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Taiwan's Dacini fruit flies: rare endemics and abundant pests, along altitudinal gradients

By Camiel Doorenweerd*, Luc Leblanc, Yu-Feng Hsu, Chia-Lung Huang, Yu-Chi Lin, Michael San Jose and Daniel Rubinoff

Abstract

Taiwan is at the north-eastern limits of the Asian center of diversity for fruit flies in the tribe Dacini, and the country has several endemic species. Between 2013–2015, we surveyed the diversity of dacine fruit flies in Taiwan using kairomone baited traps and found fifteen species. We report four species for the first time in Taiwan and figure them: *Bactrocera nigrifacia* Zhang, Ji & Chen 2011, *B. rubigina* (Wang & Zhao 1989), *B. dorsaloides* (Hardy & Adachi 1954) and *B. bhutaniae* Drew & Romig 2013. For the species that are classified as pests, we explored how their spatial distribution correlates with elevation. The oriental fruit fly, *Bactrocera dorsalis* (Hendel 1912), is the most abundant pest on the island, but decreases sharply in abundance at higher elevations. Other pest species occur in much smaller numbers and respond differently to elevation and latitude. We also re-evaluated all records of previously recorded species and add our records to provide a checklist with thirty species of Dacini that occur in Taiwan. All species are regarded as native, six are endemic, and seven are agricultural pests. Historical records were georeferenced and plotted on maps along with records from the 2013–2015 survey to collate all known distribution data. We briefly discuss the state of knowledge of the fruit flies in Taiwan and how the distribution and host usage of Dacini may change in the future. Finally, considering the economic importance of the group, our understanding of their diversity and distributions is surprisingly poor.

*Corresponding Author E-mail: camiel.doorenweerd@hawaii.edu

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Introduction

Taiwan spans the 22nd to the 25th north parallel off the east coast of China and has a relatively small surface area of 36,193 km^2. Typically, the diversity of an island is a function of its surface area and the distance to the nearest large land mass, with increased island endemism with distance (eg Jønsson and Holt 2015, Merckx et al. 2015). The biodiversity of Taiwan, however, is extraordinarily rich for its size: its elongated north-south shape and steep central mountain range provide a remarkably diverse cline of abiotic factors. The northern areas have a temperate climate with four seasons, while the south is protected from winter cold and exposed to tropical conditions with wet and dry seasons, including frequent typhoons. Elevational gradients crossing the island from east to west go from sea level to 3,952 m at the highest point and steeply back to sea-level. The vegetation of Taiwan has accordingly been divided into many different forest types (Tsukada 1966). Subtropical rainforest occurs up to 500 m and is characterized by the tree genera: *Liquidambar*, *Trema*, *Mallotus* and *Diospyros*. Warm-temperate forest can be found between 500–1,800 m and has *Castanopsis*, *Cyclobalanopsis*, *Lauraceae*, *Theaceae* and tree ferns. Cool-temperate forest is found between 1,800–2,400m and supports *Quercus*, *Ulmus*, *Zelkova*, *Symplocos*, *Juglans*, *Carpinus*, *Salix* and a variety of conifers. Above 2,400 m is boreal forest, typically with *Tsuga*, *Abies*, *Picea* and *Pinus*. Because of historical connections to the continent, each climate zone boasts a fauna reflective of the temperature and precipitation climate regimes across the island. Taiwan grows tropical fruit trees and vegetables (e.g., Cucurbitaceae), but also deciduous fruit trees at higher elevations, all of which are potential hosts for a diversity of Dacini fruit flies across a remarkably small region.

Dacini fruit flies are all frugivorous or florivorous and the majority of the species cannot survive freezing winter temperatures. The group is most species-rich in the tropical and sub-tropical regions of South-East Asia and tropical Africa, and Taiwan marks the north-eastern boundary of the Asian center of diversity. Dacini are mostly known for their pest taxa, with approximately 90 species noted as pests on edible plants and fruits (Vargas et al. 2015), but this represents only about 10% of the group's entire diversity

(Doorenweerd et al. 2018). Shiraki (1933) published an extensive treatment of Tephritidae (as 'Trypetidae') of the Japanese empire, which at the time included Taiwan (Formosa), for which he listed 27 species, many of which were new to science. A more recent checklist of and illustrated keys to Taiwanese Dacini, by Tseng et al. (1992), included 35 species. Several of these species names have since been synonymized, mostly by Drew and Romig (2013). No checklists have been published in over 25 years, although the distribution and host preferences of *Zeugodacus tau* (Walker 1849), and partly those of *Z. cucurbitae* (Coquillett 1899), in Taiwan have been studied in detail (Liu and Lin 2001, Lin et al. 2005, Lin 2006, Lin and Liu 2012). Additionally, six of the common Dacini species in Taiwan, viz. *Zeugodacus synnephes* (Hendel 1913), *Z. cucurbitae*, *Z. tau*, *Z. arisanicus* (Shiraki 1933), *Z. cilifer* (Hendel 1912) and *B. dorsalis* (Hendel 1912), were included in a pictorial key (Lin et al. 2005).

Tephritidae are generally known for their elaborate, diagnostic, wing patterns, but Dacini are a notable exception to this rule and have mostly clear wings. The few other visible characteristics are often highly variable within species, making them notoriously difficult to identify (Drew and Romig 2013). There thus appears to be widespread convergent evolution in the group, especially in the polyphyletic *Bactrocera dorsalis* complex but, at present, little is known about potential evolutionary drivers that could be involved (White 2000, Leblanc et al. 2015a). Some of the species are known to be obligate pollinators of *Bulbophyllum* orchids (Tan and Nishida 2000, 2012), and while this has not yet been documented in Taiwan, 21 species of *Bulbophyllum* are present (EFloras 2018) with the potential for ecological and evolutionary relationships with Dacini. The diet breadth differs greatly between Dacini species, some are known to be monophagous, while others, primarily the pest species, are highly polyphagous, and for many there are no host records at all. Given the extreme ecological diversity of Taiwan, and its place at the edge of the Dacini's native diversity, it is of particular importance for understanding the factors affecting the biogeography of these important and diverse flies. We surveyed the diversity of Dacini fruit flies throughout the islands of Taiwan and Lanyu between 2013–2015 using kairomone baited traps. The attraction of male Dacine flies to plant-derived kairomones resulted from a mutually beneficial pollinator relationship with flowering plants, in particular orchids (Tan et al. 2002). The male flies sequester the

kairomones into compounds that enhance reproductive success (Royer et al. 2017) and incidentally provide an efficient way for surveying. To create an overview of the diversity, we re-evaluated all previously published species records, georeferenced them, and add our records to provide an up-to-date checklist and distribution maps that can function as a basis for further studies into evolutionary and ecological aspects of the group. We additionally explored how the abundance of species that are marked as pests follows elevational gradients, as a first step towards predictive modeling of species distributions.

Material & Methods

Collecting and collections

At the majority of the collecting localities, we used two bucket traps constructed from 5-oz urine sample cups containing either methyl eugenol (ME) or cue-lure (CL) [= synthetic analog of raspberry ketone] kairomone bait and a 10x10mm piece of dichlorvos insecticide strip attached to the lid using a hook made of 12-gauge galvanized wire (Leblanc et al. 2015b). At two sites, we placed an experimental third trap baited with zingerone (ZN) which attracts Dacini species not attracted to ME or CL (Royer et al. 2017). Zingerone was only used at two sites because at the time it was only recently discovered to be a potential attractant. Protein lures have been used in the past to target females of non-kairomone attracted species, however, we opted to not use protein traps because their range of attraction is small and not stronger than naturally present protein sources. Furthermore, protein traps would have required longer periods to be effective than our rapid assessments permitted, and frequently provide specimens with degraded DNA from mold and rot. The kairomone traps were set in transects alongside hiking trails or mountain roads and collected after two to five days in the field. Because our primary goal was to collect as much diversity as possible, and not compare collecting localities per se, we placed the traps across different habitats types and we did not use a predefined random or transect sampling scheme. One to 44 sets of 2–3 different traps were placed at each locality, depending on local

habitat variation and accessibility. We targeted natural areas because previous research has shown that this surveys agricultural pests as well, whereas agricultural areas lack the majority of non-pest species (Leblanc et al. 2016). In some cases, only methyl eugenol was used or specimens were collected by hand. It is important to note that although collecting flies using these attractants is efficient, species that are not attracted to any of the known lures will be missed. Previous workers may have found other species because they used other methods including sex attractants, food (protein) attractants, malaise traps, sweeping, and rearing flies from falling fruit (Shiraki 1933, Tseng et al. 1992). Given the broad geographic goals of our surveys, these methods were not practical since we wanted to cover a greater area of the island and more of its altitudinal range. Specimens collected during the 2013–2015 surveys are deposited in the University of Hawaii Insect Museum (UHIM) collection, representatives of each species are deposited in the National Taiwan Normal University Collection as well. Specimens were initially identified to species based on morphology and, for a subset of species representatives, DNA was extracted and a fragment of the mitochondrial COI gene was sequenced to verify identifications. Where the molecular results proved ambiguous, the morphology was re-examined and a total-evidence identification was made (Rubinoff and Holland 2005). Photographs were taken using a Nikon D7100 camera attached to an Olympus SZX10 microscope. Pictures from different focal plains were merged using Helicon Focus pro v6.7.1.

Checklist

Species in the checklist are presented by genus and species. The taxonomy and nomenclature of Dacini have recently been in flux (e.g. Schutze et al. 2015, 2017, Virgilio et al. 2015, San Jose et al. 2018), and we follow the classification as published by Doorenweerd et al. (2018). The most notable change of this classification compared to other works (e.g., Drew and Romig 2013) is the elevation of *Zeugodacus* Hendel to genus and assignment of all *Zeugodacus* subgeneric group species to this genus (De Meyer et

al. 2015). These changes, for the most part, do not impede the efficacy of the most recent dichotomous key that may be used to identify species for South-East-Asia (Drew and Romig 2016), and may be used for Taiwan. We list the known hosts from literature, except for the highly polyphagous species, for which we restrict the list to plant families. We apply the nomenclatural interpretations from The Plant List (Theplantlist.org 2018) for the host plant records. Country distribution records are compiled from Shiraki (1933), Tseng et al. (1992), Drew and Romig (2013), the Bernice Bishop Museum (Honolulu, Hawaii) collection and our 2013–2015 surveys.

Pest categories

To indicate the economic importance of the species, we use the four pest categories defined in Vargas et al. (2015): A- widespread invasive polyphagous generalists, or highly destructive specialists that have become established outside of their native range, B- polyphagous fruit pests or destructive specialists more restricted in distribution, but with invasive potential, C- oligophagous or specialist fruit or cucurbit pests that cause relatively minor damage and D- species that have been occasionally bred from commercial/edible fruit. It should be noted that these categories are defined based on invasion potential and the agricultural importance of host plants, and not on (potential) abundance in infested areas. Species outside the categories are those that are not known to attack any fruit or flowers that are edible, or, of commercial importance, and are indicated as 'non-pest'.

Maps and graphs

Bar plots and distribution maps were created using the Basemap, Pandas, Numpy and Matplotlib libraries for Python 2.7 distributed through Anaconda (2018). Only localities where both ME and CL traps were used were included for the gradient graphs. The 'World_Shaded_Relief' map from the ArcGIS Representational State Transfer (REST) Application Programming Interface (API) v10.11 service (ArcGIS 2018) was used as a base layer for the maps. Historical records from localities published in Shiraki (1933), Tseng et al. (1992) and Drew and Romig (2013) were georeferenced using Google Earth, when GPS coordinates were originally not provided. When the original record was not specific beyond a county, we did not include it in the maps. A

Github repository with the reproducible data and scripts is available at DOI: 10.5281/zenodo.1183808.

Results

Survey results

We conducted surveys in Taiwan between 2013 and 2015, with a total of 251 kairomone-baited traps set out along trails in 22 localities, 11 additional localities were opportunistically sampled by authors or collaborators (Fig. 1A). Zingerone baited traps were used in two localities only, 128 were baited with ME, and 118 with CL. Eight specimens of *Z. synnephes* were hand-caught across four different localities, and a single *B. dorsalis* was hand-caught. In total 8,023 specimens were collected and identified to species (for detailed collection records see Supplemental table 1 at DOI: 10.5281/zenodo.1183808). During the surveys, we collected fifteen of the thirty species known to occur in Taiwan. Four of the species we collected are new for Taiwan. The vast majority (94%) of collected specimens were *B. dorsalis* [7,527 individuals], followed by *Z. cucurbitae* (3%), *Z. synnephes* (2%) and *Z. tau* (1%) (Fig. 1B). The kairomone baits methyl eugenol and cue-lure attract different species with little overlap between the two. Methyl eugenol almost exclusively attracts *B. dorsalis* (Fig. 1C). In cue-lure traps there is more diversity, although three species [viz. *Z. cucurbitae*, *Z. synnephes* and *Z. tau*] together make up 91% of the specimens (Fig. 1D).

<<Fig. 1 near here>>

Altitudinal gradients

We explored the correlation between abundance and altitude for the five species that have been classified as pests. (Fig. 2A, B). The correlation differs between the species. *Bactrocera dorsalis*, a category A pest, was caught in large numbers but with a strong decline above 600 m where the subtropical forest is replaced by warm temperate flora. The four other pests that were encountered during our surveys were always collected in much smaller numbers. *Zeugodacus cucurbitae* is a category A pest that was mostly found below 200 m, *Bactrocera occipitalis* and *Zeugodacus tau* are classified as category B pests, and *Z. scutellatus* is a category C pest. *Zeugodacus tau* is present in relatively constant low numbers from sea-

level up to 1,500 m. *Zeugodacus scutellatus* is found in small numbers up to 1,200 m. *Bactrocera occipitalis* and *Z. cucurbitae* are not found above 1,000 m and are most abundant below 400 m. Localities above 1,800 m were not sampled because this group of flies is not known to occur at such high elevations at Taiwan's latitude.

<< Figure 2 near here>>

Checklist

Genus *Bactrocera* Hendel

1. *Bactrocera bhutaniae* Drew & Romig 2013. Figs. 3A–E, 7A.

Distribution: Taiwan (Lanyu Is.) [**New record**], Bhutan, India (Andaman Is.), Bangladesh, Vietnam, Thailand.

Male attractant: Cue-lure.

Hosts: Unclear. It has been reported to have been bred from "*Xylosma brachystachys* [Flacourtiaceae]" (Drew and Romig 2013), but that name is unresolved (Theplantlist.org 2017). The genus *Xylosma* has been moved to Salicaceae and no new designation of the species has been made. Specimens have supposedly also been collected from Icacinaceae in India; this host is listed as label data in Drew and Romig (2013), but is not listed as a host under the "hosts" section and thus remains uncertain.

Pest status: Non-pest.

Survey results: *Bactrocera bhutaniae* was found at only one location during our surveys: 11 specimens at 722 m altitude, in Nantou county, at Yuchi, Lianhuachi.

Notes: Before it was described in 2013, Taiwanese specimens of *B. bhutaniae* were possibly confused with *B. rubigina* or the red scutum variant of *B. dorsalis* (see Leblanc et al. 2015a).

<<Figure 3 near here>>

2. *Bactrocera costalis* (Shiraki 1933).

Distribution: Taiwan, Philippines.

Male attractant: Cue-lure.

Hosts: *Cayaponia laciniosa* [Cucurbitaceae], *Solanum surattense* [Solanaceae] (Shiraki 1933).

Pest status: Non-pest.

Survey results: Not collected during the 2013–2016 surveys.

Notes: The type locality is not specific beyond a county: “Hualien, Taitung”. The designated lectotype was collected at “Kuranu”, and a paralectotype is from “Pinan” (Drew and Romig 2013). “Pinan” is a Japanese word applied to the locality and people living in Taitung County. “Kuranu” is likely a misspelling of Kuraru, which is an old name for a colony of aboriginal people within today’s Kenting National Park, close to the southern tip of Taiwan. Neither Kuranu nor Kuraru is mentioned in the original species description (Shiraki 1933).

3. *Bactrocera dorsalis* (Hendel, 1912) Fig. 7B.

Distribution: Over 65 countries in Southeast Asia, Africa and the Pacific region (CABI 2018).

Male attractant: Methyl eugenol.

Hosts: Almost all (sub)tropical fleshy fruits, including many commercially grown. Recorded from over 300 host plants from 59 families (CABI 2018).

Pest-status: Category A.

Survey results: *B. dorsalis* was present at all surveyed localities, except two in Nantou county. Trapping abundances ranged from a single fly to 75 per trap per day (Fig. 2A).

Notes: Commonly known as the Oriental fruit fly, this species is one of the most economically important pests of fleshy fruits. First described from Taiwan, the country demarks the north-east limit of the native distribution of *B. dorsalis* (Vargas et al. 2015). *Bactrocera dorsalis* is widely distributed in Taiwan, but with quickly decreasing abundance at higher altitudes (Fig. 2A). During our surveys, we collected several of the known variant forms of *B. dorsalis*: some with red thorax instead of (predominantly) black, some with a dark abdomen instead of a clear black ‘T’ on a yellow base, and some with the costal band on the wings overlapping vein R_{2+3} (San Jose et al. 2013, Leblanc et al. 2015a).

4. *Bactrocera dorsaloides* (Hardy & Adachi 1954) Figs. 4A–E, 7C.

Distribution: Philippines (Luzon Is.), Taiwan (Lanyu Is.) [**New record**].

Male attractant: Cue-lure [**New record**].

Host: *Pouteria duklitan*; *P. macranthum* [Sapotaceae] (Drew and Hancock 1994).

Pest status: Non-pest.

Survey results: Two specimens were collected during the 2013–2015 surveys, in two traps on Lanyu Island.

<<Figure 4 near here>>

5. *Bactrocera hyalina* (Shiraki 1933) Fig. 7D.

Distribution: Japan (Kyushu), China, Thailand, Taiwan.

Male attractant: unknown.

Hosts: *Cinnamomum camphora*, *C. insularimontanum*, *Machilus thunbergii* (Ito 1983), *Ocotea lancifolia*, *Litsea verticillata* [Lauraceae] (Liang et al. 1993), *Osmanthus insularis* [Oleaceae] (Drew and Romig 2013)

Pest status: Non-pest.

Survey results: Not collected.

Notes: *Bactrocera hyalina* was previously recorded from Taiwan under the name *Dacus* (*Bactrocera*) *hsui* (Shiraki 1933), but was synonymized with *B. hyalina* by Drew and Romig (2013). *Dacus hsui* was described by Shiraki from a single female and without host records.

6. *Bactrocera latifrons* (Hendel 1915) Fig. 7H.

Distribution: Pakistan, Sri Lanka, India, Bangladesh, China, Taiwan, Thailand, Laos, Vietnam Laos, Malaysia (peninsular), Singapore, Indonesia (Kalimantan, Sulawesi). Introduced to Hawaii, Japan (Yonaguni Is.) and Africa (Tanzania).

Male attractant: latilure.

Hosts: Recorded from plants in nine host plant families; Lythraceae, Myrtaceae, Oleaceae, Passifloraceae, Rhamnaceae, Rutaceae, Sapindaceae, Solanaceae and Verbenaceae (Allwood et al. 1999).

Pest status: Category A.

Survey results: Not collected.

Notes: *Bactrocera latifrons* is a major pest of *Capsicum* and *Solanum* [Solanaceae] (Drew and Romig 2013) and such plants can be found across Taiwan. We have not encountered *B. latifrons* during our surveys, likely because it is not attracted to any of the lures that we used. Also, we did not survey agricultural fields with any of its hosts, where they may have been caught by hand. The Lectotype of *B. latifrons* was collected in Taiwan with locality data "Tainan, iii.1912'; 'Formosa, Sauter', which is not specific beyond the county Tainan. There are no records of the species since the early 1900's, and it is not certain that it still occurs in Taiwan [but see comments under *B. parvula*].

7. *Bactrocera nigrifacia* Zhang Ji & Chen 2011 Figs. 5A–E, 7E.

Distribution: Bangladesh, China, Thailand, Taiwan (Lanyu Is.) [**New record**].

Male attractant: Cue-lure.

Hosts: *Callicarpa arborea* [Lamiaceae], *Capparis sepiaria* [Capparaceae], *Zehneria wallichii*, *Flueggea virosa* [Phyllantaceae] (Drew and Romig 2013).

Pest status: Non-pest.

Survey results: One specimen on Lanyu Island.

Notes: The species is part of the *B. nigrotibialis* complex, which is characterized by having largely dark femora. *Bactrocera nigrifacia* can be distinguished from the others in the complex by having the entire fore femur black.

<<Figure 5 near here>>

8. *Bactrocera obscurata* (de Mejeire 1911) Fig. 7I.

Distribution: Indonesia (Java), Japan (Iriomote Island), Taiwan.

Male attractant: Unknown.

Host: *Diospyros maritima* [Ebenaceae] (Drew and Romig 2013).

Pest status: Non-pest.

Survey results: Not collected.

Notes: Previously recorded for Taiwan under the name *Bactrocera heppneri*, which was synonymized with *B. obscurata* by Drew and Romig (2013). The georeferenced locality (Fig. 7I) indicates the type locality of *B. heppneri*.

9. *Bactrocera occipitalis* (Bezzi 1919) Fig. 8A.

Distribution: Philippines (Luzon island), Malaysia (Sabah), Brunei, Indonesia (Kalimantan), Taiwan.

Male attractant: Methyl eugenol.

Hosts: Supposedly polyphagous, but this requires confirmation. Possibly restricted to *Mangifera indica* [Anacardiaceae], *Psidium guajava* [Myrtaceae] (Drew and Hancock 1994), *Citrus japonica* [Rutaceae] (Allwood et al. 1999).

Pest status: Category C.

Survey results: We collected 18 specimens in traps on Lanyu Island and two specimens at Fushan, Yilan county.

Notes: *Bactrocera occipitalis* has been reported as a major pest species (Drew and Hancock 1994, Drew ad Romig 2013) and has therefore been classified as a category B pest (Vargas et al. 2015). It was reported to be present in Taiwan by Tseng et al. (1992) but not by Drew and Romig (2013). We confirm its presence in Taiwan, but we consider it a category C pest because of the low occurrence and lack of evidence for major damage.

10. *Bactrocera parvula* (Hendel 1912) Fig. 8B.

Distribution: Taiwan [**Endemic**]

Male attractant: Unknown

Hosts: Unknown

Pest status: Non-pest

Survey results: Not collected.

Notes: We did not find *B. parvula* during our surveys, likely because it is not responding to any of the lures we used. Tseng et al. (1992) reported it to be "frequently found throughout Taiwan" but they did not specify their surveying methods for this species specifically. *Bactrocera parvula* has been synonymized with *B. latifrons* in the past (White and Liquido 1995), but was reinstated later (Drew and Romig 2013). *Bactrocera parvula* differs from *B. latifrons* in having dark fuscous patterns around the apices of all femora and more extensive dark markings on the abdomen. Some specimens of *B. latifrons* are known to be darker as well, but those usually only make up a small proportion of the population (LL pers. observation in Hawaii). The fact that (typical) *B. latifrons* have not been collected recently in Taiwan, whereas *B. parvula* is rather common (Tseng et al. 1992), argues against a synonymization, even though there may be overlap in morphological characters. A third species, *Bactrocera citima* (Hardy 1973), is also very similar to *B. latifrons* and *B. parvula* and differs only in the smaller width of the mesopleural stripe and having a needle-shaped ovipositor [lateral teeth on the ovipositor in *B. parvula* and *B. latifrons*]. A molecular genetic approach will likely be necessary to further elucidate the taxonomic status of these species.

11. *Bactrocera pernigra* Ito 1983 Fig. 7F.

Distribution: Japan, Thailand, Taiwan.

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: Previously recorded as *Dacus* (*Bactrocera*) *tenuivittatus* for Taiwan in Tseng et al. (1992), which has been synonymized by Drew and Romig (2013) with *B. pernigra*.

12. *Bactrocera rubigina* (Wang & Zhao 1989) Fig. 7G.

Distribution: Bangladesh, China, Bhutan, Thailand, Vietnam, Taiwan [**New record]**.

Male attractant: Cue-lure.

Host: *Litsea verticillata* [Lauraceae] (Liang et al. 1993)

Pest status: Non-pest.

Survey results: Collected in three localities; 15 specimens from several traps on Lanyu Island, one specimen on Alishan mountain in Chiayi county and one specimen in Huisun experimental forest, Nantou county.

Notes: Previously recorded as *Dacus* (*Bactrocera*) *ferrugineus* by Tseng et al. (1992) and noted it to be widely distributed but not abundant, which fits with our findings.

Genus *Dacus* Fabricius

13. *Dacus bispinosus* (Wang 1990)

Distribution: China, Taiwan.

Male attractant: Unknown.

Hosts: *Cyanchum paniculatum* [Apocynaceae] (Shiraki 1939).

Pest status: Non-pest.

Survey results: Not collected.

Notes: *Dacus bispinosus* was already reported from Taiwan in 1939 (Shiraki 1939), long before it was described, but was at that time misidentified as *Mellesis esakii*. It is, however, possible that *D. bispinosus*

is a synonym of *Dacus* (*Mellesis*) *esakii* (see discussion in Drew and Romig [2013]). We were not able to georeference the historical records beyond a county.

14. *Dacus formosanus* (Tseng & Chu, 1983) Fig. 8C.

Distribution: Taiwan [**Endemic**].

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: We collected a single specimen of *D. formosanus* at in Chiayi county on Alishan mountain at 955 m elevation, close to the locality where specimens have been collected during previous surveys.

15. *Dacus nummularius* (Bezzi 1916)

Distribution: Philippines (Luzon Island), Malaysia (peninsular), Taiwan.

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: We did not encounter *D. nummularius* during our surveys, but see Drew et al. (1998) for citation of this species in Taiwan. Shiraki (1933) collected it in Taiwan under its synonym *D. apicalis*, these specimens are now part of the syntype series.

16. *Dacus satanas* (Hering, 1939) Figs. 6A–E, 8D.

Distribution: China, Vietnam, Taiwan [**New record**].

Male attractant: Zingerone.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: 26 specimens at one trap in Chiayi county, Alishan mountain at 445 m elevation (N 23.4219 E 6156).

Notes: Previously known from northern Vietnam (Hoa binh province) and China (Yunnan Province), we found 26 specimens of *D. satanas* at one locality in central Taiwan in a Zingerone-baited trap. The specimens we collected have fully dark postpronotal lobes, matching specimens identified as *D. satanas* that we have collected in Vietnam. The descriptions of *D. satanas* and the similar looking *D. crabroniformis* (Bezzi 1914) in Drew and Romig (2013) state that the postpronotal lobes of *D. satanas* are yellow with a dark inner margin, and fully yellow in *D. crabroniformis*. We believe that fully dark postpronotal lobes are within the variation of *D. satanas*, and that the more yellow postprotonal lobes may be more common in China.

<<Figure 6 near here>>

Genus *Zeugodacus* Hendel

17. *Zeugodacus ambiguus* (Shiraki 1933) Fig. 8E.

Distribution: Taiwan [**Endemic**].

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: Shiraki described *Z. ambiguus* from a single specimen collected in 1918. In Tseng et al. (1992) the species was recorded for Taiwan as *Dacus* (*Zeugodacus*) *ambiguus* [two specimens from Fushan, Yilan county in 1978] and *Dacus* (*Zeugodacus*) *pauleiensis* [one specimen, the holotype, collected at Paulei, Kaoshiung county in 1978], the latter has since been synonymized with the former (Drew and Romig 2013). Thirteen specimens were collected in Nantour, Band county (Drew & Romig 2013), also in 1978. There are no published collection records of this rare species since 1978.

18. *Zeugodacus arisanicus* (Shiraki 1933) Fig. 8F.

Distribution: Thailand, Taiwan.

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: One specimen in Nantou county, Xitou experimental forest at 1249 m.

Notes: No females of *Z. arisanicus* are known. In Tseng et al. (1992) it was recorded under two names: *Dacus* (*Zeugodacus*) *arisanicus*, and its synonym: *Dacus* (*Zeugodacus*) *parvifoliaceus*. The synonym was designated by Drew and Romig (2013). According to Tseng et al. (1992), *Z. arisanicus* is probably widely distributed in central and southern Taiwan from 600 m to 1200 m elevation.

19. *Zeugodacus cilifer* (Hendel 1912) Fig. 8G.

Distribution: China, Laos, Thailand, Vietnam, Malaysia (peninsular), Indonesia (Sumatra), Taiwan.

Male attractant: Cue-lure.

Host: Flowers of *Thladiantha hookeri* [Cucurbitaceae] (Drew and Romig 2013).

Pest status: Non-pest.

Survey results: Seven specimens in Pingtung county, Kenting National Park, one specimen in Chiayi county, Alishan mountain at 528 m., and one specimen in Taitung county, Lungtien.

Notes: In addition to our findings, there are historical records from all over Taiwan and this is likely a common and widespread species.

20. *Zeugodacus cucurbitae* (Coquillett 1899) Fig. 8H.

Distribution: Pakistan, Sri Lanka, India, Bangladesh, Nepal, Bhutan, Myanmar, China, Japan, Thailand, Laos, Vietnam, Cambodia, Philippines, Malaysia, Brunei, Indonesia, Australia, Papua New Guinea, Taiwan. Introduced to Solomon Islands, the Mariana Islands, Hawaii, Mauritius, Reunion Island, Seychelles, and continental Africa.

Male attractant: Cue-lure.

Hosts: Recorded from fruits and flowers in twelve plant families: Asparagaceae, Capparaceae, Cucurbitaceae, Fabaceae, Malvaceae, Moraceae, Myrtaceae, Rhamnaceae, Rutaceae, Sapotaceae, Solanaceae and Vitaceae (Allwood et al. 1999).

Pest status: Category A.

Survey results: One to 39 flies per trap per day in trapping localities in Taitung, Chiayi, Pingtung and Nantou counties.

Notes: Commonly known as the melon fly, this is another major Cucurbitaceae pest. Previously recorded from Taiwan in Tseng et al. (1992) as *Dacus* (*Zeugodacus*) *cucurbitae* (page 23) and under its synonym *Dacus* (*Zeugodacus*) *yuiliensis* (page 66). Although this is one of the major pest species, we found that it is not as abundant as *Bactrocera dorsalis* (Fig. 1, 3). *Zeugodacus cucurbitae* is widespread across Taiwan, but abundances were always less than 40 trapped flies on average per day (up to 188 for *B. dorsalis*) and we did not find any specimens at localities above 1,000 m, where some of the other pest species still can be found. This is congruent with trapping records from 2001-2002 by Lin and Liu (2012), who placed traps up to 2,000 m. but did not collect *Z. cucurbitae* above 500 m.

21. *Zeugodacus depressus* (Shiraki 1933) Fig. 8I.

Distribution: Japan, Korea, Taiwan.

Male attractant: Unknown.

Hosts: *Cucurbita moschata*, *C. maxima*, *Trichosanthes kirilowii* [Cucurbitaceae] (Drew and Romig 2013).

Pest status: Category C.

Survey results: Not collected.

Notes: Commonly known as the pumpkin fruit fly, *Z. depressus* is a species of mountainous regions where it primarily feeds on wild Chinese cucumber (*Trichosanthes kirilowii*), and has become a major pest of pumpkins in Korea and Japan (Mun et al. 2003). Our research indicated that only three specimens

are known from Taiwan, which include the lectotype and a paralectotype, and were collected in 1925, 1924 and 1910. It is unclear if *Z. depressus* is still present on Taiwan, and if so, it does not appear to be a damaging pest.

22. *Zeugodacus diaphorus* (Hendel 1915) Fig. 9A.

Distribution: India, Sri Lanka, China, Indonesia, Malaysia (peninsular), Thailand, Vietnam, Bhutan, Taiwan.

Male attractant: Cue-lure.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: Previously recorded for Taiwan by Tseng et al. (1992) as *Dacus* (*Zeugodacus*) *diaphorus* (page 28) and under its synonym *Dacus* (*Zeugodacus*) *lunulatus*. *Strychnos nux-vomica* [Loganiaceae] is possibly a host (Allwood et al. 1999). The type locality is noted as "Tapani; Suisharyo", but these are two different localities and could not be georeferenced. Tapani is in Tainan City and is now called Yujing, Suisharyo is also called Shueisheliao and is in the Alishan area in Chiayi County.

23. *Zeugodacus lipsanus* (Hendel 1915) Fig. 9B.

Distribution: Taiwan [**Endemic**]

Male attractant: Cue-lure [**new record**]

Hosts: Unknown

Pest status: Non-pest

Survey results: We collected two specimens of *Z. lipsanus* on Lanyu Island in a cue-lure baited trap.

Notes: Aside from our two specimens this rare species was only known the from the (syn)type series of five specimens collected between 1908 and 1912 in southern Taiwan (Drew and Romig 2013).

24. *Zeugodacus mundus* (Bezzi 1919) Fig. 9C.

Distribution: Philippines, Taiwan.

Male attractant: Unknown.

Hosts: Unclear. *Trichosanthes wawrei* [Cucurbitaceae] is listed by Allwood et al. (1999), but this is an unresolved name in The Plant List (Theplantlist.org 2017).

Pest status: Non-pest.

Survey results: Not collected.

Notes: *Z. mundus* is historically known from one locality in central Taiwan in the mountains, and from Lanyu Island.

25. *Zeugodacus nigrifacies* (Shiraki 1933) Fig. 9D.

Distribution: Taiwan [**Endemic**].

Male attractant: Unknown.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: According to Tseng et al. (1992), *Z. nigrifacies* is distributed in central Taiwan between 600 m to 2,500 m.

26. *Zeugodacus okunii* (Shiraki 1933) Fig. 9E.

Distribution: Indonesia (Java), Taiwan (Lanyu Is.).

Male attractant: Unknown.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: Only known from Lanyu Island (Tseng et al. 1992).

27. *Zeugodacus scutellatus* (Hendel 1912) Fig. 9F.

Distribution: China, Japan, Bhutan, Thailand, Vietnam, Taiwan.

Male attractant: Cue-lure.

Hosts: An oligophagous flower pest on Cucurbitaceae, including *Cucurbita moschata* (Allwood et al. 1999) and *Trichosanthes pilosa* (Ito 1983).

Pest status: Category C.

Survey results: Two specimens in Hualien county and eight specimens in different traps in Chiayi county.

Notes: Previously also recorded from Taiwan under its synonym *Dacus* (*Zeugodacus*) *pseudoscutellatus* (Tseng et al. 1992). We encountered it at different localities but always in small numbers (Fig. 2B).

28. *Zeugodacus synnephes* (Hendel 1913) Fig. 9C.

Distribution: Indonesia, Malaysia (peninsular), Philippines, Thailand, China, Taiwan.

Male attractant: Cue-lure.

Hosts: *Cayaponia laciniosa*, *Zehneria japonica* [Cucurbitaceae] (Shiraki 1933).

Pest status: Non-pest.

Survey results: Four specimens in three traps in Nantou county, eight specimens in five traps in Pingtung county, 19 specimens in ten traps across Lanyu Island, 85 specimens in 16 traps or hand-caught in Chiayi county.

Notes: According to Tseng et al. (1992) the species is widely distributed below 900 m.

29. *Zeugodacus tappanus* (Shiraki 1933) Fig. 9H.

Distribution: Taiwan [**Endemic**].

Male attractant: Unknown.

Hosts: Unknown.

Pest status: Non-pest.

Survey results: Not collected.

Notes: Previously recorded for Taiwan by Tseng et al. (1992) under two names: *Dacus* (*Bactrocera*) *tappanus* (page 46) and its synonym *Dacus* (*Bactrocera*) *paratappanus* (page 38). It has been noted to be easily found in Taiwan, probably distributed between 500 m and 1,800 m (Tseng et al. 1992).

30. *Zeugodacus tau* (Walker 1849) Fig. 9I.

Distribution: China, India, Sri Lanka, Indonesia, Bhutan, Brunei, Malaysia, Vietnam, Taiwan, Thailand, Laos, Cambodia.

Male attractant: Cue-lure.

Hosts: Polyphagous on twenty fruiting plant families in laboratory conditions, in natural conditions primarily found on Cucurbitaceae. For a full list of the hosts in Taiwan and results from choice tests see (Lin et al. 2005, Lin 2006).

Pest status: Category B.

Survey results: Between one and seven specimens were caught per trap per day in Tainan, Hualien, Changhua, Chiayi, Pingtung and Nantou counties (Fig. 2B).

Notes: *Zeugodacus tau* is widely distributed in Taiwan and a major cucurbit pest. It was previously recorded for Taiwan by Tseng et al. (1992) under three names: *Dacus tau* and its two synonyms, *Dacus flavus* and *Dacus elegantis*. It can be found at elevations over 2,000 m and is particularly common in the northern half of Taiwan (Fig. 9I, see also Lin and Liu [2012] for additional records).

<<Figure 7,8,9 near here>>

Discussion

Origin of Taiwanese diversity

The distributional overlap of Dacini species with neihbouring countries shows that the diversity of fruit flies in Taiwan is a composite of influences from surrounding areas and some species that likely evolved on the island (Merckx et al. 2015, Vargas et al. 2015). With 30 species, it is relatively rich in Dacini, for example compared to South Korea, which only has three species (Han et al. 2017). There is also a high rate of endemism, with at least six species that are only found on Taiwan, 20% of the diversity. Most of the non-endemic species in Taiwan are shared with countries at a similar longitude in Asia, such as, (southern) China, Vietnam, Thailand, Laos, Bangladesh and Nepal. Other species have a shared distribution with regions to the South, such as *Bactrocera costalis*, *B. occipitalis* and *B. dorsaloides* with the Philippines, or *Zeugodacus okunii*, which is only -apparently- disjunctly shared with Java in Indonesia. Thirdly, there is a group of species that reflects a northerly component, such as *B. obscurata* and *Z. depressus* that can be found in Japan or Korea, but most of the species in this group can also be found in countries to the west and/or south of Taiwan. This all fits with the prevailing biogeography of Taiwan as a crossroads of northern and southern biota.

Faunistic knowledge of Dacini fruit flies in Taiwan

From our, and previous, surveys (Shiraki 1933, Tseng et al. 1992, material listed in Drew and Romig [2013]), the list of Dacini fruit fly species that occur in Taiwan is now probably fairly exhaustive but may be missing species distributed in regions that are yet unsampled. Our surveys added four new country records and now thirty species of Dacini are recorded for Taiwan in the present checklist. All are regarded as native, six are endemic, and seven are pests. We collected 15 of the 30 known species during three 'snap shot' surveys over the course of three years. Most of the 15 species not collected during our surveys are not attracted to the lures that we used. *Bactrocera dorsalis* is by far the most commonly collected, with 7,527 specimens it makes up 94% of the relative abundance in our trapping. Despite targetting natural areas, four pest species, viz. *B. dorsalis*, *Z. cucurbitae*, *Z. scutellatus* and *Z. tau* made up 97.4% of the total collected specimens. The fifth species classified as a pest that we collected, *B. occipitalis*, is

likely of lesser concern and represents 0.2% of the catches. Three species, viz. *B. nigrifacia*, *Z. arisanicus* and *D. formosanus*, were represented by singletons and we did not have an opportunity to add traps to the same locality to confirm the presence of a population or to look for potential host plants. Lanyu Island proved to be a rich and diverse area for Dacini with nine species, of which three, viz. *Bactrocera nigrifacia*, *B. dorsaloides* and *Zeugodacus okunii*, have not been encountered on the main island of Taiwan. Two of the seven species categorized as pests were not collected during the 2013–2015 surveys, likely because they are rare, not attracted to any of the lures that were used, or, in the case of *Bactrocera latifrons* specifically, because it may not be present in Taiwan at all. There is a lure available specifically for *B. latifrons*, aptly named 'latilure' (alpha ionol), which could be used in future research to confirm its presence, although the lure is apparently not very attractive. Overall, despite our collecting efforts, the distribution records for most of the species are still sparse, and host records are largely incomplete. It will therefore be invaluable to continue to collect specimens to gain better understanding of the occurrence, frequency and distribution of fruit flies in Taiwan, although our results suggest some populations might be highly localized. In particular, the rare endemic species and their hosts may reveal how species evolved in relation to the availability of hosts and inform how future changes in the flora could promote shifts onto novel host plants. Despite our limited use of the kairomone lure Zingerone, this lure collected numerous specimens of *D. santanas*. Zingerone has been shown to collect species that are not attracted to the other common lures for Dacini, viz. ME and CL, (Royer et al. 2017) and we suggest including this lure in any future surveys to get a better understanding of Dacini diversity. We also advocate that future collecting efforts should not solely rely on lures, because not all of the species are attracted to any of the (known) kairomones and ideally include rearing from as many forest- and commercially grown fruits and flowers as possible.

Excluded species

Aside from the synonymized species, four other species were previously published as resident in Taiwan but are not included in the current list. *Zeugodacus caudatus* (Fabricius 1805) was listed for Taiwan in Drew and Romig (2013), but without noting any studied specimens under the 'materials studied' header,

nor reference to other published material. *Zeugodacus caudatus* is a category C pest species of Cucurbitaceae flowers that is found in many countries in South-East Asia, including Indonesia and Vietnam. We did not encounter it during the 2013–2015 surveys, even though the species is known to be attracted to cue-lure. Because there are no traceable specimens or otherwise verifiable records, we do not list it as present in Taiwan. *Bactrocera expandens* (Walker 1859) was listed by Tseng et al. (1992) but is absent from Taiwan (see explanation in Drew and Romig 2013). *Bactrocera pedestris* (Bezzi 1913) was also listed as present in Taiwan by Tseng et al. (1992). However, their record was based on specimens attracted to methyl eugenol, whereas *B. pedestris* is attracted to cue-lure. The species was therefore not listed by Drew and Romig (2013) and we follow that same interpretation. Chen and Zia (1955) reported the Japanese orange fly, *Bactrocera tsuneonis* (Miyake 1919), for the Taiwanese fauna, but Tseng et al. (1992) excluded it. It is a species that is known from China and Japan, including the Ryukyu Islands. There are unpublished reports of outbreaks of the species in Citrus farms prior to 1955 on the Japanese islands of Kyushu and Amami (Tseng et al. 1992), but no confirmation of it ever being present on Taiwan could be found. We did not encounter it during our 2013–2015 surveys and follow the reasoning in Tseng et al. (1992) for excluding it.

Shifting climatic conditions

The Pleistocene climate conditions in Taiwan were cooler than present (Tsukada 1966) and may have been largely unfavorable for most species of Dacini, which depend on host plants that grow in subtropical and tropical conditions. Our surveys showed that pest fruit flies currently found in Taiwan generally are most common in subtropical zones below 600 m. The only exception appears to be *Zeugodacus tau*, which occurs up to 1,600 m. The future climate of Taiwan is expected to become warmer from the effect of greenhouse gases, which is only slightly mitigated by the cooling effect from aerosols (Hsu and Chen 2002). This will likely lead to the expansion of the range, increased abundance, and likely the virulence of the two most important pest species, *Bactrocera dorsalis* and *Zeugodacus cucurbitae*. For *B. dorsalis* there have been extensive distribution modelling studies in Africa, showing that climate is the primary factor determining the flies' range (De Villiers et al. 2016). Additionally, in central China, a northward

range extension for *B. dorsalis* has already been documented, likely related to the increasing number of milder winters (Han et al. 2011). Two of the other pest species, *Zeugodacus tau* and *Z. scutellatus*, appear to be less sensitive to elevational changes, or highly migratory, and can currently be found at low densities up to 1,400 m and 1,600 m, respectively. Overall, the expected climatic changes further emphasize the need to track the trends in both the abundances and distribution of populations of fruit flies in Taiwan. Accurate faunistic data can be used to prepare appropriate control measures that reduce agricultural damage and improve our understanding of the impacts of climate change on host specific herbivores.

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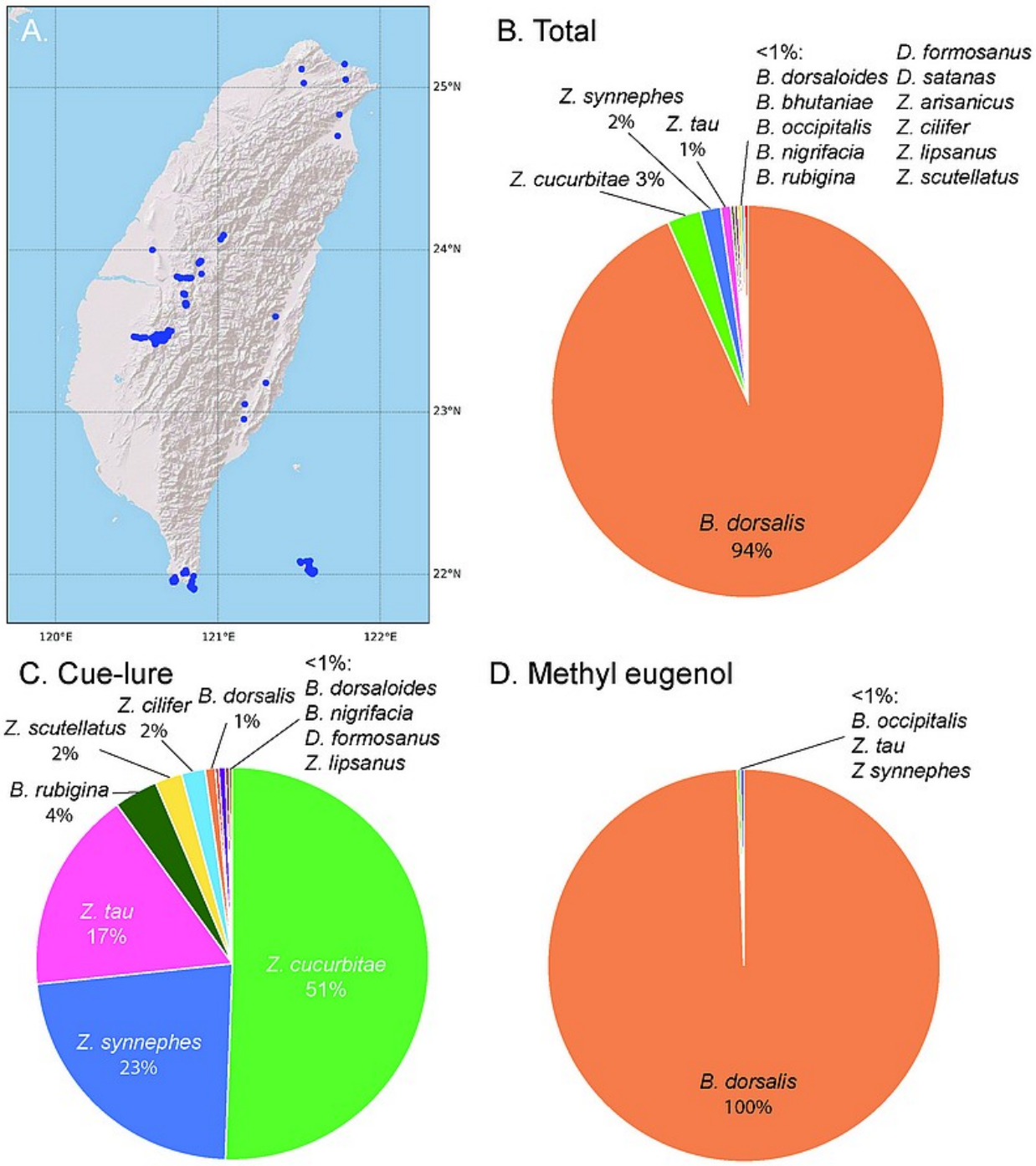

Figure 1: Overview of the results of the 2013-2015 surveys. A. Map of Taiwan with the localities that were sampled indicated with blue dots. The small island with sampling points South-East of Taiwan is Lanyu. B. Relative abundance of species from the different collecting methods, i.e. methyl eugenol, cue-lure, zingerone traps and hand-caught specimens. C. Relative abundance of species caught in cue-lure traps. D. Relative abundance of species caught in methyl eugenol traps.

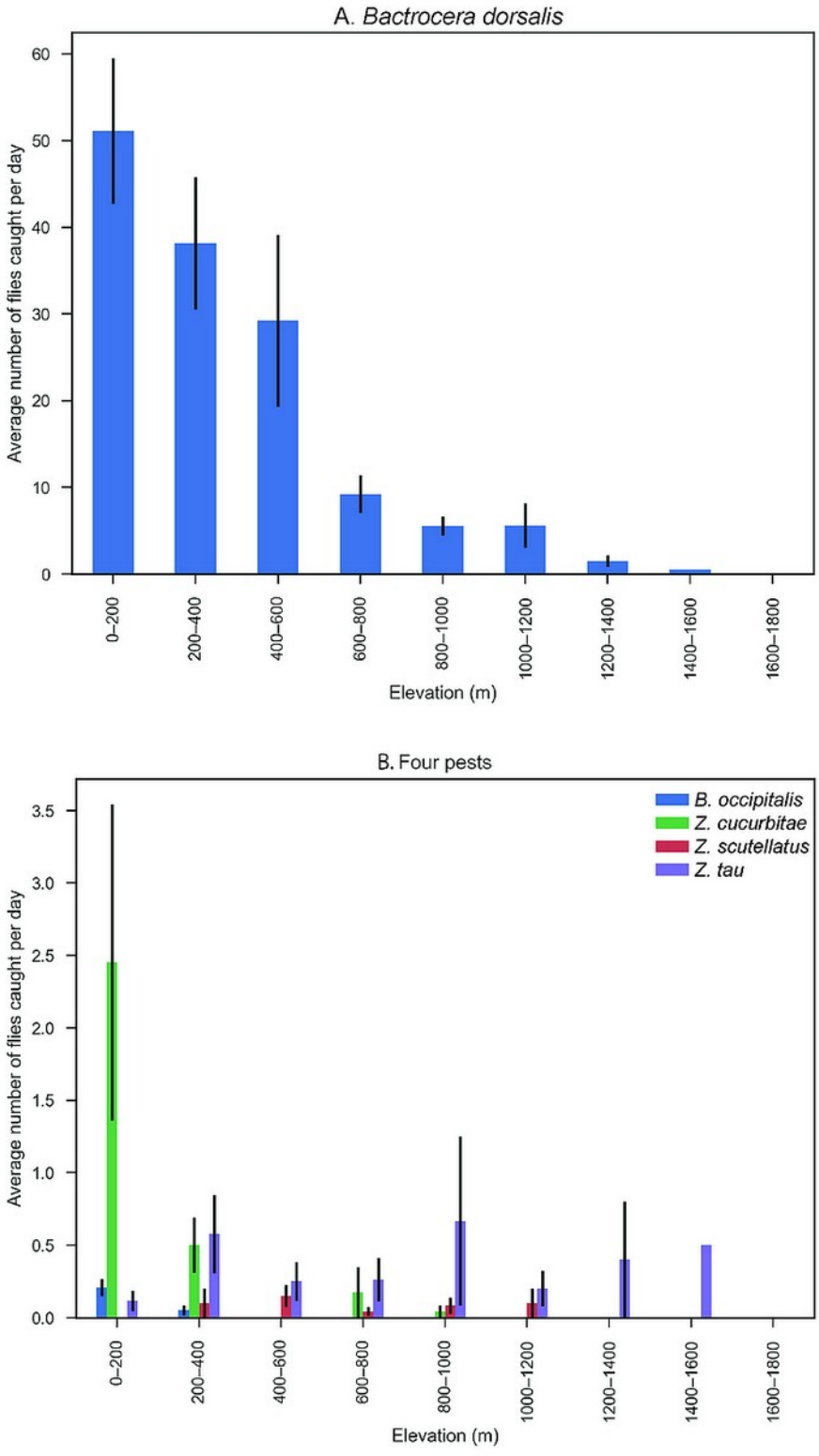

Figure 2: Bar plots showing the average number of flies caught per elevation bin of 200 m for the collected species that are categorized as pests, with standard error bars. A. Number of flies per trap per day elevation bin for *B. dorsalis*. B. The other species four pest species represented in our trapping: *B. occipitalis*, *Z. cucurbitae*, *Z. tau* and *Z. scutellatus*.

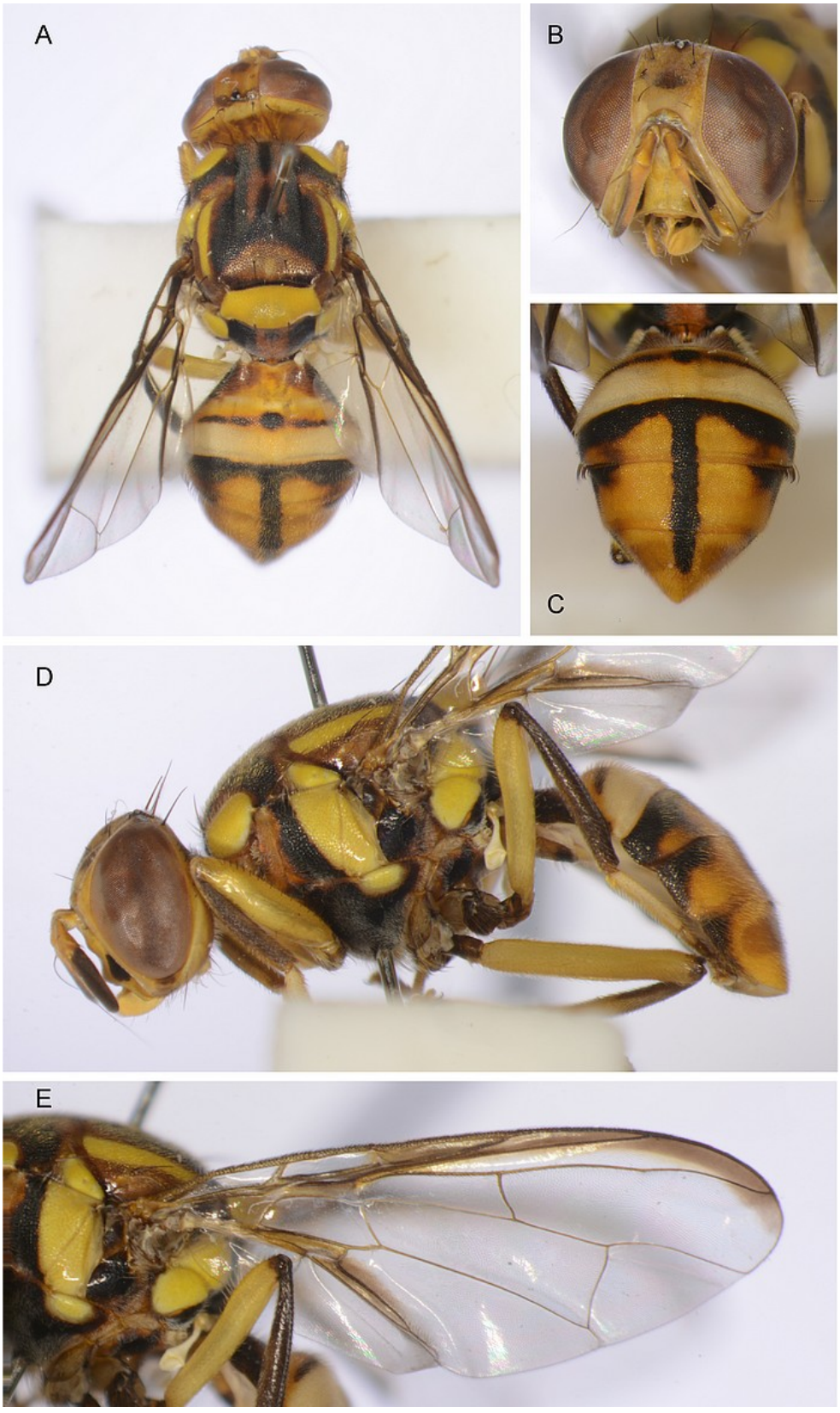

Figure 3: *Bactrocera bhutaniae*, voucher number ms4348, first record for Taiwan. A. dorsal view, B. head, frontal view, C. abdomen detail photo, dorsal view, D. lateral view, E. detail photo of the wing.

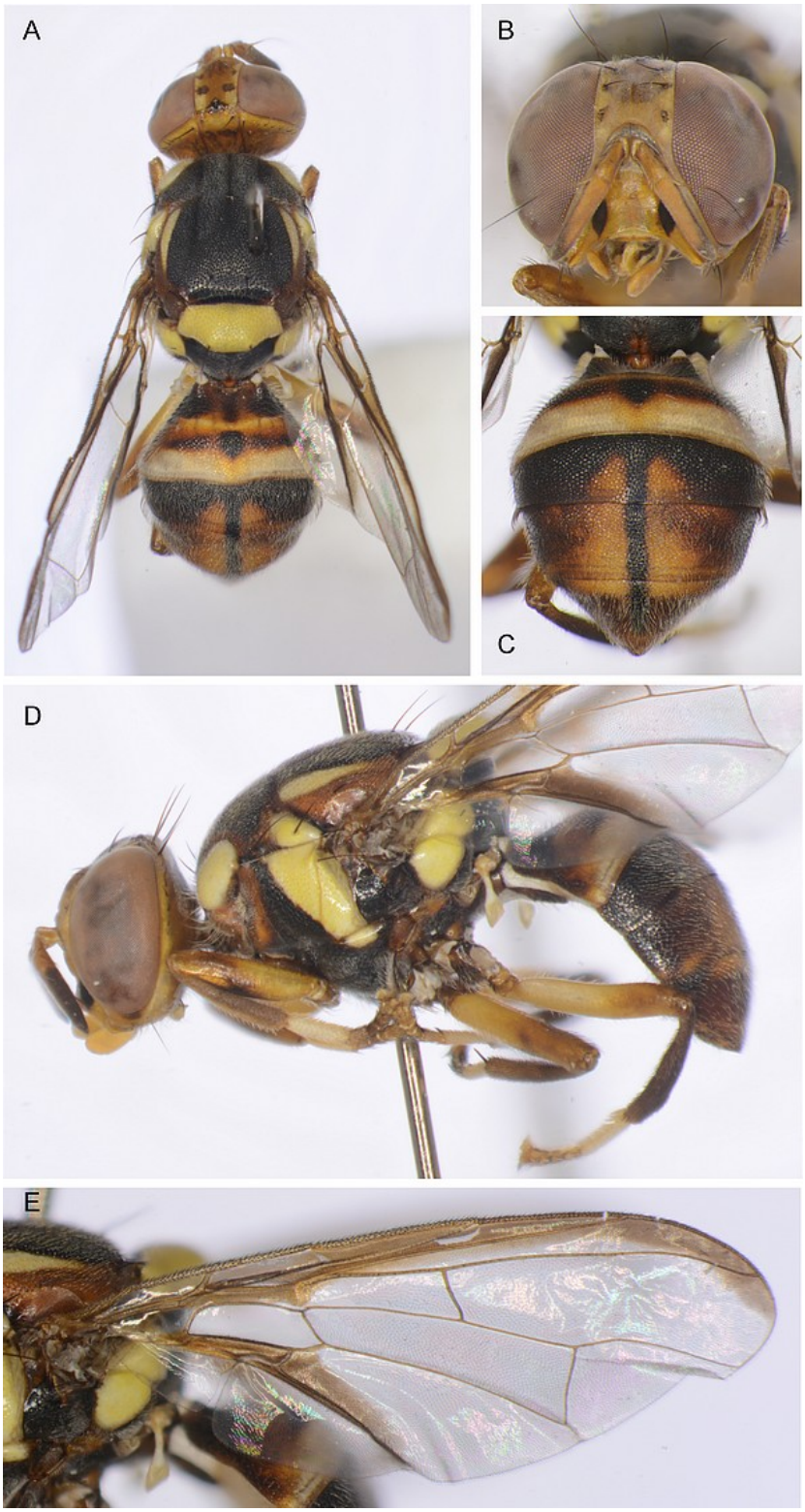

Figure 4: *Bactrocera dorsaloides*, voucher number ms4389, first record for Taiwan. A. dorsal view, B. head, frontal view, C. abdomen detail photo, dorsal view, D. lateral view, E. detail photo of the wing.

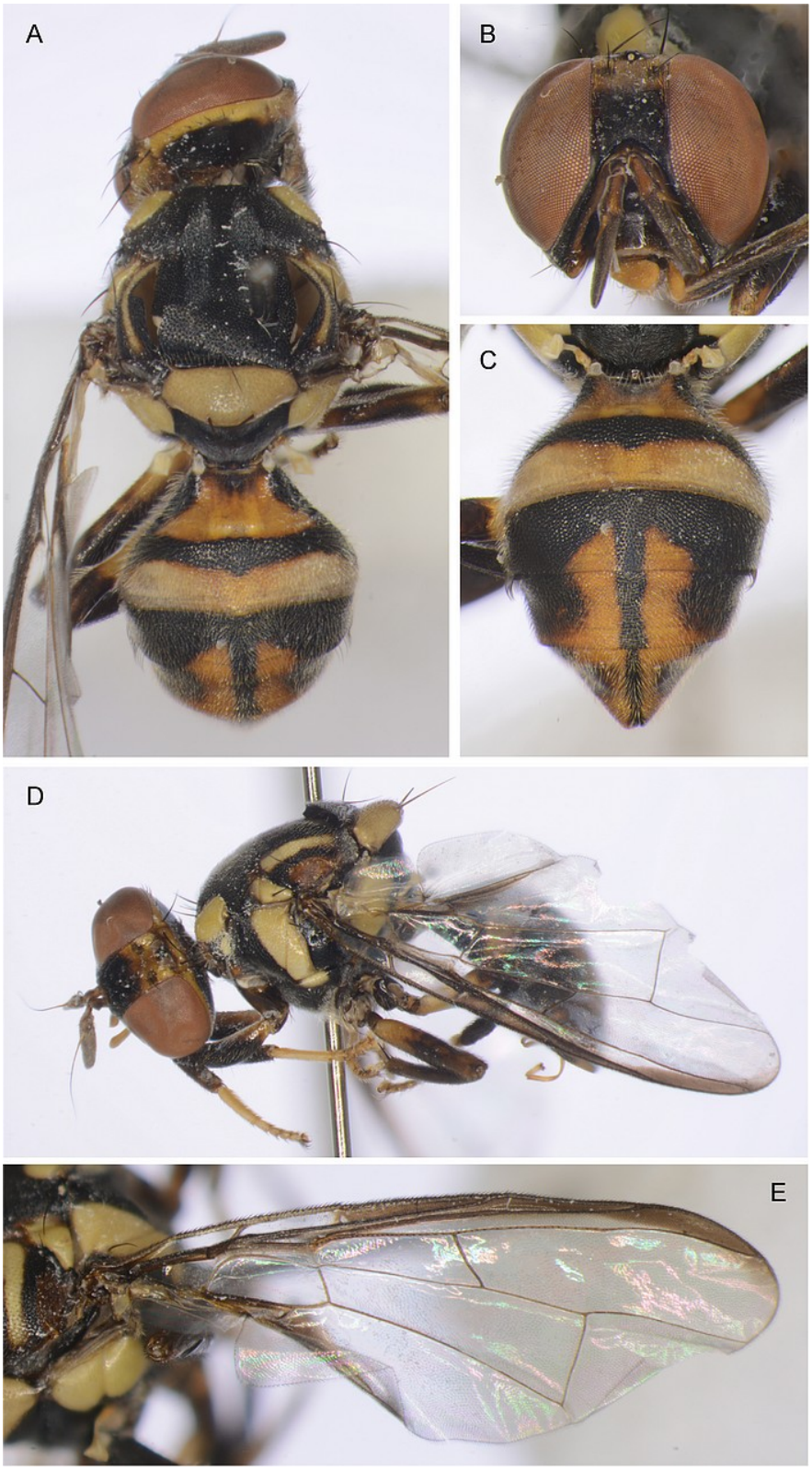

Figure 5: *Bactrocera nigrifacia*, voucher number ms4390, first record for Taiwan. Specimen is slightly damaged with a crushed thorax, but all the diagnostic characters are present. A. dorsal view, B. head, frontal view, C. abdomen detail photo, dorsal view, D. lateral view, E. detail photo of the wing.

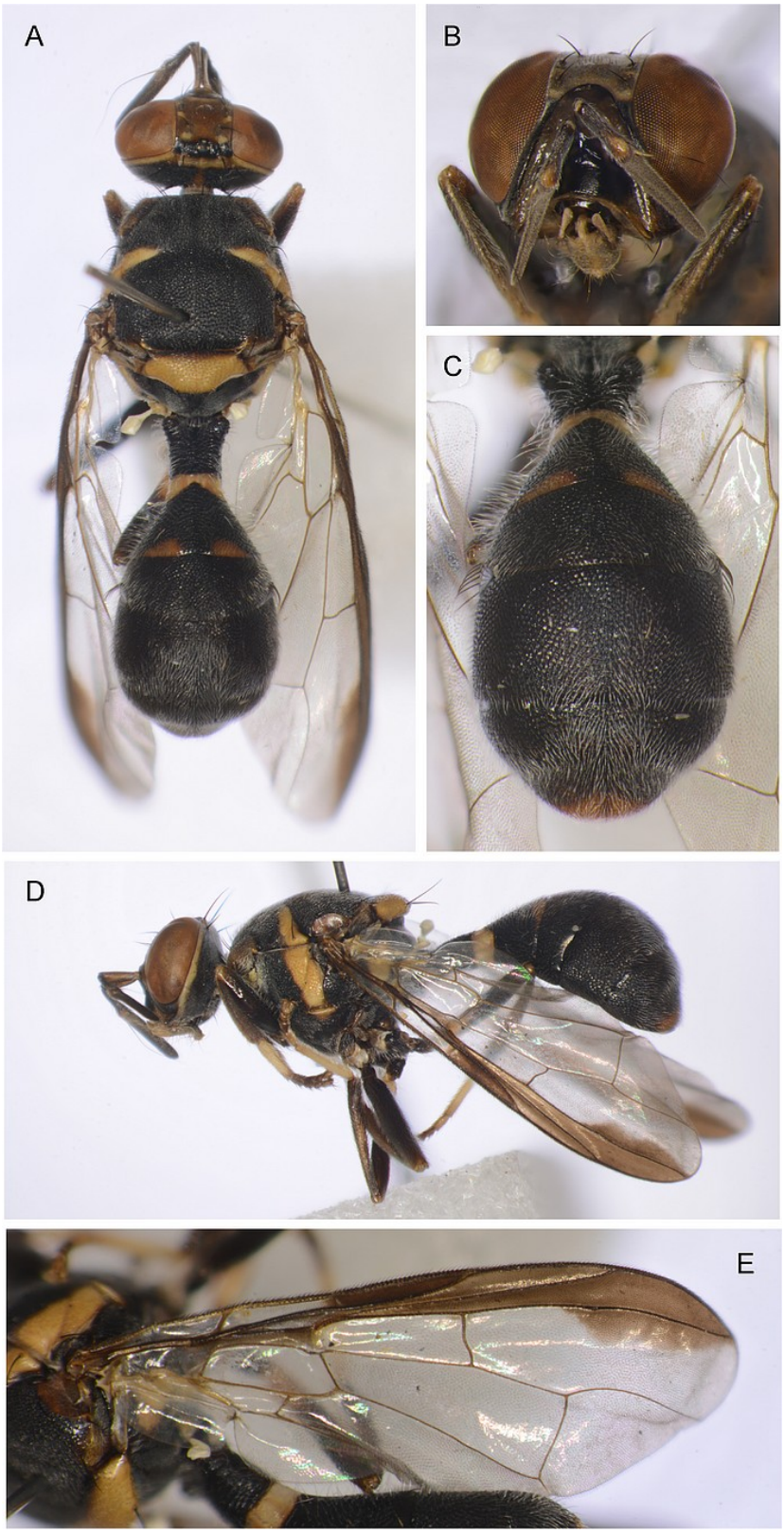

Figure 6: *Dacus satanas*, collected at locality FF237, Taiwan, Chaiyi Co., Alishan mountain, 6-8.xiii.2014, first record for Taiwan. A. dorsal view, B. head, frontal view, C. abdomen detail photo, dorsal view, D. lateral view, E. detail photo of the wing.

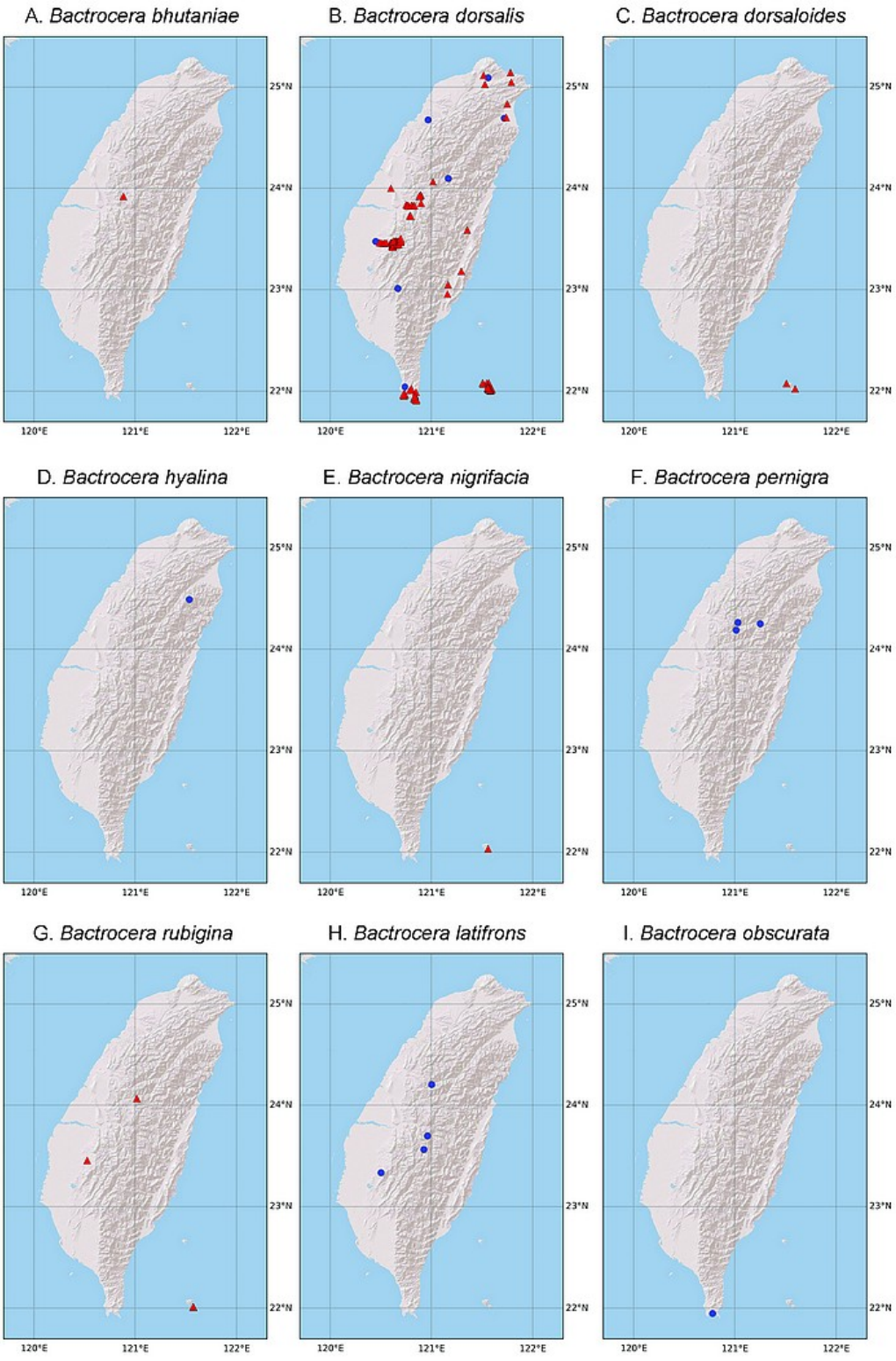

Figure 7: Distribution maps. Red triangles indicate localities where the species was observed during the 2013–2015 surveys, blue dots indicate historical records. A. *Bactrocera bhutaniae*, B. *Bactrocera dorsalis*, C. *Bactrocera dorsaloides*, D. *Bactrocera hyalina*, E. *Bactrocera nigrifacia*, F. *Bactrocera pernigra*, G. *Bactrocera rubigina*, H. *Bactrocera latifrons*, I. *Bactrocera obscurata*.

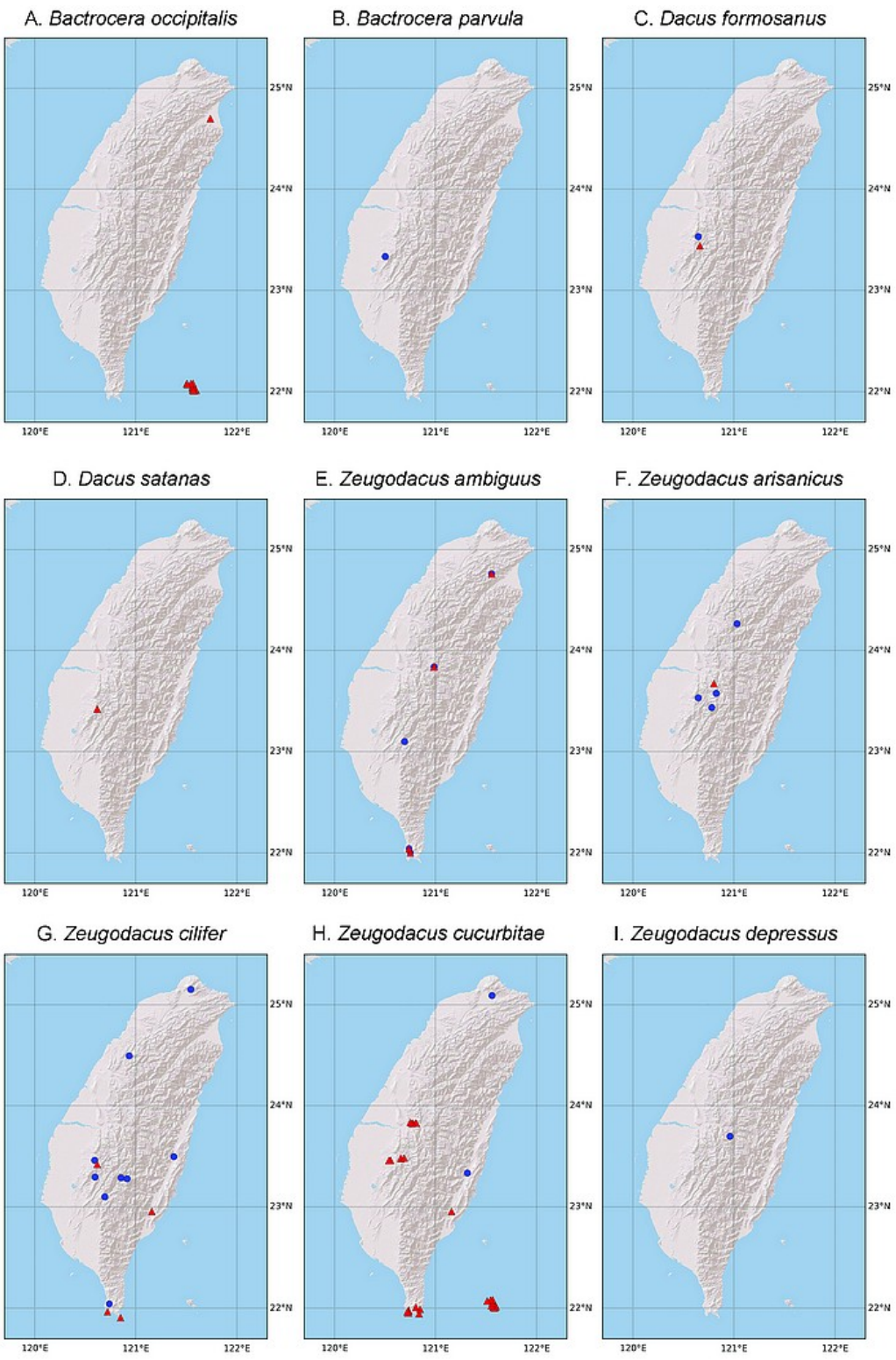

Figure 8: Distribution maps. Red triangles indicate localities where the species was observed during the 2013–2015 surveys, bue dots indicate historical records. A. *Bactrocera occipitalis*, B. *Bactrocera parvula*, C. *Dacus formosanus*, D. *Dacus satanas*, E. *Zeugodacus ambiguus*, F. *Zeugodacus arisanicus*, G. *Zeugodacus cilifer*, H. *Zeugodacus cucurbitae*, I. *Zeugodacus depressus*.

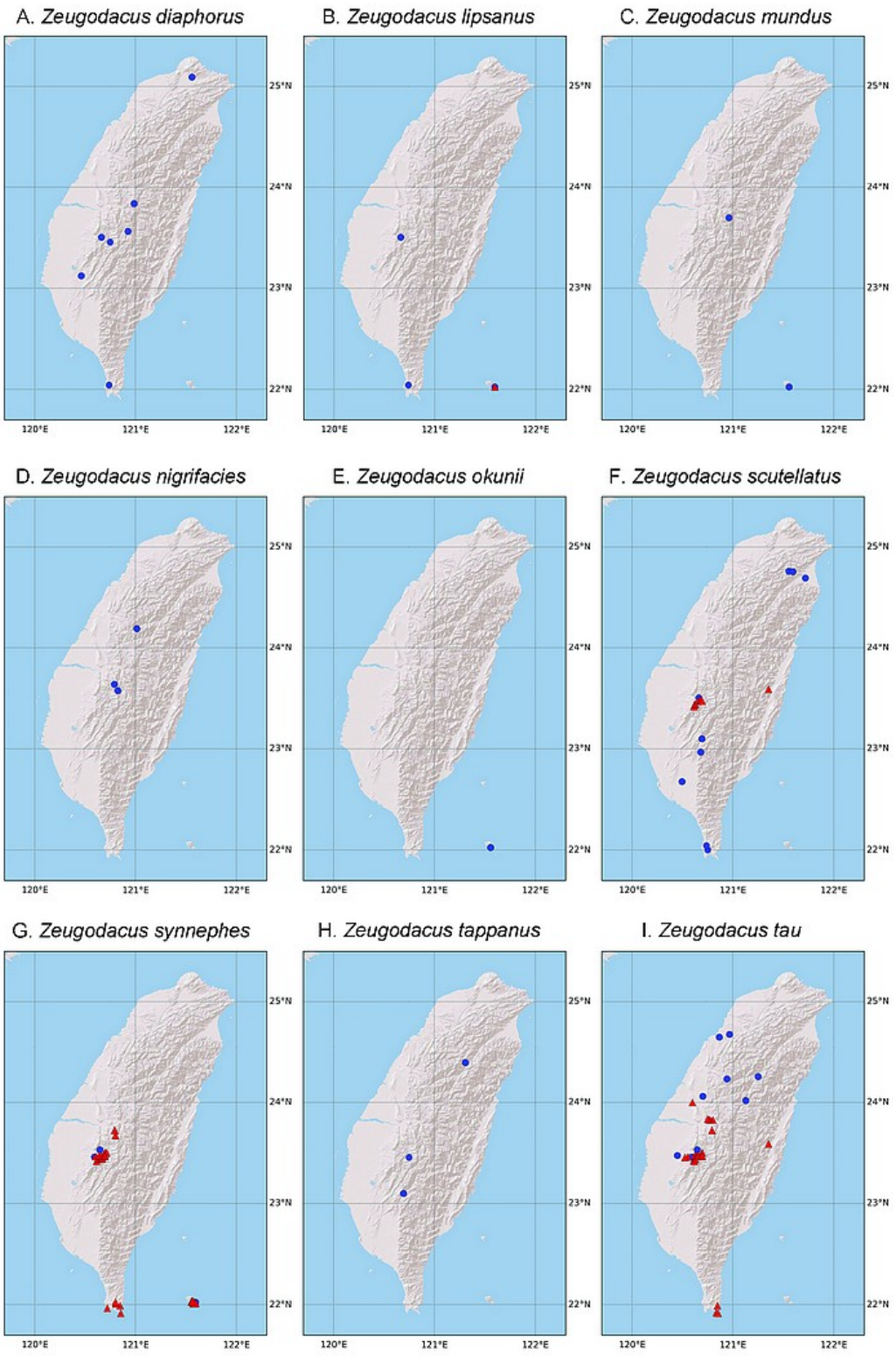

Figure 9: Distribution maps. Red triangles indicate localities where the species was observed during the 2013–2015 surveys, blue dots indicate historical records. A. *Zeugodacus diaphorus*, B. *Zeugodacus lipsanus*, C. *Zeugodacus mundus*, D. *Zeugodacus nigrifacies*, E. *Zeugodacus okunii*, F. *Zeugodacus scutellatus*, G. *Zeugodacus synnephes*, H. *Zeugodacus tappanus*, I. *Zeugodacus tau*.