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LARVAL DEVELOPMENT, METAMORPHOSIS AND PARASITISM IN THE HAWKMOTH, *ENPINANGA BORNEENSIS* (BUTLER) (LEPIDOPTERA: SPHINGIDAE: MACROGLOSSINAE)

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INTRODUCTION

The hawkmoth, *Enpinanga borneensis* (Butler, 1879), is widely distributed in Southeast Asia, being recorded from Thailand, Peninsular Malaysia, Sumatra, Java and Borneo (Inoue et al., 1996), and also more recently from the Philippine island of Palawan (Brechlin, 2000). Thus far, its only documented caterpillar foodplants are *Dillenia suffruticosa* and *Tetracera indica*, both of which belong to the same plant family, Dilleniaceae (Yunus & Ho, 1980; Diehl, 1982). In Singapore, the shrub, *Dillenia suffruticosa* (Malay vernacular names: daun tempeh, simpoh air), is widespread and occurs from secondary forests to forest edges in many parts of the island. The climber, *Tetracera indica*, is also well distributed along forest fringes. Consequently, it is logical to predict that thriving populations of *Enpinanga borneensis* occur in this country.

OBSERVATIONS

Encounters with both adults and larvae of this particular sphingid species have mostly been at the Kent Ridge Campus of the National University of Singapore (NUS). Both adult males and females of this sexually dimorphic species have occasionally been observed resting on walls along the corridors of the Department of Biological Sciences (DBS), NUS. In the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research (RMBR), NUS, specimens from Singapore of this species abound. The earliest specimen (ZRC.LEP.6, male) was collected by "Miss Burkill" from "Gardens Singapore" in May 1922. More recent collections comprise a fair proportion of male (ZRC.LEP.7–13) and female (ZRC.LEP.14–20) specimens, some of which have been contributed by the author. These were either found as adults or reared from caterpillars encountered at various stages of development. Most of the caterpillars were found from Kent Ridge, on the foodplant, *Dillenia suffruticosa*. Other caterpillars have also been seen and/or reared from collections made from the MacRitchie Reservoir forest trails in the Central Catchment Nature Reserve. However, not all caterpillars were reared through to the adult stage. Some were preserved in various instars to serve as comparative reference material, along with their corresponding exuvia and pupal cases (ZRC.LEP.21–34), including larvae that succumbed to attack by parasitoid wasps.

Fig. 1. Very early instar of *Enpinanga borneensis* (family Sphingidae), well camouflaged along the secondary leaf vein of its host plant, *Dillenia suffruticosa* (family Dilleniaceae). Found on Kent Ridge, 22 Nov.2007.

Fig. 2. Mid-instar larva found on Kent Ridge on 5 Sep.2007. Note the initial lateral protrusions (pale yellow) at the thoracic segments and its straight, sharp, tapered horn at the posterior.

Fig. 3. Final instar from Kent Ridge. Note the pronounced, bright orange lateral expansions on the thoracic region. The tail horn is now thicker and down-curved. The final instar may attain a length of 80 mm, with its tail horn measuring 15 mm.

Fig. 4. Pre-pupal coloration prior to the final larval moult and transformation into the pupa. Note the darkening of its entire body, with the appearance of three, lateral pairs of deep green patches on the thoracic segments.

Fig. 5. Ventral view of pupa, reared from a caterpillar collected on Kent Ridge.

Fig. 6. Lateral view of pupa. Note the granular texture of the head region.

The earliest larval instars of *Enpinanga borneensis* are seldom seen, most certainly owing to their ability to remain undetected by blending in with the secondary veins on the underside of *Dillenia suffruticosa* leaf blades. At this stage, its body is pale green, and the tail horn is thin, straight and reddish-brown (Fig. 1). As it progressively moults into subsequent instars, the larvae begin to exhibit increasingly pronounced lateral expansions in the thoracic region. A pale, creamy, dorsolateral stripe is now visible along each side of the body, below which is a series of indistinct, oblique, pale yellow lines (Fig. 2). Its tail horn still retains the straight, tapered form, characteristic of the earlier instars. When the caterpillar enters its last instar, the thoracic expansions become very well developed and take on a striking orange colour, encompassing a pair of small black markings toward the rear (Fig. 3). In addition, these lateral protrusions are highlighted along the edge with a ridge of closely spaced, whitish granules. The tail horn is now thicker, bluish-grey and its distal end is blunt and down-curved. Final instar caterpillars of *Enpinanga borneensis* have a body length (excluding tail horn) of 75–80 mm and a tail horn length of 12–15 mm.

In the field, the more advanced instars of *Enpinanga borneensis* display a particular defensive behaviour if disturbed. They raise the thoracic portion of their bodies and emit droplets of clear, dark green liquid from their mouths. This chlorophyll-rich fluid is most certainly derived from the accumulation of fresh leaf matter that had been previously ingested. Prior to pupation, a noticeable darkening of the body of the final instar caterpillar occurs. The most distinct changes are witnessed in the thoracic region, where three dark green patches appear on the lateral protrusions (Fig. 4). At this point, the appetite of the caterpillar is reduced drastically and it begins pacing around, in search of a place to pupate. Over two days, the body of the caterpillar gradually contracts and emits excessive fluids from within. The last instar larval skin is then sloughed off, revealing a freshly formed pupa, which soon hardens and darkens to a golden-brown (Figs. 5 & 6). A typical pupa is 34–37 mm long. The pupal head is blunt and has a conspicuously granular texture.

The duration of the pupal stage is 11–17 days. Upon emergence, the adult moth quickly scrambles to the nearest available branch or leaf to find a vertical perch from which to hang and expand its wings. In the newly emerged male moth, the conspicuous retinaculum on the underside of the forewing may be readily observed while its wings are still held back over its dorsum (Fig. 7). The time taken from the point of pupal emergence to complete expansion of wings is

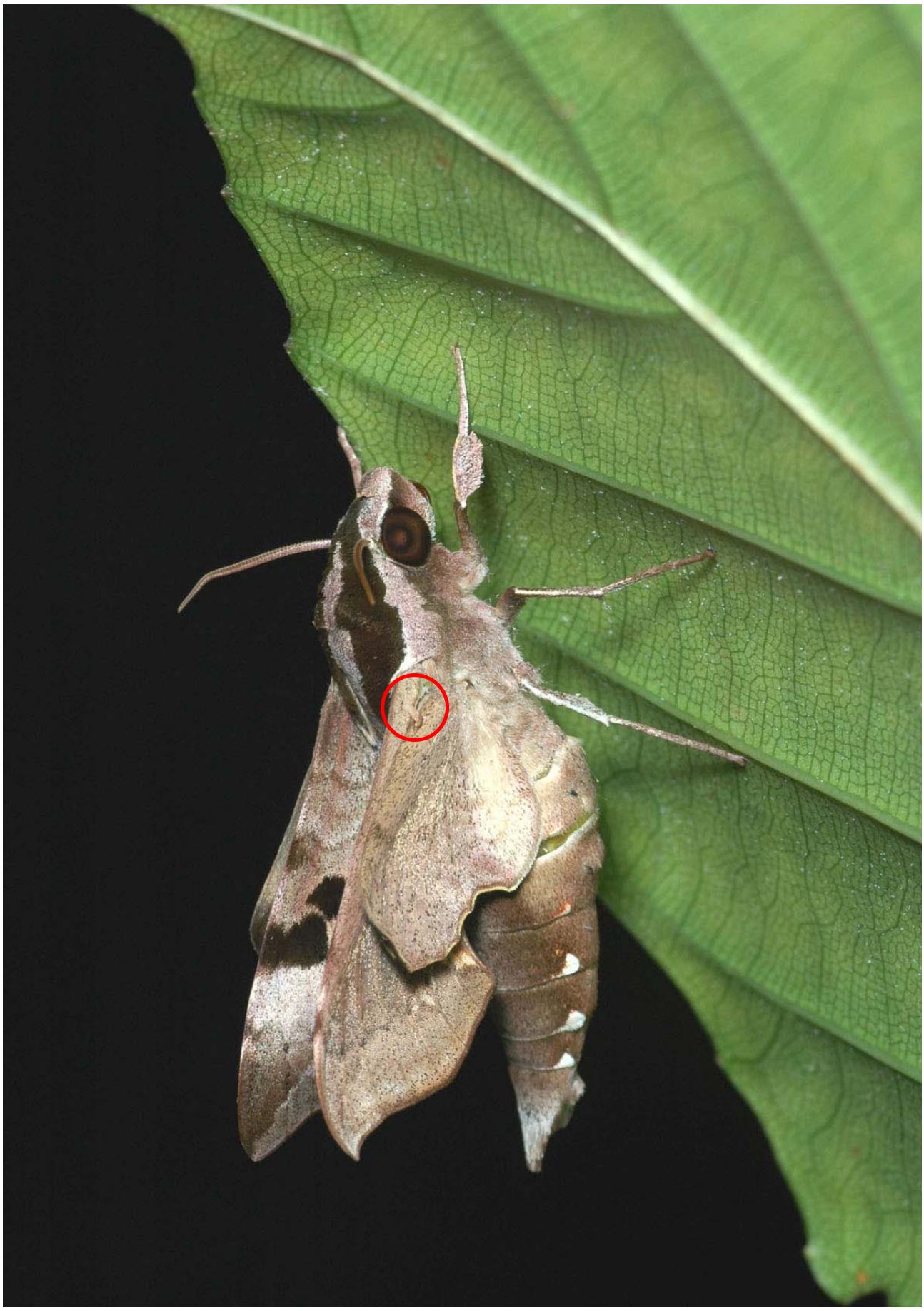

Fig. 7. A freshly emerged adult male *Enpinanga borneensis* with its wings being expanded. This particular individual was reared from a caterpillar from Kent Ridge. It emerged from its pupa on the night of 22 Sep.2007 at about 2040 hrs. In this position, the retinaculum and frenulum are clearly visible on the underside (circled red).

usually less than 10 minutes. *Enpinanga borneensis* is a species that displays sexual dimorphism and the gender-specific wing patterns are clearly distinguishable between the male (Fig. 8) and female (Fig. 9).

Fig. 8. The same male (as in Fig. 7) with its wings fully expanded, in typical sphingid resting posture.

Fig. 9. This female emerged on the night of 29 Sep.2007. It was also reared from a caterpillar found on Kent Ridge. Note the significant difference in wing markings and pattern from that of the male (Fig. 8) in this sexually dimorphic species.

In the course of my search for lepidopteran larvae among foliage in suitable habitats, I have had numerous encounters with a wide variety of parasitic wasps (mostly in the family Ichneumonidae), many of which were observed to be seeking out a suitable caterpillar host in which to deposit their eggs.

On 8 Oct.2007, an early instar of *Enpinanga borneensis* was found on foliage from Kent Ridge at about 1000 hrs. It was transferred to the laboratory to be reared, but was observed to be rather sluggish in behaviour and fairly unresponsive. Its body length was 31 mm, and its tail horn 18 mm long. When observed against the light, a single, dark ellipse was noticeable within. This internal dark area was about 8 mm from the posterior end and a tiny yellow dot was visible externally on the right side. At about 1100 hrs, a parasitic larva began to emerge from the right body wall of the caterpillar. It was pale, ivory-white and its body tapered towards a narrow head (Fig. 10). With its posterior end remaining within the caterpillar's body, the wasp larva began to deposit a series of shiny, gold threads onto the skin of the caterpillar and the leaf surface (Fig. 11).

At about 1200 hrs, fabrication of the posterior half of a silken mesh basket had almost been completed (Fig. 12). After another half hour, the wasp larva eventually extricated its entire body from the caterpillar host. It then proceeded to crawl into the silken mesh framework and make a tight turnaround to face outwards, with its body bent in half (Fig. 13). The next phase of construction was focused on completing the anterior half of the silk mesh. By about 1245 hrs, the wasp larva was adding the finishing touches to this mesh basket (Fig. 14). As soon as the wasp larva had secured itself within the confines of the external mesh, it then began to secrete additional layers of even finer, white silk from within. By about 1400 hrs, the cocoon had become opaque and the wasp larva was no longer visible from the outside (Fig. 15). In total, the entire process of wasp larva emergence and cocoon construction took approximately three hours. Throughout this process, the caterpillar host displayed no signs of distress and remained virtually still. This caterpillar would not have subsequently survived the departure of the parasitoid and was preserved as a voucher specimen (ZRC.LEP.23).

Approximately two weeks later, the adult parasitic wasp emerged from the cocoon, but flew off before it could be photographed. Exit from the cocoon was via a cleanly sliced transverse lid at the anterior, or top, end of the elliptical cocoon (Fig. 16). Earlier observations of such parasitism on *Enpinanga borneensis* in Singapore were from caterpillars encountered at the Central Catchment Nature Reserve forests. I have also witnessed a similar scenario of wasp parasitism of the larva of another sphingid (*Eupanacra* species) while in Sarawak, Malaysia (Borneo) in Dec.2007. In the Indo-Australian region, at least 16,000 species of ichneumonid wasps are estimated to occur (Townes et al., 1961). Considerable efforts have been focused on the slug and nettle moth caterpillars (family Limacodidae) as hosts for ichneumonid parasitoids (Gauld, 1987), but many other lepidopteran families have yet to receive such devoted attention. Abundant opportunity remains for the study of the diversity and ecology of parasitic wasps of Lepidoptera in Singapore and the Southeast Asian region and I hope this paper stimulates further study of this fascinating biological interaction.

Fig. 10. On 8 Oct.2007, at about 1100 hrs, a parasitoid wasp larva (possibly Ichneumonidae) emerged head-first from the right posterior abdominal segment of its ill-fated host, an early instar of *Enpinanga borneensis* (ZRC.LEP.23; body length: 31 mm, tail horn: 18 mm) from Kent Ridge.

Fig. 11. At about 1145 hrs, the parasitoid larva had attached the preliminary silken threads onto the caterpillar host, as well as the leaf surface. These fine threads were produced from the mouth and were gold in colour.

Fig. 12. At about 1200 hrs, the posterior half of the external silken mesh was almost complete. All this time, the posterior end of the parasitoid larva had remained within the body cavity of the caterpillar host, serving as an anchorage point.

Fig. 13. At about 1230 hrs, the parasitoid larva eventually emerged from its host entirely. It then manoeuvred itself to fill the space available within the posterior silk mesh, folding its body in half in the process. From this position, it resumed the task of secreting additional silk threads.

Fig. 14. At about 1245 hrs, the wasp larva is close to completion of the external silk lattice.

Fig. 15. By about1400 hrs, the entire wasp cocoon had been completed. The larva continued to weave additional layers of silk from within, until its body was completely shrouded and not visible externally.

Fig. 16. Vacated cocoon of the parasitoid wasp, upon successful emergence of the winged adult. Note the thickened stalk of silk deployed for secure attachment to the leaf surface. At the top end, a precise transverse cut has been made around almost the entire circumference of the cocoon, creating a lid from under which the adult wasp climbed out. The lid remains hinged to the cocoon.

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