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Biology of the sineguelas leaf beetle, *Podontia quatuordecimpunctata* (L.) (Chrysomelidae: Galerucinae: Alticini), on *Spondias purpurea* L. (Anacardiaceae) in the Philippines

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Biology of the sineguelas leaf beetle, *Podontia quatuordecimpunctata* (L.) (Chrysomelidae: Galerucinae: Alticini), on *Spondias purpurea* L. (Anacardiaceae) in the Philippines

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Abstract. *Spondias purpurea* L. (Anacardiaceae), native to the Neotropical region, is cultivated in the Philippines for the edible fruits and the tree is economically significant. The adventive leaf beetle, *Podontia quatuordecimpunctata* (L.) (Chrysomelidae: Galerucinae: Alticini), has become a major defoliating pest of the tree in the country. The Philippines government has initiated study of the pest, now locally called the sineguelas leaf beetle (SLB). This paper reports the results of a one-year field study on the biology of SLB on *S. purpurea* (red sineguelas), in Batangas City, Philippines. The SLB eggs hatch in 5–7 days. The larval period is 14–16 days with 4 larval instars, the pre-pupal period is 2–3 days, and the pupal period is 15–22 days. The total life cycle from egg to adult emergence is completed within 36–48 days. Host-choice experiments revealed that different stages of SLB do not feed on carabao mango (*Mangifera indica* L.) or pili (*Canarium ovatum* Engl.), however, they fed a little but did not survive or reproduce on cashew (*Anacardium occidentale* L.). A predatory bug (*Eocanthecona furcellata* Wolff., Hemiptera: Pentatomidae) is a potential natural enemy. Unidentified fungi infecting the pupae and adults of SLB were also recorded.

Key words. Flea beetle, pest, entomopathogen, economic botany, biocontrol.

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Introduction

Spondias purpurea L., 1762 (Anacardiaceae) (Fig. 1–2, 5) is an economically important fruit crop in the Philippines. It is a tropical fruit tree native to Central America (Rodrigues et al. 2018). However, due to its popularity as an edible fruit, it has been introduced to many other parts of the world, including Asia and Africa, where it is now cultivated as a commercial crop (Florido and Cortiguerra 2003; Plants of the World Online 2023). It has naturalized in many tropical regions around the world, earning it the status of a pantropic species. Its fruit, known as mombin, plum, ciruela, or cirguela, is often eaten fresh or used in culinary preparations. *Spondias purpurea* was introduced to the Philippines about 300 years ago and is grown widely in both commercial and backyard settings (Pancho and Gruezo 2006). Three species of *Spondias* are grown in the Philippines: *S. purpurea* (red sineguelas), *S. dulcis* Parkinson, 1773 (yellow sineguelas, Fig. 3) and *S. pinnata* (L. *f.*) Kurz, 1875 (Libas, Fig. 4). Red sineguelas, cultivated throughout the Philippines, is found in Indo-Malesia, Indo-Australia, Polynesia, and other tropical countries. *Spondias pinnata* is found throughout the Philippines in primary forests at low altitudes; it also occurs in India, Celebes, Java, and the Moluccas (Pancho and Gruezo 2006). The sineguelas fruit industry in the Philippines, based on these three tree species, is a thriving one, as many "barangays" (villages) depend on trade of the fruit as their major source of income (Adorada et al. 2023).

The Regional Crop Protection Center-IVA (= DA-RCPC-IVA) first noted an outbreak of a beetle pest in Laiya, San Juan, and Batangas in August 2016 and in Agoncillo in August 2017 (Sandoval unpublished report). Both adult and larval stages of this beetle defoliate the tree (Fig. 5–6) and damage the fruit (Fig. 7–8). In 2019, this beetle wreaked havoc to fruit farmers in San Miguel, Batangas City, the largest sineguelas fruit producing area in the country. This outbreak prompted an investigation that revealed that the pest was sighted in that city as early as May 2009 (Adorada et al. 2023). A parallel outbreak was recorded in Brookes Point, Palawan in 2007–2008. The increasing frequency of outbreaks prompted a detection survey by Adorada et al. (2023) and additional outbreaks were detected in Iloilo and Pangasinan, other large fruit-producing areas. Author Calcetas sent specimens in 2017 to chrysomelid expert, Charles Staines, USNM, who identified it as *Podontia quatuordecimpunctata* (L., 1767) (Fig. 10–12) (Chrysomelidae: Galerucinae: Alticini: *Blepharida*-group).

Podontia quatuordecimpunctata is distributed in South and South-east Asia (Fig. 13 Mohamedsaid 2004; CABI 2022). A nationwide survey was carried out in the Philippines during May 2021–October 2022 to map the distribution of the three *Spondias* spp. and the beetle pest, *P. quatuordecimpunctata* (Fig. 31). The common name, sineguelas leaf beetle (SLB), was coined (Adorada et al. 2023) to ease communication in the Philippines.

The beetle has become a major defoliator of all the three species of sineguelas in the Philippines, resulting in significant economic loss. After three years of SLB infestation in Batangas City, Roy (2015) and Adorada et al. (2023) indicated that there is no viable control measure except application of costly, broad spectrum chemical insecticides. Currently, SLB has not been reported on other regionally-important tree crops such as soursop or "atis" (*Annona muricata* L., 1753, Annonaceae), mango (*Mangifera indica* L., 1753, Anacardiaceae), and banana (*Musa sapientum* L. 1753, Musaceae), cashew, or pili (*Canarium ovatum* Engl., 1883, Burseraceae) (Alvarez and Serquina 2022, unpublished report), but it is possible that SLB could threaten them, especially those in the cashew family. Understanding the biology and ecology of *P. quatuordecimpunctata* is crucial for developing Integrated Pest Management (IPM) strategies to mitigate the infestation.

We report the natural history and biology of *P. quatuordecimpunctata* based on field, laboratory, and screen house observations in the Philippines.

The genus *Podontia* Dalman, 1824 belongs to the informal *Blepharida*-group within the Alticini (Furth 1992, 1998; Furth and Lee 2000). Adults of this genus group are robust and brightly colored, with a bifurcate prosternum, saddle-shaped mesosternum, and closed forecoxal cavities (Pramanik and Basu 1973; Furth 1992; Medvedev 1999; Becerra 2004; Prathapan and Chaboo 2011; Biondi et al. 2017). The larvae have a dorsally positioned anus and cover their dorsum with feces, a unique defensive behavior (Paterson 1943; Prathapan and Chaboo 2011). *Podontia* is characterized by the emarginate anterior margin of the metatibial apex; elongate-oval eyes, convex, chrysomeline appearance of the body, and the spermathecal morphology (Lee and Yu 2021) (Fig. 10–12). Previously, *Podontia* comprised 16 species which were distributed from Indonesia to Indochina, with one species occurring in northern Australia (Baly 1865; Heikertinger and Csiki 1940). However, Medvedev (1999) redefined *Podontia* to include ten Asian species from Indonesia to Indochina, of which one turned out to be a junior synonym, thus reducing the total number of valid species to nine (Lee and Yu 2021). Recently, Lee and Yu (2021) redescribed *Podontia lutea* (Olivier, 1790) and *Podontia dalmani* Baly, 1865. Pramanik and Basu (1973), was one of the first complete life cycle, phenology, biology studies of any species in the *Blepharida*-group. Prathapan and Chaboo (2011) reviewed biological information. Lee and Yu (2021) noted the biology of *P. lutea*.

Three *Podontia* species are considered serious pests: *Podontia affinis* (Gröndal, 1808) on *S. dulcis* in Indonesia, *P. lutea* on "Chinese lacquer tree" *Toxicodendron vernicifluum* (Stokes) F.A. Barkley, 1940 (Anacardiaceae) in China, and *P. quatuordecimpunctata* on *Spondias* spp. (Prathapan and Chaboo 2011). *Podontia quatuordecimpunctata* is regarded as a pest in peninsular Malaysia, India (north-east India, West Bengal, Andaman Is.), Nepal, Myanmar (Burma), Thailand, Laos, Cambodia, and Japan (Mohamedsaid 2004; Prathapan and Chaboo 2011; Minami et al. 2018; Ray and Banerjee 2023) (Fig. 13). It is widely referred to as the hog plum beetle in that area (Sardar and Mondal 1983; Deka and Kalita 2002a; Roy 2015, Islam et al. 2023). Prathapan and Chaboo (2011: Table 1), based on literature, listed 12 host plants of this pest on four plant families – Anacardiaceae, Burseraceae, Lythraceae, and Moraceae – however, only species of *Spondias* have been confirmed. Adorada et al. (2023) added *S. purpurea* to this list.

Materials and Methods

The biological study of *Podontia quatuordecimpunctata* (SLB) on *Spondias purpurea* L. involved field surveys, greenhouse rearing and feeding experiments. Multiple Philippines government and university agencies were involved in the studies on SLB and we reference them by their acronyms:

BUCAF	Bicol University, College of Agriculture and Forestry, 8-Pan-Philippine Hi-way, Guinobatan, Albay
DA-RFO-IVA	Department of Agriculture, Regional Field Office-IVA-CALABARZON, Marawoy, Lipa City, Batangas
DA-RCPC-IVA	Department of Agriculture, Regional Crop Protection Center IVA-CALABARZON, Marawoy, Lipa City, Batangas
DA-BPI-LBNCRDPSC	Department of Agriculture, Bureau of Plant Industry-Los Baños National Crop Research Development Production Support Center, BPI-Economic Garden, Timugan, Los Baños, Laguna
DA-PAES	Department of Agriculture, Palawan Agricultural Experiment Station, South Road, Puerto Princesa City, Palawan
CAO-PPC	City Agriculturist Office, Puerto Princesa City, New City Hall Building, Sta. Monica Heights, Puerto Princesa City, Palawan
OCVAS	Office of the City Veterinary and Agricultural Services, Bolbok, Batangas City

***Spondias purpurea* L., sineguelas tree in the Philippines (Fig. 1–2).** The genus *Spondias* L. comprises 18 species (Plants of the World 2023), of which five occur in the Philippines—*S. dulcis* (golden apple or yellow fruit variety), *S. mombin* L., 1753 (hog plum), *S. pinnata* (hog plum), *S. philippinensis* (Elmer) Airy Shaw and Forman, 1967, and *S. purpurea* (red fruit variety) (Pancho and Gruezo 2006). *Spondias purpurea* grows between 10–2,000 m ASL and wild populations at 1,800 m ASL are associated with deciduous forests and semideciduous tropical forests (Rodrigues et al. 2018). *Spondias* trees are deciduous, growing to 5–15 m (Pancho and Gruezo 2006) and ~80 cm diameter at breast height (Rodrigues et al. 2018). Sineguelas trees are intercropped with other crops and trees such as mango, banana, soursop, duhat or Java plum (*Syzygium cumini* (L.) Skeels, 1912, Myrtaceae), and papaya (*Carica papaya* L. 1753, Caricaceae).

In the Batangas area, southern Luzon, sineguelas trees are planted in terrain that is flat, moderately sloped, or steep. The average annual temperature, relative humidity and the total precipitation in Ambulong, Batangas Weather Station from 1991–2020 were 27.70 °C, 82.00%, and 1,816.10 mm, respectively (PAG-ASA 2020).

The undergrowth in these plantations comprises *Paspalum conjugatum* P.J. Berguis, 1772 (Poaceae), different species of broadleaved weeds such as *Synedrella nodiflora* (L.) Gaertn., 1791 (Asteraceae), *Mimosa pudica* L., 1753 (Fabaceae), dense thickets of *Chromolaena odorata* (L.) R.M. King and H. Rob., 1970 (Asteraceae) and *Lantana camara* L., 1753 (Verbenaceae) (Calcetas 2022, unpublished notes). The tree is allowed to grow without pruning and the dead branches and twigs are removed annually. Extensive growth of vines such as *Coccinia grandis* (L.) Voigt, 1845 (Cucurbitaceae) and various liana species (multiple families) often smother the canopy of the trees. Traditionally, no manure or fertilizer is applied in sineguelas plantations. Farmers do allow their cattle to roam freely under the trees, which results in both deposition of cow dung and reduction of undergrowth. Elsewhere in the Philippines, goats are pastured to manage weeds while the young leaves of sineguelas are collected for their fodder.

Economic significance of sineguelas in the Philippines. In regions we surveyed, the leaves are used as fodder for cows and goats while the fruits infested with fruit flies or SLB are fed to pigs and other livestock. The tree canopy is cleaned before the onset of flowering (Fig. 1) in January–February (Adorada et al. 2023). The ripe fruit (Fig. 9) is edible and the seed is surrounded by a soft, sweet, and aromatic juicy pulp (Rodrigues et al. 2018). The fruit is a good source of vitamins, antioxidants, and dietary fibers (Koziol and Macia 1998; Pire et al. 2010). The community of farmers, vendors, and fruit retailers depends on sineguelas for their sustenance. Fruiting begins 2–3 years after planting (OCVAS 2022, unpublished report) and fruits are harvested every other day using an improvised bamboo pole (salungsong in Batangas or sundong in Iloilo) (~3½ m long), with a small bamboo woven basket or "buslo" at the tip. The fruits are subsequently sorted to remove damaged, pest infested, deformed, unripe, overripe, or deformed ones from the salable ones. The unmarketable fruits are fed to livestock while the marketable fruits are packed and delivered to the market to be retailed and sold. Fruits are eaten raw, processed into jam which is mixed with coconut milk to enhance the taste (Acuzar 2022, personal communication). Fruits are also used for the treatment of tonsillitis and stomatitis in children (Ragasa et al. 2001).

Rearing of SLB. Adults (~50) collected in Batangas City were maintained on potted plants in the screenhouse of the SLB Project Laboratory, DA-BPI-LBNCRDPSC, Timugan, Los Baños, Laguna. Life stages obtained from this initial culture were used to determine the life cycle as well as the feeding and consumption studies of SLB. Ten individuals were used in each experiment and replicated five times (10 × 5 = 50 individuals).

Rearing cages (Fig. 14–15). These were made of rolled plastic acetate- or mineral-water containers and nylon net sleeves. The cages had nets pasted together to prevent larvae and adults from escaping and a window was cut on one side to ease larval measurement. In plastic and nylon net cages to rear adults, no window was cut to prevent escape of the beetle, and each cage was labeled. Fifty sineguelas stem cuttings were bought from farmers in 2021, examined to be free of pests, and were raised in large plastic polyethylene pots.

A sineguelas twig with several leaves and leaflets was placed inside each rearing container. The upper end of the nylon net was tied with electrical tie wire to prevent escape. The net was attached to a galvanized iron wire or nylon net cord/string using an office metal binder clip that was attached to a nylon cord that was placed overhead for each row of sineguelas seedlings since the combined weight of the plastic container and nylon net is too heavy for the twig to support. The tail end of the net below was also secured on the stem of the seedlings using an electrical tie wire.

The concrete floor of the greenhouse was covered with plastic and banana and palm leaves. This covering was frequently sprinkled with water to cool the surrounding area.

Rearing of SLB eggs (Fig. 16). We reared more than 50 adults (50 males and 50 females) in a large nylon net cage, and we obtained five egg clusters. These were attached to ten seedlings enclosed in a rearing cage. One cluster was placed in a small transparent plastic petri dish and allowed to hatch inside the SLB Laboratory. Ten larvae were selected per replication for a total of two replications. One larva was placed in each cage and observed and measured daily. The setup was repeated for another two replications and with the last replication to collect and measure daily the larva's body and pronotum sizes (destructive sampling) and verify the number of instars based on measurement.

Rearing of SLB larvae (Fig. 17–26). The newly emerged larvae (n = 50) (Fig. 17–18) from our greenhouse egg clusters were measured, counted, weighed, and allowed to feed for about 30 minutes before they were transferred individually to the rearing cages or containers using a fine camel brush.

The size of each larva was measured daily using digital photography. A plastic ruler was placed beside the larva on the upper or inner leaf surface and photographed using a Nikon® D-7100 DSLR 24.71-megapixel camera either lengthwise and crosswise. To accurately estimate different larval instars (n = 20; 1 larva/day), the larva's body, head, and pronotal size (length and width) were independently determined by collecting, preserving, and measuring. Using this method, >4050 cohort larvae (3× the estimated days of the larval life cycle) were reared in several rearing cages. On each day (after 24 hours) up to one individual larva was sampled in each cage and preserved in a glass vial with 85% ethyl alcohol until the last surviving larva. The size of the body, head, and pronotum of these collected larvae was measured in millimeters using a dial caliper or stainless-steel ruler. Larval feeding damage was documented using various devices such as cellphones, digital microscopes, and cameras. Additional observations were noted. Labeled specimens were photographed with digital cameras and reviewed on a large monitor. The larvae were measured using a stainless-steel metal caliper and a plastic transparent ruler, with length, width, and other attributes recorded in millimeters.

Collecting larval exuviae. It is difficult to sample the larval exuviae since removal from the body may affect insect survival and biology. After each pupation, dried fecal matter was collected from each rearing cage to extract the exuviae. We placed a large plastic basin (length = 33.00 mm; width = 24 mm) underneath the posterior sleeve. The latter was then untied and shaken several times for the dried feces to fall from the cage. To sustain the availability of insect specimens for other experimental setups (e.g., feeding rate), a large nylon net rearing cage was constructed measuring (length = 2.30 m, width = 1.46 m, height = 2.15 m) with several sineguelas seedlings inside.

Collected materials were transferred to Petri plates or sorting dishes and sorted using a Nikon® SMZ645 stereomicroscope and the exuviae were collected by forceps or fine camel brush. The exuviae were photographed, measured, and grouped by instar, then labeled and preserved for characterization. The larval fecal coat was also observed, photographed, and filmed throughout the experiment. Good photo quality and alignment are crucial for accurate measurements, including avoiding blurred photos and ensuring both the insect and ruler are visible and properly aligned. Regular review and label checking of photos are necessary to avoid mix-ups.

Determination of number of instars. We used body size (length and width) and weight to sort larval instars. The head and pronotum help to precisely determine instars I, II and III. The size of instars III and IV are the same and did not change at all, however the weight is distinct to all stages except to larvae that still feed but undergo the pre-pupal stage where significant reduction in size and weight can be observed, in addition to thickening and shrinking of the integument. To determine the significance of larval weight to estimate different larval instars, each preserved larva (wet weight) was weighed in grams using a scientific electronic balance at three decimals (0.000) capability.

Rearing of SLB pupa (Fig. 27–30). Both prepupae and pupae were kept in the laboratory in a round plastic container (diameter = 110.0 cm) with nylon net cover. However, it appears that the soil and the pupal case became too dry, making it difficult for the adults to emerge from the hardened pupal case. Thus, we reared larvae in both field and laboratory settings.

Set-up of nylon net in the field. Mature larvae were transferred to the open field to simulate the natural environment (we considered that rainfall and moisture may be important to maintain the earthen pupal cases to ease escape of the adults). To protect from potential predators, each pupal case was placed inside a rectangular nylon net (length = 20 mm; width = 13 mm) tied with nylon cord and placed on the soil surface; these are shaded with some ornamental plants to prevent desiccation from the sun and too much water from heavy rainfall. The rectangular nylon container was filled 1/4 full of sterilized garden soil to prevent entomopathogenic fungi infection. The final instar larvae were covered with fresh sineguelas leaves to provide food, if these larvae were still feeding, and to offer shade against bright sunlight. Unfortunately, high mortality was observed (only few adults emerged from these pupal case). In nature, the larvae pupate near the base of the tree trunk where they are exposed to ambient moisture and are covered from direct rainfall by the tree canopy.

Set-up of nylon net rearing cage. Sterilized soil was placed at the base of the nylon-net rearing cage to reduce physical intervention and avoid damage to the newly constructed, soft pupal case. The start date of pupal case construction, duration of construction, and adult emergence were recorded and filmed. Mortality, emergence rate, and other pupal maladies, such as entomopathogen infection, were also documented.

Random sampling of pupal cases. Twenty pupae were sampled in the field and observed for emergence or reasons for their death.

Determining the fecundity and longevity of SLB adults. The emerging teneral adults' sex was identified and recorded. Twenty teneral adults were moved to a rearing container without a side window to prevent accidental escape. Ten male-female pairs were separately observed for courtship, mating behavior, duration of mating, female fecundity, and both adults' longevity. The number of eggs laid by a female in her lifetime was recorded and tabulated daily until both individuals died. Egg clusters were collected, examined, and counted.

Feeding consumption, feeding/resting cycle of SLB larvae and adults. The feeding habit, rate, and leaf consumption of instars I–IV SLB larvae (*n* = 12; 3 for each instar) and adults (*n* = 6; 3 males and 3 females) were observed in rearing cages for three consecutive days. Observations were done after a 24-hour period and damage was assessed using a percentage feeding damage rating of 1–100%. Afterward, damaged leaves were removed. The feeding and resting cycle were observed in the laboratory using a continuous digital video recording camera with a time display recorded on its monitor and taking notes of their feeding behavior.

No-choice experiments for alternate hosts of SLB. A no-choice experiment was conducted for adults of SLB on mango, cashew, rubber tree, and pili (Fig. 33–35). Three seedlings each were placed inside a nylon net cage measuring (length = 0.74 m, width = 0.74 m, height =1.20 m) with either a steel or wooden frame. Leaves with feeding damage were removed. Five male and five female adults were placed on each plant, replicated three times, and observed for feeding damage and longevity. Five individuals of each larval stage were placed on each plant species and were observed for feeding damage, longevity, and if the life cycle can be completed on the host plant. Each stage was placed and tested separately. Other potential alternate hosts of SLB in the field were also surveyed and recorded in Batangas City and during the detection survey in different regions of the country.

Field survey of arthropods on *Spondias*. The arthropod pests and other disease and fungal pathogens were monitored weekly starting from August 2021–December 2022 in two sineguelas plantations in Barangay San Miguel and Sto. Nino, Batangas City, and visits to other places. Specimens were sampled using visual count through inspection of leaves, stems, trunks, flowers, and fruits during the day and at night using light traps and ocular/manual sampling with the aid of a lamp and sweep net. Adult insects were collected by hand, placed in glass vials, and preserved in 80% ethyl alcohol. Immature insects were reared and fed in plastic cups with fresh sineguelas foliage covered with nylon mesh or in rearing cages; they were later dried and pinned. Disease pathogens and entomopathogens were grown on an agar medium, mounted on slides, and labeled properly. Undetermined fungi specimens were sent to the University of the Philippines Los Baños for morphological or molecular diagnosis to the species level.

Specimen vouchers. SLB specimens identified by Dr. Charles Staines of USNM are vouchered at the DA-RCPC-RFO-IVA-CALABARZON, Marawoy, Lipa City, Batangas and a few at USNM. More vouchers will be deposited at the University of the Philippines Museum of Natural History (UP-MNH) and the University of the Philippines Los Baños, National Crop Protection Center (NCPC), College, Laguna. Some voucher specimens have been deposited with Michael Schmitt, University of Greiswald, Germany for further morphological study.

Imaging. We observed the daily activities of larvae and adults via a digital microscope video camera enabling us to record feeding, resting habits, and feeding cycle. Color images of SLB and associated arthropods' habitus and morphological characters were captured using a Nikon® D7100 DSLR camera, equipped with Nikon® Micro 40 mm and 105 mm 1:2.8G lenses and mounted on a microscope arm track stand. The camera was remotely controlled with Helicon Remote® software and set to time-lapse photography at predetermined intervals. LED ring lights and bulbs provided lighting, and images were combined and digitally enhanced using Helicon Remote® (ver. 3.9.12 M) and Helicon Focus® (ver. 7.7.4) software. Adobe Photoshop Elements® 2020 was used to crop, clean, and store the TIFF format images.

Results

Our field and laboratory studies determined the life cycle and phenology (Fig. 31) of SLB and permitted collections of specimens of all stages. Our experimental work addressed the biology, ecology, and host range. The geographic distributions of *Spondias* spp. and SLB (Fig. 32) are based on data of Adorada et al. (2023) for the Philippines.

Biology of *Podontia quatuordecimpunctata* in the Philippines. *Oviposition* (*n* = 20). Females usually deposit eggs on different parts of the leaf but were often near the leaf apex or middle of the leaf. When the sineguelas tree defoliates (November–June), the female lays eggs on adventitious shoots, stems and even on fruits (Fig. 16). Females laid eggs mostly on the abaxial surface, sometimes on the adaxial surface, on young and smaller stems, and even on other non-organic objects on the sineguelas tree (e.g., yellow plastic tags, nylon nets, and the aluminum sheets used as cages and labels).

One female was observed laying eggs on the leaves several minutes after emergence from the pupal case without any chance of mating. This female did not deposit the eggs in clusters but simply scattered the eggs randomly (crawling fast) on the leaf surface. A female laying viable eggs is slow and careful while ovipositing. However, this female laid these unfertilized eggs as if disposing of a biological waste; these eggs failed to hatch.

The egg cluster is arranged in two layers, with more eggs in the bottom layer (average of 19.45 (n = 20), and 2.95 eggs (n = 20) in the upper layer. We observed one female ovipositing an egg cluster in three layers of 31, 20, and 5 eggs. The egg clusters can be rounded or irregular shaped or even arranged in a row, but we observed one female depositing adjacent clusters of eggs (with 4, 11, 8, 13, 5 eggs). The average number of eggs oviposited by the female is 24.46 (n = 28) per cluster with a range of 11–47. The females that oviposited three egg clusters (n = 2) had an average of 23.30 eggs and a total of 70 eggs oviposited, while females that laid two egg clusters had an average of 43.00 (n = 2). To deposit eggs on the upper layer, the female climbs atop the egg cluster in the backward direction and deposits the eggs while moving forward. The hindlegs are positioned higher or stretched out when the eggs are laid on top of each other while the hindlegs are in a lower position when they are deposited on the substrate. Females immediately leave after oviposition, with no further care of eggs. Leaflets where eggs are deposited usually exhibited several feeding episodes which is interesting since damaged leaves offer less area for oviposition. Eggs are laid in an upright position (Fig. 16) and eventually the larval head is oriented at the top. Eggs are pasted on the leaf surface and stacked together side-by-side while the female is moving in the forward direction during oviposition. The female secretes an adhesive genital fluid while laying eggs. Typically, the larva emerges from the top of the egg, but we observed one larva emerging from the bottom—perhaps the female laid the egg in an upside-down position.

Egg (Fig. 16). It is elongate-ovate, wider in the middle, round on both ends, and measure about 1.82 × 0.85 mm (n = 10). They are light yellow when newly laid; after 15 minutes (based on time-lapse video). Most of the eggs turn whitish, off-white, creamy to chalky white, and then turns yellowish brown when ready to hatch. However, close observation of individual eggs showed that it turns white after ~five minutes. The upper part of the chorion hardens first and turns white from tip to base. Newly laid yellowish eggs are wet, then drying and turning white. It appears that light and surrounding temperature affect this hardening process. The central point at both ends is the last to harden or turn white leaving a tiny opaque dot.

Embryo and hatching. The developing embryonic fluid inside the eggshell is yellowish to orange when prematurely hatched or dissected. It takes about six hours for all the live and viable larvae to emerge from the egg cluster. More eggs hatch during day light hours (65%) than at night (35%) (n = 20 egg clusters). Hatch was heaviest from 6–7 AM (45%) compared to 20% in the afternoon (n = 20 egg clusters).

The eggs of SLB hatched in 4 (8.11%) to 7 (2.70%) days (n = 38). The majority hatch on days 5 (35.14%) and 6 (51.35%) (n = 37). This finding is similar to other findings—5–7 days on *S. pinnata* (Deka and Kalita 1999, 2002c; Roy 2015); 7–9 on *S. pinnata* (Pramanik and Basu 1973; Singh and Misra 1989); and 7–8 days on *S. dulcis* (Corbett and Yusope 1921) and 6.62 and 5.15 ± 0.20 days (Hossain et al. 2004). A much earlier incubation period of 3.50–6 days was recorded on *S. pinnata* (Islam et al. 2023). This variation could simply be temperature dependent across the vast region.

Survival. The total percent hatchability is 88.53% (n = 28). A much higher rate of 90.19% was recorded by Islam et al. (2023). However, the percent hatchability of eggs deposited on the lower surface of the egg cluster is 94.36 compared to those on the upper surface (87.58, n = 20). There is a chance of high mortality of eggs oviposited in the first layer since they are overlapped by eggs of the second layer. Larvae may have difficulty escaping from the lower layer. We observed instances of some larvae failing to emerge from these crowded and overlapping conditions. However, chrysomelids may lay sterile eggs as peripheral rows, likely to protect interior eggs (Chaboo and Nguyen 2004).

Egg loss. We did not observe any predators, parasites, or parasitoids of SLB eggs during the study. Several SLB egg clusters in the laboratory were subjected to parasitism by *Trichogramma evanescens* Westwood, 1833 (Hymenoptera: Trichogrammatidae), including newly oviposited eggs (minutes old eggs that are still soft and yellow). All these eggs failed to be parasitized by the hymenopterous wasp; comparing the SLB eggs and wasp showed that the chorion is too thick and hard to be penetrated by the minute wasp ovipositor. However, Deka and Kalita (2003, 2004) reported *Trichogramma evanescens minutum* Riley, 1833 in India, and recorded 18.33% and 19.66% egg parasitism in 1999 and 2000. Egg hatch failure may be due to drying or shriveling fungal infection or other causes, we also observed in the field that small undetermined black ant species (Hymenoptera: Formicidae) are breaking and feeding on unhatched eggs embryo.

Larva (Fig. 17–26). The larva is plump, wrinkled and golden yellow, contrary to Beeson's (1941) statement of yellowish-brown. Our rearing confirmed there are four larval instars, each covered with their own excrement, as first reported by Beeson (1941). We confirmed four larval instars, agreeing with some reports (Deka and Kalita 2002c; Hossain et al. 2004; Roy 2015), but contradicting other reports of three instars (Deka and Kalita 1999; Pramanik and Basu 1973) and five instars (Singh and Misra 1989).

Duration of larval period. We found that the SLB larval stage lasted from 14–16 days (n = 50; five replications at 10 individuals per replicate) on sineguelas. Deka and Kalita (1999 and 2002c) in India recorded a larval period of 11–15 days on hog plum. Corbett and Yusope (1921) and Singh and Misra (1989) observed similar results of 11–18 days while Roy (2015) recorded a duration at 11–19 days. Pramanik and Basu (1973) reported 12–20 days on hog plum. Hossain et al. (2004) reported an average of 14.4 ± 0.5 days. Recently, Islam et al. (2023) reported an average of 12.50–15.50 days.

We observed one larval specimen's life was prolonged from 16–19 days after it stopped feeding, grew slowly, and died on the 19th day, with a possible fungal infection as evidenced by white mycelial growth on its mouth (observed with stereo microscope). However, this data point was removed as an outlier result for our life table study.

Larval morphology (Fig. 23–26). The larval head and pronotum are heavily sclerotized, blackish, heart-shaped, and with an inverted "Y"-shaped ecdycial line at the head's middle portion. Clypeus is off-white in color and the labrum notched mesally. Maxillary palpi with four palpomeres and labial palpi with two palpomeres. The pronotum is heavily sclerotized, blackish, band-shaped, and with mesal division. Pro-, meso-, and metathoracic legs are blackish. Meso- and metasternual plates blackish, distinctly sclerotized, slit-like in the instar I, round in the second and instar III, and clover-like in instar IV. Thorax with one pair of spiracles above the prothoracic legs. Abdomen yellowish orange with 12 distinct segments, eight pairs of spiracles, and 9 pairs of lateral setal spots.

Anus. It is dorsally located at the 12th abdominal segment and caudal leg with round propygidial leg in the first and instar II and with distinct pair of propygidial legs in the instars III and IV which serves as larva's anchorage to foliage.

Molting and importance of the head and pronotum on the determination of larval instars on SLB. A newly molted larva has a yellowish head and pronotum, a semitransparent integument showing a network of trachea and its body and head are entirely covered with wet feces. The larval exuviae are incorporated into its feces. The exuviae along with feces may detach from the insect's body and dry on the foliage or on the ground. The head, pronotum, and legs of exuviae are blackish and can be easily distinguished from the semitransparent integument and sorted out from the feces. The size (length and width) of the head and pronotum is an accurate indicator of the larval instars aside from the larval body size (length and width) (Table 2).

Larva, instar I (*n* = 50) (Fig. 16, 18). The young larvae feed on the chorion to break the head free first (Fig. 16). It then feeds on other parts of the chorion. The neonate pulls the anterior part of the body forward to exit the chorion. Often the exit hole is just wide enough for the neonate to exit. After emergence from the egg, the larvae mostly have the habit of raising the tip of their abdomen into the air for a while before crawling away from the egg cluster in search of young shoots and leaves. They prefer to feed and roam around on young shoots and young leaves.

The neonate has a large black head, rectangular black pronotum, yellowish abdomen, and black legs. The head and pronotum appear like one unit, and the combined length is almost half of the body. The body is ovoid, widest at the midpoint when relaxed, and becomes elongate when crawling or moving since the upper body dragged the rest of the body forward while it is anchored on the leaf surface, and the body contracts and moves forward upon release (Table 2, length ~2 mm × width 0.5 mm).

It has a body length average of 2.94 ± 0.86 mm (range of 1.80–4.50 mm). It has a body width average of 1.19 ± 0.59 mm (range of 0.50–2.05 mm). The head and pronotum are now distinct and can be observed completely separated. The length of the head is 0.70 mm and the width of 0.60–0.70 mm. The length of the pronotum is 0.60–0.70 mm and the width of 0.50 mm. The mesometasternal plate on the dorsum is blackish and slit-like. The larva weighs 0.001–0.100 g. The combined length of the head and pronotum is almost half of the body.

Feeding behavior. Neonate larvae feed mostly on the abaxial surface of light green, young leaves but some were observed on the adaxial surface of leaves. They gregariously feed on the abaxial surface of leaves and scrape and feed only at the upper portion of the leaf; these young larvae do create holes in the leaf and often leaving the whitish plastic-like part of the leaf (Fig. 17–18). The neonate feeds only on the adaxial surface (cuticle, upper epidermis, and palisade layer) and does not bite through to the lower portion (lower epidermis and spongy layer) for the first 24 hours; after a day it can punch holes on the leaf. Older instar I larvae feed in smaller groups (<5) compared to the neonates that feed in higher numbers (up to 17).

Feeding damage. They create irregular feeding holes (round to longitudinal). They prefer young shoots and leaves or the set of leaflets from six or seven leaves from the actively growing tip. After one day, the larva can grow approximately one millimeter and its mandibles can create feeding holes in the leaf. Most of the neonate larvae prefer feeding on the 10th and 11th leaves from the apical shoot while a few (one each) are feeding on the 5th and 6th leaves from the apical shoot. Neonates that were placed on older leaves (40th leaf from the apical shoot) (n = 30) create the same characteristic feeding damage to young shoots and leaves. Some larvae migrate to much younger leaves to feed gregariously. They can also consume the lateral veins of the leaf and feed randomly on a different portion of leaves (leaf margin, inner surface, lower, middle, or upper portion of leaves). The larvae may consume the leaves leaving only the midribs (Beeson 1941). The feeding site appeared larger and turned brownish after 24 hours, giving the appearance of scarred leaves.

Instar I larva lasts for three days. The green irregularly rounded feeding areas dried and turned brownish after a few days. Feeding damage coalesced due to their aggregated feeding behavior. When not allowed to feed, newly emerged larvae died within 24 hours.

Instar I larva soon cover their entire dorsum with their own feces (Fig. 18). The body shows peristalsis (wave-like) movement at this stage and may explain how individuals move their feces and anal fluid from the caudal area towards the anterior and entirely cover the body. The body fluid appears to prevent the feces from drying and falling to the ground and facilitates its adherence to the body of the larvae. Wet or dried fecal pellets were commonly observed on the leaf surface.

Larva, instar II (*n* = 50) (Fig. 18, 20). This stage lasted for four days and the body, head and pronotum measurements as well as the weight of the larva are summarized in Table 2. The meso-metasternal plate on the dorsum is blackish and round. The larva has much stronger and more well-developed mandibles that can punch holes and consume both the upper and lower portion of leaves. However, this instar does not eat veins and midribs, confirming Deka and Kalita (2002b). The larva feeds on different leaflets, sometimes adjacent or widely separated.

Larva, instar III (*n* = 50) (Fig. 22–23). This stage lasted for three days and the body, head and pronotum measurements as well as the weight of the larva are summarized in Table 2. The meso-metasternal plate on the dorsum is blackish and round. The larva weighs 0.083–0.217 g (Fig. 23).

Larva, instar IV (*n* = 50) (Fig. 24–25). This lasted 4–6 days and the body, head and pronotum measurements as well as the weight of the larva are summarized in Table 2. Some individuals still feed on the foliage and can cover the body with feces; on closer study, the integument seems to be in the pre-pupal stage: the body is wrinkled, the pronotum thickened and the body size is significantly reduced from the 14th day (length 23.00 mm, width 6.00 mm) to the 16th day (17.00 mm length, 5.00 mm width). The mesometasternal plate at the dorsum is blackish and round. The mesometasternal plate at the dorsum is blackish and clover-like. The larva weighs 0.363–0.540 g. Late instar larvae have an orange body color, yet they are mostly covered with fecal matter (Fig. 24–25). When nearing pupation, the larva stops feeding and the body becomes bare of fecal material. Deka and Kalita (2002c) observed that instars III–IV larvae are voracious feeders, consuming veins and midribs, and can easily consume the whole leaf. The head and pronotum stop growing at instars III–IV and remain the same size. However, their sizes increase further during their last molt inside the pupal case.

The total duration of the larval stages of SLB is 14–16 days and the pre-pupal stage is 2–3 days for a total of 16–19 days before entering the pupal stage.

Larval fecal ecology of SLB (Fig. 20–26). The fecal mass or covering of SLB larvae is dark green, soft, moist or wet, bacilliform or sausage-like. Fresh feces are dark yellowish, then turn blackish and thread-like when dried or fallen off the larva's body. Under the stereomicroscope, we can see leaf partly digested and undigested fragments of leaf veins and midrib. Early instar larvae have finer feces compared to the coarser texture of later instars and adult feces. The size and volume of the larval fecal mass indicates the voracity and speedy growth of the larva. Feces are produced almost continuously as the larva feeds and accumulate at the back of the head; some may fall off from any part of the larva's dorsum, depending on the body position. Feces fall off easily when the larva is positioned upside down. The late instar larva stops feeding before pupating and so it loses its fecal covering.

Larvae that are not feeding for a longer period shed their fecal covering; this can be attributed to the loss of moisture that adheres and binds the feces together to the integument of the larva. Thus, the late instar larva that is ready to pupate ceased feeding, lose the moisture and its fecal coat and exposed its full integument. A naked larva, without feces, is an indication that the individual has not fed for a longer period, probably several hours, while if it is completely covered with feces is an indication that it has fed continuously and gregariously. Fecal material deposited only at the caudal or posterior end of the body indicate that it recently fed continuously while if it is deposited near the head only indicates that it has not fed for quite a while. A voracious feeding larva has a large thick volume of feces, and its body grows fast; a sluggish feeder or unhealthy-looking larva has a thin, thread-like, and small amount of fecal matter. For instance, one larva was observed growing slowly and feeding abnormally compared to others, it had fewer fecal coats and did less feeding damage. It failed to survive, and we observed its mouth with fungal growth, perhaps an entomopathogen affecting its system.

Exuviae are sometimes incorporated into the fecal covering especially when the larva is newly molted but are often quickly discarded. All feces were recovered from each rearing cage to determine the number of instars of SLB. The cast exuvial skins of SLB are not retained in the fecal covering as in other species of the *Blepharida*-group (Paterson 1943; Takizawa 1978); exuviae fall to the leaves and ground after reaching the caudal area. If the larvae are actively feeding in an inverted position, the accumulated lump of fecal mass on the dorsum can be mistaken for an exuvial mass; sooner or later it detaches from the body.

When observed under a microscope, the feces are too wet to obtain a clear image. It appears to be covered by a film of liquid covering. We found small insects may accidentally stick to it. For instance, a tiny dead midge (Diptera: Cecidomyiidae) was found incorporated into one of the larva's feces, possibly attracted to the feces and accidentally stuck. It is unclear at present what could be the effectiveness of control sprays on larvae of SLB if the fecal cover interferes with spray reaching the body.

Larval locomotion (Fig. 24–25, Film 1). Pramanik and Basu (1973) reported that *P. quatuordecimpunctata* larvae use the pseudopod at the "anal extremity" to clasp and adhere to leaves. Larvae are often hard to collect by hand, forceps, or camel brush as they stick to the leaf surface. Gustafson and Chaboo (2009) compared this attachment structure to the adhesive anal disc of the pygopods in some chrysomelids; it serves as a holdfast organ during locomotion and minimizes the risk of falling off the plant.

Feeding behavior in larvae and adults (n = 50). *Larvae* (n = 50) feed voraciously and gregariously, growing fast, with an average length increase of 1.24 mm per day (n = 50) and an average width increase of 0.49 mm per day (Fig. 19–22, 26) (Table 2). Neonate larva feed on young shoots and young leaves (upper portion of twigs); they often fail to consume the entire set of leaves but randomly consume only a few or several leaflets. The young shoots, tender, and light green leaves are most preferred by the larvae compared to the mature dark green leaves (lower portion of twigs). The larvae migrate from other adjacent stems or twigs in search of more preferred shoots and young and tender leaves. At times when pest populations are high, the later instar larvae were forced to feed on older leaves that are available but often leaving the leaves at the bottom of the twig (very old leaves) undamaged. Large larvae were frequently observed crawling and migrating on networks of large stems and tree trunks. Twigs not producing shoots and having few young leaves were inhabited by adults and older or late instar larvae.

Our observations concur with Deka and Kalita (2002b) who reported that instar I–II larvae prefer to feed on tender and half matured leaves compared to matured leaves. Instars III–IV and adult beetles prefer to feed on tender, half matured and matured leaves with high preference on half matured and matured leaves. SLB loses the preferences due to competition for available food resource. A similar trend was reported by Hossain et al. (2004) who studied the mean leaf consumption of the beetle (measuring larval weight) on hog plum (*S. pinnata*) and recorded a value of 3.56 g during their entire larval period of 14.4 days. Instar IV larva is the most voracious at 2.06 g of leaves followed by instars I–III at 0.072, 0.680, and 0.750 g of leaves. The residual population of larvae and adults forced to feed on the fruits during times when leaves are either scarce or absent during the fruiting season (Fig. 8–9)

Instar II were observed actively feeding continuously on the leaves for a period of 4.0–7.0 minutes (average = 5.0 minutes) (*n* = 3) then rest, stop feeding, and are immobile or 25.0–37.0 minutes (average = 30.0 minutes). One instar IV continuously fed without a break for nearly 11 minutes on tender leaves and rested for 56 minutes and resumed feeding. The cycle of feeding and resting is continuous; one larva repeated the same set of activities three times while the other larva repeated it twice. The cycle was interrupted by crawling or moving around the leaves, petioles, and stems for 6.0–15.0 minutes (average = 10.0 minutes) (*n* = 3).

Adult (*n* = 50). They preferentially feed on the abaxial surface of the leaves probably, evading sunlight, as observed by Pramanik and Basu (1973). However, we observed feeding on the adaxial surface, producing small to large, rounded feeding holes on the leaf surface. They were frequently resting and not doing anything. They either sit on top the leaf, feeding by scraping on the adaxial surface and undersurface or by clinging to the sides of the leaf and positioned longitudinally to it (Fig. 6). The adults cut and chew the leaf lamina margins in an up-and-down motion using the large, strong, black mandibles. This creates a round, concave shaped feeding scar on the leaf margin. The adults advance during of feeding until they have consumed a wide portion of the leaf. They can completely devour the leaf lamina, blade, and veins, leaving only the tougher midrib or some larger veins of mature leaves.

Adults appear to prefer to feed on young and tender (light green), and mature leaves (dark green) of sineguelas. Like the larvae, they feed and rest alternately. Thus, they are often observed in the field that most of the time if the SLBs are not feeding or mating, they are just simply resting and immobile on top or underside of the leaves, under-brush weeds and grasses. Adults rest for approximately 30 minutes and groom and clean their head (antennae, compound eyes, and mouthparts) and legs for another 30 minutes or more. This leg-cleaning habit was observed often in the field while they rested. The adult used the outer side base of the tibiae, equipped with fringed short hairs to clean these sides of the body while it is rubbing both the tarsal pads to clean the base of the tibiae and the tarsal pads as well. The insect alternately cleans both parts to ensure that they are free from dirt, debris, or possibly mites or other parasitic arthropods.

The leaf-feeding consumption of male and female adult beetles was compared over 24 hours for three consecutive days. Female SLBs are three times more voracious feeders than males. Females consumed an average of 10.00 leaflets at 19.42% (*n* = 3) average feeding damage per day compared to males at 3.58 leaflets at 15.10% (*n* = 3) average feeding damage per day. Deka and Kalita (2002b) reported similar patterns with the male less voracious and consuming an average leaf area in its lifetime at 239.00 cm^2 compared to the female consumption at 303.27 cm^2. Hossain et al. (2004) computed the mean, leaf consumption of an adult at 8.23 g, and it consumed 11.79 g of leaves during its lifespan.

The sineguelas tree defoliates in November and December and starts to produce flowers and fruits from January to May. However, during these periods, the tree produces few new shoots or adventitious shoots which serves as female's preferred egg oviposition sites and food. Once foliage is devoured, larvae and adults of SLB will even shift to feed on the developing fruits.

Pupa (*n* = 20). The pre-pupal stage does not cover their body with fecal matter. It takes 2–3 days before the mature larva (pre-pupa) constructs its pupal case and transforms to a pupa (Fig. 27–30). However, Islam et al. (2023) recorded a much higher range of 5–6 days on *S. pinnata*. Mature instar IV larva may fall freely from the tree or crawl down to the base of the tree trunk. We observed that this instar larva descends the tree when it is time to pupate; it does not feed after this stage and the body starts to shrink. If this sensitive period was significantly delayed, the larvae will be unable to construct their pupal case; they simply coil around the soil, become immobile, die, shrink, and show infection with either parasitic fungus or entomopathogens.

The majority of larvae pupated on the soil surface while some pupated underground, within the upper 2.0 cm of soil. Most pupate singly. The pupal cases may be found individually or grouped around the base of the tree

(Fig. 29). We also observed that group pupation in the soil near the base of the tree, within clusters of two and four an average of 3.43 ($n = 7$) pupae per aggregate. This was observed on sineguelas trees in montane of Batangas and Guimaras, coastal areas of Guimbal, Iloilo, Brookes Point, and Puerto Princesa City, Palawan, hilly areas of Ilocos Sur and Los Baños, Laguna, and flat plains of Malaybalay, Bukidnon, La Carlota City, Negros Occidental, Florida Blanca, Pampanga, Manaoag, Pangasinan, Nueva Ecija, and Sablayan, Occidental Mindoro. Hossain et al. (2004) commented that pupation in normal conditions on hog plum (*S. pinnata*) was at 5–15 cm depth in Bangladesh. Hossain et al. (2004) measured the average length of the pupa as 10.2 ± 0.12 mm and width of 3.15 ± 0.01 mm.

Pupal case (Fig. 27, 29). It is grayish outside. When dissected after adult emergence, we observed that the inner wall surface is smooth and blackish. A brownish pupal case was observed in Puerto Princesa City, Palawan. The pupal cell has average length of 15.61 ± 1.80 mm ($n = 40$) and average width of 10.39 ± 0.62 mm ($n = 40$). The minimum length is 12.68 mm ($n = 40$) while its maximum length is 17.70 mm ($n = 40$), its minimum width is 8.89 mm ($n = 40$) and its maximum width is 12.48 mm ($n = 40$). The average weight with the insect inside is 0.749 ± 0.017 g ($n = 20$) and ranges from 0.526–0.959 mm; the empty case weighed an average of 0.621 ± 0.016 g and ranges from 0.401–0.914 mm ($n = 20$). The width of the pupal case exit hole for the developed adult is much wider compared to its base. This posterior end is where the final (instar IV) exuviae is deposited.

Pupal case construction. Once the larvae reach the soil, they dive head-first into a small crevice in the soil or digs and inserts into the easy-to-penetrate looser upper soil. They tend to aggregate at the base of the tree. The larva compacts soil particles by pushing and rolling them around the body, creating the egg-shaped ball. The larva smooths the inner walls by turning its own body inside the pupal case. The larva ingests fine and loose soil particles while moving around its case, and later excretes wet or moist feces. The larva position themselves in a coiled posture in the case; its mouth has easy access to feces extruding from the anus. The larva continues ingesting more soil until case increases in size and volume. The fecal materials are temporarily held by the anus, legs, mouth, and ventral side of the integument so they do not fall or touch the surrounding dry soil, so preserving moisture content. The larva continuously moistened the fecal mass with buccal fluid. Then the larva continues building the pupal case by the catch, pass, and paste method using its legs, maxillary and labial palpi, and mouth on the surrounding wall of the pupal case. The mouthparts move in an up-and-down motion while continuously pasting a big chunk of wet and sticky soil mass onto the wall (sides), floor (lower portion), and ceiling (upper portion) of the case. The larva continues moving around the case several times and, remarkably, sometimes even exits the case to harvest more soil particles, then re-enters the case to complete and seal it with more dirt and feces. The internal or external surface of the case when viewed under the stereo microscope is a continuous complex of mound-shaped soil structures individually pasted together. This is the result of the individual ball of wet soil that is gathered, carried, and pasted by the larval mouth to complete the mosaic-like surface. The external surface (Fig. 27) is rough with lumpy protrusions. The cases are distinct within the soil, easily distinguished by the color and shape and easily separated by hand.

We noted that the larvae apparently utilized earthworms' fecal material (= vermicast) that is commonly found at the base of sineguelas trees in our three mountainous sampling areas. Earthworm's vermicompost is a solid mass of fine soil particles that are lumped together while SLB pupal case is round, hollow inside, and with a round opening (Fig. 27, 29) where the adult exits. Dissecting and crushing several pupal cases revealed that it is composed mostly of soil, fine sand particles, stones, and pebbles with other associated and incidental particles such as quartz crystals, fine root, and grass or weed fibers, small snail shells, exoskeletons of SLB and other insects' integuments, e.g., ants and fungal spores. It is possible that ready-to-pupate larvae utilize and regurgitate soil particles or even use old pupal cases since these are numerous, scattered around the base of the tree. Thus, the beetles can be exposed to larvae, pupa, and adults that were previously infected with entomopathogens and other fungal parasites.

We documented a larva stealing the fecal mass from another larva when both were building their pupal cases side-by-side in a plastic basin. One larva encircled around and stole the moist fecal mass located at the belly of the other larva and. This may be a form of competition at times when fine soil particles are scarce and larger soil clumps and rock particles dominate the landscape.

Several pupal cases were collected from the field, placed in a plastic container, and reared in an air-conditioned laboratory room but failed to emerge. When dissected, these pupal cases were dry and may have been too hard for the adult to emerge. Pupal cases that are too dry are hard and requires a strong force to break or cut which may impede the adult from exiting. We hypothesize that the adult releases copious amount of body fluid from its mouth to soften the upper interior part of the soil while inside the pupal case before it can break free. However, in nature, the availability of high moisture and relative humidity at night and rainfall keeps the pupal case moist and probably makes it easy for the adults to emerge from the case.

Empty pupal cases were observed being used as a preferred nesting site for some species of black ants on the ground. We collected a few pupal cases far from the tree base. Most of pupal cases are found around the base of the tree trunk and creeping root system and branches that fell and spread all over the area due to strong winds and the frequency of typhoon occurrence in the Philippines.

Role of pupal case (Fig. 27, 29). This earthen-fecal structure encloses the vulnerable pupa and protects it from other predators, parasitic insects, entomopathogenic fungi, natural elements like rainfall, heat, moisture, and other nuisance arthropods that may disturb the pupation process. This case is crucial to SLB survival. Pupation within hard earthen cocoons is widespread among flea beetles and may reduce susceptibility to predators and parasites and minimize desiccation (Prathapan and Chaboo 2011).

Pupal survival. Several factors contribute to death during pupation. Some larvae inside the pupal case simply shrink and dried, others are mummified; we observed some to have yellowish or cottony white fungal growth on their body while others turned brownish. Many were dried and mummified and failed to emerge from the pupal case while others are blackened. Results of the random pupal sampling showed that 60% (n = 12) of the larvae inside the pupae simply died and dried probably due to an undetermined species of parasitic fungus; 20% (n = 4) were infected with undetermined species of fungus, and only 20% (n = 4) of the adults were able to emerge and survive from the pupal case. Other nuisances include ants, symphylans, collembolans, mites, wasps, and even other SLB larvae, for they compete for the same limited space and fine soil particles available at the surrounding base of the tree (O. Calcetas 2022, pers. obs.)

In the laboratory we observed that adequate moisture is crucial to adult survival when rearing from pupae. Dry pupal cases prolongs the pupal duration, and dries the developing pupa. Pupae were reared outside of the laboratory to ensure enough moisture and enclosed in a nylon net to protect them from natural enemies. Disturbing the pupal case in a small plastic container with sterilized soil for observation under the microscope in the laboratory increases mortality. In high temperatures the duration of the pupal stage increases from the normal 15–22 days to a 41–51 days (n = 14). In addition to temperature stress, the enclosed seedling was also infested with an undetermined species of scale insect (Hemiptera: Coccidae) and an undetermined species of mealybugs (Hemiptera: Pseudococcidae) that defoliated leaves early (Table 5). Thus, producing smaller sized adult offspring. The total life cycle of the beetle is 35–48 days from egg to adult emergence (Table 3).

Adults (*n* = 50). SLB is a robust and brightly colored flea beetle (Fig. 10–12). The head and pronotum are yellow and the elytra are either salmon pink, light orange, dark orange, yellow and with yellow legs. The upper part of the incisors of the mandibles is black, starting from the exarate form as pupa until adulthood. There are 14 collective black, irregularly rounded spots on the elytra. However, counting the individual black spots, finds nine on each elytron for a total of 18 spots. The elytra of a live and healthy beetle are either salmon pink or orange and they turned dark or light orange after death, however, individuals with yellow elytra turned cream after death.

The antenna has eleven antennomeres There are also ten distinct longitudinal punctate striae on each elytron. The male has U-shaped genital opening on the last abdominal segment while the female has no U-shaped genital opening. The 3rd, 4th, and 5th abdominal segments are U-shaped in males and nearly straight in females. Adults are not active flyers (Pramanik and Basu 1973).

Morphological and color variations. Some adult SLB show morphological variations especially on their elytra. Some have missing spots on the middle portion; others have distinctly large spots compared to others while one adult male had a large blackish band on one elytron, instead of several black spots.

Sexual dimorphism. The adult female is slightly longer than the male. Males have an average body length of 12.63 ± 1.27 mm (n = 20) (range 10.76–15.54 mm) and an average body width of 7.99 ± 0.53 mm (n = 20) (range 6.52–9.64 mm). Females have an average body length of 13.38 ± 1.34 mm (range 11.22–15.19 mm) and an average body width of 7.86 ± 0.66 mm (*n* = 20) (range 6.11–9.20 mm). Live adult males weigh slightly less than females (difference of 0.045 g) and have an average body weight of 0.223 ± 0.001 g (*n* = 20) (range 0.159–0.258 g) while females have an average body weight of 0.268 ± 0.001 g (range 0.207–0.358 g). The dead weight of adults was determined while differences in weight through natural death and starvation were also compared for both sexes. Results showed that adult males' weight through natural death significantly differs from adult males' weight from a three-week starvation period at (0.091 and 0.060 g respectively). Indicating that males lose more muscles and tissues when not feeding adequately. Adult females' weight through natural death does not differ significantly from adult females' weight that was subjected to three weeks of the starvation at 0.081 and 0.085 ± 0.001 g respectively. Moreover, adult females that were starved weigh more at 0.004 g, indicating that females lose more body tissues and muscles through egg production than starvation.

Mating behavior. We observed mating pairs (*n* = 20) in diverse sites on the sineguelas tree: hanging on the underside of leaves, on top of leaves, and clinging to stems of various sizes. We also observed mating pairs on grasses and sedges at the base of the tree; when disturbed, both fell to the ground but remained in copula. We observed mating often with threesomes of one female mobbed by two males in the field.

Mating position. Mating was prolonged; one pair was observed in copula continuously for three days while another pair mated for nearly two days (1 day and 21 hours). Singh and Misra (1989) observed pairs *in copula* for three days and frequency (six times during a 29-day observation period). Pramanik and Basu (1973) reported a mating of from 30–120 minutes. Khan (2017) reported that the average mating frequency, mating duration and mating interval were 11.2, 30.5 hours and 60.3 hours, respectively.

The female feeds on the leaf during mating. The female anchored all claws on the substrate while the male mounted female's elytra using its tarsi. The inserted male genitals also support the male's weight while the female carries him during mating. However, during mating, the male pro-claws cling to the female's elytra and its metalegs anchor to the tree surface (leaves or stems) while its mesolegs sway up and down from time to time. The male genitalia is inserted and retracted into female organ which pushes the abdomen of the female up and down. The female usually does not move during mating, in contrast to the male.

When the female moves, she carries the male on her back. During mating, males may groom their legs by rubbing the fore- and mesolegs and mesolegs and metalegs one at a time. The female sometimes walks during mating; she terminates mating by wiggling the male side-to-side or jerking her body until the male genitalia is detached from her genitals. The female may kick the male on its back using her hindlegs, although it is difficult to reach the male. Singh and Misra (1989) observed different methods used by the females to disengage from mating—by rubbing the males on branches and by jerking movements or kicking up her hind legs. One odd behavior is that both male and female excreted feces during mating.

On several occasions, males were observed to mate with an already dead female beetle in the field and laboratory, a case of necrophilia (reported in cicadas, Shen-Wang and Meyer-Rochow 2021).

Female fecundity (*n* = 6). The six females laid eggs sporadically for 8–26 days (average = 17.33 days) and oviposited an average of 696.33 (*n* = 6) eggs. These females produced ~36.33 egg clusters, with an average of 19.53 eggs per cluster. One prolific female even produced 53 egg clusters with a total of 1,071 eggs in her lifetime.

The females collectively laid eggs for a period of 69 days (August 05–October 13, 2022) (Table 4). Pramanik and Basu (1973) recorded 80–200 (average = 120) eggs produced by female *P. quatuordecimpunctata* in her lifetime. Kalshoven (1981) noted that female *P. affinis* lives for three months and produced 500 eggs on *Spondias* sp. in Indonesia. This high production explains the potential population outbreak capacity of the pest on *S. purpurea*, the massive damage it inflicts on the plant, and how one or few viable and surviving females can trigger an outbreak.

Prathapan and Chaboo (2011) considered that the large size of the beetle and the fecundity of these species contributed to their defoliating impacts on the plant. However, competition for a limited resource can reduce this high potential fecundity of females in the field. There are more males oviposited by the female at 66.67% compared to females at 33.33% (*n* = 15) and the sex ratio is computed at 6.6:3.3. In addition, nearly the same trend was computed from a collection of adults in one, large sineguelas tree in San Miguel Batangas City on August 16, 2022, for the botanical pesticide trial set up. There were more males sampled at 58.86% (93) compared to females at 41.14% (65) (*n* = 158). Based on our cumulative life cycle data, SLB has 7.60–10.43 (35–48 days) or an average of 8.80 generations per year on sineguelas in Batangas City.

Adult longevity and survival (*n* = 20). The rearing cage experiment for fecundity also provided data for adult male and female longevity in the screenhouse. Females live longer than males. Adult male longevity was from 21–78 days (average 37.17) (*n* = 8) while female longevity was from 58–180 days (average 129.00) (*n* = 8) (Table 4).

Longevity data are available on *S. pinnata* on the Indian subcontinent where males last 21.4 ± 1.75 days and females last 39.4 ± 14.87 days (Hossain et al. 2004), both males and females of 40–52 days in Bangladesh (Sardar and Mondal 1983), 5 months (150 days) for laboratory-reared *S. pinnata* (Pramanik and Basu 1973), 53–168 days (1.76–5.60 months) (Singh and Misra 1989), and 73.50–104.50 days in males and 77.50–115.50 days in females (Islam et al. 2023).

We tested the beetle's ability to survive, travel, and colonize new areas. Different life stages, including five males and five females, were starved, and tested, while field-collected adults were assumed to be fed and placed in a petri dish. Results showed an average survival of 13.9 days (range 8–22 days) for all ten beetles. In another test, two adult beetles, assumed to be satiated, were placed in a petri dish without food and water and survived for 28 and 57 days, respectively. These results suggest that adult beetles fed enough in the field can survive transport over long distances.

One newly emerged adult was not fed and was subjected to the same test and died after 24 hours. This indicates that without food reserves, adults have a low chance of survival. The adults continuously expel urine and feces while in the petri dish. Newly emerged larvae died within 24 hours of not feeding (*n* = 40). In the choice experiments, larval instars II–IV can survive for 3–4 days without feeding (*n* = 20) but continuously lose weight. Larval instar IV that are ready to pupate need to find suitable soil to construct their pupal case to survive. Pupae left bare or without a soil covering simply die due from desiccation or infected with entomopathogen.

Flight behavior. Chrysomelids show a range of tactics to escape from predators and observers, the adults either jump backward or fall to the ground from the underside of the leaf. When on the top of the leaf, the adult beetle became motionless before jumping, flying, or falling to the ground and hiding and crawling on foliage. This mechanism is called thanatosis and is a widespread escape response among leaf beetles (Prathapan and Chaboo 2011). Weeds, grasses, vines, and other vegetation serve as a good cover for the beetle to evade vertebrate predators such as chickens which are voracious feeders of the pest in different parts of the country. However, adult SLB seldom fly, or they are not active flyers and most of the time they feed, mate, or are simply motionless for long periods.

Host range of SLB (Fig. 1–4). The most available host of SLB in the Philippines is the red sineguelas, *S. purpurea*, since they are the most cultivated species. The yellow sineguelas, *S. dulcis*, commonly observed in Ilocos Norte, are less prevalent elsewhere and less preferred by farmers since the fruit is less sweet, slower to ripen, less firm, and with lower market value. This is in contrast to red sineguelas which are sweeter, take longer time to ripen, much firmer, and with higher market value. The yellow sineguelas trees monitored in Pagudpud, Ilocos Norte were pest-free at the time of monitoring (December 2021). However, to prolong the shelf life of the fruit and maintain its freshness, it is recommended to refrigerate them inside the vegetable compartment (Calcetas 2022, unpublished notes). *Spondias pinnata,* or locally known as "Libas", is another alternative host of SLB and is more prevalent in the Bicol region (Camarines Sur, Albay, and Pio Duran) where they are planted in mountainous and coastal areas. The fruit of *S. pinnata* is considered too sour to be eaten by humans and unmarketable compared to the two other species but the young shoots are used as a popular souring agent in the Bicol region (Lupi Agricultural Technicians 2022, personal communication).

No-choice experiments for SLB and visits to large plantations. The Philippine Carabao Mango (*Mangifera indica* L., 1753) and cashew (*Annacardium occidentale* L., 1753), like *Spondias*, are members of Anacardiaceae. Anacardiaceae tree crops in the Philippines are prime exports and dollar earners. Thus, a no-choice experiment was done with the fruit along with cashew, rubber tree (*Ficus elastica* Roxb. ex Hornem., 1819; Moraceae), and pili (*Canarium ovatum* Engl., 1883; Burseraceae) which is a relative of Anacardiaceae and a host of the SLB pest in other countries (Prathapan and Chaboo 2011) (Fig. 33–35).

Results showed that all SLB instar I larvae failed to feed on the four test plants and died after 24 hours in the rearing cage. However, instar IV larvae did not feed but wandered around the plant and nylon net cage and descended to the soil to pupate early; they do not feed on mango, pili, and rubber tree. Larval instars II–III fed on a small portion of the leaves of cashew while they did not feed on mango, rubber, or pili and they all died after 3–4 days. Adults were able to survive for an extended period and females were able to live longer than males.

Results of field monitoring. The SLB was not sighted in these areas; interviews with seasoned researchers, nursery caretakers, and local agricultural technicians in the area yielded nothing on the presence of the pest on these important commodities. However, the pest was detected in high numbers on red sineguelas in these areas. Several trees and seedlings of "Batwan tree" *Garcinia binucao* (Blanco) Choisy, 1849 (Clusiaceae) were monitored in Guimaras island province and La Granja, La Carlota City, Negros Occidental but showed no indication of the presence of SLB. This contradicts a report of the pest on this tree crop in Masbate during our interview in Pio Duran, Camarines Sur, however, Prathapan and Chaboo (2011) reported a Clusiaceae host for *P. congregata* Baly, 1865 in India so we will continue monitoring.

Status of SLB on rubber tree (*Hevea brasileinsis* (Willd. Ex A. Juss) Müll. Arg, 1865, Euphorbiaceae) and ornamental varieties of rubber plant (*Ficus elastica* Roxb. ex Hornem., 1819, Moraceae). This is an important plantation crop in Mindanao for export; for example, the export volume of rubber for 2020–2021 is at 206.99 thousand MT indicating a 30.7% annual increment and its value of PhP 8.16 billion (US$ 148,363,363.00) was higher by 67.4% than its previous year's level (Philippine Rubber Industry Roadmap 2017–2022, 2023). The reports of pest presence on rubber trees are contradictory (present according to Stebbing (1914) but doubted by Medvedev 1999; Deka and Kalita 2002a; Prathapan and Chaboo 2011) so our team tried to verify the presence of the beetle on the plant. Five males and five females of SLB were starved for nearly ten days and introduced unto three different ornamental varieties of rubber plant. They did not feed at all. We surveyed of thousands of rubber seedlings and hundreds of trees on plantations and a large nursery in Malaybalay, Bukidnon in November 2021, and no SLB was found. We interviewed several farmers of rubber; photos of the pest were shown to all participants, but no one recognized the pest with the plant. However, SLB was numerously sampled in nearby villages with sineguelas trees. Thus, the rubber tree as an alternate host of SLB is still questionable and we concur with others (Medvedev 1999; Deka and Kalita 2002a; Prathapan and Chaboo 2011) that it needs further confirmation.

Other insect pests and disease pathogens associated with sineguelas in the Philippines. The population dynamics study monitored other major insect pests of sineguelas in the Philippines and our findings are reported in Table 5. A separate publication will report the complete list of other insects, spiders, and pathogens associated with sineguelas in the Philippines (Calcetas, in prep.).

Before the introduction of SLB to the Philippines, the fruit fly *Bactrocera* spp. (Diptera: Tephritidae) was considered the most important insect pest of sineguelas, especially during the fruiting season (April to June) (Calcetas 2022, arthropod survey notes). Another pest observed, especially from June to August, is the capsid bug (*Helopeltis bakeri* (Poppius, 1915), Hemiptera: Miridae). The production of more shoots and young leaves during this time increases the incidence of shoot tips and young shoot burning or blackening caused by nymphal and adult feeding. The pest was observed in Batangas City, Los Baños, Laguna, Iloilo, Guimaras, and La Carlota City, Negros Occidental. An undetermined Microlepidoptera species was found to feed on the inside of rolled leaves and shoots of sineguelas in Batangas City, Iloilo, Guimaras, and La Carlota City, Negros Occidental; we are now calling this insect the sineguelas shoot roller (SSR). At least four different species of tussock moth (Lepidoptera: Erebidae: Lymantriinae) were observed gregariously feeding on sineguelas foliage in Los Baños, Laguna, Batangas City, Pampanga, Pangasinan, and Iloilo. In the towns of Brgy, Sineguelasan, Bacoor, and Cavite a massive outbreak of undetermined species of tussock moth (Lepidoptera: Erebidae: Lymantriinae) based on the collection of arthropod photos of pests shown to elderly residents in the 1940s defoliated a majority of the sineguelas trees planted in the area, which became a nuisance to residential houses, and prompted the government military to spray the tussock moth with insecticides to control the pest (Concepcion and Chua 2022, personal communication). In addition, an undetermined species of bagworm (Lepidoptera: Psychidae) was observed in numbers in Cagayan de Oro in 2021. Another insect pest of sineguelas in Western Visayas are June beetles or "salagubang" or "labog" (*Leucopholis* spp., Coleoptera: Scarabaeidae). In Iloilo, residents observed them in high numbers feeding on foliage from May to July. An undetermined species of Psychidae (Lepidoptera) in Miagao, Iloilo was observed feeding on foliage in high numbers. The tree is adjacent to a Talisay tree or Indian almond (*Terminalia cattapa* L., 1753, Combretaceae) which was heavily infested by this insect pest. A farmer in Espinosa, Guimaras collected rhinoceros beetle (*Oryctes rhinoceros* L., 1758, Coleoptera: Scarabaeidae) is an important insect pest of coconut (*Cocos nucifera* L., 1753, Arecaceae), and an undetermined species of scarab grubs infesting the roots and scavaging on dead trees (Narida 2022, personal communication). Recently, an undetermined species of elaterid larva (Coleoptera: Elateridae) was caught feeding near the base of a stem with canker-like symptoms in Batangas City. We observed that enclosed sineguelas seedlings (nylon net, screenhouse, or glasshouse for an extended periods) are prone to a massive infestation by different mealybugs and scale insects (Hemiptera). The absence of predators and parasites inside these enclosed rearing cages exponentially increases their population that then become a serious pest and cause the death of the affected seedlings (Table 5).

Adults and nymphs of the predaceous bug (*Eocanthecona furcellata* (Wolff, 1811), Hemiptera: Pentatomidae) were observed feeding on different larval instars of SLB (refer to Table 6) (Fig. 36–39). The bug was observed in multiple sites in the country. Prathapan and Chaboo (2011) observed a different pentatomid (*Eocanthecona parva* (Distant, 1902), Hemiptera: Pentatomidae), preying on the larva of *P. congregata* Baly, 1865 on Malabar Tamarind (*Garcinia gummi-gutta* (L.) N. Robson, 1968, Clusiaseae) in India.

We documented several natural enemies for different stages of the pest from different parts of the country (Table 6). These include multiple fungi species; we await more precise identifications by experts. This is in addition to Prathapan and Chaboo's (2011: Table 7) comprehensive list of the different natural enemies of the beetle.

Discussion

As part of the ongoing monitoring of SLB in the Philippines, we report here the first detailed study of the natural history and biology of *P. quatuordecimpunctata* based on one year of field, laboratory, and screen house observations in the Philippines.

The life cycle of SLB is similar to other *Blepharida*-group beetles (Pramanik and Basu 1973; Furth 1992, 1998; Furth and Lee 2000; Prathapan and Chaboo 2011), including pupal cases, four larval instars, terrestrial or underground pupation in a fecal-soil case. The adults are large and colorful. The entire life cycle lasts 35–48 days and follows the seasonal pattern of the host trees (Fig. 31).

We documented that all four larval instars of SLB retain their feces (Fig. 18, 20–23). This fecal body coat is known for all the documented *Podontia* juveniles (Barlow 1900; Corbett and Yusope 1921; Pramanik and Basu 1973; Takizawa 1978; Singh and Misra 1989; Prathapan and Chaboo 2011) and distinguishes the *Blepharida*-group lineage (Prathapan and Chaboo 2011) within the large subfamily Galerucinae (10,000 species, Lingafelter and Konstantinov 2000). Fecal-retaining behaviors and different constructions appear in four other chrysomelid subfamilies (Cassidinae, Criocerinae, Cryptocephalinae, and Lamprosomatinae) (Vencl et al. 2004; Brown and Funk 2005). The structures have been explained as camouflage, offensive barriers to predators and parasites and may enhance environmental conditions (protection from rain, wind, and sun) for the individual (Olmstead and Denno 1992; Hilker 1992; Olmstead 1994, 1996; Vencl and Morton 1999; Müller and Hilker 2003, 2004; Prathapan and Chaboo 2011). These coats may deter predators, parasitoids and parasites of SLB and must be considered in any pest management strategy. We found that the large mass of feces is evidence of actively feeding larvae; the fecal coat is lost in larvae that are not feeding well or in late instar IV at that stage nears pre-pupation. No other materials (trichomes, plant fragments, fungi, exuviae) were found in the fecal coats.

We revealed the construction of the terrestrial and subterranean pupal case. Many chrysomelids pupate underground and this aspect is challenging to study. We discovered that these larvae use their mouthparts and legs to manipulate soil and their feces to build the case. Their feces may be imbibed with chemicals that help to cement and harden the case. We discovered that the case is crucial to survival since naked pupae die due from desiccation or become infected with an entomopathogen.

We documented several natural enemies for different stages of the pest from different parts of the country (Table 6). Two remarkable associations of *Blepharida* group beetles are known: 1) Lebiine carabids (Coleoptera: Carabidae) (Koch 1958) where these carabid adults are parasitoids of the terrestrial pupae, and 2) some members are used as hunting poisons in indigenous hunting of San bushmen in southern Africa (Chaboo et al. 2016, 2019). The carabid-Blepharida-group association is an example of aggressive mimicry as the carabids closely resemble their prey/hosts in size and color patterns (Lindroth 1971). Attempts have been made to exploit this predatory-parasitoid carabid behavior to control populations of the economically significant potato pest chrysomelid, *Leptinotarsa* (Weber et al. 2006, 2008). We did not collect any carabids in our survey of arthropods on the sineguelas tree (Table 6) nor did we find any carabid parasitoids in the pupal cases. It is possible that a carabid predator-parasitoid of SLB may exist in the native range. Perhaps, we may yet uncover a native Philippines carabid species that may adopt SLB as a host.

What makes SLB a successful pest?

The adults can survive starvation (1–2 months) without any food or water in confinement and its longevity (6 months). The reproductive capacity or fecundity is high (average = 696.33 eggs; from 05 August to 13 October 2022). The larvae and adults‘ can extensively defoliate their hosts are alarming characteristics of an invasive pest species, especially in an introduced environment with diverse potential host plant species to adapt.

Possible integrated pest management strategies to manage SLP on the red sineguelas tree crop in the Philippines

Fruiting season (January to May). *Removal of adventitious shoots*. We observed that red sineguelas trees completely shed their leaves during flowering and fruiting but some new shoots emerged as new sprout, or adventitious shoots. The number of shoots produced by each tree may depend on the frequency and amount of rainfall in a particular area. These shoots serve as the SLB females‘ residual population‘s most preferred ovipositional site and larva‘s food for its growing period of ~two weeks (14–16 days). Once they completely devoured the available foliage they will even shift to feed on the developing fruits (Fig. 7–8). Thus, without new shoots, no new eggs will be oviposited and no new larvae will emerge to feed on the fruits. After 24 hours without feeding neonates die. Thus, we highly recommend a strategy of regular removal of these unwanted shoots or sprouts manually or by sickle.

Vegetative season (June to October). *Undetermined species of fungal entomopathogen.* At the onset of the wet season, the sineguelas tree starts to produce new shoots and foliage which become a food source for SLB. After oviposition, the eggs hatch after 4–7 days (approximately 1 week) and for the next two weeks or 14–16 days, larvae go down at the base of the tree to congregate, construct pupal case, and pupate. Due to the topography of the sineguelas plantations in Batangas City and the cost of transporting water we recommend a drench application of an aqueous solution of the fungus species around the base of the tree. One 250 gram plastic bag of entomopathogen for two sineguelas trees (divided into two) is suggested. Based on our trial the fungus continues to grow and reproduce on the substrate, we recommend spreading the corn substrate or growing media of the entomopathogen around the base of the tree. This prolongs the presence and increases the establishment of the fungus, thereby increasing the SLB infection rate. The fungus grows on the body of the adult beetle and kills the pest after 5–7 days of application or getting the entomopathogen. We are examining the effectiveness of spraying on larvae that are protected by their fecal coat.

Insecticide spray. With heavy beetle infestation, we suggest spraying of recommended insecticides to reduce the pest population. The application of pesticides in the soil/at the base of the tree to control the pest can also be tried. Initial results showed that SLB adults die after 9 to 14 minutes after spraying. The use of Insect Growth Regulator (IGR) insecticide which is effective for the immature forms is also highly recommended.

Pentatomid bug. The bug *Eocanthecona furcellata* feeds on different immature or larval stages of the pest. Therefore, we recommend mass rearing of this bug in government facilities for its release and distribution to sineguelas fruit farmers.

Manual collection of SLB. The SLB is not an active flyer and are often seen resting or mating on top of the leaves. The pest can be easily caught by beating branches and foliage so insects fall or feign dead below. These SLB can be collected manually, fed to chickens and ducks or fish, or drowned in soapy water. Additionally, regular collection of the pupae deposited around the base of the tree can significantly reduce their population and infestation. The adult beetles can also be fed to chickens.

Conclusions

Podontia quatuordecimpunctata is now an established invasive pest of sineguelas tree crops (*Spondias* spp.) in the Philippines. Several government and university agencies are collaborating on long-term efforts to study the biology of the host trees and the beetle towards control measures. This is our second contribution, after Adorada et al. (2023). We determined the life cycle, characteristics of each stage, types of damage, and established the phenologies of both host plant and SLB in the Philippines situation. Our next steps are to report on the population dynamics of the pest population, phenology of the sineguelas tree, natural enemies, other major arthropod pests, foliar disease, soil-borne entomopathogens including their mass production, other parasites and their effects on the overall population of SLB. We will continue to monitor the beetle's alternate hosts.

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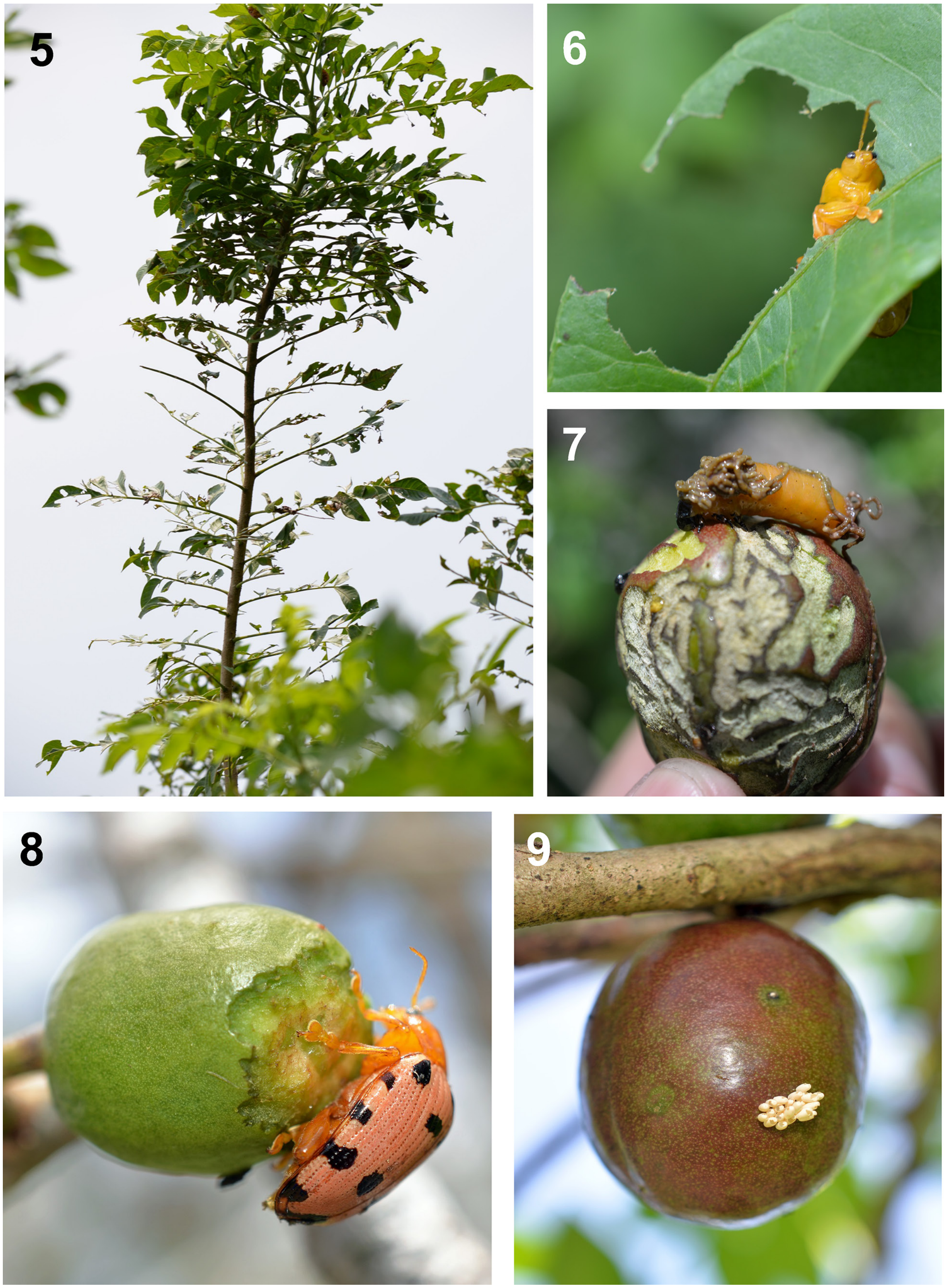
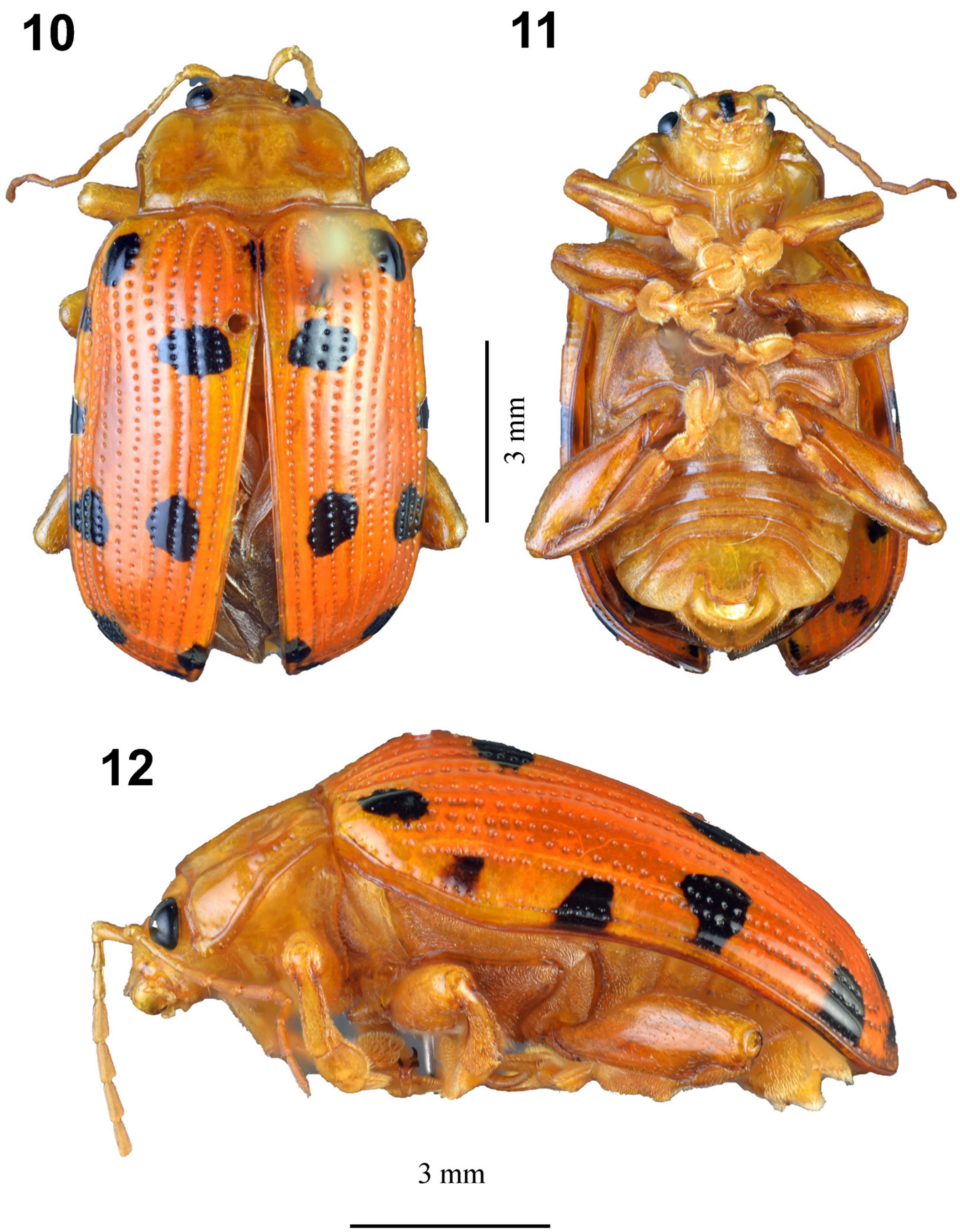
Figures 1–4. Plants associated with the sineguelas leaf beetle **1)** A typical sineguelas tree (*Spondias purpurea* (L.) with foliage (June to November). **2)** Fruits (April to June) in the Philippines. **3)** Fruits of yellow sineguelas (*Spondias dulcis* Parkinson). **4)** Fruits of "Libas" (*Spondias pinnata* (L.f.) Kurz). (Photographs courtesy of SLB project).



Figures 5–9. Beetle damage to sineguelas tree in the Philippines. **5)** Defoliation from herbivory of adult and larvae. **6)** Adult eat the entire leaf. **7)** Herbivory on fruit by the larva. **8)** Herbivory on fruit by an adult. **9)** Adult oviposits on fruits. (Photographs courtesy of SLB project).



Figures 10–12. Adult of sineguelas leaf beetle (SLB) (*Podontia quatuordecimpunctata* (L., 1767). **10)** Dorsal habitus. **11)** Ventral habitus. **12)** Lateral habitus. (Photographs courtesy of SLB project).

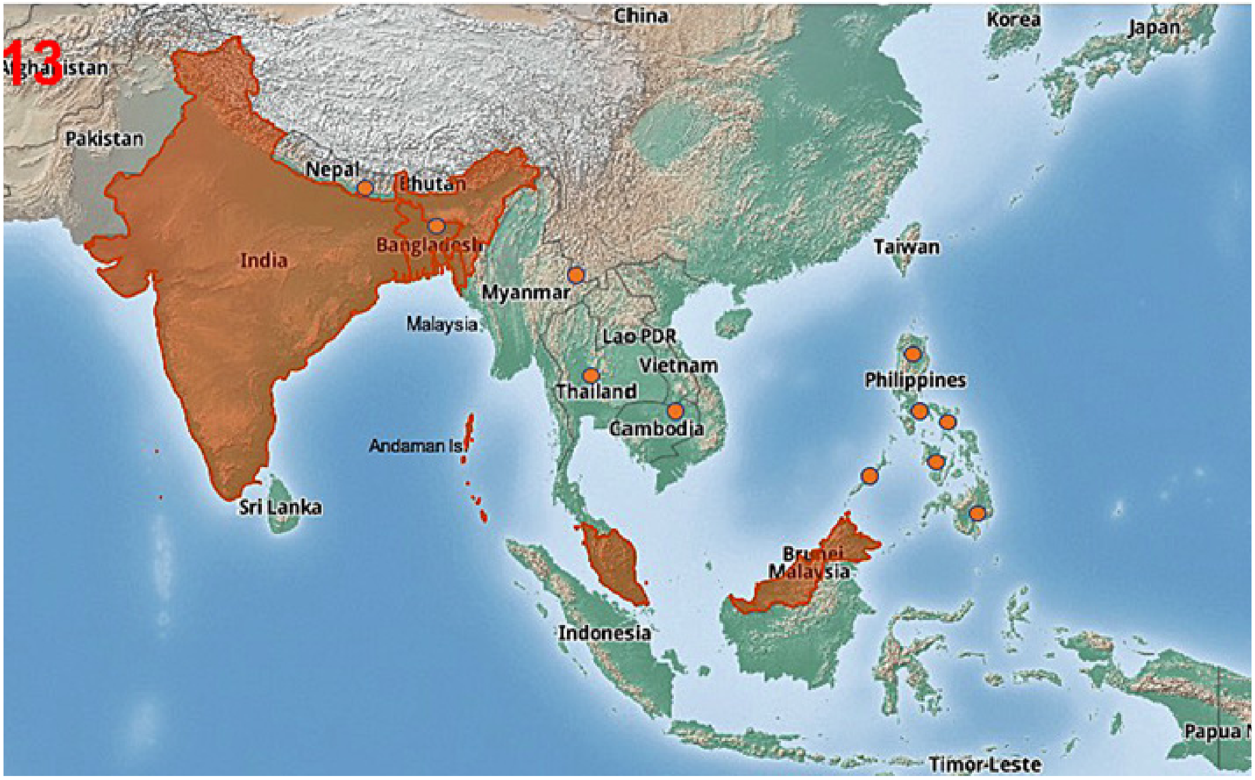
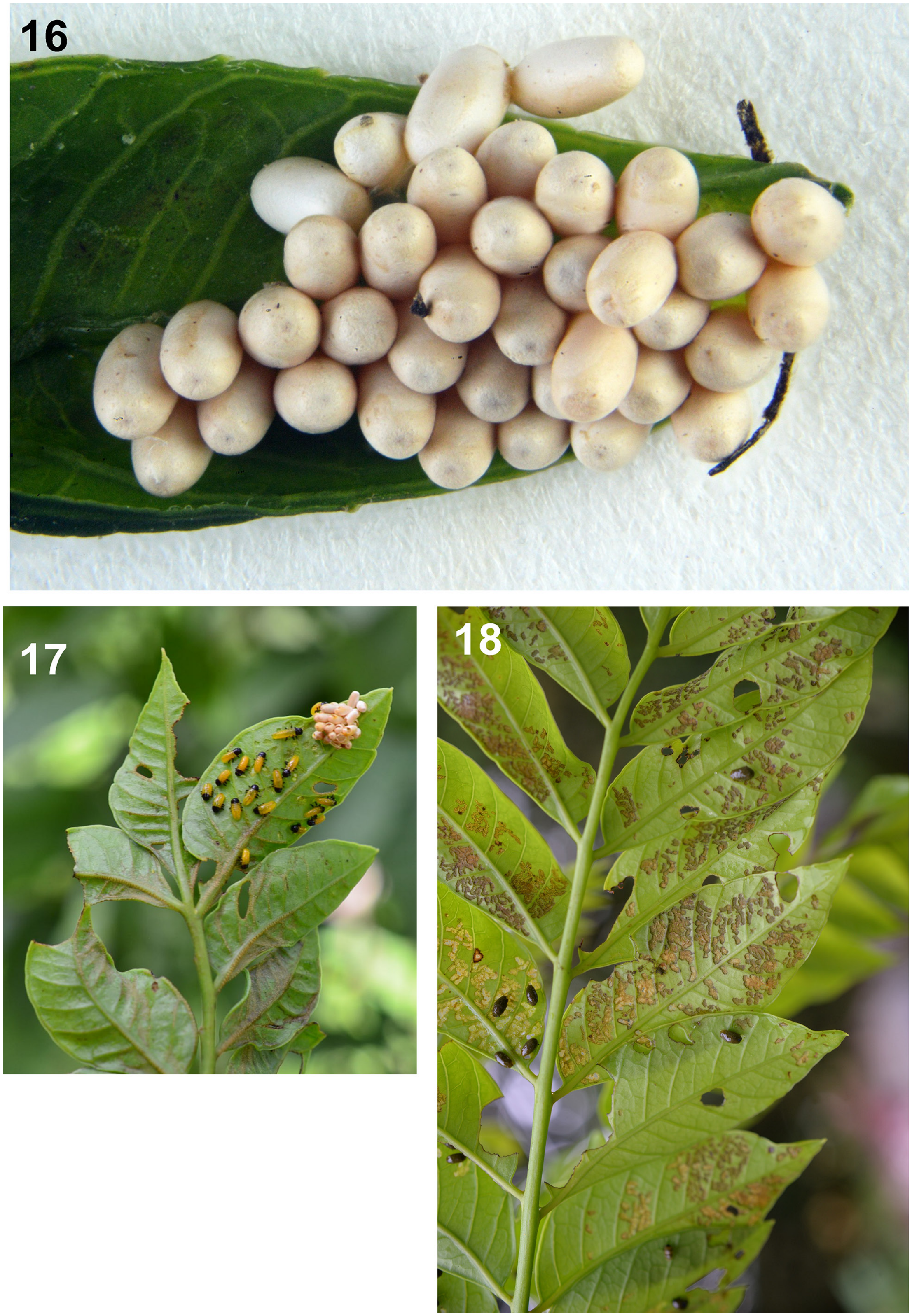
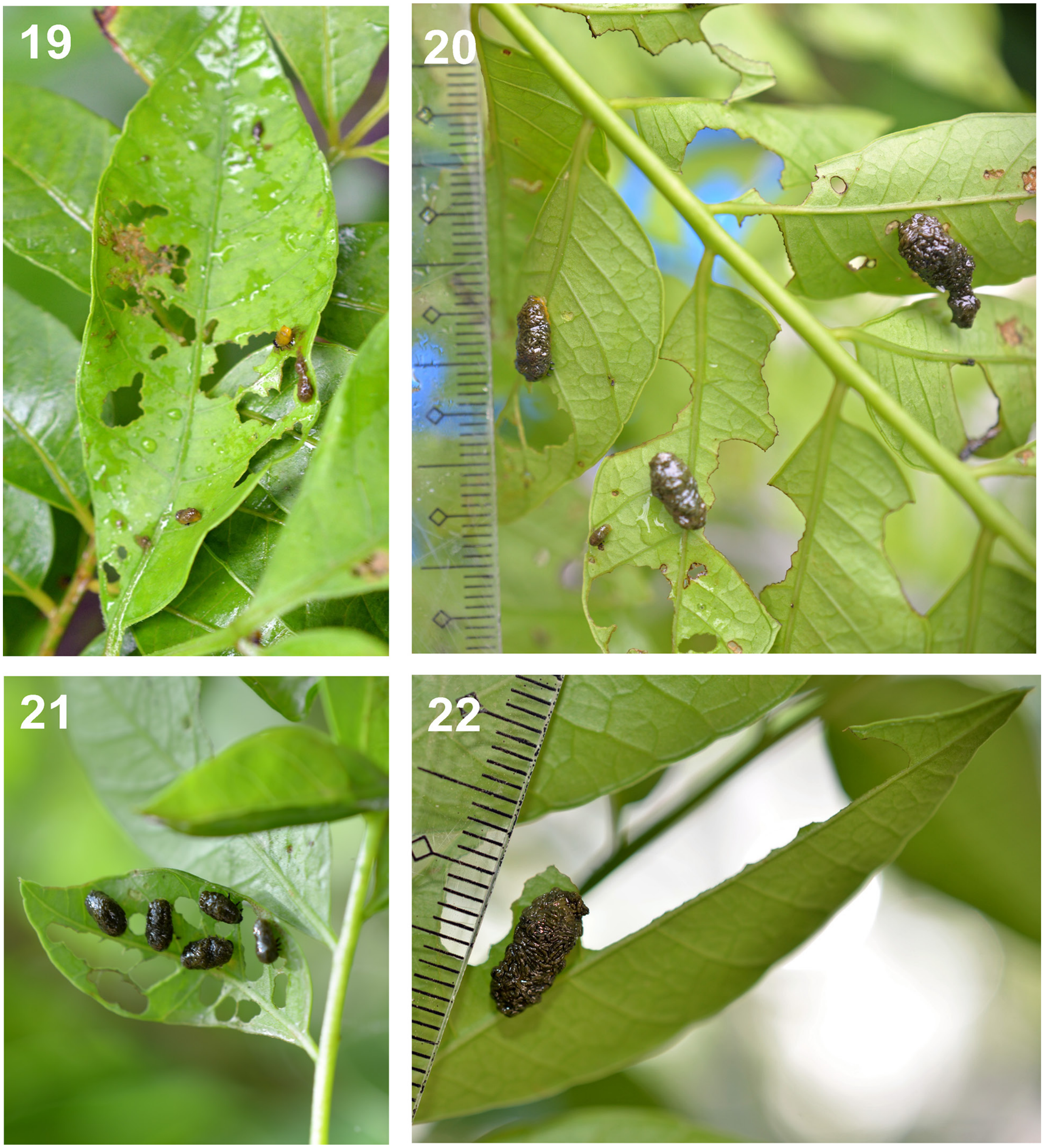


Figure 13. Geographic Distribution of sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) in South, Southeast Asia (CABI 2022). Added in the map are the countries of Nepal, Myanmar, Lao, Thailand, Cambodia, different islands of the Philippines and Andaman Island where the pest is also present (Mohamedsaid 2004).

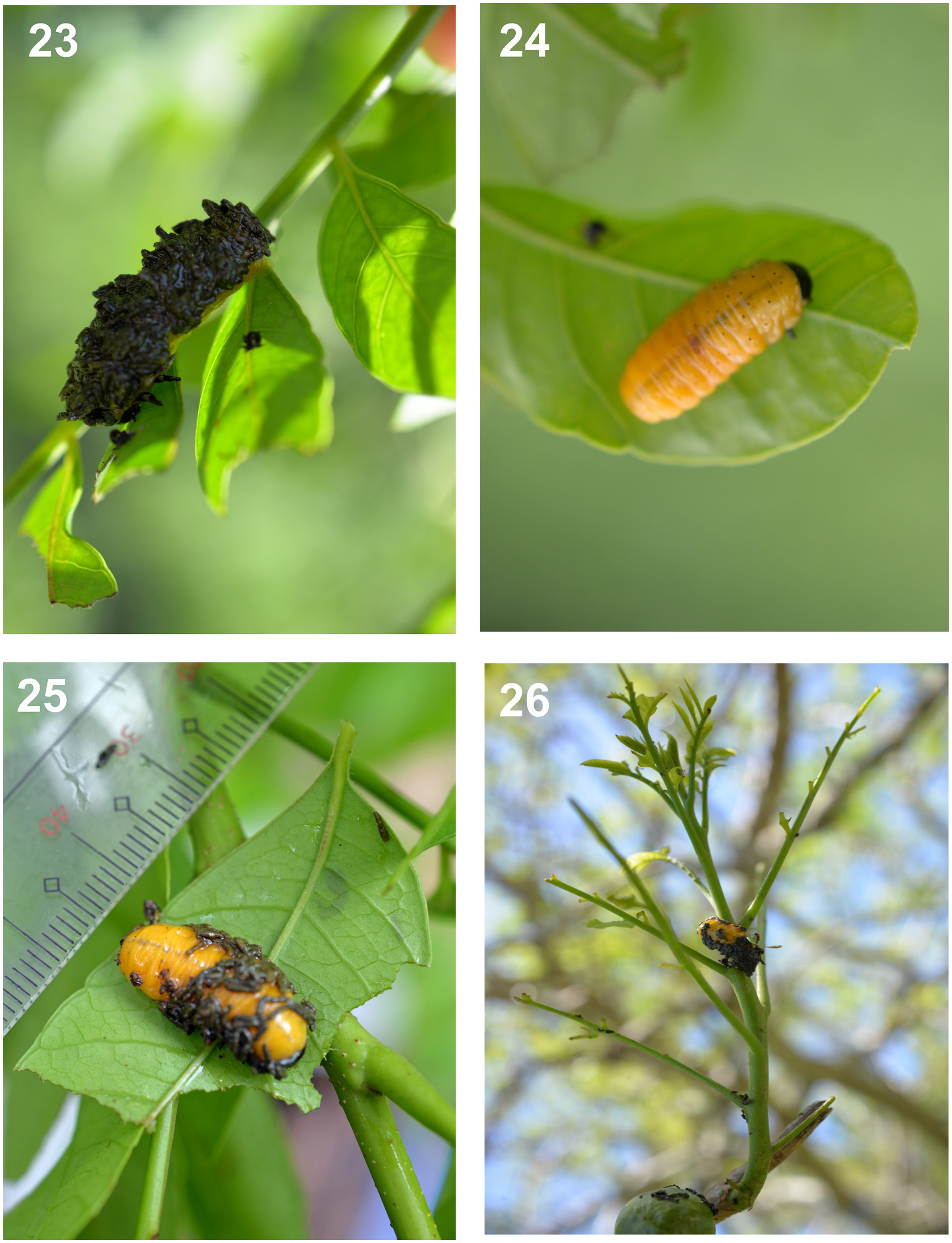
Figures 14–15. Leaf beetle rearing cages. **14)** Sineguelas leaf beetle rearing cage with sineguelas (*Spondias purpurea* (L., 1767) seedling as food and soil at the base of the twig for pupation. **15)** Rearing cages where the study of its biology was conducted. (Photographs courtesy of SLB project).



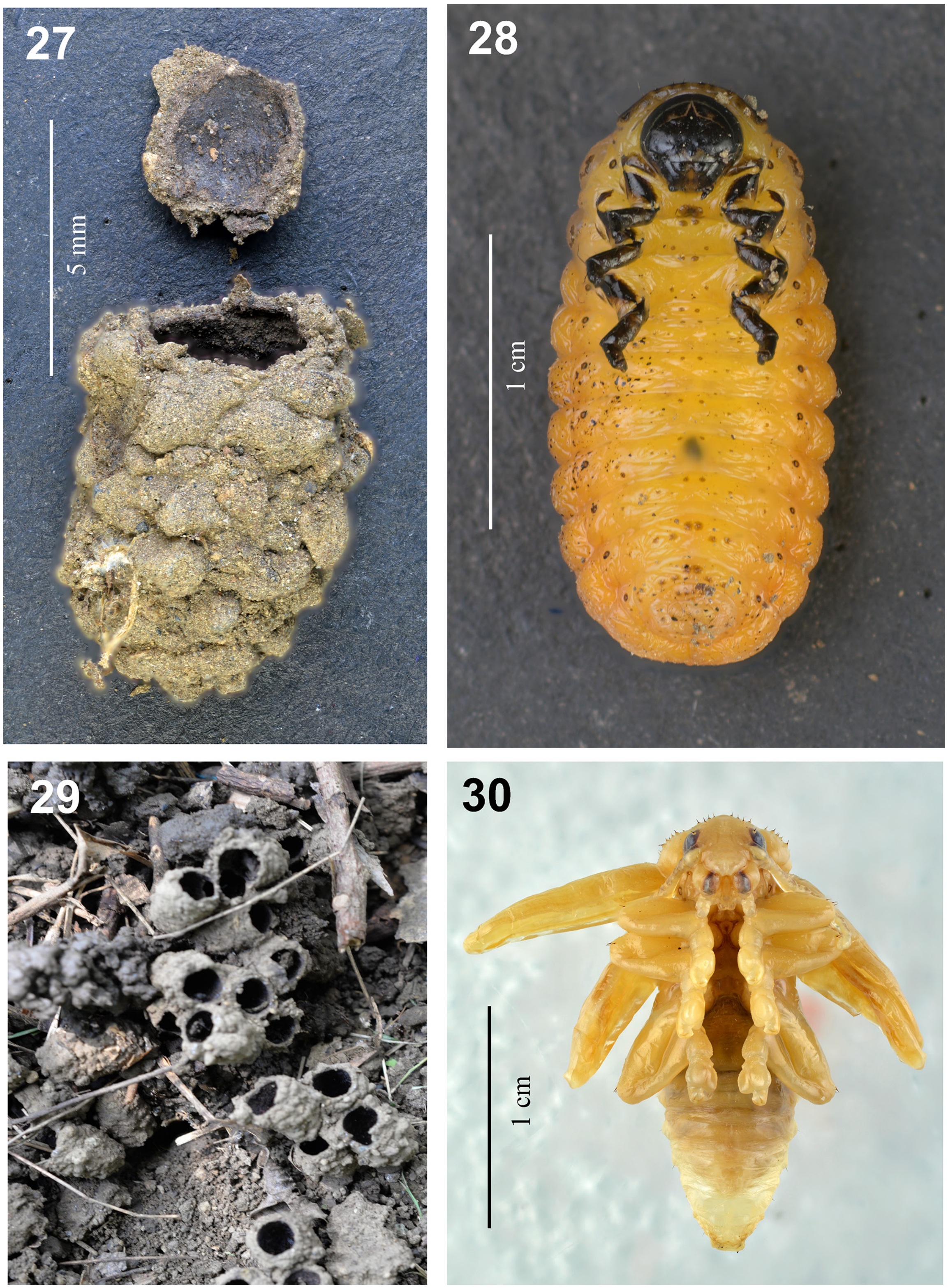
Figures 16–18. Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) on sineguelas (*Spondias purpurea* L.). **16)** Egg cluster. **17)** Neonate larvae. **18)** Feeding damage of neonate larvae (Photographs courtesy of SLB project).



Figures 19–22. Larvae and their feeding damage of sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) on sineguelas (*Spondias purpurea* L.). **19)** Instar II larvae. **20)** Instar II larvae. **21)** Instar II larvae. **22)** Instar III larvae. (Photographs courtesy of SLB project).



Figures 23–26. Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) on sineguelas (*Spondias purpurea* L.). **23)** Third instar larva. **24)** Fourth instar larva. **25)** instar IV larva. **26)** Late instar larvae of SLB can defoliate the twig and leave only midribs and stems. (Photographs courtesy of SLB project).



Figures 27–30. Pupae and pupal cases of sineguelas leaf beetle (SLB) (*Podontia quatuordecimpunctata* (L., 1767). **27)** Pupal case constructed from soil by the pre-pupal larva. **28)** Mature larva extracted from pupal case. **29)** Pupal cases at the base of a tree of sineguelas (*Spondias purpurea* L.) in field. **30)** Pharate adult inside pupal case. (Photographs courtesy of SLB project).

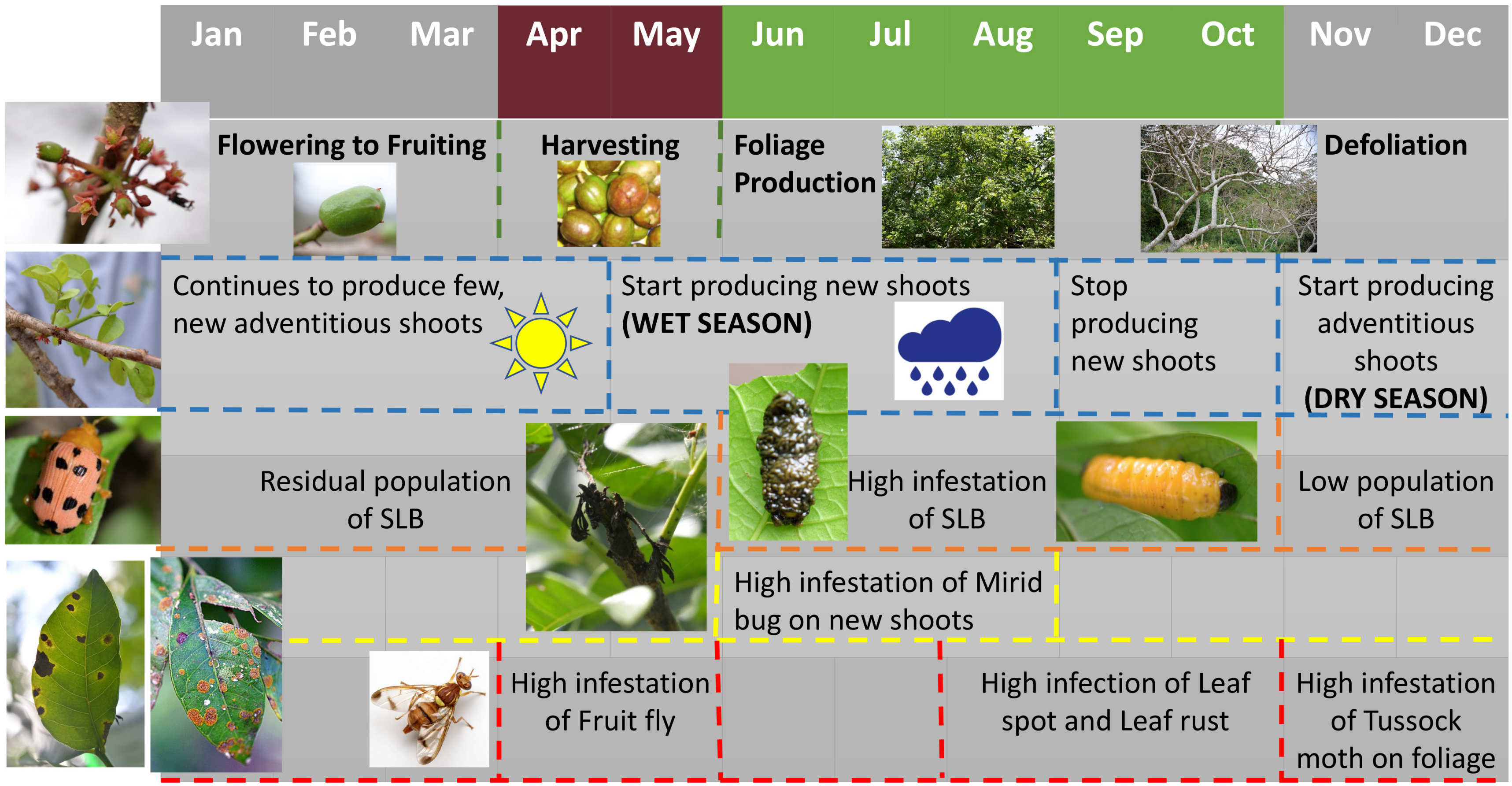


Figure 31. Phenology of sineguelas (*Spondias purpurea* L.) and seasonal abundance of sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) and other insect pests and disease pathogens in the Philippines (Photographs courtesy of SLB project).

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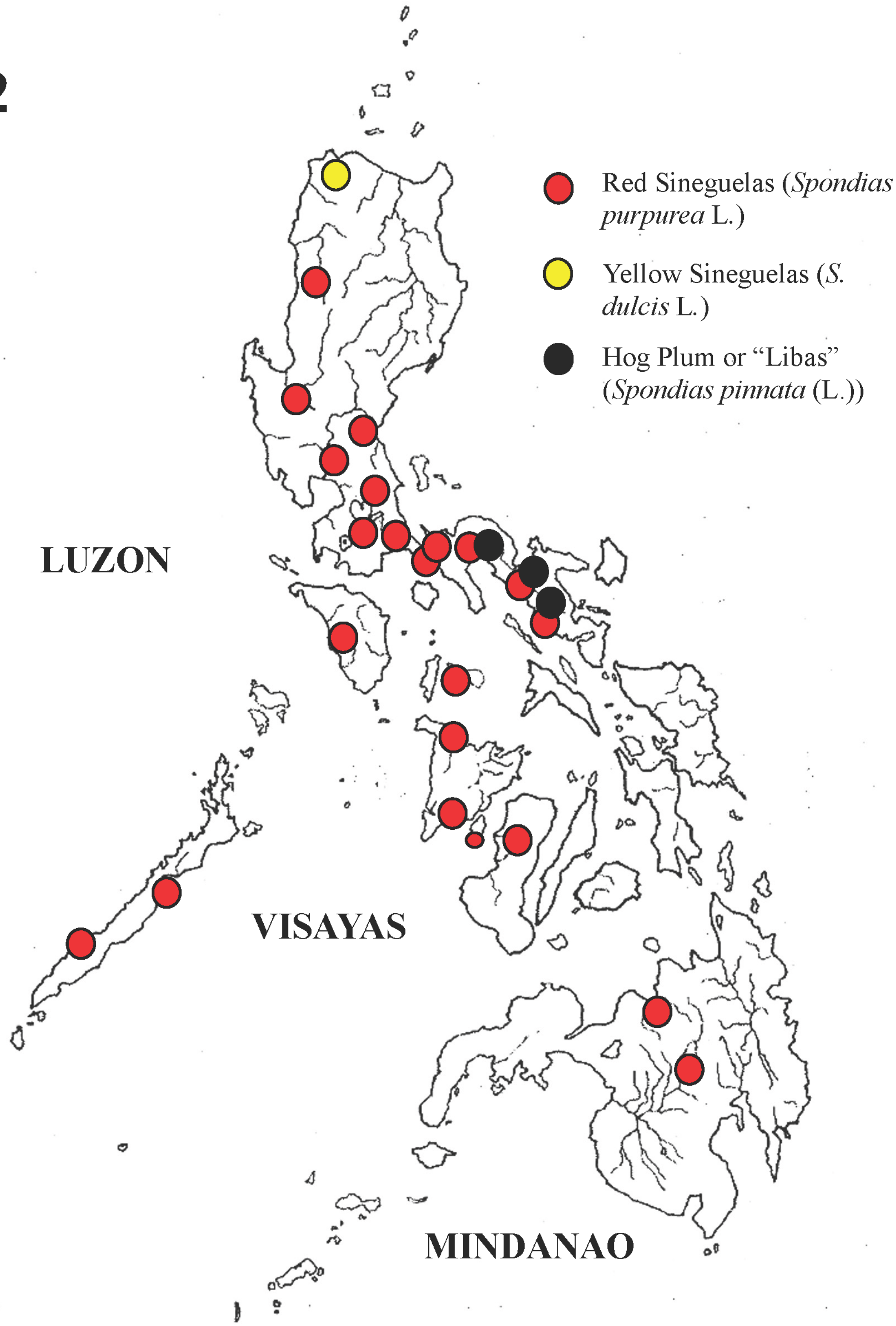
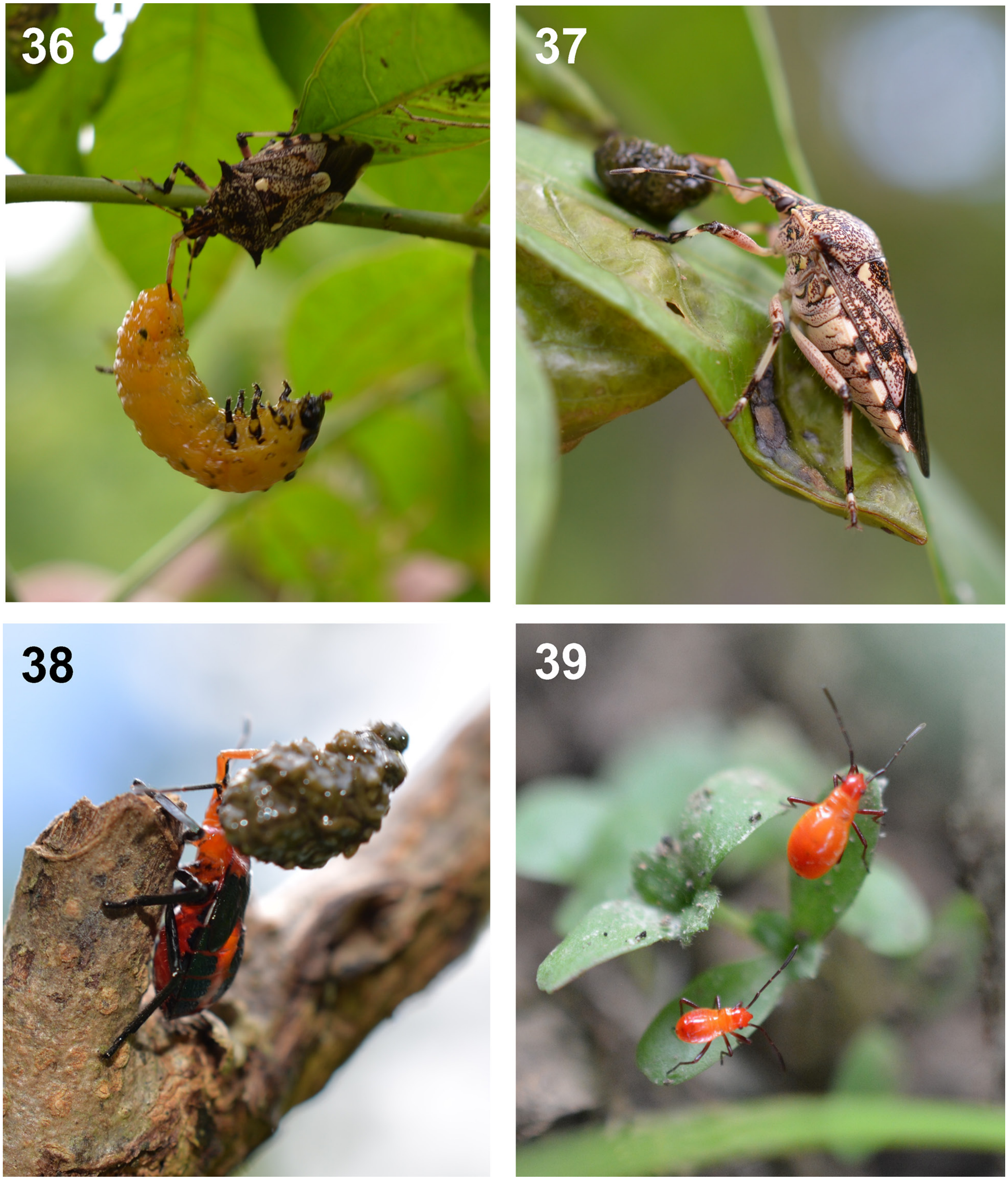


Figure 32. Infestation of sineguelas leaf beetle (SLB) (*Podontia quatuordecimpunctata* (L., 1767) on Red sineguelas (*Spondias purpurea* L.) (red circle), Yellow sineguelas (*S. dulcis* Forst.) (yellow circle), and hog plum or "libas" (*S. pinnata* (L.)) (black circle) in the Philippines. (Map courtesy of Dr. Sheryl A. Yap of IWEP-UPLB, Los Baños, Laguna, unpublished thesis 2004) (Adorada et al. 2023).

Figures 33–35. No choice experiments. **33)** Carabao mango (*Mangifera indica* L.). **34)** Cashew (*Anacardium occidentale* L.). **35)** Pili (*Canarium ovatum* L.). (Photographs courtesy of SLB project).



Figures 36–39. Pentatomid bug (Hemiptera: Pentatomidae: *Eocanthecona furcellata*) preying on the larval stages of sineguelas leaf beetle (SLB) (*Podontia quatuordecimpunctata* (L., 1767). **36-37)** Adults preying on 4th and 2nd instar SLB larvae. **38)** Nymph preying on 1st instar larva. **39)** Early instars of pentatomid bug. (Photographs courtesy of SLB project).

Table 1. Host plants of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767)) (after Prathapan and Chaboo 2011).

Host Plant	Reference
Anacardiaceae: *Mangifera* L. sp.	Furth 1998
Spondias L. sp.	Kalshoven 1951; Takizawa 1978; Medvedev 1999
Spondias cytherea Sonn.	Yunus and Hua 1980; Daulmerie 1994; Furth 1998; Khatun et al. 2016
Spondias dulcis Forster	Corbett and Yusope 1921; Maulik 1926; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Mohamedsaid 1989, 2004; Singh and Misra 1989; Baksha 1997; Medvedev 1999; Roy 2015; Rahman et al. 2022; Adorada et al. 2023
Spondias pinnata (L.f.) Kurz (=*Spondias mangifera Willd.)*	Barlow 1900; Maxwell-Lefroy 1909; Stebbing 1914; Beeson 1919, 1941; Corbett and Yusope 1922; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Husain and Ahmad 1977; Sardar and Mondal 1983; Singh and Misra 1989; Howlader 1993; Baksha 1997; Deka and Kalita 1999, 2002a-b, 2003, 2004; Hossain et al. 2004; Uddin and Khan 2014; Roy 2015; Rani et al. 2021a-b; Adorada et al. 2023
Spondias purpurea L.	Adorada et al. 2023
Burseraceae: *Canarium* L.	Yunus and Hua 1980; Furth 1998
Moraceae: *Ficus elastica* Roxb. ex Hornem.	Stebbing 1914; Beeson 1919, 1941; Scherer 1969; Baksha 1997; Singh and Misra 1989
Ficus L.	Beeson 1919; Medvedev 1999; Deka and Kalita 2002a
"fruit trees" (native and imported)	Fletcher 1920, 1921; Susainathan 1923
Lythraceae: *Duabanga sonneratioides* Buch.-Ham. (Syn *D. grandiflora* (Roxb. Ex DC) Walp.	Ahmad 1939; Beeson 1941; Bose 1953; Singh and Misra 1989; Baksha 1997
Lythraceae: *Sonneratia apetala* Bunc.-Ham	https://eol.org/pages/2885296

Table 2. Head and pronotum size and weight of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767)).

Larval Instar	Head (mm)		Pronotum (mm)		Weight (g)
	Length	Width	Length	Width	
1st	0.70	0.60–0.70	0.60–0.70	0.50	0.001–0.10
2nd	1.00	1.00–1.30	1.20–2.00	0.70–1.00	0.011–0.040
3rd	2.00	2.10–2.20	3.50	2.00	0.083–0.217
4th	2.00	2.20	3.50	2.00	0.363–0.540

Table 3. Life cycle and body size of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) on Sineguelas (*Spondias purpurea* L.) in the Philippines.

Stages/Larval Instar	Range (mm)		Average (mm)		No. of Days
	Length	Width	Length	Width	
Egg					4–7
Larva					14–16
1st	1.80–4.50	0.50–2.05	2.943 ± 0.86	1.195 ± 0.59	(3)
2nd	4.00–10.20	1.50–4.00	6.587 ± 1.76	2.787 ± 0.63	(4)
3rd	8.30–17.50	2.90–5.33	11.214 ± 2.52	4.376 ± 0.74	(3)
4th	13.78–23.00	5.00–8.70	17.974 ± 2.46	6.645 ± 0.90	(4–6)
Pre–pupa					2–3
Pupa					15–22
Total					**35–48**

Table 4. Fecundity and longevity data of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) on Sineguelas (*Spondias purpurea* L.) in the Philippines.

No.	Number of eggs laid	Number of egg clusters laid	Average number of eggs	Number of days oviposited	Longevity
1	1,071	53	20.21	26	180
2	470	27	17.41	8	180
3	754	31	24.32	15	58
4	645	28	23.04	19	98
5	679	48	14.15	20	78
6	559	31	18.03	16	180
Average	**696.33**	**36.33**	**19.53**	**17.33**	**129**

Table 5. Insect pests of singuelas (*Spondias purpurea* L.) found during monitoring period (May 2021–November 2022) in the Philippines.

Scientific name	Common name	Life stage involved	Type of damage	Major incidence sites
Bactrocera spp.	Fruit fly	larva	Puncture and feeding damage on fruits	Cosmopolitan
Coccidae	Scale insects	adults and nymphs	Feeding on leaves and stems	Batangas City, Los Banos, Laguna
Elateridae	Click beetle	larva	Feeding on bark and stems	Batangas City
Helopeltis bakeri (Poppius)	Capsid bug	adult and nymphs	Necrotic lesions on young shoots	Cosmopolitan
Lymantriidae (4 undetermined species)	Tussock moth	larva	Feeding and defoliating leaves	Bacoor, Cavite Pampanga, Pangasinan, Los Banos, Laguna, Batangas City, Iloilo
Leucopholis irrorata (Chevrolat) and *L. pulverulenta* (Burmeister)	June beetle	adults	Feeding and defoliating leaves	Batangas City, Iloilo
Melolonthinae	Whitegrub	larva	Feeding on roots and scavaging on dead trees	Guimaras
Microlepidoptera	Sineguelas shoot roller	larva	Feeding and clumping of rolled new shoots and young leaves	Batangas City, Iloilo, Guimaras, La Carlota City, Negros Occidental
Oryctes rhinoceros (L.)	Coconut rhinoceros beetle	larva	Feeding on roots and scavaging on dead trees	Guimaras
Pseudococcidae	Mealybugs	adults and nymphs	Feeding on leaves and stems	Batangas City, Los Banos, Laguna
Psychidae	Bagworm	larva	Feeding holes	Iloilo

Table 6. List of natural enemies of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767) found during the monitoring period (May 2021–November 2022) in the Philippines.

Natural Enemies	Reference
Aspergillus sp. (Trichocomaceae) Parasitic fungus	Gallegos 2002, unpublished report
Beauveria sp. Entomopathogenic fungus	Adorada et al. 2023
Jumping spider (Four undetermined species) (Araneae: Salticidae)	Recorded in the survey
Penicillium sp. (Trichocomaceae) Parasitic fungus	Recorded in the survey
Preying mantis (Two undetermined species) (Mantodea: Mantidae)	Recorded in the survey
Oecophylla smaragdina F. (Hymenoptera: Formicidae)	Recorded in the survey
Orb-weaver spider (Araneae: Araneidae)	Recorded in the survey
Oxyopid spider (Araneae: Oxyopidae)	Recorded in the survey
Pentatomid bug *Eocanthecona furcellata* Wolff. (Hemiptera: Pentatomidae)	Adorada et al. 2023
Sheet web spider (Araneae: Lyniphiidae)	Recorded in the survey

Table 7. List of natural enemies of Sineguelas leaf beetle (*Podontia quatuordecimpunctata* (L., 1767)) (after Prathapan and Chaboo 2011).

Natural Enemies	Reference
Apanteles sp. Foerster (Braconidae)	Deka and Kalita 2003, 2004
Meteorus sp. Haliday (Braconidae)	Deka and Kalita 2003, 2004
Trichogramma evanescens Westwood (Trichogrammatidae)	Deka and Kalita 2003, 2004
Lynx spider (Oxyopidae)	Deka and Kalita 2003, 2004
Chalcid wasp (Chalcididae)	Corbett and Yusope 1921
Eulopid wasp *Pediobius* sp. Walker (Eulophidae)	Baksha 1997
Encyrtid wasp *Ooencyrtus corbetti* Ferr. (Encyrtidae)	Corbett and Miller 1933, Singh and Misra 1989 and Baksha 1997
Undetermined pentatomid bug (Pentatomidae)	Prathapan and Chaboo 2011
Mantis *Stagmomantis* sp. (Mantidae)	Deka and Kalita 2003, 2004
Mermithid nematode *Mermis* sp. Dujardin (Mermithidae)	Singh and Misra 1989, Daulmerie 1994, Baksha 1997
Birds (*Corvus splendens* Vieillot and *Acridotheres tristis* (L.))	Deka and Kalita 2003, 2004
Laboulbenia podontiae Thaxter (Laboulbeniaceae)	Thaxter 1914
Cephalosporium sp. (Hypocreaceae)	Singh and Misra 1989, Daulmerie 1994, Baksha 1997
Entomopathogenic nematode *Photorhabdus temperata* (Morganellaceae)	Fischer-Le Saux et al. 1999; Asaduzzaman et al. 2018