

Performance of larval parasitoid *Habrobracon hebetor* Say (Hymenoptera: Braconidae) on *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae): potential use as Bio-control agent

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Abstract

The parasitoid *Habrobracon hebetor* is a polyphagous parasitoid of several lepidoptera larvae, including *Spodoptera* species. *H. hebetor* is already used to control several economically important insect pests. It has also been reported on the fall armyworm (FAW), but its utilization against the FAW requires further investigation. First, we assessed the acceptability of different larval instars of *S. frugiperda* for parasitism by *H. hebetor*. Second, we assessed the parasitism of *H. hebetor* on *S. frugiperda* in comparison to *Corcyra cephalonica*, the factitious host on which the parasitoid is mass cultured. Finally, we tested the parasitic ability of *H. hebetor* progeny developing from *S. frugiperda* larvae. The *H. hebetor* female paralyzed and killed all 3rd -6th instar larvae of *S. frugiperda* but parasitized and laid eggs only on the 5th and 6th instar larvae. With respect to parasitism and laying eggs, *H. hebetor* has a marked preference for *C. cephalonica* larvae. Likewise, *H. hebetor* developing on *S. frugiperda* larvae had lower performance than parasitoids that have been reared on the factitious host, *C. cephalonica*. However, because *H. hebetor* is relatively easy to mass rear, it could still be considered a potential supplementary biological control agent with other parasitoids against the FAW.

Graphical Abstract



Female Habrobracon hebetor laying eggs on 5th instar larva of S. frugiperda

Keywords Spodoptera frugiperda · Habrobracon hebetor · Corcyra cephalonica · Biological control

Extended author information available on the last page of the article

Abbreviation

FAW Fall armyworm

Introduction

Habrobracon hebetor Say (Hymenoptera, Braconidae) is a polyphagous, parasitoid of many lepidopteran larvae. It is a parasitoid of stored product Pyralidae species, Plodia interpunctella Hübner, Cadra cautella Walker, Ephestia kuehniella Zeller, Corcyra cephalonica Stainton, Galleria mellonella Linnaeus and Gelechiidae, Sitotroga cerealella Olivier. It is also a parasitoid of field crop insect pests, Helicoverpa armigera Hübner (Lepidoptera: Noctuidae), Spodoptera species (Lepidoptera: Noctuidae), Earias vittella Fab. (Lepidoptera: Noctuidae), Diatraea saccharalis Fab. (Lepidoptera: Crambidae), Cydia leucostoma Meyrick (Lepidoptera: Tortricidae), Pempelia morosalis Saalmüller (Lepidoptera: Pyralidae), Opisina arenosella Walker (Lepidoptera: Xyloryctidae), Ectomyelois ceratoniae Zeller (Lepidoptera: Pyralidae), Palpita unionalis Hübner (Lepidoptera: Pyralidae), and Heliocheilus albipunctella de Joannis) (Lepidoptera: Noctuidae) (Ghimire and Philips 2010; Kishani-Farahani et al. 2012; Saxena et al. 2012; Saadat et al. 2014a; Dehliz et al. 2016; Mansour et Saber 2017; Gahukar et Ba 2019; Lettmann et al. 2021). Usually, a female of H. hebetor first stings and injects venom into the host larvae before laying eggs on paralyzed host larvae (Ghimire and Phillips 2014; Kabore et al. 2019). Sometimes, it stings and feeds on the liquid that oozes out but does not lay eggs (Kabore et al. 2019). One H. hebetor female can produce an offspring of 200-400 individuals (Yu et al. 1999; Chen et al. 2011; Kabore et al. 2019). The rapid growth rate, short generation time, high fecundity, and easiness to mass multiply on factitious hosts at low cost make *H. hebetor* an ideal parasitoid for augmentative/inundative releases against field insect pests. H. hebetor is used in the control of several economically important insect pests, including the carob moth, E. ceratoniae, on pomegranate (Saadat et al. 2014a), H. armigera on tomato, the tea looper, Biston suppressaria Guenée (Lepidoptera: Geometridae) (Alam et al. 2021), and the millet head miner, H. albipunctella (Ba et al. 2013, 2014; Baoua et al. 2014; Kabore et al. 2017; Amadou et al. 2017). Releases of *H. hebetor* against the millet head miner can lead to a 34% increase in grain yield in the Sahel region (Baoua et al. 2014).

Since the invasion of the fall armyworm, *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), in Africa in 2016, many options have been tested for controlling the pest (Harrison et al. 2019; Rioba and Stevenson 2020; Kasoma et al. 2021; Chawanda et al. 2023), such as biological control (Kenis et al. 2023). Numerous egg and larval parasitoids have been identified as potential candidates for biological control (Amadou et al. 2018; Kenis et al. 2019; Sisay et al. 2019; Laminou et al. 2020; Koffi et al. 2020; Agboyi et al. 2021; Colmenarez et al. 2022), including H. hebetor (Cruz et al. 2018). Given that *H. hebetor* is already used in augmentative biological control of the millet head miner in the Sahel region (Guerci et al. 2018; Gahukar and Ba 2019), it could, if effective, be easily reared and released for augmentative control of FAW using the existing bio-factories (Guerci et al. 2018; Gahukar and Ba 2019). In fact, H. hebetor and the related Bracon brevicornis Wesmael have been reported as biological control agents of Spodoptera litura Fab. and Spodoptera exigua Hübner (Kaur and Kaur 2013; Punia et al. 2020; Fathipour et al. 2020; Ghosh et al. 2022). Thus, it is important to understand the suitability of S. frugiperda for H. hebetor parasitism. A comprehensive study on H. hebetor performance on S. frugiperda is presented. We first tested the acceptance of different larval instars of S. frugiperda for parasitism by H. hebetor. Larval instars that supported parasitism were further tested for H. hebetor development compared with larvae of the rice moth, C. cephalonica, the factitious host on which the parasitoid is mass cultured. The potential utilization of H. hebetor for control of S. frugiperda in field conditions is further discussed.

Material and method

Origin and rearing conditions of the insects

The experiments and insect rearing were carried out in the entomology laboratory of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), *Sadoré* in Niger, under controlled environmental conditions (temperature= 29 ± 0.47 °C; relative humidity= $60.8\pm1.19\%$ and photoperiod=12 h).

Spodoptera frugiperda was reared from larvae collected in a sorghum field in late 2017 at the ICRISAT research station in Sadoré. First-instar larvae were fed Tobacco Budworm artificial diet (Product# F9781B, FrontierTM Agricultural Sciences, Newark, DE, USA). From instar two onwards, the larvae were fed solely with fresh castor bean *Ricinus communis* L. (Euphorbiaceae) leaves, using the rearing procedure described by Laminou et al. (2020; 2023).

Habrobracon hebetor was initially collected from a culture established from field-collected larvae of *H. albipunctella*. Habrobracon hebetor larvae were reared on fourth and fifth instar larvae of the rice moth, *C. cephalonica*, using the technique described by Ba et al. (2014). Rice moths were reared on pearl millet grain and flour using the technique described by Ba et al. (2014).

Acceptability of different larval instars of *S. frugiperda* for parasitism by *H. hebetor*

The experiment was conducted with mated H. hebetor females, aged less than 24 h, and 3rd -6th instar larvae of S. frugiperda. For each larval stage tested, 23 larvae and 23 H. hebetor females were used. Each S. frugiperda larva of a given instar was confined individually with a mated H. hebetor female in a Petri dish for 24 h. The parasitoid female was then removed from the Petri dish, and the larva was checked for paralysis and/or parasitism. Thus, the number of unparasitized, paralyzed, and parasitized larvae was recorded. Larvae parasitized by H. hebetor were easily distinguished by the presence of cocoons, while paralyzed larvae are killed by a host-feeding mechanism with no deposition of eggs (Kabore et al. 2017). The number of eggs laid per parasitized larva was recorded, and the parasitized larvae were incubated until H. hebetor progeny emerged. The number and sex of emerging adults were recorded.

Parasitism of *S. frugiperda* larvae by *H. hebetor* as compared to larvae of the factitious host, *C. cephalonica*

The parasitoid *H. hebetor* was offered larvae of *S. frugiperda* and *C. cephalonica* for parasitism in no-choice and choice conditions.

Based on the findings of the previous experiment, H. hebetor female was given either the 5th or 6th instar larvae of S. frugiperda or the 5th or 6th instar larvae of C. cephalonica, the factitious host for parasitism. The experiment was conducted concomitantly with 92 Petri dishes as follows: (i) 23 dishes with a single 5th instar larva of S. frugiperda in each; (ii) 23 dishes with a single 5th instar larva of C. cephalonica in each; (iii) 23 dishes with a single 6th instar larva of S. frugiperda in each; and (iv) 23 dishes with a single 6th instar larva of C. cephalonica in each. A single 24-h-old mated H. hebetor female was released in each Petri dish for parasitism. After 24 h exposure of C. cepahlonica / S. frugiperda larvae to H. hebetor parasitism, the parasitoids were removed from the boxes, and the larvae were incubated for 3 days. The larvae were checked for the number of parasitized larvae and the number of eggs laid per larvae by the parasitoid.

Under the choice condition, both the 5th instar larva of *C. cephalonica* and *S. frugiperda* were placed together in one box and submitted to one *H. hebetor* female for parasitism for 24 h. Concomitantly, both the 6th instar larvae of *C. cephalonica* and *S. frugiperda* were put together in another box and submitted to one *H. hebetor* female for parasitism for 24 h. The experiment was replicated 23 times. After exposure to *H. hebetor* parasitism, the females were

removed from the boxes, and the host larvae incubated for 3 days and checked for the number of parasitized larvae and number of eggs laid per host-larvae.

Fitness of *H. hebetor* female emerging from *S. frugiperda* larvae

The fitness of *H. hebetor* females emerging from *S. frugiperda* larvae (from previous experiments) was compared to counterpart *H. hebetor* females continuously reared on *C. cephalonica*. In both cases, *H. hebetor* females were provided 4th -5th instar *C. cephalonica* larvae for parasitism. The parasitoid females were kept individually with the host larva in a Petri dish for 24 h and moved each day to a new Petri dish with another *C. cephalonica* larva until the female died. To ensure females' fertilization, they were always accompanied by a male. Adult parasitoids were fed with a 10% honey solution. The parasitized larvae were incubated until new *H. hebetor* progeny emerged. Parental female life span, number of eggs laid per female, number of emerging adults, and sex ratio of offspring were recorded.

Statistical analysis

The normality and homogeneity of the data were checked by the Shapiro–Wilk and Bartlett tests, respectively, using RStudio software version 4.0.3. When data were found to be normally distributed, an independent t-test for two samples was applied (α =0.05). Percentage data that did not fit normal distribution were subjected to arcsine transformation before being subjected to a t-test. When the dataset did not fit normal distribution and did not meet the criteria for transformation, the non-parametric Wilcox independent test for two samples was applied. Likewise, the non-parametric Wilcox independent test for two samples was applied for choice tests.

Results

H. hebetor female paralyzed and killed all 3rd -6th instar larvae of *S. frugiperda* within 24 h of exposure (Table 1). However, only the 5th and 6th instar larvae of *S. frugiperda* were parasitized by *H. hebetor* but with no significant difference for the two larval stages (Table 1). Likewise, *H. hebetor* female laid a similar number of eggs on the 5th and 6th instar larvae of *S. frugiperda* (Table 1). Moreover, *H. hebetor* development was completed in the same number of days on the 5th and 6th instar larvae of *S. frugiperda* (Table 1).

In a no-choice situation, *H. hebetor* female parasitized twice more 5th larvae of *C. cephalonica* than *S. frugiperda* (Table 2). Likewise, significantly more 6th instar

<i>S. frugiperda</i> larvae instar	% paralyzed larvae (% ± SE)	% parasitized larvae (±SE)	No eggs (±SE) laid per host-larvae	<i>H. hebetor</i> egg to adult development time $(d \pm SE)$
3rd instar	100	-	-	
4th instar	100	-	-	
5th instar	100	56.52 ± 10.57 a	9.38±1.55 a	12.90 ± 0.18 a
6th instar	100	69.57±9.81 a	13.31±2.18 a	12.57 ± 0.20 a
	-	$t_{1-43.76} = -0.90; P = 0.37$	$t_{1-25.82} = -1.46; P = 0.15$	W=45; <i>P</i> =0.27

Table 2 Parasitism ($\% \pm S.E$) of 5th and 6th instar larvae of S. frugiperda and C. cephalonica by H. hebetor in choice* and no-choice** conditions.Columns bearing different letters were significantly different according to a non-parametric Wilcox independent test at P < 0.05

	% parasitized larvae (±SE)			
Host-larvae	No-choice		Choice	
	5th instar	6th instar	5th instar	6th instar
S. frugiperda	56.52±10.57 a	69.57±9.81 a	21.74±8.79 a	26.09±9.36 a
C. cephalonica	100 b	100 b	$91.30 \pm 6.01 \text{ b}$	100 b
	W=379.5; P=0.0004	W=345; P=0.005	W=448.5; P<0.0001	W=460; P<0.0001

* S. frugiperda and C. cephalonica larvae are given together to H. hebetor for parasitism

** S. frugiperda and C. cephalonica larvae are kept and submitted separately to H. hebetor parasitism

Table 3 Number eggs laid (\pm S.E) by *H. hebetor* on parasitized 5th and 6th instar larvae of *S. frugiperda* and *C. cephalonica* in choice* and no-choice** conditions. Columns bearing different letters were significantly different according to an independent t-test or non-parametric Wilcox independent test at *P*<0.05

	No. eggs laid on host-larvae (±SE)			
	No-choice		Choice	
Host-larvae	5th instar	6th instar	5th instar	6th instar
S. frugiperda	9.38±1.56 b	13.31±2.18 b	4.14±0.51 b	6.83 ± 0.79 b
C. cephalonica	16.35 ± 0.75 a	18.17 ± 0.70 a	15.78 ± 0.51 a	15.17 ± 0.49 a
	W=245.5; P=0.002	t $_{1-18.14} = 2.12; P = 0.04$	W=161; P<0.0001	W=138; P=0.0002

* S. frugiperda and C. cephalonica larvae are given together to H. hebetor for parasitism

** S. frugiperda and C. cephalonica larvae are kept and submitted separately to H. hebetor parasitism

Table 4 *H. hebetor* adult emergence ($\% \pm SE$) from parasitized 5th and 6th instar larvae of *S. frugiperda* and *C. cephalonica* in choice* and nochoice** conditions. *H. hebetor* (%) emergence data in no-choice conditions were subjected to arcsine transformation prior to analysis. Within a column, means with different letters were significantly different according to an independent t-test or non-parametric Wilcox independent test at *P*<0.05

	% <i>H. hebetor</i> adult emergence $(\pm SE)$			
	No-choice		Choice	
Host-larvae	5th instar	6th instar	5th instar	6th instar
S. frugiperda	31.99±5.31 b	32.51±6.13 b	$46.19 \pm 13.30 \text{ b}$	34.78±4.64 b
C. cephalonica	90.10 ± 1.89 a	89.60 ± 1.27 a	91.71±1.35 a	94.55±0.99 a
	$t_{1-17.99} = 8.59; P < 0.0001$	$t_{1-18.43} = 8.07; P < 0.0001$	W=138; P=0.005	W=138; P=0.0002

* S. frugiperda and C. cephalonica larvae are given together to H. hebetor for parasitism

** S. frugiperda and C. cephalonica larvae are kept and submitted separately to H. hebetor parasitism

larvae of *C. cephalonica* were parasitized than *S. frugiperda* (Table 2). Regardless of larval instars, *H. hebetor* female parasitized 3-4-fold more *C. cephalonica* larvae than *S. frugiperda* in a choice situation (Table 2). In both no-choice and choice situations, *H. hebetor* females laid more eggs on the 5th and 6th instar larvae of *C. cephalonica* than *S. frugiperda* (Table 3).

Under no-choice conditions, *H. hebetor* adult emergence was three times higher on the 5th and 6th instar larvae of *C. cephalonica* than *S. frugiperda* (Table 4). Under choice conditions, *H. hebetor* emergence is 2–3 times higher on 5th and 6th instar larvae of *C. cephalonica* than *S. frugiperda* (Table 4). However, in general, the sex ratio of emerging adults was not affected by host larvae species in both

Table 5 *H. hebetor* emerging female ($\% \pm SE$) when developing on 5th and 6th instar larvae of *S. frugiperda* and *C. cephalonica* in choice* and no-choice** conditions. Within a column, means with the same letters were not significantly different according to an independent t-test or non-parametric Wilcox independent test at P < 0.05

	% female (±SE)			
Host-larvae	No-choice		Choice	
	5th instar	6th instar	5th instar	6th instar
S. frugiperda	55.95±5.89 a	59.68±2.68 a	52.78±13.20 a	51.67±6.67 b
C. cephalonica	62.69 ± 1.78 a	59.61±1.84 a	65.12 ± 1.44 a	64.09 ± 1.85 a
	$t_{1-11.87} = 1.09; P = 0.30$	$t_{1-21.31} = -0.02; P = 0.98$	W=101.5; P=0.084	W=91.5; P=0.04

* S. frugiperda and C. cephalonica larvae are given together to H. hebetor for parasitism

** S. frugiperda and C. cephalonica larvae are kept and submitted separately to H. hebetor parasitism

Table 6Lifespan of *H. hebetor* female emerging from *S. frugiperda* and *C. cephalonica* larvae and total number eggs laid when given *C. cephalonica* larvae to parasitize and corresponding, % emerging adults and %female in the progeny. Emerging adults' (%) data were subjected to arcsine transformation prior to analysis. Columns bearing different letters were significantly different according to an independent t-test or non-parametric Wilcox independent test at P < 0.05

Origin of <i>H. hebetor</i> parental female	Female lifespan (days±SE)	Total number eggs laid per <i>H. hebetor</i> female	% Emerging adults (±SE)	% Female in the progeny (\pm SE)
S. frugiperda	20.86 ± 0.94	156.72 ± 10.70 b	47.87±2.50 b	54.77±1.76 b
C. cephalonica	19.78 ± 0.42	262.9 ± 12.02 a	79.68±3.86 a	60.44±1.55 a
	$t_{1-30.34} = -1.06 = P = 0.30$	$t_{1-56.46} = 6.60; P < 0.0001$	$t_{1-43.21} = 6.94; P < 0.0001$	$t_{1-56.45} = 2.49; P = 0.016$

no-choice and choice situations, except for 6th instar larvae in choice condition (Table 5).

H. hebetor females emerging from *S. frugiperda* live as long as those continuously reared on *C. cephalonica* larvae (Table 6). However, females reared continuously on *C. cephalonica* laid significantly more eggs than those emerging from *S. frugiperda* (Table 6). Likewise, adult emergence was much higher on *H. hebetor* continuously reared on *C. cephalonica* than the parasitoid emerging from *S. frugiperda* larvae (Table 6). Ultimately, the proportion of females was much higher when the parental female of *H. hebetor* developed on *C. cephalonica* larvae (Table 6).

Discussion

Our results show that all 3rd -6th larval instars of *S. frugiperda* were paralyzed and ultimately killed by *H. hebetor*. These results are consistent with Alam et al. (2021) findings, who reported paralysis of all 4th -6th larval instars of *S. frugiperda* by *H. hebetor*. This is particularly promising given that not all late instar larvae of host species are paralyzed by *H. hebetor* in other settings (Magro and Para 2001; Ghimire and Phillips 2014). Likewise, *H. hebetor* paralyzed all 5th and 6th instar larvae of *S. frugiperda*, even in the presence of the factitious host *C. cephalonica* larvae. This is in line with *H. hebetor* typical behavior; it stings and injects venom to paralyze the host-larvae before choosing to lay eggs or not (Kabore et al. 2019; Baker and Fabrick 2000; Allahyari et al. 2020; Cantori et al. 2022).

As documented by Cantori et al. (2022), paralysis efficacy is a poor criterion to rule out on parasitism activity. Interestingly, our results show that the parasitoid lays eggs and completes life cycle on 5th -6th larval instars but not on early developmental stages. This clearly shows that H. hebetor has a marked preference for 5th -6th instar larvae of S. frugiperda. In general, H. hebetor prefers late larval stages of its host species for parasitism (Akinkurolere et al. 2009; Mbata et Warsi 2019). With the related parasitoid species Bracon brevicornis Wesmael, parasitism was observed on 3rd -6th instar larvae of S. frugiperda (Ghosh et al. 2022; Lekha et al. 2022). Differences may be due to experimental conditions, as H. hebetor performance is more affected by temperature than B. brevicornis (Lettmann et al. 2021). However, differences may be related to intrinsic species characteristics. On both 5th and 6th instar larvae of S. frugiperda, egg-to-adult development of H. hebetor was completed in days comparable to what Magro and Para (2001) observed on the same host but higher than what was reported with most storage insect pest species in other settings (Ghimire and Phillips 2014).

However, when it comes to laying eggs, *H. hebetor* has a marked preference for *C. cephalonica* larvae. This is in line with Magro's and Para's (2001) observations. Since *S. frugiperda* larvae are bigger than those of *C. cephalonica*, they are likely more vigorous and require more energy to get parasitized by *H. hebetor*. Similar observations have been reported when comparing parasitism of *H. hebetor* on *H. armigera* vs. *E. kuehniella* (Saadat et al. 2014b), S. *litura* vs. *G. mellonella* (Abou El-Ela et al. 2021)d *litura* and *S. littoralis* vs. *C. cephalonica* (Muslim et al. 2017). The host preference could also be influenced by *H. hebetor's* rearing history, given that the parasitoid has been reared on *C. cephalonica* for several generations. Similar findings have been reported with H. hebetor in other settings (Saadat et al. 2014b). The host preference may also be due to nutritional/antinutritional factors of the host larvae as observed with different parasitoids (Vinson and Iwantsch 1980; Harvey et al. 2011), including *H. hebetor* (Baker and Fabrick 2000; Magro et al. 2006; Kaur and Kaur 2013; Borzoui et al. 2016). This is corroborated by the fact that a lower number of offspring emerged from S. frugiperda than C. cephalonica larvae. The poor quality of S. frugiperda larvae for H. hebetor development has likely impaired the fitness of the emerging adults. In fact, H. hebetor females emerging from S. frugiperda larvae have a lower fecundity, and they produced less progeny and fewer females as compared to females continuously reared on C. cephalonica. This is in line with previous findings suggesting that parasitoid offspring performance can be affected by maternal rearing conditions (Wang and Messing 2004; Najafpour et al. 2018). According to Visser et al. (2023), when provided with poor larval hosts, the parasitoid's ability to accumulate fat could be affected, resulting in poor performance.

Successful parasitism results from a series of behaviors that lead to the location and acceptance of suitable hosts for progeny development. In the case of the millet head miner, H. hebetor can search for inconspicuous 5th -6th instar host larvae in the millet head for paralysis, host feeding, and subsequent parasitism (Kabore et al. 2017). In the case of S. frugiperda, the parasitoid can clearly develop on 5th -6th larval instars. Interestingly, the damage caused by early instars of FAW on maize is insignificant, and most damage to the plant is caused by the later instar larva (Abrahams et al. 2017). Thus, parasitism of later instars of FAW by *H. hebetor* is amenable as it attacks the larval stage of FAW that causes the most damage and is the most difficult to control. However, as Bracon's successful host searching depends on several factors, including experience and volatiles released by the host plant (Zaki et al. 1998; Faccoli and Henry 2003; Saadat et al. 2014b, 2016; Magalhães et al. 2019), the question is whether H. hebetor will be able to search S. frugiperda larvae in a hidden location, such as the whorl of maize plants, for parasitism. Early studies in Bangladesh suggested successful host searching by H. hebetor in the maize field (Alam et al. 2021). The same study reported a 45% reduction in FAW larval populations after releases of H. hebetor in maize fields. This needs to be confirmed in other settings, emphasizing the weight of larval paralysis and larval parasitism on overall pest population reduction. Finally, the use of H. hebetor in integrated management approaches for effective control of FAW needs further evaluation, particularly in terms of yield protection. The assessment could also explore the combined use of *H. hebetor* with egg parasitoid Telenomus remus Nixon (Hymenoptera: Platygastridae).

Conclusions

Habrobracon hebetor paralyzes and ultimately kills all 3rd -6th larval instars of *S. frugiperda*, but the parasitoid lays eggs and completes development on only 5th -6th larval instars. However, *H. hebetor* performs less on *S. frugiperda* than *C. cephalonica*, the factitious host on which it is being reared. Further investigations will be needed to assess the possible use of *H. hebetor* in biological control of the fall armyworm.

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Declarations

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