lamps at night (Shimoda and Honda 2013). The combination of nighttime lighting and the release of *M. pulchricornis* might be more effective than either treatment alone. However, the effects of nighttime lighting on the oviposition behavior of the nocturnal *M. pulchricornis* have yet to be evaluated.

Mass rearing of natural enemies is important for biological control, especially through augmentation. Rearing *M. pulchricornis* on target pest insects is costly, but *E. kuehniella* seems to be a feasible alternative host for the mass rearing of this parasitoid (Nakano et al. 2018). However, certain technical issues, e.g., how to make wasps oviposit on usually concealed *E. kuehniella* larvae and how to enlarge host larvae about 20% more, remain to be solved. For instance, rapidly heating food grain might help driving *E. kuehniella* larvae out for oviposition, and juvenile hormone analog treatment will increase their size for sufficient growth of their parasitoids (our unpublished data).

As pointed out by Stouthamer (1993), asexual strains are expected to be more effective than sexual strains in biological control because of the so-called twofold cost of sex. In contrast, certain traits useful in biological control may occur exclusively in the more genetically variable sexual strains, which could serve as a rich source of genetic variation to improve asexual strains as natural enemies (Lommen et al. 2017). A future objective will be the crossing of sexual (arrhenotokous) and asexual (thelytokous) strains of *M. pulchricornis* for genetic improvement in biocontrol use.

Concluding remarks

Meteorus pulchricornis is a highly polyphagous endoparasitoid of caterpillars. This is an extreme but not rare case of polyphagous koinobiosis. For example, a common braconid endoparasitoid *Cotesia vestalis* (Haliday) [= *C. plutellae* (Kurdjumov)] was considered highly specific to the diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Pluteliidae), a serious pest of crucifers, but it can also parasitize many other lepidopteran species to varying degrees of efficacy (Cameron et al. 1997; Nixon 1974). Therefore, further studies are required to assess the utility of *C. vestalis* as a biocontrol agent against *P. xylostella* (Arvanitakis et al. 2014). On the other hand, recent studies have revealed that the host ranges of idiobiont ectoparasitoids, such as *Bracon* and *Habrobracon* species (Braconidae), are narrower than that expected previously (Chomphukhiao et al. 2018; Matsuo et al. 2016). Host specificity of parasitoids in relation to koinobiosis or idiobiosis will be a challenging issue to be discussed again.

Studies on the biology of parasitoid wasps have been conducted on host

specialists rather than host generalists (Kuramitsu and Kainoh 2018). Polyphagous koinobiosis, however, will be a novel perspective to help elucidate the evolution of parasitoids interacting with multiple adaptive agents and evaluate them for use as biocontrol agents in changing ecosystems. Probably due to its high polyphagy, *M. pulchricornis* shows high genetic diversity and environmental plasticity in adult melanism (Abe et al. 2013). Genetic bases of polyphagy and associated traits of parasitoid wasps are scarcely known, but the application of next-generation sequencing technologies will help answer these questions (Wachi et al. 2018).

It has been argued that polyphagous natural enemies are generally inferior to monophages or oligophages. Polyphages may be relatively less effective at maintaining pest populations at low equilibrium levels and may pose a comparatively greater threat to non-target organisms. Nevertheless, they may survive long using alternative hosts and effectively control the re-invaded pest populations (Kidd and Jervis 2007). In fact, many polyphagous predators, that is to say, carabids, bugs, mites, and spiders, among others, are effective biocontrol agents in conservation and augmentation. As a highly polyphagous parasitoid, likely with genetically interconnected sexual and asexual strains, *M. pulchricornis* could serve as a highly adaptable biocontrol agent against a wide variety of pest caterpillars.

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Table 1 Host records of <i>Meteorus pulchricornis</i> *				
Superfamily	Family	Species	Regions or countries ^a	References ^b
Yponomeutoidea	Plutellidae	<i>Plutella xylostella</i>	J, NZ, in laboratory	5, 11, 25, 30
Gelechioidea	Gelechiidae	<i>Hypatima rhomboidella</i>	E	27
Pterophoroidea	Pterophoridae	<i>Amblyptilia acanthadactyla</i>	E	27
Choreutoidea	Choreutidae	<i>Anthophila fabriciana</i>	E	27
Tortricioidea	Tortricidae	<i>Ctenopseustis obliquana</i>	NZ	5
		<i>Epiphyas postvittana</i>	NZ	4, 5
		<i>Harmologa oblongana</i> -group	NZ	4, 5
Papilionoidea	Papilionidae	<i>Papilio macilentus</i>	J	16
	Lycaenidae	<i>Arhopala ganesa loomisi</i>	J	16
		<i>Artopoetes pryori</i>	J	16
		<i>Chilades pandava</i>	J	21
		<i>Thecla betulae</i>	E	13
	Nymphalidae	<i>Charaxes jasius</i>	E	13, 27
Pyraloidea	Crambidae	<i>Evergestis forficalis</i>	?J	26
		<i>Glyphodes cf. onychinalis</i>	NZ	5
		<i>Herpetogramma licarsisalis</i>	NZ (association only)	5
		<i>Musotima aduncalis</i>	NZ	32
		<i>Musotima nitidalis</i>	NZ	32
		<i>Musotima</i> sp. 1	NZ	32
		<i>Uresiphita gilvata</i>	E	27
		<i>Uresiphita polygonalis maoralis</i>	NZ	5, 22, 32
	Pyralidae	<i>Ephestia kuehniella</i>	In laboratory	23
		<i>Galleria mellonella</i>	In laboratory	1
Lasiocampoidea	Lasiocampidae	<i>Lasiocampa quercus</i>	E	19
		<i>Lasiocampa trifolii</i>	E	27
		<i>Poecilocampa populi</i>	E	13
Geometroidea	Geometridae	<i>Agriopis aurantiaria</i>	E	13, 27
		<i>Agriopis leucophaearia</i>	?E	13
		<i>Austrocidaria bipartita</i>	NZ	32
		<i>Austrocidaria</i> sp.	NZ	32
		<i>Bedellia psammisella</i>	NZ	5
		<i>Cleora scriptaria</i>	NZ	5, 32
		<i>Cyclophora</i> sp. on <i>Quercus</i>	E	27
		<i>Epiphyryne verriculata</i>	NZ	32
		<i>Eupithecia nanata</i>	E	13
		<i>Eupithecia</i> sp. on <i>Juniperus</i>	E	27
		<i>Operophtera brumata</i>	E	13, 27
		<i>Operophtera fagata</i>	E	27
		<i>Pasiphila lunata</i>	NZ	32
		<i>Pseudocoremia suavis</i>	In laboratory	3
		? <i>Asaphodes</i> sp.	NZ	5
Noctuoidea	Erebidae	<i>Eilema</i> sp (as <i>E. sororcula</i>)	?J	26
		<i>Lymantria dispar</i>	E, J, K	2, 4, 9, 13, 16, 19, 20
		<i>Orgyia thyellina</i>	NZ	4, 5
	Noctuidae	<i>Spilosoma imparilis</i>	J	12, 16
		<i>Teia anartoides</i>	A, NZ	5, 8, 10
		<i>Agrotis ipsilon</i>	In laboratory	5
		<i>Anarta myrtilli</i>	E	27
		<i>Arcte coerula</i>	J	16
		<i>Austramathes purpurea/ Feredayia graminosa</i>	NZ	32
		<i>Chrysodeixis eriosoma</i>	NZ	5
		<i>Diarsia intermixta</i>	NZ	32
		<i>Eupsilia transversa</i>	E	13, 27
		<i>Graphania mutans</i>	NZ	5
		<i>Graphania ustistriga</i>	NZ	5
		<i>Helicoverpa armigera</i>	NZ, In laboratory	4, 5, 15, 30
		<i>Helicoverpa</i> spp.	J	29
		<i>Heliothis maritima</i>	J	16
		<i>Hipoepa fractalis</i>	J	16, 26
		<i>Lycophotia porphyrea</i>	E	13, 27
		<i>Mamestra brassicae</i>	In laboratory	17, 31
		<i>Mythimna separata</i>	J, in laboratory	11, 16, 26, 28
		<i>Orthosia camipennis</i>	J	16
		<i>Orthosia cruda</i>	E	27
		<i>Spodoptera exigua</i>	C, in laboratory	14, 31
		<i>Spodoptera littoralis</i>	In laboratory	31
		<i>Spodoptera litura</i>	C, J, NZ, T	5, 6, 7, 16, 24, 28
		<i>Thysanoplusia orichalcea</i>	NZ	5, 30
	Nolidae	<i>Nola cuculatella</i>	E	13
		<i>Uraba lugens</i>	NZ	18

*Host records before Marsh (1979) and Huddleston (1980), who revised species delimitation within the genus *Meteorus*, are not cited here.

^a A, Australia; C, China; E, Europe; J, Japan; K, Korea; NZ, New Zealand; T, Taiwan

^b 1, Askari et al. 1977; 2, Balevski 1999; 3, Barraclough et al. 2014; 4, Berry 1997; 5, Berry and Walker 2004; 6, Chen and Hwang 2015; 7, Chen et al. 2011; 8, Chhagan et al. 2008; 9, Fuester et al. 1993; 10, Gerard et al. 2011; 11, Harvey et al. 2010; 12, Hondo 1992; 13, Huddleston 1980; 14, Liu and Li 2006; 15, Liu and Li 2008; 16, Maeto 1989a; 17, Malcicka and Harvey 2014; 18, Mansfield et al. 2005; 19, Marsh 1979; 20, Minami et al. 1999; 21, Miyake 2010; 22, Mundaca 2011; 23, Nakano et al. 2018; 24, Nguyen et al. 2005; 25, Okada 1989; 26, Stigenberg and Ronquist 2011; 27, Stigenberg and Shaw 2013; 28, Suzuki and Tanaka 2006; 29, Takashino et al. 1998; 30, Walker et al. 2004; 31, Harvey et al. 2015; 32, Hartnett et al. 2018

Table 2 Comparison of the main biological traits of three major lineages of braconids parasitizing exophytic caterpillars			
Subfamily	Euphorinae	Microgasterinae	Rogadinae
Main genera including parasitoids of exophytic caterpillars	<i>Meteorus</i> , <i>Zele</i>	<i>Cotesia</i> , <i>Glyptapanteles</i> , <i>Microplitis</i>	<i>Aleiodes</i> , <i>Macrostomion</i>
Modes of parasitoidism			
Koinobiont or idobiont	koinobiont	koinobiont	koinobiont
Endoparasitic or ectoparasitic	endoparasitic	endoparasitic	endoparasitic
Solitary or gregarious	mainly solitary	mainly gregarious	mainly solitary
Host range of each species	one or occasionally many families	usually one genus or family	usually one genus or family
Regulation of host physiology			
Ovary associated factors	virus-like particles (VLPs)	polydnaviruses (PDVs)	unknown
Host immune suppression	hemocyte apoptosis	egg coating, hemocyte regulation	unknown
Teratocytes	present	present	absent
Modification of host development	slight	often highly elaborated	unknown
Defense tactics during and after cocoon spinning			
Manipulated host behavior	passive, if present	often very aggressive	unknown
Cocoon structure	suspended with a silk thread or formed within the host's pupal chamber	often forming a large communal cocoon mass	formed within a mummified host skin
Adult reproduction and behavior			
Egg maturation	synovigenic; middle-sized eggs	pro-ovigenic; small eggs	synovigenic; fairly large eggs
Daily activity	usually nocturnal (and crepuscular)	diurnal	usually nocturnal
Host location	mainly by visual cues	mainly by semiochemical cues	little known
Host feeding	no	no	yes
Sources: Marsh (1979), Quicke (2015), Shaw and Huddleston (1991) and others cited in the text			

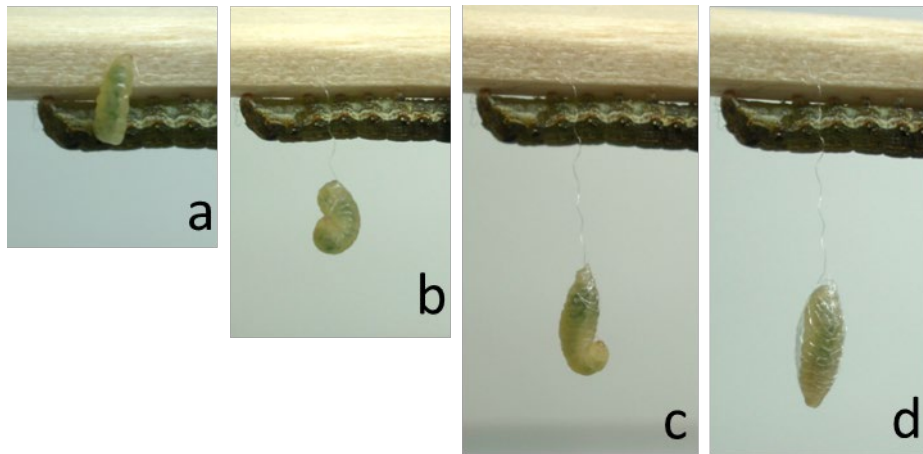


Fig. 1 Construction of a suspended cocoon by *Meteorus pulchricornis*. A mature larva emerging from *Spodoptera litura* and anchoring a silk thread to the substrate (a), elongating the thread (b), hooking the thread at the tip of the abdomen (c), and spinning a cocoon (d). Courtesy of Shunsuke Shirai



Fig. 2 Female *Meteorus pulchricornis* attacking a larva of *Spodoptera litura*. Courtesy of Masaki Yamamoto and Kentaro Itokawa

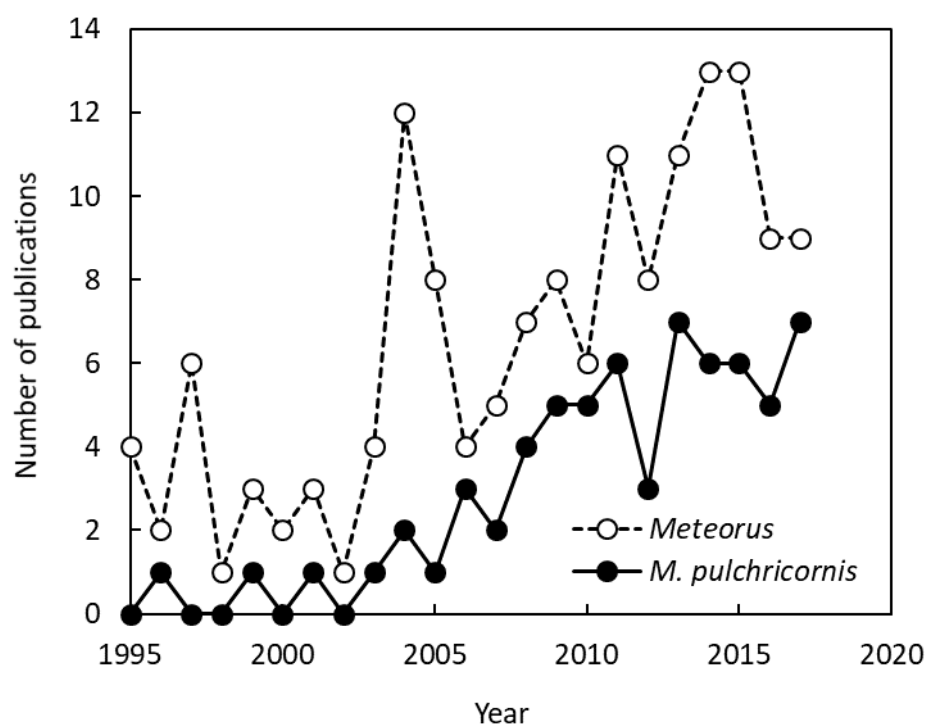


Fig. 3 Annual changes in the number of publications with topic "*Meteorus*" or "*Meteorus pulchricornis*" in the Web of Science Core Collection, Clarivate Analytics, Philadelphia.

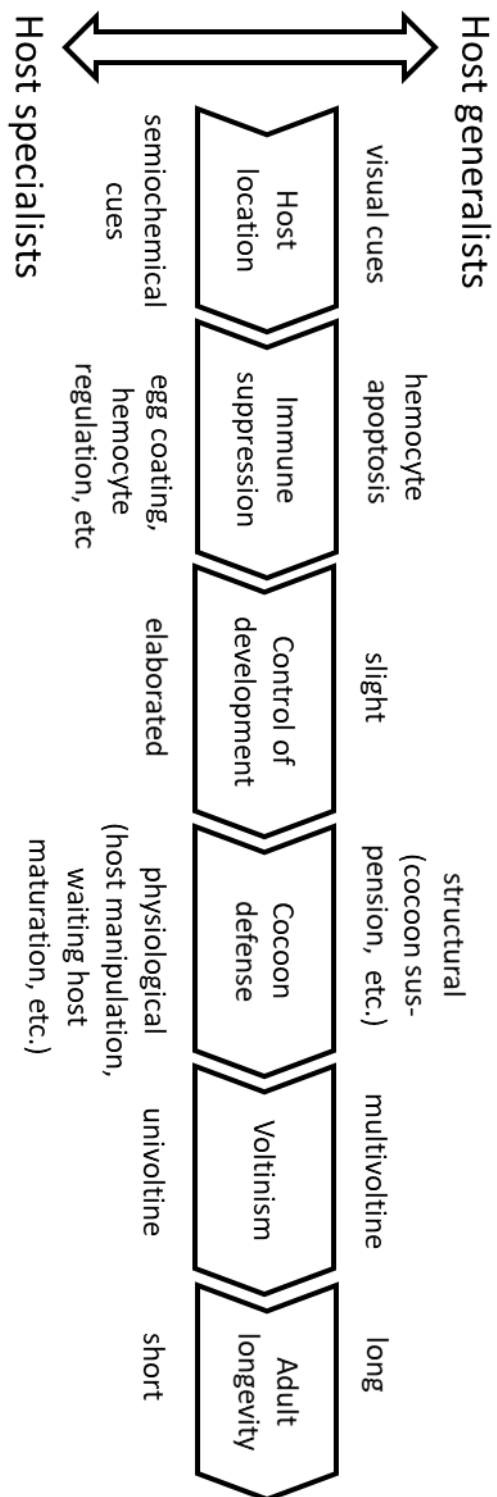


Fig. 4 Contrasting factors involved in the evolution of host specialists or host generalists for exophytic caterpillars

Supplementary Video 1 Female *Meteorus pulchricornis* pursuing a rubber dummy host, performing oviposition, and finally thrusting its ovipositor to the dummy host. Courtesy of Masaki Yamamoto

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