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A new lycaenid butterfly exclusively associated with the subalpine sclerophyllous oak forests in Taiwan (Lepidoptera, Lycaenidae, Theclinae)

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(Accepted 25 December 2003)

Abstract

Subalpine sclerophyllous oak forest grows at high elevation in Taiwan, distantly separated from similar forest communities found in western China, Tibet and India. An investigation on bud-breaking phenology of oaks and associated phytophagous insects in this community revealed an undescribed species of *Teratozephyrus* lycaenid. This and other oak-associated insects suggest that the presence of this oak community in Taiwan resulted from a more widely distributed community. The newly discovered *Teratozephyrus* turned out to be most closely related to *T. nuwaii*, described from western China, and is described below as *T. elatus* sp. nov. Two other species of *Teratozephyrus* also inhabit Taiwan, but both are associated with broad-leaved oak forests. Of them, *T. arisanus* is widespread both in China and Taiwan, is morphologically distinct from the other *Teratozephyrus* species and is exclusively associated with broad-leaved oaks. The other, *T. yugaii*, probably gained its broad-leaved oak association secondarily as no similar species is found in the broad-leaved oak communities on continental Asia, and it favours cool, higher-elevation environments even though its host plant ranges into far lower elevations.

Keywords: *Bud-breaking phenology, host association, Matsumura's Type Collection, Systematics, Tadao Kano*

Introduction

It is generally believed that sclerophyllous vegetation is an adaptation to drought in areas with a prolonged dry season, notably in the Mediterranean climate (Cox and Moore 1993). Nevertheless, a similar vegetation type is found in India (Rawal and Pangtey 1994), Tibet, south-western China and Taiwan, where no prolonged dry season is present (Wu and Wang 1980). In Taiwan, such vegetation is termed “montane evergreen sclerophyllous forest”, and contains two *Quercus* oak species, namely *Quercus spinosa* David and *Q. tarokoensis* Hayata, which dominate these plant communities. The former represents the oak species that grows at the highest elevations in the subalpine zones of Taiwan, ranging from 2300 m up to 3200 m (Hsu et al. 2001). Another form, namely *Q. “tatakaensis”*, is

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sometimes treated as a distinct species (e.g. Liao 1994, 1996), but is regarded as an ecotype or phenotype of *Q. spinosa* by others (e.g. Yang et al. 1997; Covaerts and Frodin 1998). Its leaf is sclerophyllous, but is less tomentose, and longer compared with typical *Q. spinosa* (Liao 1994, 1996). This insular population of subalpine sclerophyllous oak is widely separated from those in south-western China (Covaerts and Frodin 1998), but its origin has thus far not been discussed. Moreover, although it represents the dominant vegetation type in the subalpine zone in Taiwan, practically no lepidopterological survey has been performed in this peculiar forest type.

In Taiwan, the tribe Theclini of Theclinae demonstrates the highest diversity amongst lycaenid butterflies. With 25 described species, it represents nearly a quarter of the overall lycaenid diversity, which has approximately 100 resident species on this island (Shirôzu and Ueda 1992). In general, the Theclini lycaenids rely heavily on the oak family, Fagaceae, as their larval hosts (Hsu and Liu 2002). Among the 24 species for which the larval hosts are known, 18 species are specialist feeders on Fagaceae, and all of them are monophagous or oligophagous, utilizing very limited host plant species (Uchida 1999). Nevertheless, none of these Taiwanese species was known to be associated with sclerophyllous oaks. So far, only species in the genera *Teratozephyrus* Sibatani, 1946 and *Esakiozephyrus* Shirôzu and Yamamoto, 1936 of the Theclini are known to be specialists on sclerophyllous oaks (Koiwaya 1996a). In Taiwan, two species of *Teratozephyrus* are currently known; *T. arisanus* is a well-known broad-leaved oak feeder (Uchida 1999), and its populations in continental China also have the same host association (Koiwaya 1996a). The other species, namely *T. yugaii*, is superficially similar to the sclerophyllous oak-associated species in western China, but Uchida (1999) has proven that the larval host of *T. yugaii* is the evergreen broad-leaved *Q. stenophylloides* Hayata. Intrigued by the discrepancy between *Teratozephyrus* and the rich presumed host resource in Taiwan, we postulated that there may be a representative of *Teratozephyrus* associated with the subalpine sclerophyllous oak forest. Therefore, during the past 2 years, field observations on the bud-breaking phenology of the oak species in the subalpine sclerophyllous oak forest were made, followed by sampling at a selected study site to determine whether there is any temporal differentiation which provides a potential larval food resource by different oak species for *Teratozephyrus* in the plant communities. *Q. "tatakaensis"* is provisionally regarded as a distinct species in this study. A survey on the sclerophyllous oaks for their associated lepidopterous insects was conducted at the same time.

Material and methods

Study site and period

Preliminary observations on bud-breaking phenology were carried out during 2002, with the search for Theclini lycaenids and other lepidopteran insects associated with these sclerophyllous oaks initiated at the same time. A study area at Xiulin (=Shiulin, altitude 2335 m), Hualian County, Taiwan (approximately at 120°20' E, 24°12' N), was selected because the evergreen broad-leaved *Q. stenophylloides*, and the sclerophyllous *Quercus spinosa* and *Q. "tatakaensis"* were sympatric, and immature material of *Teratozephyrus* was found. The study area is approximately 1500 m × 60 m.

Bud-breaking phenology

Oak trees found at the study site were randomly sampled during 2000 to investigate bud-breaking phenology. Trees of the *Quercus "tatakaensis"* ecotype were sampled separately.

The length of new shoots was taken as the measurement of host plant availability for the larva of *Teratozephyrus*, because Theclini larvae are known to be specialized for feeding on fresh and soft leaves (Fukuda et al. 1972). Leaf size is not considered to be a good indicator because in these oak species it varies considerably both within and among species (Liao 1994). Sampling was stopped when leaves became hardened.

Sampling of Theclini lycaenids and the other phytophagous insects

Eggs of *Teratozephyrus* were collected in winter and brought back to our laboratory at the Department of Life Science, National Taiwan Normal University at Taipei, then stored at 8°C. They were brought out for hatching when budding of the hosts began at the study site. Samples of *Teratozephyrus* larvae and the other lepidopterans were collected at the same time that observations of bud-breaking were made. Larvae were reared in plastic containers (15 × 8 × 4.5 cm). The rearing records adopted the system used by Powell and De Benedictis (1995). Each collection of immatures was labelled according to the collecting year and month: e.g. 01F16 refers to the 16th collection in June 2001. This system employs alphabetical letters to represent months in sequence. The other reared oak-feeding insects were identified and saved for other studies.

Taxonomic methods

The emerged *Teratozephyrus* specimens were compared with all the described species of the genus using specimens, including types, deposited in various institutes as well as literature to determine the taxonomic affinity of the material. Dissection of genitalia was performed by removing the entire abdomen and placing in 10% KOH at room temperature for 24 h to dissolve the soft tissue, then transferring it to cellusolve for another 24 h for descaling, before finally placing it in 70% ethanol for dissection. The dissected parts are preserved in 70% ethanol. A ISI ABT DS-130S was used for scanning electron microscopy (SEM) illustration. Terminology follows Nijhout (1991) for wing patterns, Klots (1970) for genitalia and Stehr (1987) for chaetotaxy of larvae. Types of the new taxon are deposited in the following institutes: BMNH, The Natural History Museum, London; IOZ, Institute of Zoology, Chinese Academy of Sciences, Beijing; NTNU, National Taiwan Normal University, Taipei; NMNS, National Museum of Natural Science, Taichung. Additional specimens for comparison were obtained from the above institutions and SEHU (the Matsumura Collection at Systematic Entomology Laboratory, Hokkaido University, Sapporo).

Results

Bud-breaking phenology

The timing of bud-break and growth of the new shoots of the oak species at the study site in 2002 is shown in Figure 1. The budding of *Quercus stenophylloides* was about 5 weeks earlier than in *Q. spinosa* and *Q. "tatakaensis"*, which did not initiate until the leaves of *Q. stenophylloides* were nearly mature. The result shows that there is a considerable time gap in availability of the potential food resource for oak-associated Theclini larvae at the study site.

Systematic accounts of Teratozephyrus found at the study site

Immatures of *Teratozephyrus* were found on all oak species at the study site. Two species are recognized; one is associated with *Q. stenophylloides* (Hsu no. 00E21, 01E48) and the other

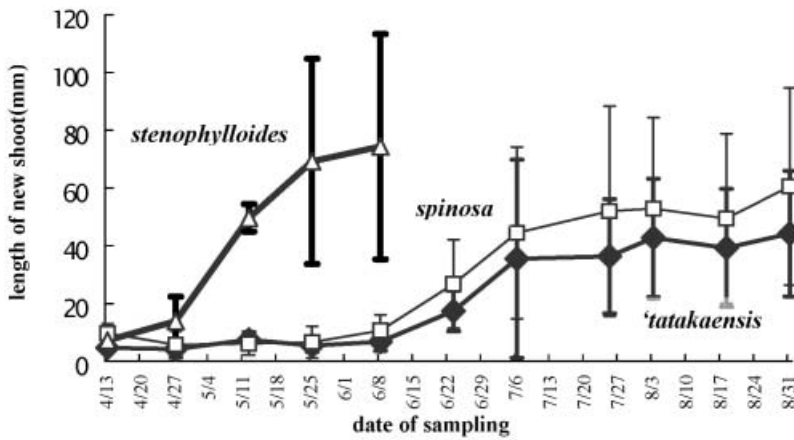


Figure 1. Bud-breaking phenology of the *Quercus* species growing at Guanyuan, Hualian Co., Taiwan, 2002. Bars represent standard errors.

is specific to *Q. spinosa* (Hsu no. 00E22, 01E46, 01F16, 02E37), with the former matching the current concept of *T. yugaii*. Samples of *Teratozephyrus* were also obtained from *Q. 'tatakaensis'*, but the quantity was too small to make a legitimate taxonomic comparison, so they are left out of this article. As a problem on the identity of the type of *T. yugaii* became apparent during the study, a discussion on the type specimens of *T. yugaii* and the other relevant names are given herein.

Problems involving the type of "Zephyrus yugaii" Kano

Prior to elucidating the identity of *Q. spinosa*-associated *Teratozephyrus*, nomenclature involving the similar species *T. yugaii* needs to be clarified. Currently two available names are synonymized with *T. yugaii* (Kano, 1928), namely *shirakiana* Matsumura, 1929 (holotype, ♂, SEHU) and *niitakana* Matsumura, 1929 (holotype, ♀, SEHU). After Kano (1928) described "*Zephyrus yugaii*", Matsumura (1929) treated both of the two taxa he described as infraspecific names of "*Zephyrus hecale*". Araki and Sibatani (1941) firstly synonymized both of Matsumura's names with *yugaii*, and still considered *yugaii* a subspecies of *hecale*, which was subsequently transferred to *Teratozephyrus* by Shirôzu and Yamamoto (1956). Fujioka (1994) revised the genus *Teratozephyrus*, and elevated *T. yugaii* to specific level based upon genitalic characters, with this species being endemic to Taiwan. Having examined the unique types of *shirakiana* and *niitakana*, we have no doubt that they are conspecific and also identical to the *Q. stenophylloides*-associated species, but not to the *Q. spinosa*-associated one. However, the key problem is that there is no available information about the whereabouts of the type specimen of *yugaii* Kano, the oldest of the three names. In a project to establish a database for endemic Taiwanese butterflies sponsored by the Council of Agriculture of Taiwan, all efforts to locate it at various institutions in Taiwan and Japan have been in vain. It was not until we carefully compared the data on the labels of Matsumura's types and the literature dealing with Kano's early expeditions in Taiwan that we gained some additional insights into this problem, which needs to be solved before the systematics of the *Q. spinosa*-associated *Teratozephyrus* in Taiwan can be worked out. In the original description of "*Zephyrus yugaii*" by Kano

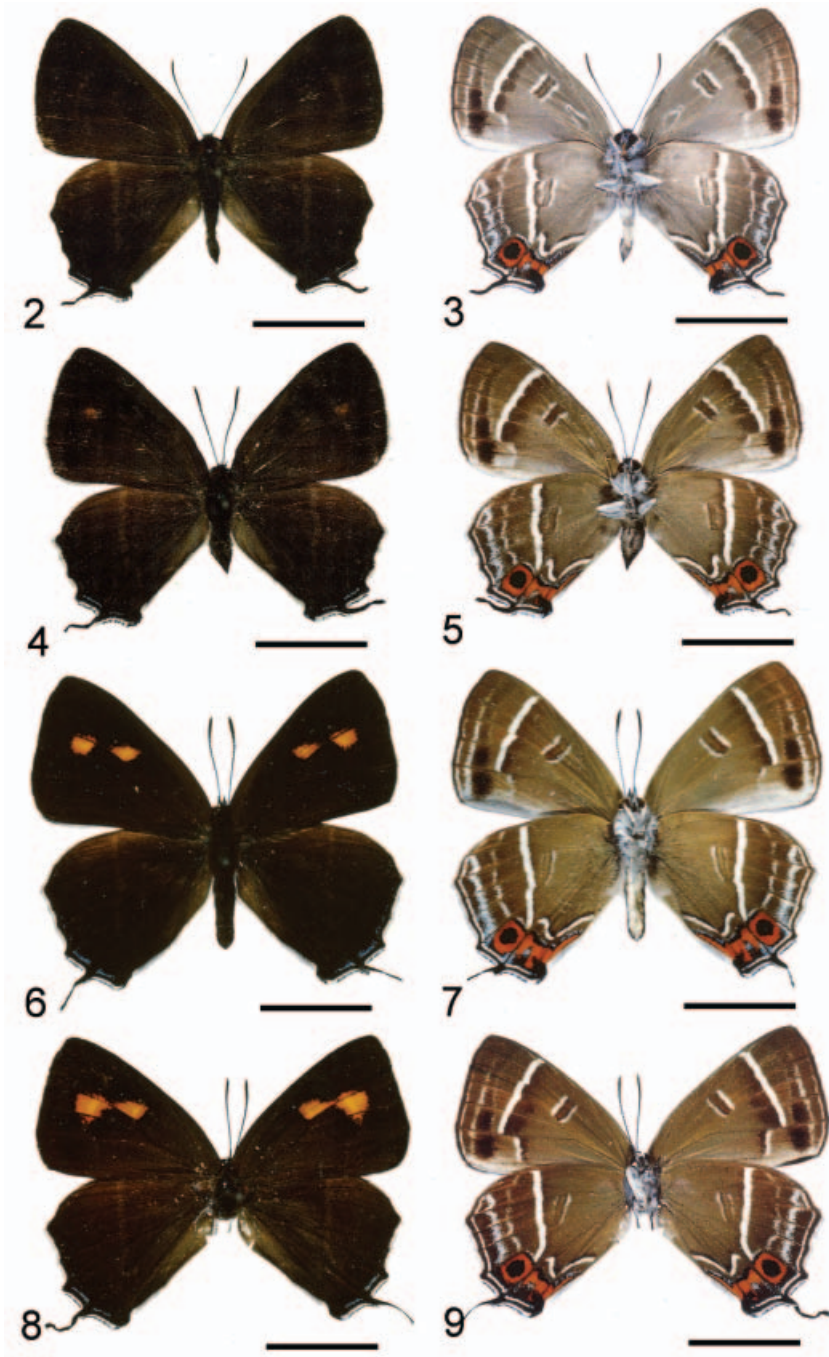
(1928), no specimen depository was specified. The description contained only three sentences and no illustrations. The single specimen on which Kano based his description was collected from the top of “Niitaka” (now Yushan, literally Jade Mountain) on 14 and 15 July 1927. Although no specimen with such a label has been located, we did find the type specimen of “*Zephyrus hecale niitakana*” which was collected by Kano, and bears a label reading “Kano 11. X, 1926 Niitaka”. Moreover, in the original description of “*Z. hecale niitakana*”, Matsumura (1929) states the data of the type as “... collected on the 11th of October, 1926, at top of Mt. Niitaka by T. Kano”. On the other hand, in Kano’s (1928) review of the faunistic research history of the Niitaka area, he clearly pointed out that he had several trips to the area in “April, 1926” and “May and July, 1927”, and only during the July 1927 trip did he twice visit the top of Niitaka. Thus it is evident that Kano could not have collected Matsumura’s “*Z. hecale niitakana*” type in October of 1926 as he did not reach the area at that time. Therefore, we came to the conclusion that the collecting data on the label of the type for “*Z. hecale niitakana*” is probably erroneous, that this specimen is the holotype of “*Zephyrus yugaii*”, and that “*Zephyrus yugaii*” Kano and “*Z. hecale niitakana*” Matsumura, which were described based on the same type specimen, are objective synonyms. *T. yugaii* Kano takes the nomenclatural priority and can be applied to the *Q. stenophylloides*-feeding *Teratozephyrus* in Taiwan.

Based upon the above discussion, no name is available for the *Q. spinosa*-associated *Teratozephyrus* in Taiwan. Having compared the material with all the other described taxa of the genus, we have reached the conclusion that it represents a new species, which is described below.

***Teratozephyrus elatus* n. sp.**

(Figures 2–5, 10–16, 20)

Description. Male (Figures 2, 3): FL 15.2–17.3 mm (mean 16.2 ± 0.8 mm, $n=5$); AL 7.3–8.2 mm (mean 7.8 ± 0.4 mm, $n=5$). Head: hairy, vertex, frons dark brown but with white mesad; a white, narrow rim surrounding eye; eye semi-oval, densely covered with long, buff setae; labial palpus correct, with third segment pointed downwards and much shorter than second segment, covered with white scaling mottled with black; scales on venter slender, long and hair-like; maxillary palpus reduced, invisible; proboscis unscaled, pale buff in colour; antenna smoothly scaled, naked at terminal end of nudum and along inner surface distad where short trichoid sensilla present. A pair of white dots at base of most flagellomeres, but attenuate toward nudum. Thorax: buff dorsad, white ventrad; tegulae covered by buff tinged with red hairs; legs covered with white scales, mottled with brown. Fore wing: termen, costa slightly concave, dorsum nearly straight. Ground colour of upperside uniformly dark brown, with underside markings barely visible by transparency. Ground colour of underside grey. Discal spot forming brown bar edged with white. Distal band of central symmetry system represented as tilted, uneven white line edged with prominent brown band proximally, running from costa toward Cu_2 ; white scales with tendency to extend basad, intersecting brown band. Submarginal band and “g”-element as defined by Nijhout (1991) fused into prominent, dark brown band edged with white, attenuate toward apex. Fringe with white cilia. Hind wing: contour of wing slightly produced at distal end of M_1 , M_3 and Cu_1 ; Cu_2 bearing long, “tail”-like projection distad (length 4.6 ± 0.3 mm, $n=5$). Ground colour of upperside uniformly dark brown, overlaid with metallic blue scaling distally in cell Cu_1 and Cu_2 , with underside markings visible by transparency. Ground colour of underside grey. Discal spot forming brown bar edged with white. Distal band of central symmetry system forming prominent white line edged with



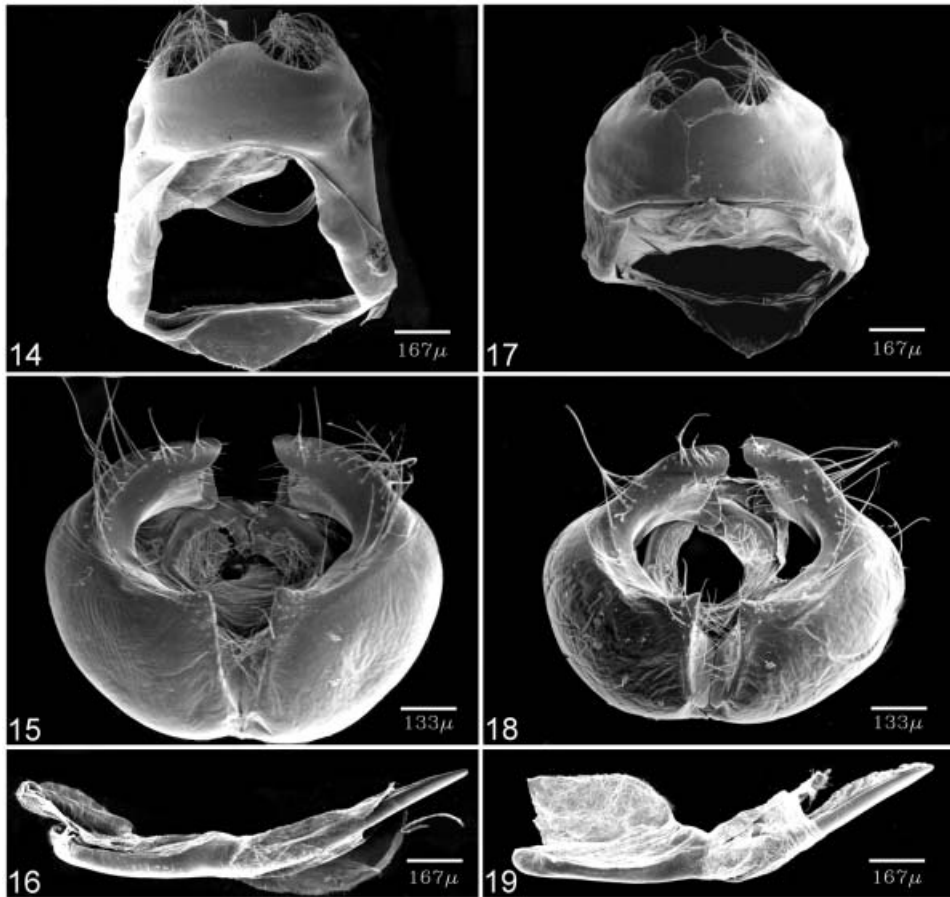
Figures 2–9. (2–5) *Teratozephyrus elatus*, n. sp.: (2) ♂ holotype, upperside; (3) ♂ holotype, underside; (4) ♀ paratype, upperside; (5) ♀ paratype, underside. (6–9) *Teratozephyrus niwai* Koiwaya: (6) ♂, upperside; (7) ♂, underside; (8) ♀, upperside; (9) ♀, underside. Scale bars: 10 mm.



Figures 10–13. Immatures of *Teratozephyrus elatus*, n. sp. (10) Ovum; (11) First instar larva; (12) Last (final) instar larva; (13) Pupa.

brown proximally, nearly straight but uneven, from dorsum to vein Cu_2 , re-bent three times in cell Cu_2 , forming a prominent “W”-shaped band. Proximal band of central symmetry system obsolete. Submarginal band consisting of faint, broad white band, a black, round dot enclosed within orange circle in cell Cu_1 , and a tornal orange patch in cell Cu_2 , both edged by black scales basad. “g”-Element forming a faint white line, mixed with some metallic blue scaling toward dorsum. Tornus with prominent black scalings. Fringe with white inner cilia, dark brown outer cilia. Abdomen: dark brown dorsad, white ventrad. Male genitalia (Figures 14–16): ring-shaped sclerites of 9+10 segments with width approximately $0.5 \times$ height, posterior end forming triangular flap dorsad of brachium; uncus a medial bump; saccus thin, flap-shaped; brachium simple, hook-shaped; valva broad, with prominent ridge ventrally; harpe forming a slightly concave cone-shaped bump; ampulla strongly curved, arm-shaped with posterior surface setose, distal end bifurcate, forming a thick, dorsal lobe with truncated end and a thin, tongue-shaped, ventral lobe. Phallus slender, upcurved posteriorly with pointed caudal end; aedeagus approximately $1.3 \times$ phallobase, cornuti absent. Juxta narrow, nearly circular but open dorsad.

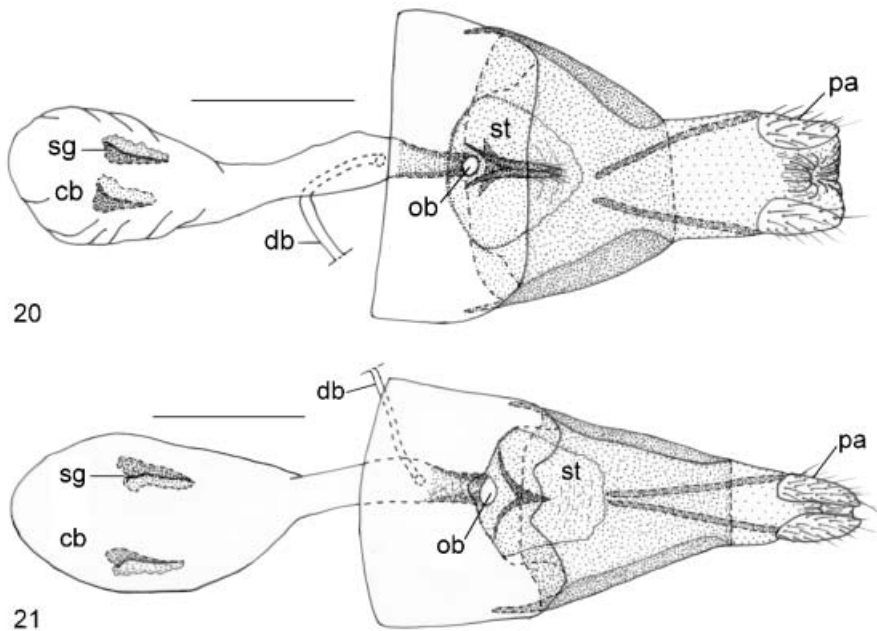
Female (Figures 4, 5): FL 16.4–17.6 mm (mean 17.2 ± 0.5 mm, $n=4$); AL 6.8–7.6 mm (mean 7.3 ± 0.3 mm, $n=4$). Body, wing patterns as described for male except scalings of underside buff, forewing upperside with a couple of barely visible orange spots in proximal end of M_2 and centre of M_3 . “Tail”-like projection of hind wing longer than that of male (length 4.7–5.2, with mean 4.9 ± 0.2 mm, $n=4$). Anterior margin of eighth tergum forming elongate, digitate process. Genitalia (Figure 20): papillae anales weakly sclerotized, oval, setose. Apophyses posteriores slender, elongate, slightly flattened at base. Sterigma forming a broad, dome-shaped, sclerotized plate containing a prominent medial, inverted, pin-like,



Figures 14–19. Male genitalia of *Teratozephyrus* spp. (14) Dorsal view of 9th and 10th segment of *Teratozephyrus elatus*, n. sp. (15) Ventral view of valvae of *T. elatus*, n. sp. (16) Phallus of *T. elatus*, n. sp. (17) Dorsal view of 9th and 10th segment of *T. nuwai*. (18) Ventral view of valvae of *T. nuwai*. (19) Phallus of *T. nuwai*.

heavily sclerotized process lying caudad and dorsad immediate of ostium. Terminal end of this process setose, bifurcate. Ductus bursae sclerotized caudad, with ductus seminalis joining immediately ahead of this sclerotized part. Corpus bursae oblong, bearing a pair of prominent, invaginated, axe-shaped signa

Immature stages: ovum (Figure 10) approximately 0.77 ± 0.02 mm in diameter, 0.49 ± 0.02 mm in height ($n=15$), spherical but slightly compressed, chorion densely covered with minute spicules, micropyle as a prominent depression dorsad, white in colour. Larva: first instar (Figure 11): body grey in colour with long, transparent primary setae, turning pale green by first moult. Legs brown. Head, T1 shield, anal lobe dark brown. T1 shield ladder shape, anal lobe pentagonal. Primary setae as follows: on T1 shield, XD 1 longer than XD2, D1 longer than D2, SD1 and SD2 not visible. L1, L2, L3 forming a straight horizontal line. On T2 and T3, D1 longer than D2, SD1 minute, SD2 absent, D1, D2 and SD1 forming a straight vertical line. L setal group forming a straight tilt line. On A1–A6, D1 longer than D2, SD1 and SD2 minute, both above spiracles. L2 shortest in L setal group, anterodorsad of L1 and L3, L1 longest. On A7 and A8, D2, SD1, SD2 absent.



Figures 20, 21. Female genitalia of *Teratozephyrus* spp. (20) *T. elatus*, sp. n. (21) *T. nuwai*. cb, corpus bursae; db, ductus bursae; sg, signum; ob, ostium bursae; st, sterigma; pa, papillae anales. Scale bar: 1 mm.

L setae as those of A1–A6. SV setal group bisetose on T1, unisetose on T2–A8. Second to fourth (final) instar (Figure 12): head brown with dorsal half pale brown tinged with yellow. Cranial sutures white. Body densely covered with short, brown or transparent secondary setae. Ground colour green with lateral, yellow chevrons, prominent yellow, longitudinal double lines present dorsad toward maturity. T1 shield, anal lobe turning green. Spiracles white. Newcomer's organ and eversible tentacles absent. Body colour turning dark green tinged with blue upon pupation. Full-grown larva 15.9 ± 0.65 mm in body length ($n=6$). Pupa (Figure 13): of typical lycaenid type, surface wrinkly, covered with short brown setae. Ground colour pale brown mottled with dark brown markings. A pair of prominent dark brown dots present on T2 dorsad. A longitudinal medial band present on abdomen dorsad. Pupal length approximately 10.32 SD 0.34 mm ($n=6$).

Phenology. Adults have yet to be observed in the wild. Field-collected larvae emerged in June.

Bionomics. The egg is laid near the base of the dormant buds of the host, approximately 30 cm up to 4 m above the ground. Larvae eclose in spring, devouring only soft tissues of the host. Older larvae possess the midrib-cutting behaviour shared by many Theclini lycaenids (Koiwaya 1996a; Hsu 2002; Hsu and Liu 2002). Larva pupated under fallen leaves under laboratory conditions.

Diagnosis. Based upon genitalic structure, *Teratozephyrus nuwai* Koiwaya (1996b) (Figures 6–9) from western China is evidently the sister species of *T. elatus*; both species share a shallowly bifid ampulla at distal end of valva and single, short, medial bump-like uncus in

male (Figures 14–19). *Teratozephyrus arisanus* (Wileman, 1909) and *T. tsukiyamahiroshii* (Fujioka, 1994), plus all species of the closely related *Esakiozephyrus* and *Iwaseozeohyrus* Fujioka, 1994 possess a bifurcate uncus. The unci of the remaining described *Teratozephyrus* species are elongate (Fujioka 1994), in contrast to the short, bump-like condition found in *T. nuwai* and *T. elatus*. *Teratozephyrus elatus* can be distinguished from *T. nuwai* by: (1) there are a pair of prominent orange spots on the fore wing upperside in both sexes of *T. nuwai* (Figures 6, 8), whereas those spots are greatly reduced or obsolete in *T. elatus* (Figures 2, 4); (2) ground colour of wing underside is buff in both sexes of *T. nuwai* (Figures 7, 9), whereas it is sexually dimorphic in *T. elatus*, buff in female (Figure 5) but grey in male (Figure 3); (3) inverted, funnel-shaped process of sterigma is longer than that of signum, with its caudal end setose and bifurcate in *T. elatus* (Figure 20), whereas it is shorter than that of signum, with caudal end pointed in *T. nuwai* (Figure 21); and (4) signa are axe-shaped in *T. elatus* (Figure 20), in contrast to sickle-shaped in *T. nuwai* (Figure 21). Within Taiwan, only *Teratozephyrus yugaii* is superficially similar to *T. elatus* in appearance, but their genitalic structures indicate they are not the most closely related to each other. They can be distinguished by the following characters: (1) the edges of the white lines on the wing undersides are uneven in *T. elatus*, but even in *T. yugaii*; (2) outer cilia of hind wing is white in *T. elatus*, whereas it is buff in *T. yugaii*; (3) distal end of valva is shallowly bifid in *T. elatus*, but deeply bifurcate in *T. yugaii*; (4) uncus of *T. elatus* is short and bump-like, whereas it is prominently protruded and digitate in shape in *T. yugaii*; and (5) sterigma forms a dome-shaped, sclerotized plate with a slender, pin-like medial process in *T. elatus*, whereas it forms an elongate, spade-shaped plate with a robust, triangular medial protrusion in *T. yugaii*.

Type material. Holotype: ♂, Taiwan: Hualien Co., Xiulin, Guanyuan, 2335 m, 16 May 2002, coll. Y. F. Hsu, emerged 3 June 2002, reared from *Quercus spinosa* (Hsu no. 02E 37, BMNH). Paratypes: 2♂, same locality as holotype, 19 May 2000, coll. Y. F. Hsu, C. C. Lu, C. Y. Hung, emerged 17/18 June 2000, reared from *Quercus spinosa* (Hsu no. 00E22, 1♂ genitalia preparation YFH 1219, NTNU); 1♀, 26 May 2001, coll. Y. F. Hsu, emerged 26 June 2001, reared from *Quercus spinosa* (Hsu no. 01E46, NTNU); 1♂, 10 June 2001, coll. Y. F. Hsu, emerged 27 June 2001, reared from *Quercus spinosa* (Hsu no. 01F16); 1♂, 16 May 2002, coll. Y. F. Hsu, emerged 3 May 2002, 2♀, emerged 5 May 2002, 1♀, emerged 6 May 2002, reared from *Quercus spinosa* (Hsu no. 02E37, BMNH, NMNS, IOZ).

Additional material. 1♂, 1♀ (wings distorted), same locality as holotype, 19 May 2001, coll. Y. F. Hsu, C. C. Lu and C. Y. Hung, emerged 18 June 2000 (Hsu no. 00E22, genitalia preparation YFH 1234 ♂/1235 ♀).

Other phytophagous insects associated with the sclerophyllous oak community

During our survey, we also found the following phytophagous species associated with sclerophyllous oak communities: *Phyllonorycter* sp. (Gracillaridae) (HSU 02E38) and a leaf beetle (Chrysomelidae) (HSU 02E39) on *Q. spinosa*, plus leaf mines of a species of *Phyllonorycter* (Gracillaridae) (HSU 02E40) and a *Stigmella* species (Nepticulidae) (HSU 02E41) on *Q. "tatakaensis"*.

Discussion

Besides *Q. spinosa*, there are another two species of evergreen sclerophyllous oaks growing on Taiwan (Liao 1994, 1996). Of them the endemic *Q. tarokoensis* is a low-elevation

species, ranging from 300 to 1250 m, thus unlikely to be a host resource for *T. elatus* as populations of this plant are out of reach for this butterfly. As a matter of fact, very few, if any, Theclini species inhabit low-elevation forests on this island (Uchida 1999). The other species, *Q. "tatakaensis"*, has a distributional range from 1500 up to 2600 m (Liao 1994, 1996), yet no difference in the budding phenology between it and typical *Q. spinosa* was observed at the study site (Figure 1). Subsequently, no matter whether *Q. "tatakaensis"* is considered a distinct oak species or not, there is no phenological difference as a potential larval food resource between this oak "form" and *Q. spinosa*. Ova of *Teratozephyrus* were collected from *Q. "tatakaensis"*, but at much lower frequency, and only a few female adults were subsequently reared out. We excluded these specimens from the type series of *T. elatus* for there were no male specimens available, but anticipate *Q. "tatakaensis"* may be a secondary, alternative host for *T. elatus*, if this material proves to be conspecific with *T. elatus*.

The distribution of the sclerophyllous *Q. spinosa* is widely disjunctive, with populations found in Taiwan and north-central to south-west continental China and Burma (Covaerts and Frodin 1998). The origin of the insular populations of this oak in Taiwan has yet to be investigated. Disjunctive distributions reflect past events, such as long distance dispersal over geographic barriers, crustal plates that drifted apart or once widespread taxa that have been reduced to surviving remnants (Brown and Lomolino 1998). It is well known that the island of Taiwan was created by an uplift due to a collision termed the Penglai Orogeny (Ho 1986) about 4 million years ago (Hsu 1990). This rules out the possibility that its sclerophyllous oak is a product of crustal plate movements. The discovery of *Teratozephyrus elatus* suggests that the insular populations of *Q. spinosa* are unlikely to be a product of long distance dispersal via natural pathways as no stages in the life history of *T. elatus* could be attached to dispersing acorns, which are the only dispersal agent of this oak that can be brought by flying animals such as birds. In addition, the fact that leaf mines of a species of *Phyllonorycter* (Gracillaridae), a *Stigmella* species (Nepticulidae) and a leaf beetle species (Chrysomelidae) were observed on *Q. spinosa* and *Q. "tatakaensis"* during the survey further rejects the possibility that insular populations of these sclerophyllous oaks under alpine/subalpine conditions in Taiwan originated from long distance dispersal, because a balanced diversity of associated fauna is not expected to be present with a long distance dispersal event. Thus the most reasonable explanation for the existence of the alpine/subalpine sclerophyllous oaks and phytophagous insect fauna associated with them in Taiwan is that they represent relict distribution resulting from the reduction from previous wider and continuous distribution with the Asiatic continent when Taiwan was connected to mainland China during previous glacial stages. Geological evidence suggests that Taiwan was connected to the Asiatic mainland for several periods of time during the Cenozoic (Shaw 1996), and many terrestrial organisms have a continental origin, although some have evolved into distinct endemic forms (Liu 1989). It is noticeable that *T. elatus* already shows many distinct morphological differences from its sister species, *T. nuwaii*, in western China, and the population of *Q. spinosa* in Taiwan is sometimes given a subspecies status (e.g. Covaerts and Frodin 1998).

Combining the checklist provided by Koiwaya (1999) and *Teratozephyrus elatus* described in the present study, the genus *Teratozephyrus* contains nine species in total. Of these, three species are known to be associated with sclerophyllous oaks, namely *T. nuwaii* with *Quercus spinosa* (Koiwaya 1996a) from China, *T. elatus* with *Q. spinosa* (the present study) from Taiwan, and *T. hecale* with *Q. engleriana* Seemen (HSU 01E70) from China. Two species are associated with the evergreen broad-leaved oaks, namely

T. arisanus with *Q. stenophylloides* (Uchida 1999) and *Q. myrsinaefolia* Blume (Koiwaya 1996a), and *T. yugaii* with *Q. stenophylloides* (Uchida 1999). Morphology of *T. arisanus* deviates from the rest of the species in the genus (Fujioka 1994), and *T. arisanus* is exclusively associated with montane evergreen broad-leaved forest both in continental China (Koiwaya 1996a) and Taiwan (Uchida 1999). *T. yugaii* and *T. elatus* can be found sympatrically in Taiwan, but they are not closely related to each other and they are

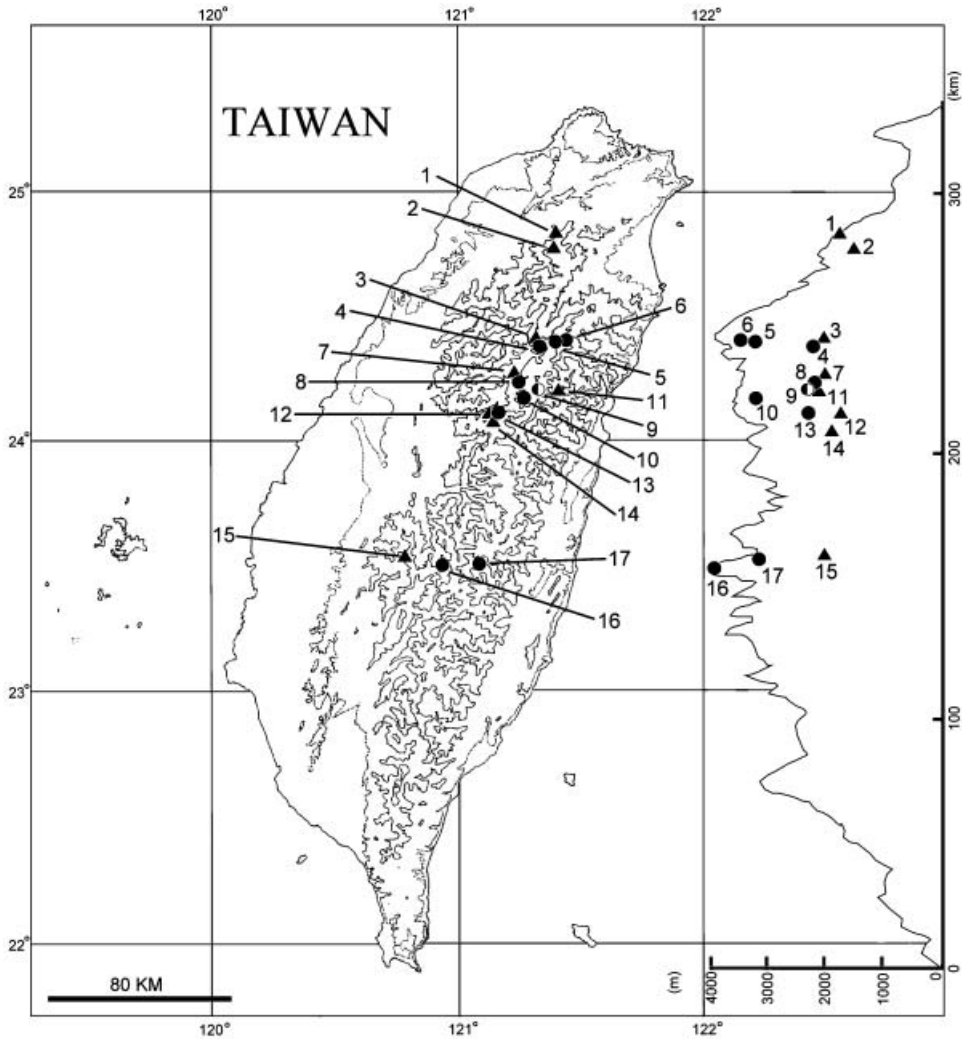


Figure 22. Distribution of *Teratozephyrus* species in Taiwan. Circle denotes *T. yugaii*; semi-open circle *T. yugaii* plus *T. elatus*; triangle *T. arisanus* (data resource: Yamanaka 1980; NTNU specimens). Locality list: 1, Taipei Co.: Sanxia, Beichatianshan, ca 1700 m; 2, Taipei Co.: Wulai, Lalashan, ca 1500 m; 3, Ilan Co.: Datong, Siyuanyakou, ca 2000 m; 4, Ilan Co.: Datong, Siyuanyakou, ca 2100 m; 5, Taizhong Co.: Heping, Shenmazhenshan, ca 3100 m; 6, Taizhong Co.: Heping, Nanhubeishan, ca 3500 m; 7, Taizhong Co.: Heping, Lishan, ca 2000 m; 8, Nantou Co.: Renai, Biluxi, ca 2300 m; 9, Hualian Co.: Xiulin, Guangyuan, 2335 m; 10, Nantou Co.: Renai, Keinanguan, ca 3200 m; 11, Hualian Co.: Xiulin, Bilu, ca 2100 m; 12, Nantou Co.: Renai, Songgang, ca 1900 m; 13, Nantou Co.: Renai, Meifeng, ca 2100 m; 14, Nantou Co.: Renai, Cuifeng, ca 2300 m; 15, Jiayi Co.: Alishan, ca 2100 m; 16, Jiayi Co.: Alishan, Yushan, 3950 m; Jiayi Co.: Zhoushe, Dashuiku, 3200 m.

associated with different oak hosts. Although *T. yugaii* is associated with the same host utilized by *T. arisanus* in Taiwan, they have never been found sympatrically in the same forest community, with the former occupying higher elevations (Figure 22) (Uchida 1999). The genitalia of *T. yugaii* have many peculiar characters among *Teratozephyrus* (Fujioka 1994), and so far it has not been possible to determine its most closely related taxon on a morphological basis. The question regarding the origin and biogeography of this species awaits answers provided by future phylogenetic studies involving *Teratozephyrus* and related genera such as *Esakiozephyrus* and *Iwasozephyrus*. Nevertheless, as noted already, three species of *Teratozephyrus*, plus a species of *Esakiozephyrus*, are known to use the sclerophyllous oaks as specific larval hosts, leading to the speculation that such host-usage strategy may be a ground plan shared by these two genera. A few recent phylogenetic studies on oaks suggest the sclerophyllous oaks may form a monophyletic group (e.g. Nixon 1993; Manos et al. 1999); therefore the common ancestor of *Teratozephyrus* and *Esakiozephyrus* might already have colonized and specialized on sclerophyllous oaks as larval hosts. If this turns out to be the case, the acquisition of evergreen broad-leaved oak as the larval host by *T. yugaii* is secondary. It is worth mentioning that although *Q. stenophylloides* ranges well down to 900 m altitude, no *T. yugaii* was ever recorded below 2000 m in elevation (Figure 22), suggesting the species is adapted to cooler habitats. The fact that the most closely related species of *T. elatus* is not *T. yugaii* demonstrates *T. yugaii* could not have evolved from a common ancestor shared by these two taxa; it seems more plausible that it was derived from an ancestor inhabiting cool environments either from continental Asia or within Taiwan. It is intriguing to observe that no species related to *T. yugaii* has yet been discovered in southern China, where a high diversity of evergreen broad-leaved oaks occurs (Li 1996; Hsu and Jen 1998), further endorsing the statement that *T. yugaii* is not likely to have derived from an ancestor associated with that type of vegetation. In contrast, *T. arisanus* is found across southern China and Taiwan, exclusively associated with the evergreen broad-leaved forests, and certainly had an origin in association with this vegetation type. No matter where *T. yugaii* originated, it probably was originally associated with non-evergreen broad-leaved oaks, and acquired the current host association along its evolutionary history.

Teratozephyrus elatus is the first known butterfly species that is exclusively associated with the sclerophyllous oak forests in Taiwan. Although it is still premature to estimate whether a high diversity of phytophagous specialist insect community is present in this well-defined vegetation type in Taiwan, the discovery of gracillarid species, which are usually host-specific (Powell et al. 1998), suggests that more host-specific Lepidoptera are to be expected from the sclerophyllous oak forests on the island.

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