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Larval behaviour and development of *Penepodium luteipenne* (Fabricius, 1804)

(Hymenoptera: Sphecidae)

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Abstract: The larval behaviour and development of *Penepodium luteipenne* (Fabricius, 1804) are described; the development is analysed in a table of life; notes on the nesting behaviour are also provided. The work is based on 63 specimens collected in the Biological Reserve of Poço das Antas (Rio de Janeiro State, southeastern Brazil), an area covered by Atlantic Tropical rain forest.

Key words: Hymenoptera, Sphecidae, Sceliphrini, *Penepodium*, larva, immature, behaviour, biology, wasp, table of life

Introduction

Although the nesting behaviour of Apoid wasps is extensively studied (see BOHART & MENKE 1976), the behaviour and development of the larvae are still poorly known. *Penepodium* Menke is a genus of cockroach-hunting solitary wasps distributed as far north as central Mexico. The biology of this genus is known only from notes on a few species (WILLIAMS 1928, GENISE 1981, GARCIA & ADIS 1993, BUYS 2006). In the present paper the larval behaviour and development of *Penepodium luteipenne* (Fabricius, 1804) are described; developmental phases are analysed in a table of life; notes on the nesting behaviour are also provided.

Material and methods

Cockroaches bearing wasp egg were collected in the Biological Reserve of Poço das Antas (city of Silva Jardim, state of Rio de Janeiro, southeastern Brazil). The prey specimens were put in transparent plastic jars lined inside with absorbent, slightly moistened paper. The prey faeces were daily removed to avoid fungi proliferation. In the case of the nests containing more than one prey specimen, each one was put in a different jar and offered to the larva one by one.

Voucher specimens of adult *P. luteipenne*, its larvae and prey were deposited in the entomological collection of the Museu Nacional – Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil. Additional adults of *P. luteipenne* were deposited in the Museu de Zoologia / Universidade de São Paulo (MZSP), São Paulo, Brazil.

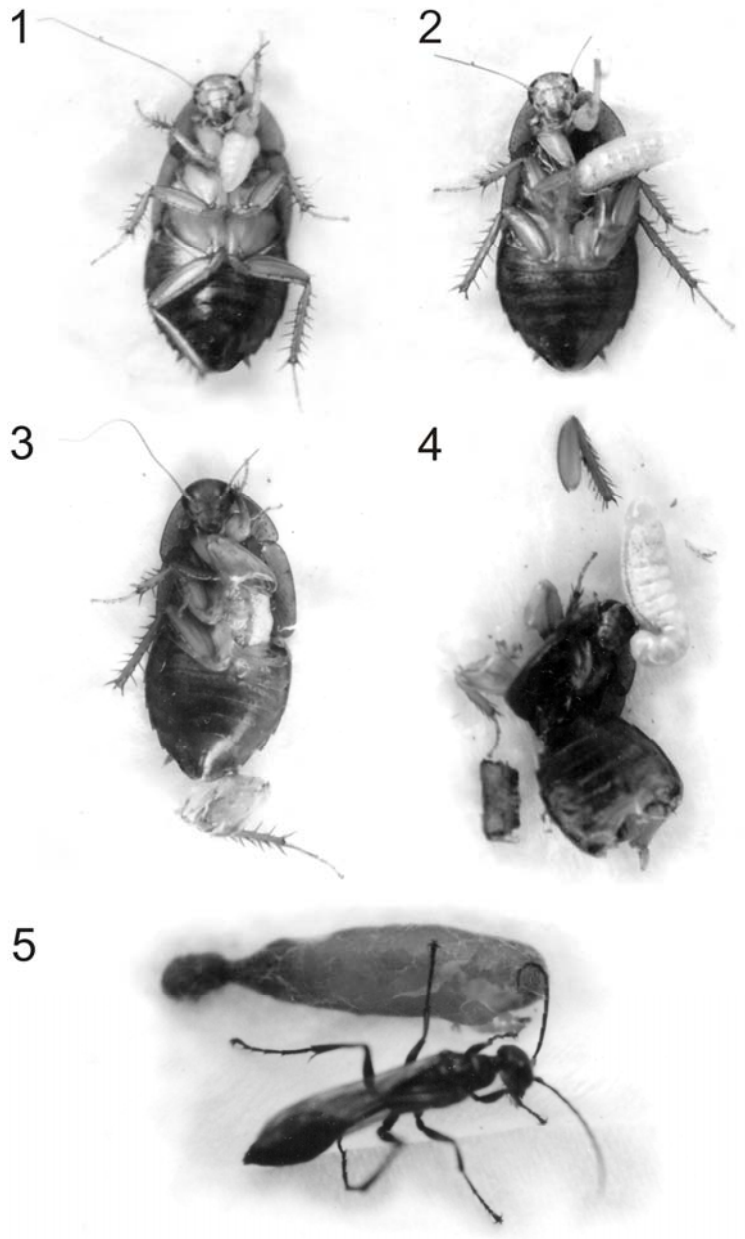
Results

The females of *P. luteipenne* were observed digging unicellular nests in compact clay soil of an unpaved road that crossed a forested area. They stored the nests with one to four nymphs or adults of *Poeciloderrhis catharina* (Shelford, 1910) or *Poeciloderrhis basistriga* (Walker, 1868) (Blattodea: Blaberidae).

The female lays her egg behind one forecoxa of the prey. The egg hatches two or three days after the oviposition. The newly emerged larva inserts the head and part of anterior portion of the body under the prey forecoxa in the point where the egg was attached (Fig. 1). Since the prey remains active and the larva stays in a hidden place, it was not possible to determine weather the first larval instar had a short external feeding phase before penetrating the prey body. The larva stays in the same place without apparent external movements during the early development. The prey remained alive for two to six days after the egg hatching. The wasp venom seems not to debilitate so much the cockroaches, because they are able to actively walk, to feed on the moistened paper used to line the rearing jar, and to defecate. As the larva grows, the prey cease to feed, its movements become slower and it finally die. With four to seven days of development, the larva reaches the last (fifth) instar and gains movement (Fig. 2). The larva in this instar sometimes penetrates entirely inside the

prey body (Fig. 3). After one or two days the last instar larva completely consumed the prey, remaining only the hardest parts of its exoskeleton (Fig. 4).

Soon after the first prey specimen has been consumed, the larva actively traverses the rearing jar moving the mandibles, behaviour that probably is a search for more food. If a new prey specimen is offered, the larva touches its body with the mouthparts before feeding on it. This behaviour could be interpreted as a chemical and/or textural recognition of the prey. The larva usually starts consuming the new cockroach for the ventral thorax, which seems to be the softer part of her exoskeleton, and after one or two days she completely consumed the prey. If the larva does not find new preys, she remains immobile for about one day and subsequently starts to spin a cocoon. Firstly she spins a silken structure, which is transparent and malleable. Due to this transparency, it is possible to observe the larva secreting a pale yellow substance from the mouth, with which she coats all the internal surface of the cocoon. Within a few days, the cocoon becomes dark brown and its texture resembles a brittle, but resistant paper. The cocoon is claviform and has a nipple-like projection in one extremity bearing an orifice through which the larva eliminates her faeces one or two days after having constructed the cocoon. The faeces remain attached to the cocoon (Fig. 5) and become hard after dried. It is not possible to observe through the cocoon wall when the larva pupates. Therefore, the duration of the pre-pupa and pupa stages can not be measured. Only when the pupa starts gradually to gain pigmentation, it is possible to distinguish her structures through the cocoon wall. The metamorphosis to adult is also not observed through the cocoon wall, but it is certain that the adult wasp remains inside the cocoon for some days. During a part of such a period, its tergites and sternites are still not imbricated, and the internal membranous region between them is exposed. Through this region, white and ovoid grains of uric acid accumulated in the stages of larva and pupa are eliminated. Inside the cocoon of a female that developed in a prey specimen with 0.55g, it were counted 52 grains with 726.4 – 1229.2 μm (mean = 859 μm) in length and 372.5 – 484.6 μm (mean = 422 μm) in width (n=10). When the adult emerges from the cocoon, his abdominal sclerites are completely imbricated. The period the wasp remained inside the cocoon from mature larva to adult was 28 to 32 days (n=5). The adult broke the cocoon wall without a definite pattern of cutting (Fig. 5).



Explanation of figures see next page.

Figs 1–5: Development of a male *Penepodium luteipenne*, consuming an adult *Poeciloderrhis catharina*. (1) Prey, still alive, with an immobile larva under her forecoxa; (2) mobile larva consuming the prey; (3) larva inside the prey body; (4) mature larva and remains of the prey exoskeleton; (5) adult wasp soon after breaks through the cocoon wall; observe the black mass of faeces attached to a cocoon extremity and the rupture of the cocoon wall made by the wasp.

Table I. Table of life of *Penepodium luteipenne* in laboratory conditions.

Phase of Development	Number of survivorship in the early of each phase	Probable factor of mortality	Number of death in each phase
Egg	63	Parasitoidism	4
Immobile larva	59	Prey death	28
		Non identified	6
Mobile larva	25	-	-
Full-grown larva	25	-	-
Pre-pupa	25	Fail in the cocoon construction	13
		Fungus proliferation	2
Pupa	10	Insufficiency of Prey biomass	2
		Fail in the cocoon construction	1
Cocooned adult	7	-	-

The pre-imaginal development of *P. luteipenne* was classified into seven phases: (1) egg; (2) immobile larva, phase in which the larva remains under the prey forecoxa without apparent external movements; (3) mobile larva, phase in which the larva gains movement and consumes the remainder of prey; (4) full-grown larva (this term is preferred, since the term ‘mature larva’ has been used to designate the last instar larva, even having not reached the limit of growth), phase between the end of feeding period and the faeces elimination; (5) pre-pupa, phase between the faeces

elimination and the pupation (as definite by others authors, as EVANS & WEST-EBERHARD 1973); (6) pupa; and (7) cocooned adult, phase in which the adult, still inside the cocoon, has his gastric sclerites still not imbricated and eliminates the metabolic debris accumulated in the stages of larva and pupa. The survivorship in each developmental phase was analysed in a table of life (Table I).

Table II. Duration in days of developmental phases of some *Penepodium* species. E. = egg; F.P.= feeding phase; P.R.= period between the feeding phase and the cocoon construction; C.C. = cocoon

	E.	F.P.	P.R.	C.C.	C.	T.	Source
P. luteipenne	2-3	5-9	1	1-2	28-32	35-44	Obtained data
P. luteipenne	2	4	-	-	-	30	WILLIAMS (1928)
P. haematogastrum	-	-	-	-	-	30-45	WILLIAMS (1928)
P. gorianum	2	6-8	1	2	29 - 39	38-48	GARCIA & ADIS (1993)

The immature survivorship rate in laboratory was very low; from 63 prey specimens bearing wasp eggs only seven adults hatched (11%). However, this low rate must be related to the artificial conditions that the larvae and her prey were submitted. All the eggs hatched, being the deaths registered in the egg phase due to the incidence of parasitoid flies, which quickly consumed the cockroaches before the egg hatching. The major part of the mortality occurred during the phase of immobile larva followed by the phase of pre-pupa (Table I). The death of the immobile larvae was, in almost all cases, preceded by the prey death, suggesting that the larva needs live prey during early development. Most of the deaths in pre-pupa occurred when the mature larvae failed in completing the cocoon construction. These pre-pupae survived for some days; one of them pupated, but died after a few days. Other two pre-pupae have died apparently due to the incidence of fungus. Their bodies, still alive, became dark in colour and the rearing jars very moistened and with the characteristic musty smell. A larva that did not construct the cocoon orifice voided her faeces inside the cocoon and died after pupating. Two larvae that consumed only one small prey resulted very smaller than the

other ones and ceased developing after pupating. Possibly, they died because consumed insufficient prey biomass.

Discussion

The duration of the developmental phases of *P. luteipenne* in southeastern Brazil is similar to that observed by WILLIAMS (1928) in *P. luteipenne* from Brazilian Amazon and that observed in other species of the genus (Table II). GARCIA & ADIS (1993) observed that *P. gorianum* sometimes gets into dormancy in prepupal stage, in this case the total development lasting 81 to 198 days. An inactive period between the feeding phase and the cocoon construction, as herein observed, was also found in *P. gorianum* (GARCIA & ADIS 1993). Other species of Sceliphrini, namely *Trigonopsis cameronii* (Kohl, 1902) (EBERHARD 1974) and *Sceliphron assimile* (Dahlbom, 1843) (DOW 1932), were observed coating the cocoon wall internally with a yellowish substance. A similar behaviour was observed in other sphecid wasps of the tribes Sphecini and Ammophilini, as well the construction of a nipple-like projection at one end (BUYS 2004). However, species of *Penepodium* are unique in voiding the faeces through an orifice of the cocoon (BUYS 2001). The classification of the larval development into discrete phases as herein proposed seems to be useful to further comparative studies on development of Apoid wasps.

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