

## Immature Biology of *Prosotas* Reveals an Ovipositing Strategy Unusual in Polyommatine Lycaenids (Lepidoptera: Lycaenidae: Polyommatinae), with a Description of a New Subspecies of *P. dubiosa* from Taiwan

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**Yu-Feng Hsu and Shen-Horn Yen (2006)** Immature biology of *Prosotas* reveals an ovipositing strategy unusual in polyommatine lycaenids (Lepidoptera, Lycaenidae, Polyommatinae), with a description of a new subspecies of *P. dubiosa* from Taiwan. *Zoological Studies* 45(3): 308-321. The immature biology of a widespread and often-abundant lycaenid in the genus *Prosotas* was heretofore poorly documented. Investigations conducted on 2 widely distributed and largely sympatric species, *P. nora* and *P. dubiosa*, revealed that both species exhibit peculiar oviposition behaviors. The females oviposit in the host inflorescence only during a critical development stage of the inflorescence. Their ova are laid within tightly arranged flower buds and are concealed with a transparent gelatinous substance, rendering the ova cryptic. Due to this peculiar behavior, host choice by *Prosotas* obviously requires a suitable inflorescence type in addition to appropriate chemical stimuli of potential host plants. In association with this ovipositional behavior, larvae of both species exit the ovum or ova laterally rather than in the usual way from the top. The papillae anales of the female genitalia are produced posteriorly and show a modification to facilitate oviposition. The ovipositional behavior and lateral eclosion of the larvae are considered potential synapomorphies of the genus *Prosotas* as they are unique among polyommatine lycaenids. A discussion on earlier misconceptions concerning the immature biology of *Prosotas* is provided. Finally, samples of *P. dubiosa* from Taiwan were compared with those from other regions, revealing that they consistently differ from those of other regions, and thus they are described as *P. dubiosa asbolodes*, ssp. nov. <http://zoolstud.sinica.edu.tw/Journals/45.3/308.pdf>

**Key words:** Female genitalia, Ovipositor, Ovum concealment, Ovum eclosion.

The genus *Prosotas* Druce 1891 comprises a group of small-sized polyommatine lycaenids widely distributed in the Oriental and Indo-Australian regions (Seki et al. 1991, Eliot 1992, Parsons 1999). Members of this genus were often confused with the speciose genus *Nacaduba* until Tite (1963) revised the *Nacaduba*-complex and confirmed its generic status based on the structure of the male genitalia (Parsons 1999). Three putative synapomorphies have been proposed to support the monophyly of *Prosotas*: 1) valva terminating in a pointed hook dorsally (Tite 1963); 2) phallus with a truncated, branch-like, ventral process

subapically (Tite 1963); and 3) ductus seminalis which is swollen near the junction with ductus bursae (Hirowatari 1992). Nineteen species are currently placed in this genus (Tennet 2003). Within the genus, most species have restricted distributions, but two of them, *P. nora* (C. Felder, 1860) and *P. dubiosa* (Semper, 1879), are particularly abundant and widespread across nearly the entire distributional range of the genus (Tite 1963, Eliot 1992). Although *Prosotas* species may be abundant where they are found, i.e., *P. nora* and *P. dubiosa* in the Malay Peninsula (Eliot 1992), India (Bean 1988), and Solomon Is. (Tennet 2002); *P.*

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*papuana* Tite, 1963 of Papua New Guinea (Parsons 1991); and *P. felderi* (Murray, 1874) in Australia (Braby 2000), the published literature on their immature biology is scanty, with the larval host plants of only 4 species previously documented (Robinson et al. 2001, Table 1). In Australia, Brady (2000) provided host-plant data and brief notes on the immatures of 3 *Prosotas* species, viz. *P. nora*, *P. felderi*, and *P. dubiosa* (Table 1), but no data on the ovipositional behavior were given. In Japan, where the biology of the rhopaloceran fauna has been comprehensively surveyed, *P. nora* is the only lycaenid species for which the life history is poorly documented (Fukuda et al. 1984, Teshirogi 1997). Igarashi and Fukuda (1997 2000) reported on *P. dubiosa*, but did not describe its ovipositional behavior. The most extensive data on immatures of *Prosotas* can be found in (Bean 1988) and in a series of notes by (Kitamura 1994 1995 2000a b), and incongruent descriptions of the oviposition biology and larval phenotypes are present in these accounts.

Intrigued by the discrepancy between the commonness of *Prosotas* and the poor knowledge of their immature biology, fieldwork and laboratory observations on *Prosotas* immatures were initiated in 2002 in Taiwan, where only *P. nora* was previously known to occur (Uchida 1991, Ho and Chang 1998). Two *Prosotas* species, *P. nora* and *P. dubiosa*, however, emerged from the material collected in Taiwan. Field observations and laboratory rearing of the immatures of the 2 species produced results inconsistent with data in the literature, and revealed that both species are specialized flower/flower bud feeders as larva with modifications of the female genitalia to cope with a peculiar ovipositing habit in ramose- or head-type inflorescences.

## MATERIALS AND METHODS

### Field observations and rearing

Ova and larvae of *Prosotas* were collected by examining leaves of potential host plants. Rearing was performed in plastic containers (15 x 8 x 4.5 cm). Rearing codes followed the system developed by (Powell and De Benedictis 1995). Each collection of immatures was labeled according to the collection year and month: e.g., HSU 04B3 referring to the 3rd collection (3) in Feb. (B) 2004 (04), with the month indicated by the letter. Inflorescences of hosts were divided into 3 parti-

tions of equal length along the longitudinal axis, and the position of ova on each was recorded.

### Taxonomic methods

Dissection of genitalia was performed by removing the entire abdomen and placing it in 10% KOH at room temperature for 24 h to dissolve the soft tissue, then transferring it to cellulose for another 24 h for descaling, before finally placing it in 70% ethanol for dissection. The dissected parts were preserved in 70% ethanol. A SPI-MODULE sputter coater (Structure Prob Inc., Wester Chester, PA, US) was used for sample coating, and a Polaron critical point drier (Quorum Technologies, East Sussex, United Kingdom) for sample drying. A Jeol JSM-5600 (Joel, Tokyo, Japan) was used for scanning electron microscopy (SEM) illustration. Terminology follows Nijhout (1991) for wing patterns, Klots (1970) for genitalia, Stehr (1987) for chaetotaxy of larvae, and Fiedler (1991) for myrmecophilous organs. Paratypes of the new taxon are deposited in the following institutes or collections: The Natural History Museum, London (BMNH), Chongqing Natural History Museum, Chongqing, China (CNHM); Forest Pest Control Station of Jiangxi Province, Nanchang, China (FPCJP); Institute of Zoology, Chinese Academy of Sciences, Beijing (IOZ); National Museum of Natural Science, Taichung, Taiwan (NMNS); Department of Life Sciences, National Taiwan Normal University, Taipei, Taiwan (NTNU); and the Tomoo Fujioka Collection, Tokyo (TF). Samples of *Prosotas* specimens from Taiwan were compared with conspecific samples and types from other regions, including: *Prosotas dubiosa dubiosa* (1 ♂ holotype, 4 ♂♂, 4 ♀♀, Queensland, BMNH); *P. d. indica* (5 ♂♂, 5 ♀♀, India, BMNH); *P. d. eborata* (1 ♂ holotype, 1 ♀ allotype, 3 ♂♂, 3 ♀♀, Solomon Islands, BMNH); *P. d. lumpura* (1 ♂ holotype, 1 ♀ allotype, Malay Peninsula, BMNH; 4 ♂♂, 2 ♀♀, NTNU); and *P. d. subardates* (26 ♂♂, 7 ♀♀, Luzon and Minor, the Philippines; 2 ♂♂, Sabah, Borneo, NTNU; 6 ♂♂, southern Sulawesi).

## RESULTS

### Immature biology of *Prosotas nora* and *P. dubiosa*

#### *Prosotas nora*

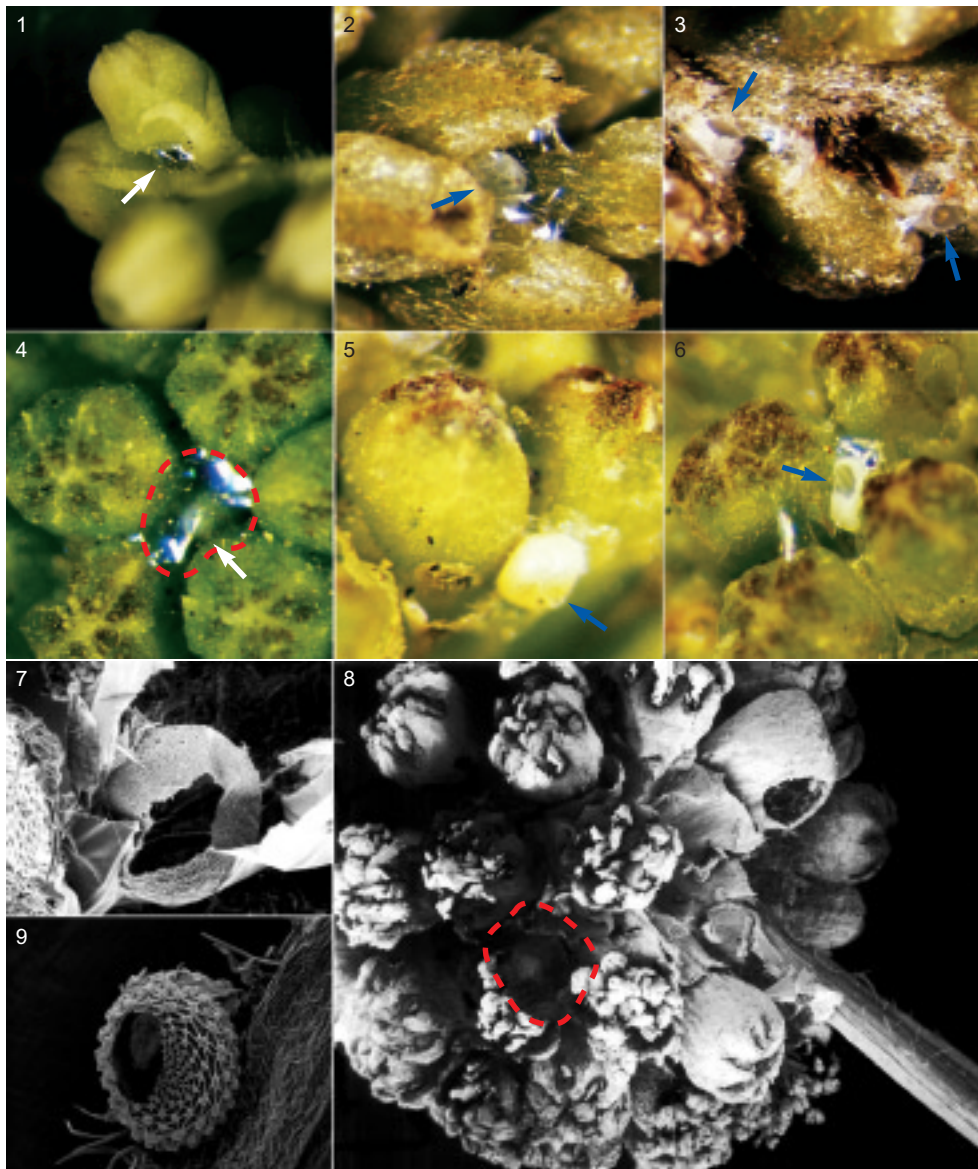
**Table 1.** Checklist of the known host plants of *Prosotas* species. The higher classification of the plants follows APG (2003)

Species	Hostplant Name	Host family	Host order	Region	References
<i>P. nora</i>	<i>Acacia caesia</i>	Fabaceae (M)	Fabales	India	Bell, 1918
	<i>Ac. catechu</i>	Fabaceae (M)	Fabales	India	Robinson et al. 2001
	<i>Ac. torta</i>	Fabaceae (M)	Fabales	India	Robinson et al. 2001
	<i>Ac. farnesiana</i>	Fabaceae (M)	Fabales	Taiwan	present study
	<i>Archidendron dulcea</i> <sup>a</sup>	Fabaceae (M)	Fabales	India	Robinson et al. 2001
	<i>Dalbergia pinnata</i>	Fabaceae (M)	Fabales	Philippines	Kitamura, 2000b
	<i>Mimosa hamata</i> ?	Fabaceae (M)	Fabales	India	Bean, 1988
	<i>Mimosa himalayana</i>	Fabaceae (M)	Fabales	uncertain	Robinson et al. 2001
	<i>Mimosa diplotricha</i>	Fabaceae (M)	Fabales	Taiwan	present study
	<i>Pomgama glabra</i>	Fabaceae (M)	Fabales	Assam	Norman, 1976
	<i>Entada phaseoloides</i>	Fabaceae (P)	Fabales	Japan	Fukuda et al. 1984
	<i>E. parvifolia</i>	Fabaceae (P)	Fabales	Japan	Fukuda et al. 1984
	<i>Rhynchosia rothii</i>	Fabaceae (P)	Fabales	Taiwan	Ho and Chang, 1998
	<i>Derris laxiflora</i>	Fabaceae (P)	Fabales	Taiwan	present study
	<i>Lespedeza formosa</i>	Fabaceae (P)	Fabales	Taiwan	present study
	<i>Adenanthera microsperma</i>	Fabaceae (P)	Fabales	Taiwan	present study
	<i>Bauhinia championi</i>	Fabaceae (C)	Fabales	Taiwan	present study
	<i>Caesalpinia crista</i>	Fabaceae (C)	Fabales	Japan	Asano and Fukaiishi, 2002
	<i>Allophylus cobbe</i>	Sapindaceae	Sapindales	Sri Lanka	Green, 1912
	<i>Sandoricum koetjape</i>	Sapindaceae	Sapindales	Philippines	Kitamura, 2000a,b
	<i>Itea oldhamii</i>	Saxifragaceae	Saxifragales	Taiwan	present study
	<i>Bischofia javanica</i>	Euphorbiaceae	Malpighiales	Japan	Asano and Fukaiishi, 2002
	<i>P. dubiosa</i>	<i>Acacia farnesiana</i>	Fabaceae (M)	Fabales	Philippines
<i>Ac. auriculiformis</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Ac. hemignosta</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Ac. leiocalyx</i>		Fabaceae (M)	Fabales	Australia	DeBaar, 1979b
<i>Ac. mangium</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Ac. polystachya</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Ac. victoriae</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Ac. maidenii</i>		Fabaceae (M)	Fabales	Australia	Schmidt and Rice, 2002
<i>Ac. confusa</i>		Fabaceae (M)	Fabales	Philippines	Kitamura, 2000
<i>Desmanthus illinoensis</i>		Fabaceae (M)	Fabales	Philippines	Kitamura, 1995
<i>Archidendron dulcea</i> <sup>a</sup>		Fabaceae (M)	Fabales	Philippines	Kitamura, 1995
<i>Ar. grandiflorum</i>		Fabaceae (M)	Fabales	Australia	Braby, 2000
<i>Dalbergia sissoo</i>		Fabaceae (M)	Fabales	Australia	Meyer, 1996
<i>D. pinnata</i>		Fabaceae (M)	Fabales	Australia	Kitamura, 2000
<i>Samanea saman</i>		Fabaceae (M)	Fabales	Taiwan	Present study
<i>Cajanus reticulatus</i>		Fabaceae (P)	Fabales	Australia	Braby, 2000
<i>Litchi chinensis</i>		Sapindaceae	Sapindales	Australia	Storey, 1977
<i>Alectryon tomentosus</i>		Sapindaceae	Sapindales	Australia	Schmidt and Rice, 2002
<i>Harpullia pendula</i>		Sapindaceae	Sapindales	Australia	Schmidt and Rice, 2002
<i>Macadamia integrifolia</i>		Proteaceae	Proteales	Australia	Common and Waterhouse, 1981
<i>Buckinghamia celsissima</i> <sup>b</sup>		Proteaceae	Proteales	Australia	DeBaar, 1979a
<i>Mallotus philippinensis</i>		Euphorbiaceae	Malpighiales	Philippines	Kitamura, 2000
<i>P. felderi</i>		<i>Acacia floribunda</i>	Fabaceae (M)	Fabales	Australia
	<i>Ac. granitica</i>	Fabaceae (M)	Fabales	Australia	Hawkeswood, 1988
	<i>Ac. leiocalyx</i>	Fabaceae (M)	Fabales	Australia	DeBaar, 1979b
	<i>Ac. penninervis</i>	Fabaceae (M)	Fabales	Australia	Hawkeswood, 1988
	<i>Ac. podalyriifolia</i>	Fabaceae (M)	Fabales	Australia	Hawkeswood, 1988
	<i>Ac. sophorae</i>	Fabaceae (M)	Fabales	Australia	Hawkeswood, 1988
	<i>Ac. disparrima</i>	Fabaceae (M)	Fabales	Australia	Schmidt and Rice, 2002
	<i>Ac. falcata</i>	Fabaceae (M)	Fabales	Australia	Schmidt and Rice, 2002
	<i>Ac. concurrens</i>	Fabaceae (M)	Fabales	Australia	Schmidt and Rice, 2002
	<i>Albizia lebeck</i>	Fabaceae (M)	Fabales	Australia	Braby, 2000
	<i>Litchi chinensis</i>	Sapindaceae	Sapindales	Australia	Common and Waterhouse, 1981
	<i>Alectryon coriaceus</i>	Sapindaceae	Sapindales	Australia	Common and Waterhouse, 1981
	<i>Cupaniopsis anacardioides</i>	Sapindaceae	Sapindales	Australia	Common and Waterhouse, 1981
	<i>Harpullia pendula</i>	Sapindaceae	Sapindales	Australia	Schmidt and Rice, 2002
	<i>Macadamia integrifolia</i>	Proteaceae	Proteales	Australia	Common and Waterhouse, 1981
	<i>Buckinghamia celsissima</i> <sup>b</sup>	Proteaceae	Proteales	Australia	DeBaar, 1979a
	<i>P. aluta</i>	<i>Dalbergia pinnata</i>	Fabaceae (M)	Fabales	Andaman/Nicobar isalands

<sup>a</sup>As *Pithecellobium dulce* in the original citation; <sup>b</sup>oviposition only; M, Mimosoideae; P, Papilionoideae; C, Caesalpinioideae.

We documented the following larval hosts for *Prosotas nora*: *Bauhinia championi* (Fabaceae: Caesalpinioideae) (HSU 00J51, 03J17, 03J33, and 03K30), *Derris laxiflora* (Fabaceae; Papilionoideae) (HSU 02E67), *Lespedeza formosa* (Fabaceae: Papilionoideae) (HSU 98J15, 03L56, and 05K49), *Adenantha microsperma* (Fabaceae: Papilionoideae), *Acacia farnesiana* (Fabaceae: Mimosoideae) (HSU 03L15.1 and 03L48.1), *Mimosa diplotricha* (Fabaceae: Mimosoideae) (HSU 03L56), and *Itea oldhamii*

(Saxifragaceae) (HSU 03G9 and 03G14), of which Saxifragaceae was recorded for the first time. On all occasions, the ova were inserted into tightly arranged flower buds of the inflorescences, either singly or several in a mass, and were concealed by a transparent gelatinous substance (Figs. 1-3), which rendered the ova inconspicuous. The larva ecloses from the egg laterally (Figs. 1-3) and feeds exclusively on inflorescences on all 6 species of host plants examined. The ground color of the larvae appeared to be correlated with the color of the



**Figs. 1-9.** Eggs of *Prosotas* species. 1. Oviposition condition of *P. nora* on the inflorescence of *Itea oldhamii*. 2. Ovum of *P. nora* on the inflorescence of *Lespedeza formosa*. 3. Egg shell of *P. nora* showing the eclosion hole. 4. Oviposition condition of *Prosotas dubiosa* on the inflorescence of *Acacia farnesiana*. 5. Ovum of *P. dubiosa*, with the gelatinous substance removed. 6. Egg shell of *P. dubiosa* showing the eclosion hole. 7. SEM observation showing the “lateral eclosion” condition in *P. dubiosa*. 8. Eggs of *Prosotas* are usually laid in a densely arranged inflorescence. 9. The general “top eclosion” condition in *Lampides boeticus*.

petals of the inflorescences upon which it was feeding: being pale green on *B. championii* (Fig. 11), olive green on *D. laxiflora* (Fig. 10), purplish red on *L. formosa* and *M. diplotricha*, green on *Ad. microsperma*, green or yellow on *Ac. farnesiana*, and white on *I. oldhamii* (Fig. 12). Prominent dark markings developed on some larvae, with the mottled form (Fig. 12) representing about 6% ( $n = 18$ , HSU 03J17, 03J33, and 03K30) on *B. championii*, 29% on *D. laxiflora* ( $n = 7$ , HSU 02E67), 0% ( $n = 7$ , HSU 03J9 and 05K49) on *L. formosa*, 100% ( $n = 3$ , HSU 03L56) on *M. diplotricha*, 0% ( $n = 4$ , HSU 04F3 and 04J5) on *Ad. microsperma*, 33% ( $n = 9$ , HSU 03L48.1 and 04B3.1) on *Ac. farnesiana*, and 44% ( $n = 16$ , HSU 03G9, 03G14, and 04F47.1) on *I. oldhamii*. Larvae left the inflorescences and pupated in debris (Fig. 13) in the laboratory.

Vouchers. 5 ♂♂, 2 ♀♀, TAIWAN: Taipei City, Beitou Dist., Junjianyan, 180 m, 13 July 2003, Coll. Y. F. Hsu; reared from *Itea oldhamii*, emerged (emgd.) 28-29 July 2003, HSU 03G9; 1 ♀, 18 July 2003, Coll. Y. F. Hsu; reared from *I. oldhamii*, emgd. 28 July 2003, HSU 03G14; 4 ♂♂, 4 ♀♀, TAIWAN: Taipei City, Wenshan Dist., Xianjiyan, 30 June 2004, Coll. Y. F. Hsu, J. R. Chen, and C. T. Chung; emgd. 17-21 July 2004, reared from *I. oldhamii*, HSU 04F47.1; 1 ♂, TAIWAN: Nantou Co., Renai, Songgang, ~1900 m, 17 Sept. 2003, Coll. Y. F. Hsu; reared from *Lespedeza formosa*, emgd. 29 Nov. 2003, HSU 03J9; 2 ♀♀, TAIWAN: Taidong Co., Yanping, Hongye, ~450 m, 30 Sept. 2003, Coll. Y. F. Hsu; reared from *Bauhinia championii*, emgd. 10 Oct. 2000, HSU 00J51; 1 ♀, 28 Sept. 2003, Coll. L. H. Wang; reared from *Bauhinia championii*, emgd. 20 Oct. 2003, HSU 03J33; 1 ♂, 26 May 2002, Coll. L. W. Wu; reared from *Derris laxiflora*, emgd. 10 June 2002, HSU 02E67; 2 ♂♂, 1 ♀, TAIWAN: Kaohsiung City, Xiaogang Dist., Dalinpu, 0-20 m, 9-10 Nov. 2003, Coll. Y. F. Hsu; reared from *Acacia farnesiana*, emgd. 21 Nov. 2003, HSU 03L15.1; 1 ♀, 29 Nov. 2003, Coll. Y. F. Hsu; reared from *Acacia farnesiana*, emgd. 12 Dec. 2003, HSU 03L48.1; 1 ♀, 29 Nov. 2003, Coll. Y. F. Hsu; reared from *Mimosa diplotricha*, emgd. 15 Dec. 2003, HSU 03L56; 2 ♀♀, TAIWAN: Nantou Co., Jiji, 7 Sept. 2004, Coll. Y. F. Hsu; emgd. 18-25 Sept. 2004, reared from *Adenantha microsperma*, HSU 04J5.

### *Prosotas dubiosa*

Larval hosts documented for *Prosotas dubiosa* include *Acacia farnesiana* (Fabaceae: Mimosoideae) (HSU 03C37, 03L15, and 03F34),

*Archidendron dulce* (Fabaceae: Mimosoideae) (HSU 03L48), and *Samanea saman* (Fabaceae: Mimosoideae) (HSU 04H40 and J15). Females demonstrated similar oviposition habits as *P. nora*, with 1 or 2 ova inserted into tightly arranged flower buds of inflorescences and concealed by a transparent glue-like substance (Figs. 4-6). The larva also ecloses laterally from the ovum and feeds exclusively on inflorescences. The ground color of the larva was pale green to green on all species of host plants examined, and dark markings of larva developed to various degrees on these plants (Fig. 14), with mottled larvae accounting for 50% ( $n = 10$ , HSU 03F34 and 04B6) on *Ar. dulce*, 80% ( $n = 5$ , HSU 04H40 and 04J15) on *Samanea saman*, and about 96% ( $n = 23$ , HSU 03L48, 04B3, and 04B7) on *Ac. farnesiana*. Pupation also took place in debris (Fig. 15) in the laboratory.

### Modification of female genitalia and oviposition strategies of *Prosotas*

Examination of the genitalia of *P. nora* and *P. dubiosa* revealed that the papillae anales of both species are produced posteriad into a shovel-like form (Figs. 18, 19), and are evidently correlated to their oviposition strategy. A similar modification has also been found in various lineages of the Lepidoptera that perform endophyletic oviposition (Powell 1984, Davis et al. 1992, Kristensen 2003, Yen et al. 2005). The only other female genitalia of *Prosotas* examined previously were those of *P. nelides* (Hirowatari 1992), which have the same form of papillae anales, suggesting that all *Prosotas* species may share the same oviposition strategy. The fact that many host plants of *P. felderi*, an Australian species similar to *P. nora*, are known (Table 1) without observation of its ova (Braby 2000) provides further evidence, because the ovum concealment may render this stage difficult to detect in the field. The observation that *P. nora* and *P. dubiosa* utilize various unrelated host plants (Table. 1) suggests that microhabitat suitability or plant inflorescence architecture is important in host choice by *Prosotas*. We found no viable ova on host plants without a suitable inflorescence architecture, suggesting that only a narrow window of opportunity exists when a host plant is a suitable oviposition substrate. In contrast, *Nacaduba*, *Catopyrops*, and *Erysichton*, the other genera placed in the *Nacaduba* complex (sensu Hirowatari 1992), are known to produce unconcealed ova (Common and Waterhouse 1981, Parsons 1999, Braby 2000), thus the substrate

texture of ovipositing location is less restricted. The females of these genera also lack the modified papillae anales (see Hirowatari 1992) suitable for endophyletic oviposition. Bell (1918) stated that the ovum of *P. nora* is laid at the base of a flower bud; however, ova of both *P. nora* and *P. dubiosa* were found at different locations along the inflorescence (Table 2). In the case of *Itea*, *P. nora* ova were found only at the distal end of the inflorescence ( $n = 17$ , HSU 03J9 and 03J14; Fig. 1; Table 2), suggesting that *Itea* presents an indefinite ramose which has tightly arranged flower buds only at the growing point of the inflorescence.

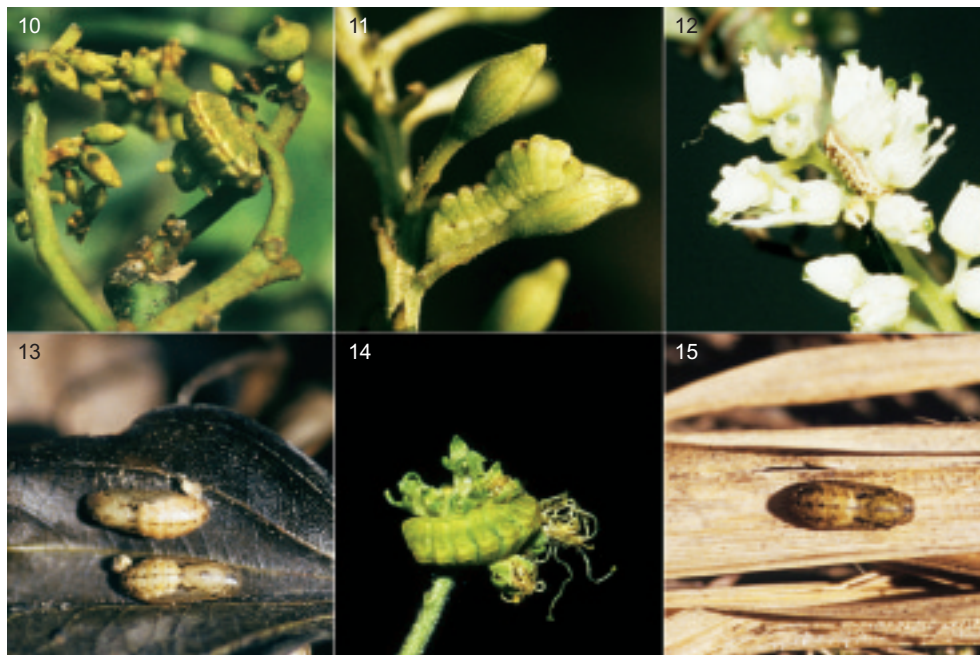
### SYSTEMATICS

The samples of *P. dubiosa* from Taiwan differ from those of other regions and thus warrant a subspecific designation.

***Prosotas dubiosa asbolodes*, ssp. nov.**  
(Figs. 4-6, 14, 15, 17, 19-23, 28, 29)

*Type material.* Holotype: ♂, TAIWAN: Kaohsiung City, Xiaogang Dist., Dalinpu, 0-20 m, 29 Nov. 2003, Coll. Y. F. Hsu; reared from *Acacia farnesiana*, emgd. 13 Dec. 2003, HSU 03L48 (BMNH).

*Paratypes:* 6 ♂♂, 1 ♀, same locality and date as holotype, associated with *A. farnesiana*; 6 ♂♂, 4 ♀♀, same locality and date as holotype; reared from *A. farnesiana*, emgd. 11-12 Dec. 2003, HSU 03L48; 3 ♂♂, 1 ♀, same locality as holotype, 9-10 Nov. 2003, Coll. Y. F. Hsu; 5 ♂♂, 7 ♀♀, same locality as holotype, 9-10 Nov. 2003, Coll. Y. F. Hsu; reared from *A. farnesiana*, emgd. 19-25 Nov. 2003, HSU 03L15; 1 ♀, 29 Aug. 2004, Coll. Y. F. Hsu; reared from *Samanea saman*, emgd. 13 Sept. 2004, HSU 04H40; 2 ♂♂, 2 ♀♀, 11 Sept. 2004, Coll. Y. F. Hsu; reared from *Samanea saman*, emgd. 25-27 Sept. 2004, HSU 04J15; 1 ♀, TAIWAN: Kaohsiung Co., Renwu, Kaotan, 8 Mar. 2003, Coll. C. C. Hsieh; reared from *A. farnesiana*, emgd. 23 Mar. 2003, HSU 03C37; 4 ♂♂, 1 ♀, Jiaxian, 250 m, 25 June 2003, Coll. Y. F. Hsu, 2 ♂♂, 1 ♀, reared from *Archidendron dulce*, emgd. 8-9 July 2003, HSU 03F34, Coll. Y. F. Hsu, 2 ♂♂, 29 June 2003, 1 ♀, 10 Dec. 2003, Coll. Y. F. Hsu and C. C. Hsieh; 2 ♂♂, Taoyuan, Weijinxi, 1000 m, 25 June 2003, Coll. Y. F. Hsu; 6 ♂♂, TAIWAN: Chiayi Co., Dapu, Zhutoushan, 300 m, 24 Sept. 2003, Coll. Y. F. Hsu, 1 ♀, 29 Oct. 2003; 1 ♂, 10 Nov. 2003, Coll. Y. F. Hsu; 1 ♀, TAIWAN: Tainan Co., Dongshan, Baihe, 80 m, 29 Oct. 2003, Coll. Y. F. Hsu; 5 ♀♀, TAI-



**Figs. 10-15.** Larvae and pupae of *Prosotas* species. 10. Fourth instar larva of *P. nora* on the inflorescence of *Derris laxiflora*. 11. Fourth instar larva of *P. nora* on the inflorescence of *Bauhinia championi*. 12. Fourth instar larva of *P. nora* on the inflorescence of *Itea oldhamii*. 13. Pupa of *P. nora* in debris. 14. Fourth instar larva of *P. dubiosa* on the inflorescence of *Acacia farnesiana*. 15. Pupa of *P. dubiosa* in debris. The arrow indicates the eclosion hole in the oval shell.

WAN: Taidong Co., Lanyu (Orchid I.), Sidaogou, 1-3 May 2003, Coll. Y. F. Hsu and Y. Lo.

**Diagnosis:** *Prosotas dubiosa asbolodes* is most similar to *P. d. subardates* (Figs. 24, 25, 30, 31) from Southeast Asia, but can be distinguished by the following characters: 1) the wing uppersides of the male are overlaid with deep-purple scales tinged with a sooty-blue sheen in *asbolodes*, whereas they are bright purple in *subardates*; and 2) the ground color of the wing undersides of *asbolodes* is brown tinged with gray, in contrast to pale brown tinged with yellow in *subardates*. The sympatric *P. nora formosana* (Figs. 26, 27, 32, 33) is also similar to *P. d. asbolodes* in appearance, but *P. n. formosana* bears a prominent tail-like projection on the hindwing, which is absent from *P. d. asbolodes*. Moreover, the submarginal band on the hindwing underside is distant from the distal band of the central symmetry system in *P. n. formosana*, but is in close contact with this system in *P. d. asbolodes*.

**Male** (Figs. 20, 26): Forewing length 8.4-11.2

mm (Table 3); antennal length 4.8-6.3 mm (Table 3). Head: Hairy, vertex and frons dark brown but with white on vertex and behind eye; a white, narrow rim surrounding eye; eye semi-oval, densely covered with long, buff setae; labial palpus porrect, with 3rd segment approximately 1/2 length of 2nd segment, covered with dark-brown scaling dorsad and dark brown mixed with white ventrad, scales on venter slender, long, and hair-like; maxillary palpus reduced, not visible; proboscis unscaled, pale buff colored; antenna smoothly scaled, naked at distal tip of flagellum; distal segments of flagellum enlarged with an inner depression and a patch of outer white scaling. A ring of white present at base of most flagellomeres. Thorax: Dark brown with long, white-tinged blue hairs dorsally and ventrally; legs slender, covered with brown scales, mottled with white, foretarsus fused into a tubular structure. Forewing: Termen and costa slightly concave, dorsum nearly straight; dorsum longer than costa. Ground color of upperside dark brown, overlaid with deep-purple scales extensively tinged

**Table 2.** Ovipositing site of *Prosotas* and inflorescence type of larval host

<i>Prosotas nora</i> Host species	distal 1/3	medial 1/3	basal1/3	inflorescence type
<i>Bauhinia championi</i>	12	15	7	ramose
<i>Lespedeza formosa</i>	0	3	0	ramose
<i>Adenantha microsperma</i>	2	0	0	ramose
<i>Mimosa diplotricha</i>	5	8	4	head
<i>Itea oldhamii</i>	17	0	0	ramose
<i>Prosotas dubiosa</i> Host species	distal 1/3	medial 1/3	basal1/3	inflorescence type
<i>Acacia farnesiana</i>	10	9	32	head
<i>Achidendron dulce</i>	2	3	5	head
<i>Samanea saman</i>	3	0	0	head

**Table 3.** Measurements of forewing length and antenna of both sexes of *Prosotas dubiosa asbolodes*, n. subsp.

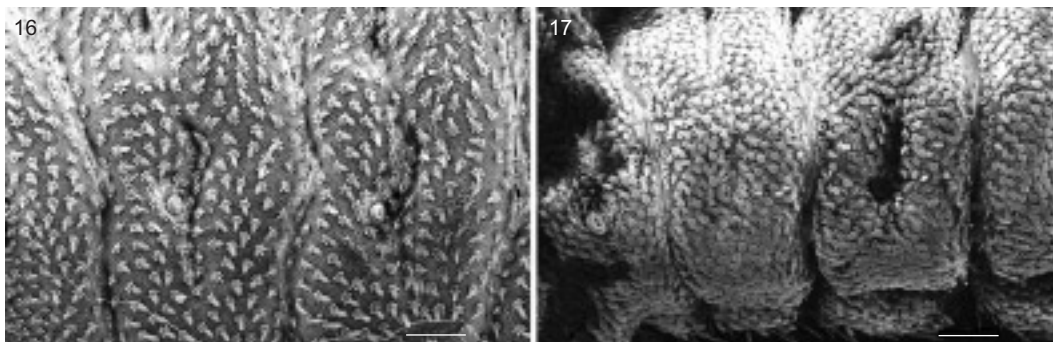
sex	mean forewing length (mm) ± SD	n
♂	10.08 ± 0.70a	34
♀	9.78 ± 0.85a	19
F = 1.92	df = 52	P = 0.1709
mean antennal length (mm) ± SD		
♂	5.56 ± 0.38a	34
♀	4.96 ± 0.45b	19
F = 22.30	df = 52	P < 0.0001

with a sooty-blue sheen, leaving narrow margins along termen. Markings of undersides barely visible due to their transparency. Fringe with dark-brown inner cilia and pale-brown outer cilia. Ground color of underside pale brown tinged with gray. Discal spot forming a bar edged by an inner brown and outer white line, with scaling within the bar paler than ground color. Central symmetry system represented as a series of bars of the same coloration as discal spot, arranged in uneven curves. Submarginal band and “g”-element as defined by Nijhout (1991) combined, forming brown band with a whitish medial line and proximally whitish lunules. Fringe pale brown. Hind wing: Contour of wing nearly circular. Ground color of upperside dark brown, overlaid with deep-purple scales extensively tinged with a sooty-blue sheen, leaving narrow margins along termen, dorsum, and around tornal area. Markings of undersides only somewhat visible due to their transparency, notably the prominent dark-brown spot in cell  $Cu_1$ . Fringe with dark-brown inner cilia and pale-brown outer cilia. Ground color of underside pale brown tinged with gray. Discal spot forming a bar edged by an inner brown and outer white line, with scaling within the bar paler than ground color. Central symmetry system represented as a series of bars of the same color as discal spot, arranged in uneven curves. Submarginal band and “g”-element as defined by Nijhout (1991) combined, forming brown band with a whitish medial line and proximal whitish lunules. A prominent, black spot crowned with orange yellow and distal metallic-pale-blue scaling at distal end of cell  $Cu_1$ ; similar but much-smaller spot present at tornus. Fringe pale brown. Abdomen: Dark brown mottled with brown, tinged with yellow dorsad, white ventrad. Genitalia (Figs. 20, 21): Ring-shaped sclerites of 9+10 segments with width approximately 0.64 times height, 9th segment produced anteriorly into

triangular extension, posterior end of 10th segment forming a pair of rectangular flaps; uncus and saccus obsolete; brachium simple, slender, hook-shaped, slightly enlarged at base; valva elongate, bearing slender, setose, up-bent caudal processes. Phallus robust, bearing a ventral, slender, digitate subapical process; cornuti composed of a patch of spicules. Juxta narrow, Y-shaped.

*Female* (Figs 21, 27): Forewing length 8.0-11.0 mm (Table 3); antennal length 4.0-5.5 mm (Table 3). Body as described for male. Foretarsus segmented, with 5 tarsomeres. Ground color of wing uppersides dark brown, with a patch of metallic-blue scaling proximally on hindwing. Wing undersides as in male. Genitalia (Fig. 19): Papillae anales setose, sclerotized, shovel-like, pointed at caudal end. Apophyses posteriores slender, elongate, longer than segment VIII. Apophyses anteriores short, stout, digitate, blunt at distal end. Sternite VIII modified mesoposteriorly into a flat, smooth piece, with ostium posterior to it. Ductus bursae broad, sclerotized, bearing a dorsal, conical, sclerotized portion leading to ductus seminalis. Corpus bursae oblanceolate. Signa absent.

*Immature stages*: Ovum (Figs. 10-15) approximately  $0.34 \pm 0.02$  mm in diameter,  $0.24 \pm 0.01$  mm in height ( $n = 23$ ). Chorion very thin, disc-like with minute, fine sculpturing on surface. Pale green tinged with yellow at first, turning white tinged with gray upon hatching. Larva: First instar: Body vermiform, pale brown with transparent primary setae on brown base; body ground color turning to yellow or pale yellow tinged with green after feeding. Legs and prolegs pale yellow tinged with green. Head nearly circular with a medial cleft at vertex, brown, glossy; stemmata and sutures dark brown. T1 shield diamond-shaped. XD1 2 times XD2 length on T1 shield. XD1 dorsal to XD2. D1 longer than D2 from T1 to A8. D1

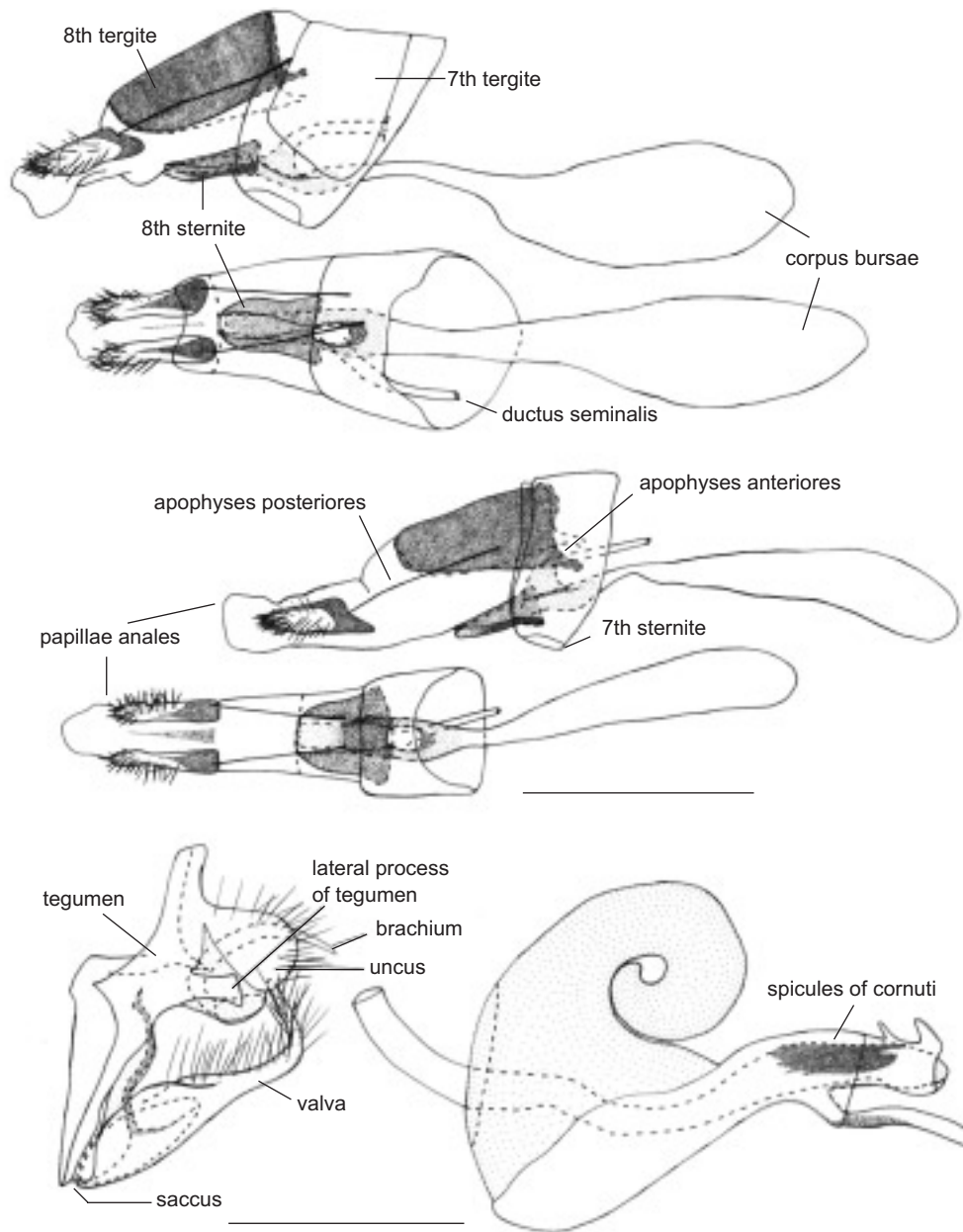


**Figs. 16-17.** Setae of the 4th instar larvae of *Prosotas*. 16. *Prosotas nora*. 17. *Prosotas dubiosa*. Scale bar = 200  $\mu$ m.



anterodorsal to D2, except on A8 where D1 immediately above D2. D group of each side of segment widely separated on T1, gradually converging posteriad, becoming side by side from A1 to A8. SD group absent from T2, unisetose on T3, bisetose but minute on A1 to A8; SD1 approximately equal to SD2 in length, with SD1 above spiracle, SD2 anterodorsal to spiracle. L group trisetose from T2 to A8, L1 longer than and ventral to L2 and L3. A9 + 10 bearing 4 L setae along posterior margin of body. SV group unisetose.

Spiracles brown. Anal lobe nearly semicircular, with weakly sclerotized oval anal plate. Second instar: Body humped dorsally, with prominent dorsal, medial groove on thorax. In addition to primary setae, secondary setae covering cuticle throughout body, but typical chalaza bearing elongate setae only present in a narrow zone laterally; majority of secondary setae with asteriform chalaza bearing short setae. Anal plate vestigial. Head turning creamy-yellow, with brown stemmata and brown mouthparts tinged with red. Body pale



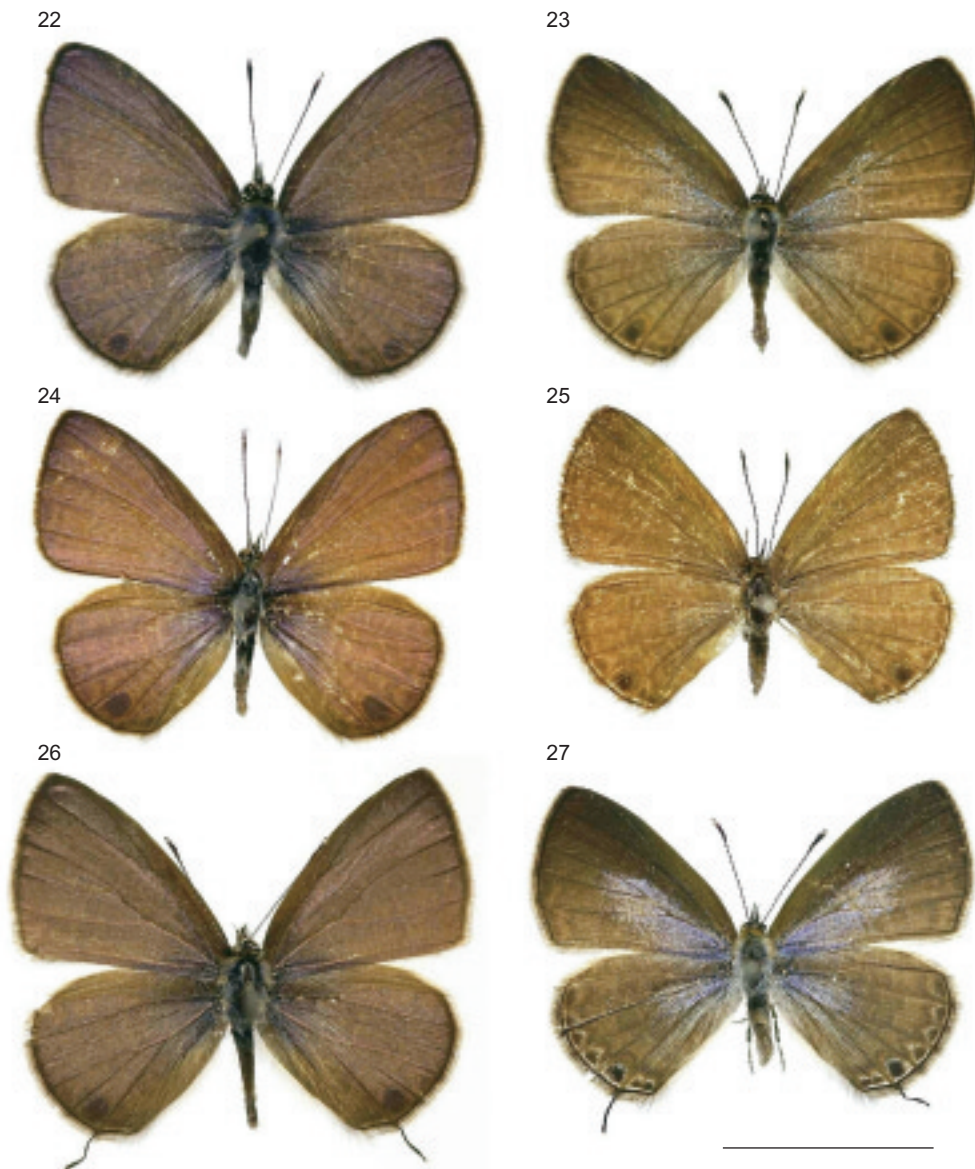
**Figs. 18-21.** Genitalia of *Prosotas*. 18. Female genitalia of *P. nora formosana*. 19. Ditto, *P. dubiosa asbolodes*. Scale bar = 0.5 mm. 20, 21. Male genitalia of *P. dubiosa asbolodes*. 20. Lateral view of 9 + 10 sclerites and left valva. 21. Phallus. Scale bar = 0.5 mm.

green or yellow. Spiracles white. Third instar: generally similar to 2nd instar but with vestigial primary setae. Asteriform chalaza more extensive than on 2nd instar. Body ground color green tinged with yellow, with yellow longitudinal lines running along dorsal midline and laterally. Faint, broken, double chevrons present laterally. Myrmecophilous organs emerged, with DNO and TOs both present. Fourth instar (Fig. 17): Asteriform setae densely covering entire body. Body coloration variable due to color of setae; generally body ground color green, with green, white,

and brown setae tinged with red arranged in a uniform or mottled appearance. Crochets represented as 2 bands of biordinal mesoserries. Pupa (Fig. 15): BL =  $6.56 \pm 0.37$  mm ( $n = 13$ ).

*Distribution*: Taiwan, from sea level to 1000 m in elevation.

*Larval host association*: *Acacia farnesiana*, *Archidendron dulce*, and *Samanea saman* (all Fabaceae: Mimosoideae) are the only documented larval hosts, but additional plant species are likely to be used because specimens were taken in habitats where those plant species were lacking.



**Figs. 22-27.** Uppersides of *Prosotas* species. **22.** *Prosotas dubiosa asbolodes*, n. subsp., holotype ♂. **23.** *Prosotas dubiosa asbolodes*, n. subsp., paratype ♀. **24.** *Prosotas dubiosa subardates* ♂. **25.** *Prosotas dubiosa subardates* ♀. **26.** *Prosotas nora formosana* ♂. **27.** *Prosotas nora formosana* ♀. Scale bar = 10 mm.

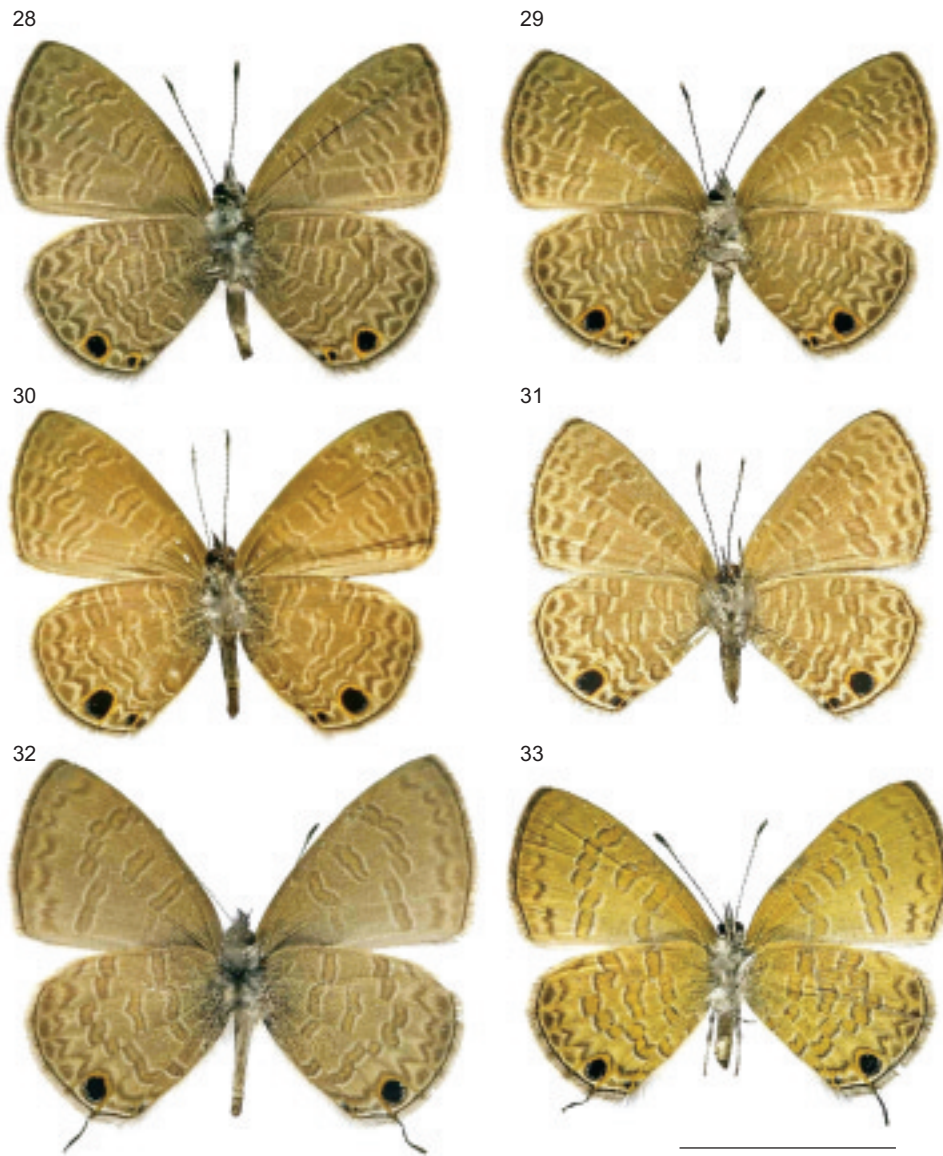
*Etymology:* An adjective of Greek, from *asbolodes* = sooty, referring to the dark, sooty wing uppersides of the males.

## DISCUSSION

### Oviposition biology of *Prosotas*

The most intriguing finding of the present study is the oviposition biology of *Prosotas*; no similar ovipositing strategy is known in any other

polyommatine lycaenid butterflies. Larvae of both *P. nora* and *P. dubiosa* eclose laterally (Figs. 3, 12) rather than from the top of the chorion, suggesting an adaptation to oviposition in tight slits. The female genitalia of both species show a unique modification of the papillae anales (Figs. 18, 19) that may correspond with this ovipositing behavior. As females of other *Prosotas* species examined (Hirowatari, 1992) also exhibit the same modification of the papillae anales, it is very likely that this morphological feature and oviposition behavior are shared by all *Prosotas* species. In



**Figs. 28-33.** Undersides of *Prosotas* species. **28.** *Prosotas dubiosa asbolodes*, n. subsp., holotype ♂. **29.** *Prosotas dubiosa asbolodes*, n. subsp., paratype ♀. **30.** *Prosotas dubiosa subardates* ♂. **31.** *Prosotas dubiosa subardates* ♀. **32.** *Prosotas nora formosana* ♂. **33.** *Prosotas nora formosana* ♀. Scale bar = 10 mm.

contrast, no female of the other genera in the *Nacaduba* complex (sensu Hirowatari 1992) possesses this modification of the papillae anales. Oviposition concealment with a transparent gelatinous covering (Figs. 4, 5) and lateral eclosion of larvae upon hatching (Figs. 1-3) are thus putative synapomorphies for *Prosotas* in addition to the 3 morphological synapomorphies suggested by Tite (1963) and Hirowatari (1992).

*Jamides bochus* (Stoll, [1782]), a species not belonging to the *Nacabuba* genus complex, is also known to conceal its ovum with froth (Bascombe et al. 1999, Hsu 1999), but its ovum is not inserted into a slit, and its 1st instar larva still ecloses from the top of the chorion. Obligatory lateral eclosion of the ovum is uncommon among lycaenid butterflies. *Shaanxiana takashimai* (see Koiwaya 1996) and *Satyrium tanakai* (see Igarashi and Fukuda 2000), both belonging the Theclinae, are known to engage in this behavior and deposit their ova into slits under bark or bud scales. The myrmecophilus polymmatine *Maculinea alcon* and *M. rebeli* are known to demonstrate peculiar oval bottom eclosion, associated with a very thick chorion (Thomas et al. 1991). The eclosion of ovum of all other polyommata lycaenids occur from the top, as demonstrated in the case of *Lampides boeticus* (Fig. 9). In contrast, the 2 *Prosotas* species reported herein demonstrate obligatory lateral eclosion of ova (Figs. 3, 12), which possess a semi-transparent and very thin chorion (Figs. 3, 12).

There is little doubt that the ancestral host association of *Prosotas* is with legumes as many closely related genera (sensu Tite 1963, Eliot 1973, Hirowatari 1992) predominantly utilize legumes as hosts (Fiedler 1991 1995, Robinson et al. 2001). Prior to the present study and a recent observation made in Japan (Asano and Fukaishi 2002), only members of the Papilionoideae and Mimosoideae were known as host plants. Chappill (1995) showed that the Mimosoideae is actually a derived clade within the Caesalpinioideae, and the polyphyletic Caesalpinioideae was not known to be colonized by *Prosotas*. We therefore hypothesized that the ancestral host-plant association of *Prosotas* began on either the Papilionoideae or Mimosoideae, followed by a saltatory host switch to the alternative legume subfamily. In the present study, *Bauhinia*, a caesalpinoid genus considered one of the most basal groups in Fabaceae (Doyle 1995), is found being utilized by *Prosotas*, so it seems that the host associations of *Prosotas* do not necessarily correlate with host-plant phylogeny, but the inflorescence structure that provides

ovum concealment. This scenario is further supported by the fact that a diverse set of plant families distantly related to the Fabaceae (Doyle 1995) are used as larval hosts by *Prosotas* (Table 1), although as many as 40 species in 16 genera of legumes have been documented as larval hosts of this lycaenid genus (Table 1).

### Past misconceptions on the immature stages of *Prosotas*

Although as many as 20 species in 3 families of plants and 22 species in 4 families respectively are known to be utilized as larval hosts by *P. nora* and *P. dubiosa* (Table 1), prior to the present study, observations on the ovum of *Prosotas* species were scanty. Bell (1918) provided the first account of ovum morphology, describing the egg of *P. nora* with reticulate cells on the chorion. Subsequent observations of this species were given by Bean (1988) and Kitamura (2000b), both based on a single ovum, and with the morphology in agreement with Bell's (1918) account. No description of the ovum of *P. dubiosa* or any other *Prosotas* species has been given. The *Prosotas* ova observed in the present study do not agree with the published literature. The ova of *P. nora* and *P. dubiosa* both appear to possess a very thin chorion with a coarse but glossy surface without conspicuous reticulated cells (Fig. 7). Moreover, the larvae of all ova investigated in the present study eclosed laterally (Figs. 1-3, 6, 7), evidently a behavior corresponding with the ovipositing condition (Figs. 1-3, 6). The morphology of the *Prosotas* ovum is likely an apomorphic adaptation correlated to the peculiar egg-concealing ovipositing behavior, as most of the known polyommata ova are exposed and possess relatively thick and prominent reticulated cells (e.g., Bascombe 1999, Braby 2000). The ovum-concealing behavior using a gelatinous substance makes the ovum nearly invisible in the field, leading Fukuda et al. (1984) to report a behavior that they termed "pseudo-oviposition" by female *P. nora*, which was observed to bend its abdomen onto the inflorescence of *Leucaena leucocephala* (Leguminosae; Mimosoideae) where "no ovum nor larva was found." Kitamura (1995) observed female *P. dubiosa* ovipositing on inflorescences of *Pithecellobium* (= *Archidendron*) *dulce* by inserting its abdomen into slits among the flower buds and applying a gelatinous substance to cover the ovum. He suspected that the "pseudo-oviposition" of *P. nora* described by Fukuda et al. (1984) may

have referred to true oviposition. Nevertheless, he later rejected his own hypothesis by reporting an ovum of *P. nora* exposed on a stipulate of an undetermined species of legume (Kitamura 2000b). The discovery of the same ovum-concealing oviposition condition of *P. nora* on 6 different host-plant species with different inflorescence types in the present study justifies Kitamura's (1995) earlier suspicion that "pseudo-oviposition" may be true oviposition. It is highly likely that all published accounts of *Prosotas* ova refer to those of other Polyommata, possibly *Acytolepis puspa*, a polyphagous lycaenid which feeds on a diversity of host plants including legumes (Fiedler 1991, Bascombe 1999, Hsu 1999, Robinson et al. 2001). The morphology of the ovum shown or described in those references agrees with that of this species.

Another hypothesis involving immatures proposed by Kitamura (2000b) is that the larvae of *P. nora* have poorly developed markings on the body despite a variable ground color, in contrast to a mottled pattern (termed "mosaic" by him) on a pale-green or pale-brown ground color of the larva of *P. dubiosa*. He suggested that such differences in color patterning may be used to distinguish larvae of the 2 species. Bean (1988) pointed out that the body coloration of *P. nora* is variable even though only a few larvae were examined. The present study confirms Bean's (1988) observation, and we found that larvae of *P. nora* and *P. dubiosa* exhibit considerable variations in the dark markings on the body, indicating that the body color pattern does not provide a reliable distinction between these 2 species. Alternatively, the form and distribution of setae on the body may represent reliable characters for separating the 2 species, which are sympatric through much of their ranges (Tite 1963). The secondary setae of the last instar of *P. nora* are slender and lanceolate and sparsely distributed, with between-setal distances largely greater than the diameter of the asteroid form setal base (Fig. 16). In contrast, the setae of *P. dubiosa* are short and predominantly ovoid in shape, densely distributed, and with between-setal distances less than the diameter of the asteroid form setal base (Fig. 17).

The pupae of *P. nora* and *P. dubiosa* are almost identical but the dark-brown markings of *P. dubiosa* are more extensive than those of *P. nora*, and a longitudinal, medial, dark-brown band is present on the abdomen in *P. dubiosa* (Fig. 15), whereas it is absent from *P. nora* (Fig. 13).

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