INTRODUCTION

Sapodilla fruit borer (SFB) is a major pest of sapodilla fruit[1]. The undescribed phycitine moth, previously name *Nephopterix* sp. [= *Mussidia pectinicornella* Hampson = *Ectomyelois ceratoniae* (Zeller) = *Myelois ceratoniae* Zeller], is congeneric with *Ceroprepes naga* Roesler & Küppers, 1979, from Sumatra, and with *Tetralopha piratis* Meyrick, 1887, from Australia (Horak personal communication). During the course of the studies on the biology of this pest, a bethylid attacking the SFB larvae was collected. This parasitic wasp was subsequently described as *Goniozus thailandensis* Gordh & Witethom[2].

Bethylidae are cosmopolitan family containing about 2,000 described species which almost exclusively parasitize larvae of Coleoptera and Lepidoptera[3,4,5,6,7,8,9]. The bethylid genus *Goniozus* comprises about 150 nominal species[10]. All *Goniozus* species are primary gregarious ectoparasitoids. These parasitoids prefer cryptic Microlepidoptera larvae, but they are not host specific[3,4,5,7,8,9]. Life history of several *Goniozus* species has been well documented[3,4,5,7,8,9,11,12,13,14,15,16].

According to the fossorial habit, *Goniozus* species are potential candidates for biological control of Lepidoptera larvae living in concealed situations[3,4,5,7,8,9]. Their effectiveness as biological control agents of Lepidopterous pests has been reported for *G. aethiops* Evans attacking *Pectinophera gossypiella* (Saunders)[5], *G. legneri* Gordh and *G. emigratus* (Rohwer) attacking *Amyelois transitella* (Walker)[17,18], *G. marasmi* Kurian attacking *Marasimia trapizalis* (Guenee)[19] and *G. jacintae* Farrugia attacking *Epiphyas postvittana* (Walker)[20].

In Thailand, studies on biology of Bethylidae have been limited only to *Goniozus* attacking the rice leaf folder, *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Pyralidae)[21].

Since *G. thailandensis* is a primary parasitoid of the phycitine SFB, its development and potential for the biological control of its host was investigated.

Voucher specimens were deposited in the institutions mentioned in Gordh and Witethom[2].

METERIALS AND METHODS

Unless otherwise stated, all observations were conducted at 26±1°C, 70-80% RH, and under a 12:12 (L:D) photocycle.

Sapodilla fruit borer culture

The method of rearing of SFB was slightly modified from Witethom and Silawatchananai[1]. After mating, seven to 10 females were transferred to each of several (2-3) oviposition cages. The clear plastic cages (16.5 cm in diameter, 24 cm high) had eight organdy-covered ventilation holes (3.2 cm in diameter) in their sides and four (2.3 cm in diameter) in their lids. Four sheets of tissue paper were hung inside each container for female oviposition. Pieces of sterilized cotton pads moistened with 10% honey solution and with water were supplied as food and water. The egg-covered tissue papers were removed and kept in labelled plastic bags. New papers were replaced daily. Water and honey were changed every two days. Adults were discarded after seven days of oviposition. One day prior to hatching, oviposited papers (100-150 eggs) were cut and placed in each of several (2-3) containers with seven to 10 unriped sapodilla fruit as larval food. The clear plastic boxes (11x11x6 cm) had one organdy-covered ventilation hole (7 cm in diameter) in their lids. Larvae were reared as described in Witethom and Silawatchananai[1]. Approximately 200 larvae in each developmental stage were continually available using these culture techniques.

According to the results of preliminary observations on optimal SFB number and instar for parasitism and oviposition (Witethom, unpublished data), two fifth instar larvae were used for parasitoid oviposition during 24-hr exposure throughout this study.

To prepare larvae hosts, six to 12 early fifth instars (two-week old) from the SFB culture were transferred individually to each lidless container (5 cm in diameter, 6 cm high) with an unriped sapodilla fruit. The larvae were then left overnight to allow larval tunnelling inside the fruit, thus simulating the natural infestation.

G. thailandensis culture

G. thailandensis culture was started with adults emerging from SFB larvae collected from sapodilla orchards on Yo Island, Songkhla (6° 17′N, 7° 56′N, 101° 30′E, 106° 20′W)[22]. Adult parasitoids that emerged from field-collected hosts were frequently added to the culture to increase genetic heterogeneity.

Eight to 12 newly emerged parasitoids were kept together in each clear-vent plastic container (9.5 cm in diameter, 20 cm high) for 24 hr to facilitate mating.

Since female parasitoids may use chemicals either from larval host plant or from host feces as cues for host searching, a sapodilla twig soaked in a bottle of water, a piece of infested fruit and host feces were provided in each parasitoid container[23].

To maintain *G. thailandensis* culture, two fifth instar SFBs were exposed to each female parasitoid (three to 10 days old). Water and honey were not supplied during oviposition. After 24-hr exposure, the larvae were seperated from female parasioids and reared until parasitoid emergence, host pupation, or death.

Survival and development of immature stages

Twenty nine parasitized SFB larvae were prepared as described in parasitoid culture. The oviposited larvae were observed daily under the stereomicroscope to determine the stage and duration of parasitoid development. The parasitoid instars were not determined. Numbers of parasitoid larvae, pupae, and adults emerged from each parasitized host were recorded to determine their survival.

To determine number of eggs deposited, 16 parasitized larvae were killed, placed in FAA for 6 hr and stored in 70% ethanol. Number of eggs laid by *G. thailandensis* females during 24-hr exposure were recorded. These data were compared to data on number of parasitoid larvae to determine egg viability.

Adult longevity and fertility

After mating, the life history of 28 females (one to five females per replicate) was observed. Each female, deprived of honey but provided with hosts daily at 2:1 host: parasitoid ratio, was monitored for : (1) the preoviposition period, (2) number of hosts attacked, (3) number of progeny produced per female and per parasitized host, and (4) sex ratio of each brood. Twenty six females were reared under the same condition but deprived of hosts. The longevity of host-deprived females were recorded and compared with those provided with hosts. The head width and total body length of both female groups were measured to determine the correlation between size and longevity. The longevity of 28 mated honey-deprived males, 1-5 males per replicate, was concurrently observed.

To determine whether *G. thailandensis* is arrhenotokous, 13 fifth instar SFB larvae were parasitized by virgin females (five to 10 days old). Number and sex of progeny emerged from parasitized hosts were recorded.

An overall estimate of sex ratio was obtained from the parasitoid that emerged during the immature development and survival as well as from the adult longevity and fertility studies.

Sex ratio of *G. thailandensis* was also determined by following the method of Green *et al*[24]. Broods were classified according to size, using only those with complete emergence. The number of single-male broods for each brood size was counted. If the number of males is binomially distributed, the probability of observing as many as k (or more) broods with exactly one male will be no larger than

$$\alpha = \sum_{x=k}^{n} \binom{n}{x} \hat{p}^x (1-\hat{p})^{n-x}$$

where $\hat{p} = (1-1/N)^{N-1}$, N is brood size, n is the frequency of brood size occurrence, k is the number of broods of size N having exactly one male, and x is the number of males.

Construction and analysis of life table

Following the death of the 28 females provided with hosts, life table statistics were calculated using the computational methods of Andrewartha and Birch[25] and Birch [26]. The pivotal age (x) was the mid point of age interval in days. Age-specific survival rate (l_x) for the immature stages was estimated from that noted in the immature survival study. Age-specific survival rate (l_x) for adult females was calculated as the number of females surviving over the initial number of females multiplied by the estimated survivorship at adult emergence. Age-specific fertility rate (m_x) was calculated as the number of progeny produced per day divided by the number of females alive on that day. The following statistics were calculated from the life table.

(1) Net reproductive rate (R_0)-the average number of female progeny produced per female during her lifetime, where

$$R_0 = \sum_{x=0}^{\infty} l_x m_x$$

(2) The intrinsic rate of natural increase (r_m) (= Innate capacity for increase)- the maximal rate of increase of a population under specified environmental conditions with unlimited food and space, where

$$\sum_{x=0}^{\infty} e^{-r_m x} l_x m_x = 1$$

(3) The capacity for increase (r_c)- the growth rate of populations with non-overlapping generations or the actual growth rate of a population founded by a single cohort females until a stable age distribution is obtained, where

$$r_c = \ln R_0 / T_c$$

The capacity for increase is an approximation of the r_m and is typically less than r_m.

(4) Finite rate of increase (λ)- number of individuals added to a population per female per day, where

$$\lambda = e^{r_m}$$

(5) Generation time (T) - time required for a population with a stable age distribution to increase by R_0, where

$$T = \ln R_0 / r_m$$

(6) Cohort generation time (T_c)- mean age of females in a cohort at the birth of female offspring, where

$$T_c = \sum_{x=0}^{\infty} x l_x m_x / R_0$$

Cohort generation time is an approximation of generation time.

Data analysis

The computer programs Stat View 512[+] [27] was used to analyze data. For sex ratio determination, binomial function was generated by computer programs in Minitab Release 5.1.1[28].

RESULTS

The oviposition behavior of *G. thailandensis* was naturally not observed since it took place within the host burrow. *G. thailandensis* females temporarily paralyzed the hosts prior to oviposition. Females laid eggs along the intersegmental membranes of the host's body, especially on the middle segment and dorsal aspect of the host's body. If the parasitoid eggs were damaged, the host developed normally.

Survival and development of immature stages

The number of eggs laid per parasitized host averaged ($\pm$SE) 10.4$\pm$0.5 (n=16 broods). The mean numbers of larvae, cocoons, and adults per parasitized host were 10.0$\pm$0.6, 9.2 $\pm$0.6, and 8.2$\pm$0.7 (n=29 broods), respectively. Thus the percentage of egg hatching was 96.1% with 78.3% of the eggs surviving to adult emergence.

The developmental period of *G. thailandensis* is presented in Table 1. The incubation period averaged 3.1$\pm$0.0 days. The larval stage lasted 4.1$\pm$0.0 days. The pupal period took 13.5$\pm$0.1 days. Total development time from egg deposition to adult emergence was not significantly different between sexes (t=0.274, df=244, P>0.05). Consequently male and female data were pooled for subsequent analyses.

Table 1 The developmental period of *G. thailandensis*
Gordh & Witethom reared on fifth instar SFBs
at 26±1°C, 70-80% RH, and under a 12:12
(L:D) photocycle (n=246)

Developmental Stage/Period	Range of Duration (days)	Mean duration±SE (days)
Egg	3-4	3.1±0.0
Incubation period		
Larva	3-5	4.1±0.0
Larval period		
Pupa	10-19	13.5±0.1
Pupal period		
Total developmental period	16-26	20.7±0.1

Adult longevity and fertility

Six specimens of mated host-provided females were lost before size measurement, so that 22 samples of this group were available for analysis.

Longevity of mated females provided with hosts and those deprived of hosts was not significantly different (t=-0.625, df=46, P>0.05). Mated host-provided females lived 7.2±0.6 days (n=22) and mated host-deprived females lived 7.7±0.5 days (n=26). Female longevity was not correlated with either head width or total body length (r_s=0.061, P>0.10, r_s=-0.109, P>0.10, n=48).

Longevity of mated males significantly differed from that of mated host-provided females (t=2.861, df=54, P<0.05). The mean longevity was 5.7±0.6 days for mated males (n=28) and 7.7±0.4 days for mated host-provided females (n=28).

The survivorship curve (l_x) derived from the life table (Table 2) resembled type I of the hypothetical survivorship curve[29]. The mortality was low during the first five days of adult life and thereafter increased (Fig.1).

G. thailandensis was arrhenotokous. Unmated females produced only male progeny averaging 8.5±1.0 males per parasitized host (n=13 broods).

The preoviposition period of *G.thailandensis* females averaged 4.4±0.4 days. The mean number of SFB larvae parasitized throughout female lifetime was 1.6±0.1 hosts (n=28), with 13.3±1.2% of hosts being parasitized. Total progeny (males and females) per female and per parasitized host were 9.1±1.3 and 5.9±0.9 (n=28), respectively. The mean female progeny produced per female and per parasitized host were 7.6±1.1 and 4.9±0.8 (n=28), respectively. The mean percentage of female progeny was 82.1±3.0 (n=23).

The frequency of one-male broods for a given brood size is shown in Table 3. For brood sizes two to thirteen, the proportion of one-male broods was, 40.6%, not significantly

Table 2 Laboratory life table of *G. thailandensis* reared on fifth instar SFBs at 26±1°C, 70-80% RH, and under a 12:12 (L:D) photocycle

	x (days)	l_x	m_x	$l_x m_x$
Immature	0.5	1.000	0.000	0.000
stage	20.5	0.882	0.000	0.000
	21.5	0.783	.....	.....
	22.5	0.783	1.200	0.940
	23.5	0.783	14.000	10.962
	24.5	0.755	14.667	11.074
	25.5	0.727	14.417	10.482
	26.5	0.643	18.000	11.577
	27.5	0.587	14.833	8.711
	28.5	0.447	4.667	2.088
	29.5	0.224	10.500	2.349
	30.5	0.140	6.333	0.886
	31.5	0.112	0.000	0.000
	32.5	0.028	0.000	0.000
	33.5	0.028	0.000	0.000

R_0 = 59.067

Table 3 Distribution of brood sizes for 36 broods of
G. thailandensis (k is the number of broods
of a given size having exactly one male and
α is an upper bound on the probability of
observing as many as one-male broods or more)

Brood size N	Frequency n	One-male broods k	α
1	1	0	-
2	2	0	1.000
3	2	1	0.691
4	3	1	0.807
5	1	0	-
6	1	1	-
7	2	2	0.157
8	2	0	1.000
9	7	3	0.558
10	5	2	0.641
11	2	1	0.622
12	2	1	0.621
13	3	1	0.765
15	1	1	-
16	1	0	-
17	1	0	-
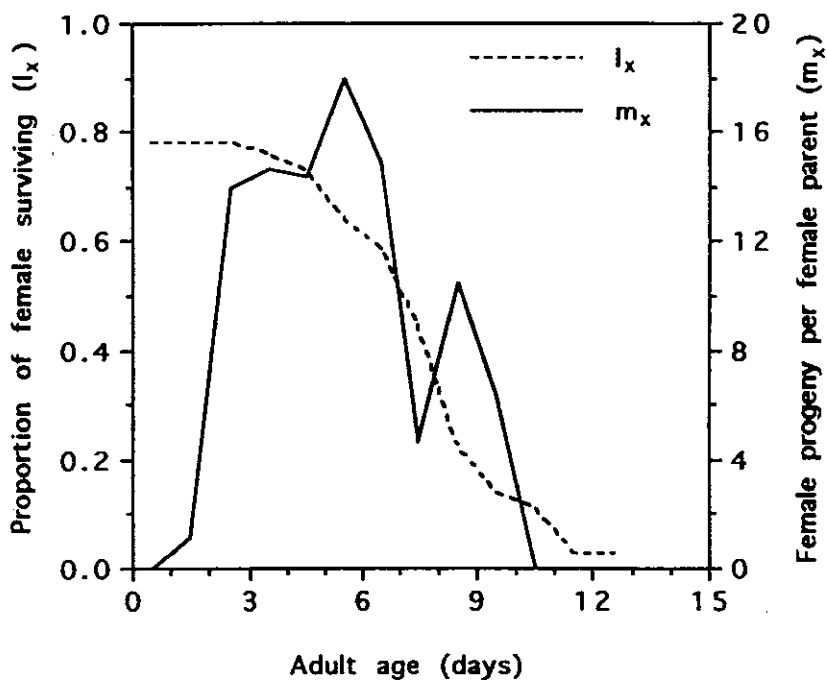
Fig. 1 Daily proportion of *G. thailandensis* females
surviving (l_x) and number of female progeny
produced per female parent (m_x) at $26\pm1°$C,
70-80% RH, and under a 12:12 (L:D) photocycle
(n=28)

greater than that expected by a binomial distribution. Thus
the sex ratio of *G. thailandensis* was randomly determined.

The daily female progeny produced per female parent
(m_x) curve for *G. thailandensis* was initiated from the life
table (Table 2). The fertility curve was bimodal. Female
progeny production was highest during the first six days of
adult life and afterwards declined. The progeny production
rose again on day eight and nine (Fig.1).

Life table statistics

The generation time (T) and cohort generation time
(T_c) of *G. thailandensis* were 25.5 and 25.7 days, respectively.
The net reproductive rate (R_o) was 59.1 females per female per
lifetime. The capacity for inacase (r_c) was almost similar to
the intrinsic rate of increase (r_m) (0.159 and 0.160 females
per female per day, respectively). The finite rate of increase
(λ) was 1.174 females per famale per day. *G. thailandensis* had
high potential to increase since the net reproductive rate and
the finite rate of increase were greater than one, the capacity
for increase and the intrinsic rate of increase were greater
than zero[30].

DISCUSSION

Paralysis of the SFB larva by *G. thailandensis* was not
permanent. The host regained mobility after the parasitoid
has oviposited. Temporary paralysis has been reported for
G. japonica Ashmead[31], *G. marasmi* Kurian[19], *G. rugosus*[32], and
G. sensorius[15,16]. Permanent paralysis has been observed in
other *Goniozus* species[4,5,7,8].

G. thailandensis resembled *G. aethiops*[5], *G. marasmi*[19],
and *G. pakmanus*[9] in depositing its eggs transversely in the
intersegmental membrane of the host. Like all *Goniozus*
species, *G. thailandensis* usually oviposited on the middle

segments of the host's body. This preference was probably
due to the host hemolymph fold[8]. Hosts oviposited by
G. thailandensis readily pupated if the parasitoid eggs were
destroyed. This phenomenon has keen reported for G. aethiops[5],
G. gallicola[4], and G. legneri[8].

Immature mortality of G. thailandensis was moderate,
22%, compared with that of G. triangulifer (67%)[14] and of
G. emigratus (10%)[7]. The immature survival of Goniozus could
be improved by providing host cencealment and decreasing
humidity of rearing conditions[5,9]. The development time of
G. thailandensis was similar to that of other Goniozus species.
The incubation period of G. indicus was three days, larval
development required 4-8 days and pupal duration took 11-12
days[11]. In G. platynotae the incubation period was three
days. The larval period lasted 5-6 days and the pupal stage
took 12-14 days[12]. The incubation period of G. columbianus
was 3.1 days and the larval feeding period was 4.7 days. The
pupal period lasted 13.7 days. The total development time
took 22.1 days[3]. The relatively shorter development time
especially inculation period has been reported in Goniozus sp.
attacking the rice leaf folder[21], G. legneri[8],
G. gallicola[4], and G. sensorius[15].

Longevity of Goniozus species varies considerably.
For example Gifford[11] found that G. indicus females lived
for 5.1 days. The longevity of G. aethiops averaged 13.4 days[5].
G. emigratus lived for 52.6 days when provided with hosts and
37.1 days when deprived of hosts[7]. Gordh et al[8] reported that
G. legneri lived substantially longer than other Goniozus
species. Mated females provided pink boll worm (PBW) hosts
lived 95.8 days and those provided navel orange worm (NOW)
hosts lived 97.4 days which were significantly different
from the host deprived group. The longevity of G. pakmanus
females provided with hosts (37 days) was greater than those
deprived of hosts (8 days)[9]. By contrast G. gallicola females
lived for 62.4 days when provided with hosts and 71.0 days

when deprived of hosts. The difference was probably due to host attack while subduing hosts[4]. In *G. thailandensis* mated host-provided females lived as long as mated host-deprived females. Similar fidings have been reported of *G. sensorius*[15] and *G. triangulifer*[14]. The influence of host feeding and type of food on *Goniozus* longevity have been reported by Gordh and Hawkins[7], and Peter and David[15].

Longevity of *Goniozus* species was different between sexes. In *G. thailandensis* mated host-provided females (7.7 days) lived significantly longer than mated males (5.7 days). These data were consistent with the findings for *G. triangulifer*[14], *G. pakmanus*[9], *G. legneri*[8], and *G. emigratus*[7].

A preoviposition period is often observed in *Goniozus* species, but its duration is greatly variable. *G. japonica* has a preoviposition period of 7 days[33], and *Goniozus* sp. about 8-9 days[34]. The preoviposition period of *G. nephantidis* was 4-5 days[35] and *G. emigratus* 3-5 days[7]. *G. legneri* has a preoviposition period of 3.1 days on NOW and 4.1 days on PBW[8]. The preoviposition period of *G. thailandensis* averaged 4.4 days which was similar to most other species of *Goniozus*. The shorter preoviposition periods have been reported for *G. gallicola* (2-3 days)[4], *G. sensorius* (1-2 days)[15], and *Goniozus* sp. (1 day)[21].

There was considerable variation in the total number of eggs laid and hosts attacked by different *Goniozus* species. *G. platynotae* parasitized 6.4 hosts and produced a mean of 24.2 eggs per female per lifetime. The mean number of eggs per host was 3.4[12]. *G. aethiops* parasilized four hosts and laid 16.2 eggs[5]. Gordh and Hawkins[7] reported that *G. emigratus* parasitized about nine hosts and laid 118.8 eggs when hosts were provided continually. *G. emigratus* attacked more hosts (15.6) and deposited more eggs (232.9) when hosts were provided with one day of host deprivation between oviposition episodes. On NOW *G. legneri* parasitized 23 hosts and produced about 149 female progeny per parental lifetime.

On PBW *G. legneri* attacked 25 hosts and produced about 170 female progeny during female lifetime[8]. *G. pakmanus* attacked 12 hosts and laid about 74 eggs[9]. *G. sensorius* parasitized about seven hosts and laid on an average 50.1 eggs[15]. The number of hosts parasitized by *G. thailandensis* throughout female lifetime was retalively low, averaging 1.6 hosts. The number of eggs laid were not recorded. However, the numbers of female progeny produced per parental female and per parasitized host during the female lifetime averaged 7.6 and 4.9 females, respectively.

Gordh and Hawkins[7] reported that the sex ratio at adult emergence in all *Goniozus* species was strongly female biased. Several *Goniozus* species have precise sex ratios and regulate the number of males produced in brood size. Generally, small broods were female biased since only one male was required to inseminate cohort females. The number of males increased as brood sizes increased to ensure enough sperm to inseminate all females of the brood[8]. Green *et al*[24] found that the number of single-male broods in *G. gordhi* differed significantly from that predicted by a binomial distribution. Brood sizes from two to nine were predominantly single-male broods; for larger broods more males emerged. Non-random sex ratio has also been reported for *G. gallicola*[4], *G. aethiops*[5], *G. emigratus*[7], *G. legneri*[8], and *G. pakmanus*[9]. *G. thailandensis* was arrhenotokous. The sex ratio was also in favor of females. For brood sizes two to thirteen, the proportion of one-male broods was, 40.6%, not significantly greater than that of binomial prediction. Similarly, random sex ratio has been reported for *G. triangulifer*[14].

Net reproductive rate (R_0) of *G. thailandensis* ($R_0 = 59.1$ females per female per lifetime) was substantially less than that for *G. emigratus* ($R_0 = 128.038$ females per female per lifetime)[7] and for *G. legneri* on PBW and NOW ($R_0 = 160.2$ and 145.1 females per female per lifetime, respectively)[8]. The cohort generation time (T_c) of *G. thailandensis*, 25.7 days,

was shorter than that of *G. emigratus* (37.1 days)[7] and of
G. legneri on PBW and NOW (51.5 and 45.1 days, respectively)[8].
Similarly the generation time (T) of *G.thailandensis* (T=25.5
days) was shorter than that of *G. emigrtus* (T=27.3 days)[7]
and of *G.legneri* (T=30.7 days)[8].

   In *G.thailandensis* the capacity for increase (r_c),
0.159 females per female per day, was almost similar to the
intrinsic rate of increase (r_m), 0.160 females per female
per day.   By contrast the substantially differences between
r_c and r_m have been reported for *G. legneri* on PBW and NOW[8]
and *G. emigratus*[7].   The differences were probably due to the
large R_o values and possibly to large variances in the $l_x m_x$
distributions[8].   The r_m value of *G. thailandensis* (r_m=0.160
females per female per lifetime) was less than that of
G. emigratus (r_m=0.178 females per female per day)[7] and
G. legneri on NOW (r_m=0.162 females per female per day)[8].
This effect was due to the lower net reproductive rate for
G. thailandensis (R_o=59.1 females per female per lifetime)
versus *G. emigratus* (R_o=128.038 females per female per life
time)[7] and *G. legneri* on NOW (R_o=145.1 females per females
per lifetime)[8].   In contrast the value of r_m for
G. thailandensis was slightly greater than that obtained
for *G. legneri* on PBW (r_m=0.157 females per female per
lifetime) even though the net reproductive rate for
G. thailandensis (R_o=59.1 females per female per lifetime)
was considerably less than that for *G. legneri* (R_o=160.2
females per female per lifetime)[8]. This effect was probably
due to the shorter generation time for *G. thailandensis*
(T=25.5 days) than for *G. legneri* on PBW (t=32.3 days*)[8].

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* calculated from Gordh *et al*[8]

CONCLUSION

The generation time of phycitine SFB host was about
34 days[1] and that of *G. thailandensis* was about 26 days.
With the host larval period of 18 days, *G. thailandensis*
will only have one generation per synchronous host
generation because the parasitoid only parasitizes the
larval stage of the host.

Despite the low percentage of parasitization (13.3%)
G. thailandensis might be a promising candidate for the
biological control of the SFB on sapodilla because of its
fossorial habit. This habit is desirable attribute for the
biological control of the SFB since the host larvae infest
sapodilla fruit and a parasitoid which locates concealed
host larvae is important in developing a biological control
program for the larval stage of this pest. In addition
G. thailandensis may act in concert with other parasitiods
and predators to control the SFB and other lepidopterous
pests that live in cryptic conditions.

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