

***Hasora anura* de Nicéville from Taiwan (Lepidoptera: Hesperidae: Coeliadinae) Representing a New Subspecies Endemic to the Island**

Yu-Feng Hsu^{1,*}, Hiroshi Tsukiyama², and Hideyuki Chiba³

¹Department of Life Science, National Taiwan Normal University, Taipei, Taiwan 116, R.O.C.

Tel: 886-2-29326234 ext. 338. Fax: 886-2-29312904. E-mail: t43018@cc.ntnu.edu.tw

²4-18, Narashoinodai # 2-203, Funabashi-Shi, Chiba Pref. 274-0063, Japan. E-mail: tsukiyama@gol.com

³Natural Science Department, Bishop Museum, Honolulu, HI 96817 0916, USA. E-mail: skipper@i.bekkoame.ne.jp

(Accepted January 16, 2005)

Yu-Feng Hsu, Hiroshi Tsukiyama, and Hideyuki Chiba (2005) *Hasora anura* de Nicéville from Taiwan (Lepidoptera: Hesperidae: Coeliadinae) representing a new subspecies endemic to the island. *Zoological Studies* 44(2): 200-209. Populations of *Hasora anura* of Taiwan possess morphological characters and larval host usage which differ from those of conspecific populations in continental Asia. They are considered to represent a new subspecies endemic to Taiwan. This new subspecies is characterized by 1) an ochreous ground color on the wing undersides; 2) creamy-yellow markings on the hindwing undersides; 3) a valva rapidly narrowing distally; and 4) arms of the uncus close at the base. It is monophagous as a larva, feeding on *Ormosia formosana* (Fabaceae), in contrast to the broader host range of the continental populations, which utilize both *Ormosia* and *Milletia* (Fabaceae) as larval hosts. Year-round observations of the occurrence of immatures of this new subspecies and documentation in literature records suggest that it is a univoltine species, in which the occurrence of immatures is synchronized with the annual budding of its host; it probably overwinters as an adult. <http://www.sinica.edu.tw/zool/zoolstud/44.2/200.pdf>

Key words: Host association, Fabaceae, Monophagy, Endemicity.

Members of the genus *Hasora* Moore, 1881 are fairly large in size among skippers and are swift, strong flyers (Eliot 1992). The species diversity of this genus is high, with approximately 28 species, and it is the 2nd-largest skipper genus in Southeast Asia (Tsukiyama 1981, Chiba 1995). Only *Celaenorrhinus* Hübner, 1819 contains more species in the region. The genus has a vast distributional range, from the Indian subcontinent, eastwards across nearly all of southeastern Asia, reaching Papua New Guinea, Australia, and Fiji (Evans 1949, Tsukiyama 1981, Eliot 1992). It reaches its highest species diversity in the Oriental tropics (Tsukiyama 1981). The ranges of only a few *Hasora* species extend northwards into southern China. Among them, just 1 species, namely *Hasora anura* de Nicéville, 1889, is a purely montane species that is restricted to northern territory,

ranging from the southern part of continental China and not extending much farther south in Indochina (Shirôzu 1960, Tsukiyama 1981). *H. anura* was previously divided into 3 geographical races, *H. a. anura* de Nicéville, 1889 (Sikkim, northeastern India, and northern Burma), *H. a. danda* Evans, 1949 (Indochina), and *H. a. china* Evans, 1949 (continental China) (Chiba 1995) (Fig. 1). Evans (1949) considered *danda* as a good species, but Chiba (1995) pointed out that the diagnostic characters of *danda* used by Evans agree with those of *anura* and concluded that the 2 taxa are conspecific.

The presence of *H. anura* in Taiwan was confirmed by Shirôzu (1943), who stated that there are differences in the wing markings between the populations of *H. anura* in Taiwan and those of the nominotypical subspecies in mainland China, but

* To whom correspondence and reprint requests should be addressed.

no treatment was suggested due to the lack of sufficient material from the Asian continent for comparison. Shirôzu (1960) subsequently adopted the name *china* for the populations of Taiwan. Authors have followed this treatment since then (e.g., Hamano 1986, Uchida 1988 1991 1995). Nevertheless, Chiba et al. (1992) and Chiba (1995) considered that the wing patterns of populations from Taiwan are distinct from those of continental Asian populations. Having compared samples of *H. anura* from Taiwan with those from continental Asia, we confirmed Chiba's (1995) observations and came to the conclusion that samples from the island differ considerably from those of the Asian continent in terms of adult morphology and larval host usage. Thus, the populations of *H. anura* from Taiwan should be regarded as a new subspecies.

MATERIALS AND METHODS

Taxonomic methods

Samples of *H. anura* from Taiwan were compared with conspecific specimens from continental Asia, including: 32 ♂ and 9 ♀ from Myanmar (Burma); 47 ♂ and 9 ♀ from Thailand; 9 ♂ and 5 ♀ from Laos; 10 ♂ and 10 ♀ from Vietnam; and 25 ♂ and 16 ♀ from China (Fig. 1). Dissection of the genitalia follows the procedures of Hsu and Liu

(2002). Terminology follows Nijhout (1991) for wing patterns, and Evans (1949) and Klots (1970) for genitalia. Types of *H. a. taiwana* subsp. nov. are deposited in the following institutes and collections: BMNH: The Natural History Museum, London, UK; HTC: Hiroshi Tsukiyama Collection, Funabashi, Japan; KU: Faculty of Agriculture, Kyushu Univ., Fukuoka, Japan; NMNS: National Museum of Natural Science, Taichung, Taiwan; NTNU, National Taiwan Normal Univ., Taipei, Taiwan; and SEHU, Systematic Entomology Laboratory, Hokkaido Univ., Sapporo, Japan.

Survey on the phenology and larval host association

A study area at approximately 700 m in elevation in Lianhuachi, Yuchi, Nantou Co., central Taiwan was selected to conduct a preliminary survey on the phenology and larval host association of *H. anura* in Taiwan. Observations were performed once a month in 2001, at a site where both the recorded larval host of *Ormosia formosana* Kanehira, 1936 (Fabaceae) (e.g., Uchida 1988 1991 1995, Igarashi and Fukuda 2000) and *Milletia nitida* Benthem, 1842 (Fabaceae), a frequently reported host plant of the continental *H. a. china* (Hill et al. 1978, Johnston and Johnston 1980, Bascombe et al. 1999), grow abundantly. Vegetation of both plants was examined for the presence of immatures of *H. anura*. Data of adult



Fig. 1. Distribution of *Hasora anura* subspecies; squares denote *H. a. anura*, circles *H. a. danda*, diamonds *H. a. china*, and triangles *H. a. taiwana*. Closed symbols indicate specimen records (HTC, KU, NMNS, NTNU, and SEHU), and open symbols indicate literature records (from Evans 1949, Smith 1994, Bascombe et al. 1999).

records were compiled from the literature. Data from 2 immature-rearing databases were used; one is maintained by James J. Young, the Hong Kong Lepidoptera Society (rearing lot abbreviated as JJY), and the other is at the Department of Life Science, NTNU (lot abbreviated as HSU).

RESULTS

SYSTEMATIC ACCOUNTS

Hasora anura taiwana, subsp. nov.

(Figs. 2, 3, 10, 11, 18-20, 30-33)

Description: Male (Figs. 2, 10). Forewing length 21.2~24.0 (22.24 ± 0.96) mm ($n = 14$); length of antenna 11.8~13.5 (12.49 ± 0.54) mm ($n = 14$). Head. Hairy, brown on vertex, chaetosemata on vertex represented as pale-brown hair tufts; additional chaetosemata behind antennae forming brown brushes. Antennae covered with brown scaling dorsally, creamy-yellow ventrally, nudum present at swollen part of flagellum. Eyes semioval, smooth. Labial palpus porrect, with short, thick 1st segment and long, stout 2nd segment, both covered with brown mixed with creamy-white scaling; 3rd segment minute, digitate, covered by brown scaling. Thorax covered with pale-brown hairs. Legs covered with brown hairs.

Forewing: Costa nearly straight but slightly bent backwards at apex; termen concave, length subequal to that of dorsum; dorsum straight. Ground color of upperside uniformly glossy brown. Central symmetry system represented by 1 or 2 minute, creamy-yellow subapical dots. Fringe dark brown. Ground color of underside brown, overlaid with ocherous scaling anteriorly and distally. Creamy-yellow subapical dot(s) present as on upperside.

Hindwing: Configuration quite circular but produced caudad, fairly straight along dorsum. Ground color of upperside uniformly glossy brown. Fringe dark brown. Ground color of underside brown, overlaid with ocherous scaling, with a narrow, grayish-white line present along tornal lobe. Parafoveal elements forming a serpentine line, with a creamy-yellowish-white dash in cell Cu2. Basal symmetry system reduced to a small, creamy-yellowish-white dot in discoidal cell. Abdomen covered with brown hairs. Genitalia (Figs. 18-20): Tegumen broad at base, extending cephalad into a vault. Uncus bearing small, setaceous, lateral bump basad; caudal end of uncus forming elongate,

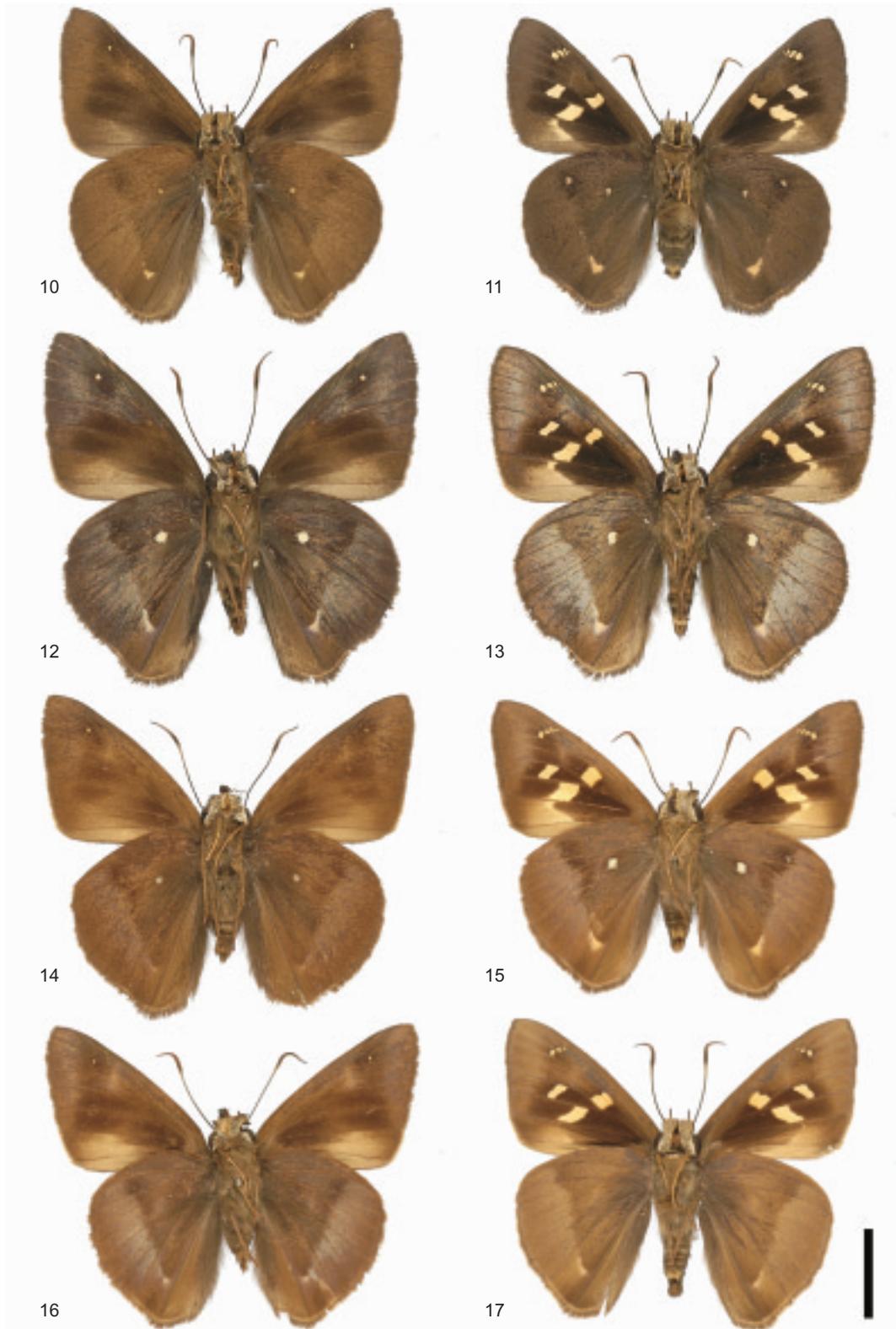
lateral, flattened arms, each twisted at terminal end and with a medial, outer protrusion. Gnathos strongly protruding posteriad, extending beyond caudal end of uncus. Valva elongate, with bifid style, forming a shallow, V-shaped depression at caudal end; dorsal extension triangular with a sharp point, ventral extension slightly serrate, circular; harpe slightly serrate dorsad, broad at base, bearing a flattened arm leading to a dorsal, elongate, triangular extension and a distal, broad, upcurved extension. Phallus straight, shorter than length of valva, with phallobase more than 2x length of aedeagus.

Female (Figs. 3, 11): Forewing length 19.0~22.7 (21.39 ± 1.22) mm ($n = 8$); length of antennae approximately 11.8~12.5 (12.11 ± 0.37) mm ($n = 7$). Head and thorax: Structure and color pattern as described for male. Wings: Configuration and ground color similar to those of male. Markings much more prominent than those of male; central symmetry system of forewing represented by 2 conspicuous, creamy-yellow, semi-transparent spots in cells Cu1 and Cu2, and a series of 3 or 4 small subapical dots of same color arranged in a line. Parafoveal elements of forewing underside diffused into broad patch of creamy-white posteriorly. Creamy-yellow dash and dot on hindwing underside more prominent than those of male. Abdomen covered with brown hairs.

Immatures: Ovum (Fig. 30): Dome-shaped, white, approximately 0.72 ± 0.01 mm in diameter, 0.52 ± 0.03 mm in height; chorion with 13~17 longitudinal ribs ($n = 10$). Mature larva (Fig. 32): Head nearly circular in shape, covered with soft, white hairs on surface; dark brown or pale yellowish-brown in color. Body cylindrical, covered with soft, white hairs, pale brown to dark brown in color. T1 shield with dark-brown transverse band. Anal plate with circular posterior margin. Four prominent, yellow, longitudinal lines present dorsally. Single, short yellow line present ventral to these longitudinal lines on T2 and T3. Similar but multiple (1~3) lines present on each abdominal segment from A1 to A8. Three prominent, longitudinal white lines present laterally, with medial line running through spiracles. Spiracles white. Body length reaching approximately 40 mm. Pupa (Fig. 33): 25.7 ± 1.4 mm in length ($n = 10$). Body robust, tapering caudad, broad and blunt cephalad. A medial digitate process on vertex, with its distal end swollen into a club. Distal end of proboscis barely touching A5. Surface smooth but bearing short, transparent setae. Ground color pale olive-green, spiracles dark brown. Additional



Figs. 2-9. Subspecies of *Hasora anura*, upperside. **2.** *taiwana*, subsp. nov., holotype ♂; **3.** ditto, paratype ♀; **4.** subsp. *china*, ♂ (Guangxi Prov., China); **5.** ditto, ♀ (Jiangxi Prov., China); **6.** subsp. *anura*, ♂ (N. Myanmar); **7.** ditto, ♀ (N. Thailand); **8.** subsp. *danda*, ♂ (N. Thailand); **9.** ditto, ♀ (Laos). Scale bar = 1 cm.



Figs. 10-17. Subspecies of *Hasora anura*, underside. **10.** *taiwana*, subsp. nov., holotype ♂; **11.** ditto, paratype ♀; **12.** subsp. *china*, ♂ (Guangxi Prov., China); **13.** ditto, ♀ (Jiangxi Prov., China); **14.** subsp. *anura*, ♂ (N. Myanmar); **15.** ditto, ♀ (N. Thailand); **16.** subsp. *danda*, ♂ (N. Thailand); **17.** ditto, ♀ (Laos). Scale bar = 1 cm.

dark-brown dots present on A1 and A2. White wax covering entire body surface.

Host association: *Ormosia formosana* Kanehira, 1936 (Fabaceae) (Uchida 1988 1991 1995, Igarashi and Fukuda 2000).

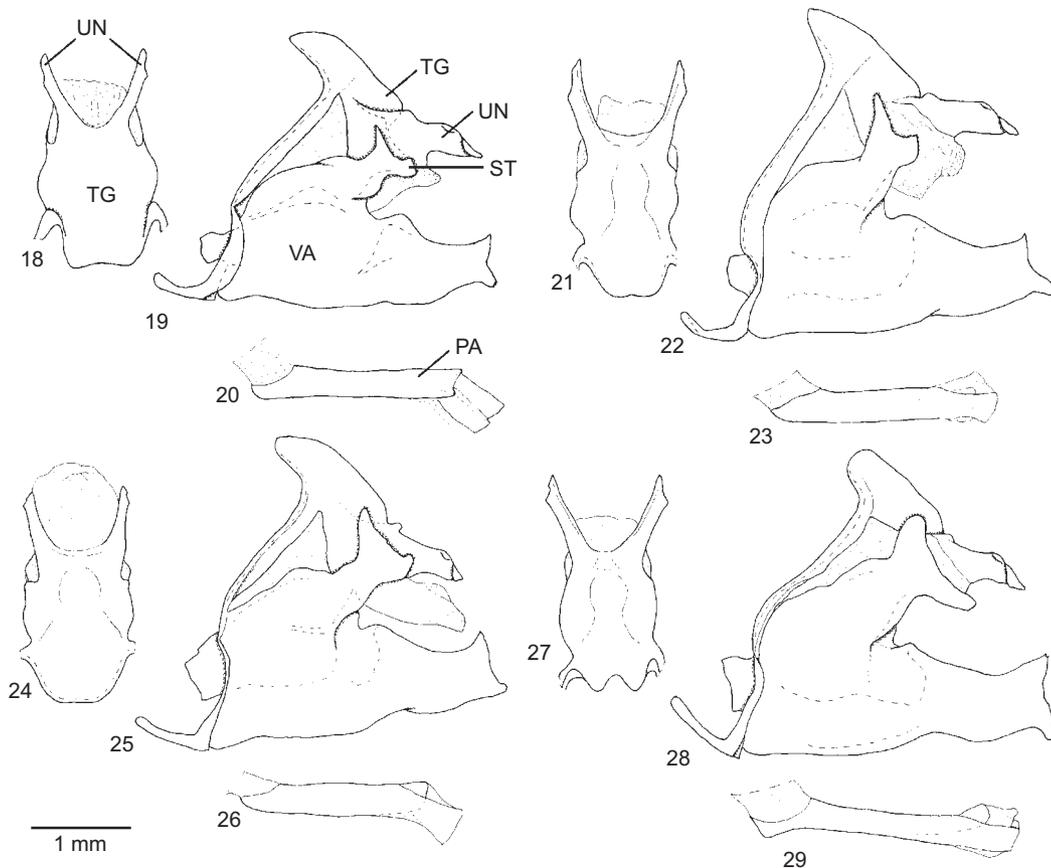
Types: Holotype ♂: Taiwan: Taizhong Co., Heping, Anmashan, 2000 m, 28 July 2003, H. C. Huang and Y. C. Hsu Coll. (BMNH).

Paratypes: 1 ♀, [Taiwan]: Taichun-shu [= Taizhong Co.], Daikoukei [= Dajixi], Urai[ruma] - Meiji [= Guguan], 30 July 1941, K. Fukushima Coll. (KU); 1 ♂, same locality as holotype, 30 Apr. 2000, C. C. Lu and C. Y. Hung coll., reared from *Ormosia formosana*, emgd. 22 May 2000, HSU 00D35 (NMNS); 1 ♀, [Taiwan: Nantou Co., Renai], Baibara [= Meiyuan], 24 Feb. 1927, Kikuchi *Hasora anura* de Nicéville Onashibiroudoseseri det. T. Shirôzu (Aug. 1952) (SEHU); 1 ♀, Taiwan: Nantou Co., Renai, Meifeng, 2100 m, 18 July 1990. C. L. Li coll. (BMNH); 1 ♂, Taiwan: Nantou

Co., Renai, Nanshanxi, ca 1000 m, 12 Mar. 1996, Y. F. Hsu coll. (HTC); 1 ♂, Taiwan: Nantou Co., Renai, Hui-Sun Forest Station, ~800 m, 6 Oct. 1996, S. C. Chen coll. (HTC); 1 ♂, Taiwan: Nantou [Co.], Renai, Sungkang [= Songgang, ~1900 m], 11 Mar. 1999. W. T. Yang coll., UV light, NMNS ENT 3151-894 (NMNS); 10 ♂, 6 ♀, Taiwan: Nantou Co., Yuchi, Lianhuachi, ~700 m, 13 May 2004, Y. F. Hsu coll., reared from *Ormosia formosana*, emgd. 31 May~11 June 2004, HSU 04E25 (NMNS, NTNU, HTC).

Distribution: Restricted to Taiwan; found only in the central part of the island from 700 to 2300 m in elevation.

Biology: Immatures were recorded and illustrated by Uchida (1995). Ovum (Fig. 30) is deposited singly, predominantly on the under surfaces of a hardened leaf, occasionally on twigs, young leaves, or the upper surface of hardened leaves (HSU 01E3; 04E25). The larva (Figs. 31,



Figs. 18-29. Male genitalia of *Hasora anura* subspecies. **18.** *taiwana*, subsp. nov., dorsal view of tegumen. **19.** ditto, lateral view of 9th + 10th sclerites. **20.** ditto, lateral view of phallus. **21.** subsp. *china* (Yunnan Prov., China), dorsal view of tegumen. **22.** ditto, lateral view of 9th + 10th sclerites. **23.** ditto, lateral view of phallus. **24.** subsp. *anura* (N. Thailand), dorsal view of tegumen. **25.** ditto, lateral view of 9th + 10th sclerites. **26.** ditto, lateral view of phallus. **27.** subsp. *danda* (Laos), dorsal view of tegumen. **28.** ditto, lateral view of 9th + 10th sclerites. **29.** ditto, lateral view of phallus. ST, style; TG, tegumen; UN, uncus; VA, valva; PA, phallus. Scale bar = 1 mm.

32) devours soft leaves and constructs a shelter with the leaves, into which the larva withdraws and rests while not feeding. Mature larvae evidently depart from the host plant for pupation (HSU 01E71, 04E25).

Diagnosis: The new subspecies can be distinguished from other subspecies by the following characters. 1) Hindwing underside and anterior 1/2 of forewing underside are overlaid with pale, slaty or purple-glossed scaling (Figs. 12-17) in the continental subspecies, whereas they are overlaid with ochereous scaling in *a. taiwana* (Figs. 10, 11). 2) The small dot and narrow dash on the hindwing underside are white in the continental subspecies (Figs. 12-17), whereas they are creamy-yellow in subspecies *a. taiwana* (Figs. 10, 11). 3) Styles of *a. taiwana* (Fig. 19) and *a. china* (Fig. 22) are similar in shape, with sharp dorsal and blunt ventral extensions nearly perpendicular to each other, whereas those extensions of the nominotypical subspecies (Fig. 25) and *a. danda* (Fig. 28) are widely separated and not sharply pointed at the tips. 4) The valva rapidly narrows toward the distal extensions in *a. taiwana* (Fig. 19), gradually narrows in *a. china* (Fig. 25) and the nominotypical subspecies (Fig. 25), and does not narrow in *a. danda* (Fig. 28). 5) Arms of the uncus are closer

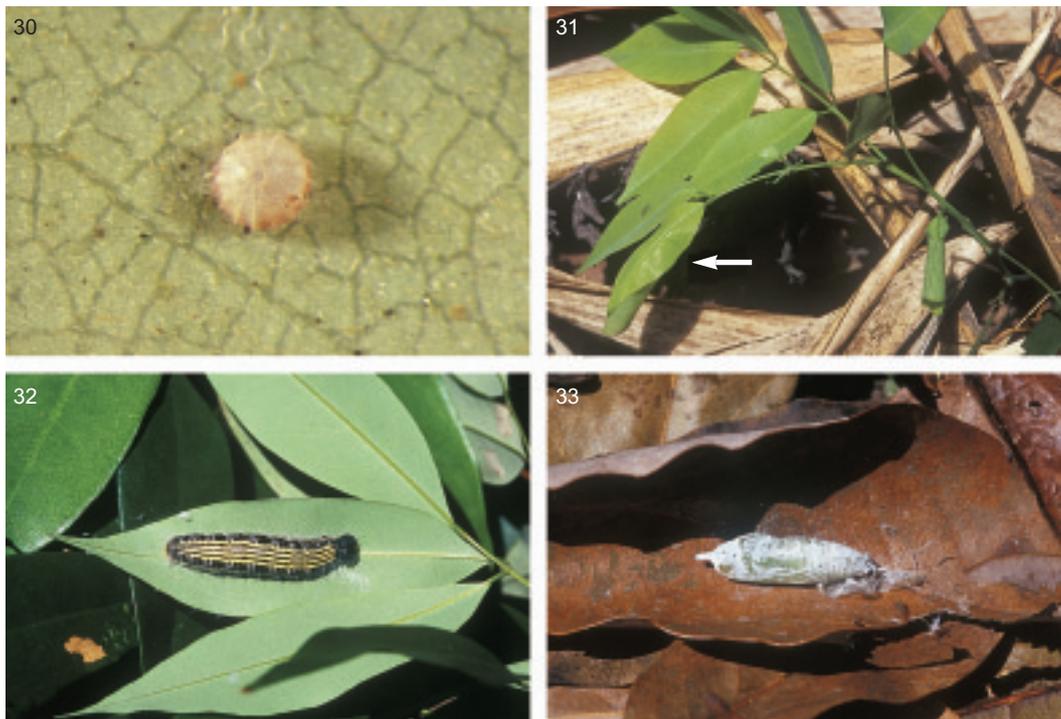
at the base and more apart distad, so that they form a V-shape in *a. taiwana* (Fig. 19), but they do not do so in the continental subspecies and form a U-shape (Fig. 28).

Key to the subspecies of *Hasora anura*

1. Hindwing underside without white dot in discoidal cell; styles with ventral extension shorter than dorsal extension, dorsal extension blunt distally.....*danda*
 - Hindwing underside with a white dot in discoidal cell*; styles with ventral extension longer than dorsal extension, dorsal extension pointed distally.....2
 2. Wing undersides with purple gloss; boundary of dorsal and ventral extension of styles poorly defined.....*anura*
 - Wing undersides without purple gloss; dorsal and ventral extension of styles perpendicular to each other.....3
 3. Wing undersides with slaty scaling; arms of uncus widely separated at base.....*china*
 - Wing undersides with ochereous scaling; arms of uncus close to each other at base.....*taiwana*
- * Occasionally the white dot is reduced in the nominotypical subspecies.

Phenology and Larval Host Association

During the study period, we only found immatures of *H. a. taiwana* in early May (HSU 01E3) in



Figs. 30-33. Immatures of *Hasora anura taiwana*, subsp. nov. 30. Ovum. 31. Larval shelter (indicated by an arrow). 32. Mature larva. 33. Pupa.

the study area (Fig. 34), whereas larvae were observed at an area outside of the study area in late Apr. (HSU 00D35). No trace of immatures of *H. a. taiwana* was found at the study site in the remaining months, although many empty shelters were observed in late May (01E71, Fig. 34).

Immatures of *H. a. taiwana* were found only on *O. formosana* during the present investigation, although *M. nitida* grows sympatrically and abundantly at the study site, suggesting that *M. nitida* might not be an appropriate host plant for *H. a. taiwana*, because soft tissue of *M. nitida* was present along with that of *O. formosana* but was not utilized by *H. a. taiwana*.

DISCUSSION

The styles of *H. a. china* (Fig. 19) and *H. a. taiwana* (Fig. 22) are nearly identical in shape, suggesting that *H. a. china* may be a sister subspecies of *H. a. taiwana*. Evans (1949) considered *danda*, which he described based on a type from Myanmar, to be a species distinct from *H. anura*, but listed only 3 weakly defined characters on the wing pattern as diagnostic features for the species, including 1) the discal line on the hindwing underside of male *danda* is not indented in “space 5” (= cell M1); 2) the [subapical] dots of the forewing are absent in *danda*; and 3) the white dot in the [discoidal] cell is absent. However, Chiba (1995) pointed out that all of these characters may be seen in *H. anura* and proposed placing *danda* within *H. anura*. As a matter of fact, we found no difference in terms of wing markings between *H. a. anura* and *H. a. danda*, except the latter presum-

ably does not possess the white discoidal spot on the hindwing underside. Problematically, some specimens from Myanmar possess the white dot while others do not, while almost all specimens examined from eastern Indochina lack the white dot (94%, $n = 34$). The genitalia structure of these eastern Indochinese specimens (Figs. 27-29, notice the structure of the styles) is distinct from that of the other 3 subspecies. We tentatively consider the form with no white discoidal spot as *H. a. danda* following Evans' (1949) diagnosis herein. However, it cannot be ruled out that the form without a white spot in Myanmar, i.e., the topotypes of *danda*, actually represents *H. a. anura* with reduced white spots, and the spotless populations in eastern Indochina represent a distinct form or taxon. To clarify this problem, examinations of long series of samples from various sites across all of Indochina and the Indian subcontinent will be necessary.

Combining the results of phenological observations with data on adults collected from the literature (Fig. 35), it is reasonable to conclude that *H. a. taiwana* is a univoltine species. The ovum of this taxon is laid in late spring and hatches in coincidence with bud-breaking of *O. formosana*. Adults of *H. a. taiwana* emerge by late May and remain active through the summer. They probably enter diapause after the summer activity, and resume activity and oviposit after the winter passes.

The larval hosts of *H. a. china* are known to be *M. nitida* in Hong Kong and continental China (Hill et al. 1978, Johnston and Johnston 1980, Bascombe et al. 1999) (JJY 2838, 2840, 3321,



Fig. 34. Phenological observations of immature appearance of *Hasora anura taiwana* at Lianhuachi, Yuchi, Nantou Co., Taiwan, during 2001. The period of time is at an interval of 1/2 a month.

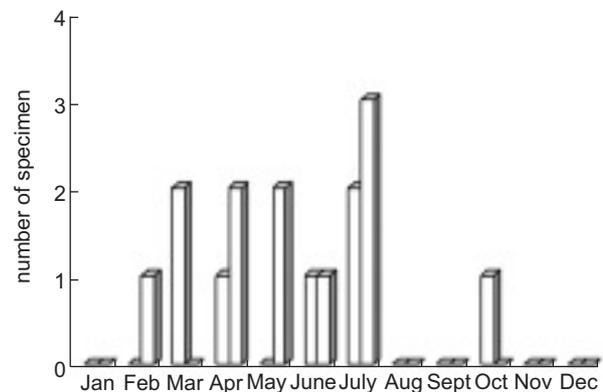


Fig. 35. Documentation of adult appearance of *Hasora anura taiwana* based on literature records (from Shirôzu 1960, Yamanaka 1980, Uchida 1991 1995) and specimens (HTC, KU, NMNS, NTNU, and SEHU). The period of time is at an interval of 1/2 a month.

3324, 3337, 3338, 3339, 3340, 3418, 4115, 4151; HSU 00D32) and *O. glaberrima* Y. C. Wu, 1940 in Guangdong, China (JJY 2480, 2481). Moreover, an additional species of *Milletia* was observed to serve as a host plant of the skipper in northern Guangdong (JJY 2939, 3617). In contrast, although *M. nitida* and other species of *Milletia* also exist and are widespread in Taiwan (Huang and Ohashi 1993), none of them has been recorded as an appropriate larval host for *H. a. taiwana*. The field survey performed in this study confirmed that *M. nitida* is not utilized as a host, suggesting that the insular race of *H. anura* is monophagous, specializing on *O. formosana*. Utilization of *O. formosana* as the sole larval host by *H. anura* provides a possible explanation for the restricted distribution of the skipper within Taiwan, where it has only been recorded from the central part of the island (Yamanaka 1980), for *O. formosana* is found only in central Taiwan (Huang and Ohashi 1993). *H. a. china* is, on the other hand, widespread and abundant as it utilizes a broader host range.

In total, larval host plants of 10 *Hasora* species are known (Parsons 1999, Braby 2000, Igarashi and Fukuda 2000, Robinson et al. 2001), and all species associate with the legume genera of *Milletia*, *Derris*, *Pongamia*, or *Fordia*, except that *H. discolor* utilizes *Mucuna* (Parsons 1999, Braby 2000). *Milletia*, *Derris*, *Pongamia*, and *Fordia* all belong to a terminal clade within the Fabaceae, named core Millettieae, as defined by Hu et al. (2000 2002), whereas Kajita et al. (2001) demonstrated that *Mucuna* is phylogenetically distant from the core Millettieae. There seems little doubt that the ground plan host association of *Hasora* is with the core Millettieae, as members of this clade are used by nearly all *Hasora* species for which the host plant has been recorded. Interestingly, *Ormosia*, the sole host plant of *H. a. taiwana*, is considered to be at a more basal position within the Fabaceae (Chappill 1995, Hu et al. 2000 2002). This host usage is evidently a derived condition, as larvae of the continental *H. anura* are known to feed on both *Milletia* and *Ormosia* as discussed in the previous paragraph, and most other *Hasora* species utilize members of the core Millettieae. Similar patterns are seen in other butterfly groups; for instance, the Rhamaceae association of *Nymphalis californica* is evidently derived from the Urticales association shared by other *Nymphalis* species (Janz et al. 2001); the *Rhododendron* association of *Howarthia* is derived from the Fagaceae association shared by the puta-

tive sister groups of the genus (Hsu et al. 2004). An interesting question remaining to be solved is why *H. a. taiwana* is specialized or at least why it shows a strong preference toward *Ormosia*, as no member of the core Millettieae is known to be utilized as a larval host by *H. a. taiwana*. Future tests on the acceptance of *Milletia* as potential hosts for *H. a. taiwana* and differences in the secondary compounds and the leaf texture of *Ormosia* and *Milletia* may possibly provide an answer.

Acknowledgments: Samples of *Hasora anura* from Taiwan were provided by Hang-Chi Huang and Yu-Cheng Hsu (The Butterfly Conservation Society of Taiwan, Taipei, Taiwan) and Chun-Lin Li (National Taiwan University, Taipei, Taiwan). James J. Young (The Hong Kong Lepidoptera Society, Hong Kong) provided unpublished rearing data of *Hasora anura china*. Mei-Ling Jan (NMNS) arranged the loan of the specimens in her care. Chih-Chien Lu (NTNU) assisted in the survey of phenological observations. Ying-Juan Yang, Chia-Chang Hsieh, Li-Wei Wu, and Jian-Ren Chen (NTNU) assisted in preparing the figures. Shen-Horn Yen (National Sun Yat-Sen University, Kaohsiung, Taiwan) provided many useful suggestions. H. Chiba thanks the late John N. Eliot for discussions on the relationship of *H. anura* and *H. danda*, and financial support from an Ernst Mayr Grant, Harvard Univ., Cambridge, MA, USA. We also appreciate helpful comments given by 2 anonymous reviewers.

REFERENCES

- Bascombe MJ, G Johnston, FS Bascombe. 1999. The butterflies of Hong Kong. London: Academic Press.
- Braby MF. 2000. Butterflies of Australia, their identification, biology and distribution. Collingwood, Australia: CSIRO.
- Chappill JA. 1995. Cladistic analysis of the Leguminosae: the development of an explicit phylogenetic hypothesis. In M Crisp, JJ Doyle, eds. Advances in legume systematics. 7: Phylogeny. Kew, UK: Royal Botanic Gardens, pp. 1-9.
- Chiba H. 1995. A revision of the subfamily Coeliadinae of the world (Lepidoptera:Hesperiidae). PhD Dissertation, Univ. of Hawaii, Honolulu, HI.
- Chiba H, YF Hsu, T Shirôzu. 1992. HesperIIDae. In JN Heppner, H Inoue, eds. Lepidoptera of Taiwan, Vol. 1, part 2: checklist. Gainesville, FL: Association For Tropical Lepidoptera, pp. 130-132.
- Eliot JN. 1992. The butterflies of the Malay Peninsula, 4th revised edn. (originally by AS Corbet and HM Pendlebury). Kuala Lumpur, Malaysia: Malayan Nature Society.
- Evans WH. 1949. A catalogue of the HesperIIDae from Europe, Asia and Australia in the British Museum (Natural History). London: The British Museum.

- Hamano E. 1986. Ecological encyclopedia of Taiwanese butterflies. Tokyo: Kodansha. (in Japanese)
- Hill DS, G Johnson, MJ Bascombe. 1978. Annotated checklist of Hong Kong butterflies. Mem. Hong Kong Nat. Hist. Soc. **11**: 1-62.
- Hsu YF, W Liu. 2002. On *Photinia*-associated *Chrysozephyrus* hairstreaks, with description of a new species (Lepidoptera: Theclinae: Theclini). Zool. Stud. **41**: 263-270.
- Hsu YF, D Din, SH Yen, ZQ Qian. 2004. Systematic problems surrounding *Howarthia melli* (Forster) (Lepidoptera: Lycaenidae: Theclinae), with description of a new species and a review of *Rhododendron*-association in lycaenid butterflies. Ann. Entomol. Soc. Am. **97**: 653-666.
- Hu JM, M Lavin, MF Wojciechowski, MJ Sanderson. 2000. Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast *TRNK/MATK* sequences and its implications for evolutionary patterns in Papilionoideae. Am. J. Bot. **87**: 418-430.
- Hu JM, M Lavin, MF Wojciechowski, MJ Sanderson. 2002. Phylogenetic analysis of nuclear ribosomal ITS/5.8s sequences in the tribe Millettieae (Fabaceae): *Poecilanthe-Cyclolobium*, the core Millettieae, and the *Callerya* group. Syst. Bot. **27**: 722-733.
- Huang TC, H Ohashi. 1993. Leguminosae. In TC Huang, ed. Flora of Taiwan, 2nd edn. Vol. 3. Taipei: Editorial Committee of the Flora of Taiwan, pp. 160-396.
- Igarashi S, H Fukuda. 2000. The life histories of Asian butterflies. Vol. 2. Tokyo: Tokai Univ. Press.
- Janz N, K Nyblom, S Nylin. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution **55**: 783-796.
- Johnston G, B Johnston. 1980. This is Hong Kong: butterflies. Hong Kong: Hong Kong Government Publication.
- Kajita T, H Ohashi, Y Tateishi, CD Bailey, JJ Doyle. 2001. *rbcl* and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and allies. Syst. Bot. **26**: 515-536.
- Klots AB. 1970. Lepidoptera. In SL Tuxen, ed. Taxonomist's glossary of genitalia in insects, 2nd edn. Copenhagen: Munksgaard, pp. 115-130.
- Nijhout HF. 1991. The development and evolution of butterfly wing patterns. Washington, DC and London: Smithsonian Institution Press.
- Parsons M. 1999. The butterflies of Papua New Guinea, their systematics and biology. London and San Diego, CA: Academic Press.
- Robinson GS, PR Ackery, IJ Kitching, GW Beccaloni, LM Hernández. 2001. Hostplants of the moth and butterfly caterpillars of the Oriental Region. London: The Natural History Museum.
- Shirôzu T. 1943. On the occurrence of *Hasora anura* de Nicéville in Formosa (Lepidoptera, Hesperidae). Entomol. World **11**: 277-282. (in Japanese)
- Shirôzu T. 1960. Butterflies of Formosa in colour. Osaka, Japan: Hoikusha. (in Japanese)
- Smith C. 1994. Butterflies of Nepal (Central Himalaya). Bangkok: Tecpress Service.
- Tsukiyama H. 1981. Miscellaneous notes on skippers of Southeast Asia (3). Gekkan-Mushi **146**: 25-29. (in Japanese)
- Uchida H. 1988. Amidst the lantana flowers: butterflies of Taiwan – nature and man. Mumazu: self-published. (in Japanese)
- Uchida H. 1991. Charms of Formosa, island of everlasting summer: butterflies of Taiwan – nature and man. Mumazu: self-published. (in Japanese)
- Uchida H. 1995. Everlasting island with beautiful butterflies - nature and man. Mumazu: self-published. (in Japanese)
- Yamanaka M. 1980. Distribution of Formosan butterflies (6). Tyô Ga **30 (Supplement 1)**: 1-143. (in Japanese)