EVOLUTIONARY STUDIES OF FRUIT-PIERCING MOTHS IN THE GENUS *EUDOCIMA* BILLBERG (LEPIDOPTERA: EREBIDAE)

by

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To Rita Marie Klem. You can do anything you put your mind to.

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ABSTRACT

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The prevalence of monoculture and landscape simplification is correlated with diminished biodiversity and increased presence of harmful pest species in crop environments. Lepidoptera is the largest clade of herbivorous insects, with many agriculturally significant species. The pest status of insects in agricultural settings is human-defined based on behaviors that may negatively impact the yield of susceptible crops. As such, both the insect behavior and the affected crop play a part in determining pest status. One helpful means of understanding pest status involves using pest injury guilds, which distinguish different pest groups based on similar kinds of injury to comparable plant tissues. Pest injury guilds defined in the literature are reviewed and then applied to agriculturally-significant Lepidoptera. Specialized Lepidoptera behaviors are reviewed within their respective injury guilds, and the systematics, ecology, and control options for fruit-piercing moths are discussed within the context of pest Lepidoptera behaviors. To address the need for distribution information for economically relevant Lepidoptera, the first annotated checklist of pest Lepidoptera is also provided for the United States and Canada. This checklist includes 80 agriculturally significant Lepidoptera species and complexes, and incorporates notes on distribution, species delimitation, natural history, and establishment.

Fruit-piercing moths in the genus *Eudocima* Billberg, 1820 have significant pest status as adults rather than as larvae, and directly injure fruits using a specially-adapted proboscis. There are at least 48 *Eudocima* species which are found in the world's tropics, but confusion persists in the classification of this genus and there are several suspected complexes. Additionally, the area of origin for this group is uncertain, although the Oriental region has been postulated. A comprehensive phylogenetic analysis of *Eudocima* is conducted using 82 morphological characters, which are each described and figured, and analyzed using parsimony. Results suggest that *Eudocima* is not monophyletic. Strongly-resolved relationships were recovered, although

these did not correspond with previous generic concepts. The Australian region is recovered as the most parsimonious area of origin for *Eudocima*, and patterns of dispersal, particularly between the Oriental and Australian regions along the Indo-Australian Archipelago, are discussed.

The *Eudocima phalonia*-complex is distributed throughout the Old World and has been the subject of increasing interest and research due to its economic impact in the tropics and status as a potential invasive species. The recent description of closely-related sister species, as well as morphological variation documented within *E. phalonia* itself, suggests possible speciation occurring within *E. phalonia* populations across its wide geographic range. To test species boundaries for this taxon, a molecular phylogeny is constructed using anchored hybrid enrichment and a next-generation sequencing approach. Sampling for this phylogeny was informed using a global range map for *E. phalonia*, which was developed using georeferenced specimen data from natural history collections. Biogeographic analyses are also conducted to investigate the area of origin and dispersal patterns of *E. phalonia*, and to examine possible speciation modes and gene flow. Georeferenced range information is also utilized along with environmental variables in constructing a correlative environmental niche model using MaxEnt, which is used to evaluate a previous mini risk assessment for environmental suitability in the continental United States for *E. phalonia* establishment. Results suggest that *E. phalonia* is monophyletic, with gene flow still occurring between populations. The area of origin for *E. phalonia* is postulated to be the Oriental region, although further investigation is needed. Range predictions for *E. phalonia* from environmental modelling were performed for both the Old World, which concurred well with occurrence data, and for the New World. Assessment of environmental suitability for *E. phalonia* in the continental United States suggests areas in Florida and along the Gulf Coast are most favorable for establishment.

CHAPTER 1.   PEST INJURY GUILDS, LEPIDOPTERA, AND PLACING FRUIT-PIERCING MOTHS IN CONTEXT: A REVIEW

1.1   Abstract

The pest status of insects in agricultural settings is human-defined based on behaviors that may negatively impact the yield of susceptible crops. As such, both the insect behavior and the affected crop play a part in determining pest status. One helpful means of understanding pest status involves using pest injury guilds, which distinguish different pest groups based on similar kinds of injury to comparable plant tissues. Pest injury guilds defined in the literature are reviewed and then applied to agriculturally-significant Lepidoptera. More specialized Lepidoptera behaviors which are economically relevant, such as leaf-rolling or stem-boring, are examined within their respective injury guilds. In this review, fruit-piercing moths are discussed within the context of pest Lepidoptera behaviors and are highlighted due to their unique means of causing economic damage. Unlike other Lepidoptera in agricultural settings, fruit-piercing moths are harmful as adults rather than larvae, and directly injure fruits using a specially-adapted proboscis. The ecology and systematics of fruit-piercing moths, as well as current control options, are also discussed.

1.2   Introduction

A comprehensive understanding of pest status is the underpinning of all successful pest management. The concept of "pest" is human-defined (Pedigo & Rice 2009) based on behaviors which are deemed harmful or that interfere with our activities. For this reason, pest status in agricultural settings involves both crop susceptibility and damaging insect behaviors which affect crop yield. In food crops, the insect behaviors which cause economic damage can be understood in the ecological context of injury guilds (Root 1967), in which similar kinds of

damaging behavior are grouped together. These guilds may be used to group insect pests based on the responses they cause in their crop hosts, allowing for greater utility when examining community structure. The use of injury guilds also incorporates both components (the insect and the plant) important to determining pest status. In this review, pest injury guilds are defined using concepts from Boote (1981), Pedigo et al. (1986), Boote et al. (1993), and Pedigo and Rice (2009), and are applied to agriculturally significant pests within Lepidoptera. When similar behaviors within a guild are evidenced, such as leaf-rolling or stalk-boring, these behaviors are further examined. Fruit-piercing moths are discussed at length due to the extraordinary position they occupy within lepidopteran pests in the fruit-feeding guild as economically damaging adults. The ecological and systematic attributes of fruit-piercing moths are discussed, and current control options for this group, which differ from other fruit-feeding pests within Lepidoptera, are summarized.

1.3   Insect pests: pest status and injury guilds

One of the most predominant global changes affected by humankind is the expansion and intensification of agriculture (Matson et al. 1997). An effect of intensive management in agricultural systems, which include field, glasshouse, orchard, and plantation crops (Alford 1999), is a tendency towards monoculture. In the United States, as in many other countries (see Matson et al. 1997), the growing extent of monoculture has its basis in economic reasons, which include the biological superiority of certain crop species in terms of yield and the streamlining of cultural practices which maximize efficiency (e.g., USDA 1973). These reasons lead to the cultivation of fewer crop species and the simplification of landscapes. Despite the advantages, pest species present in both natural and agricultural ecosystems can reach high, damaging densities and severely impair plant processes when few plant species are present; this is especially the case in monocultures for insect herbivores with a narrow hostplant range (Matson et al. 1997). However, although a pest's population is important to understanding its impact in an agricultural setting, the intensity of the impact is not based solely on numbers (e.g., Higley & Pedigo 1996). Pest management, which sets out to solve this problem, is founded on an understanding of whether an insect is a pest and "how serious a problem it causes"; in other words, on determining pest status (Pedigo & Rice 2009).

In agricultural systems, the mere presence of a species is not usually a cause for concern (Pedigo & Rice 2009). Rather, "most insect pests of agriculture… are those species whose activities, enhanced by population numbers, cause economic losses" (Pedigo & Rice 2009); the activities of large numbers of insects in the same place, particularly activities which cause a deleterious plant response, are the basis for a pest gaining economic or agricultural significance. This is especially true if the pest insects have aggregating behaviors (such as armyworms, e.g., Kergoat et al. 2012). In gaining an understanding of pest status, Pedigo and Rice (2009) identify several important contributing factors, which can be grouped into insect factors and crop factors. Factors which are crop-related are the species, market value of the crop, and the crop's susceptibility to damage (Pedigo & Rice 2009). The other factors are insect-related, and include species, population numbers, and feeding and/or oviposition characteristics of the insect, as well as the cost of management, a factor which may fluctuate due to changing economics (Pedigo & Rice 2009). These factors together highlight the importance of both the pest and the crop in determining a pest's impact. The properties of each, whether inherent to the organism or defined by economics, help determine the reasons for the significance of the pest; this is because the concept of pest is one which people define based on behaviors that impair or obstruct our activities (see Pedigo & Rice 2009).

The way insects alter the physiology of affected crops, and by doing so reduce crop yield, is instrumental to their success as pests (Pedigo et al. 1986, Higley & Pedigo 1996, Pedigo & Rice 2009). Understanding the relationship between pest and plant host is crucial for defining pest status (Higley & Pedigo 1996). The crop factors discussed by Pedigo and Rice (2009) which contribute to pest status are all heavily influenced (if not defined) by human activities. Market value is determined by economics, and a crop's natural susceptibility to damage is mitigated or affected by cultural practices, such as irrigation or fertilization procedures (Pedigo & Rice 2009). The crop species can also be considered a product of human activities, since the plants we grow are selected by humans in response to our needs. Plant host range, or the variety of crop species utilized by an insect, is an important consideration for determining pest status, especially when considering phytophagous insects (Fenemore 1982). Plant host range includes acceptable host plants the insect will attack or use during development, particularly for feeding but also for oviposition. The plant host range for a species may be wide or narrow, but some discrimination

always exists and no insect will accept every plant (Fenemore 1982). Of the insect species with narrow hostplant ranges, many insect species which are said to be monophagus actually feed on a group of closely related plants, making true monophagy rare (Fenemore 1982). A more common behavior is oligophagy, which involves feeding on plants within a single family, or polyphagy, where a variety of hosts from many plant families are accepted (Fenemore 1982). Establishing plant host range is important for determining pest status; some pests attack many different plants, and when an infestation in one crop develops, other cultivated plants in the area could be at risk from the same species (Fenemore 1982). As noted by Beirne (1971), the economic importance of a highly polyphagous species in any region depends on which crops are most valuable there.

The importance to pest status of both insect behaviors and plant host response may be examined in terms of the injury inflicted by the pest and the damage to the plant host. Pedigo et al. (1986) define injury as "the effect of pest (insect) activities on host physiology that is usually deleterious", while damage is defined as "the measurable loss of host utility, most often including yield quantity or quality or aesthetics". Therefore, injury relates to the insect behavior, while damage relates to the plant response (Fenemore 1982, Pedigo et al. 1986, Higley & Pedigo 1996, Pedigo & Rice 2009). Injury may be in one of two categories: acute injury, which is inflicted over a short period of time and causes a stress response due to one or few instances of injury, and chronic injury, which takes place over an extended period of time and causes a stress response due to the combined effect of many instances of injury (Higley & Pedigo 1996). An advantage of distinguishing between acute and chronic injury when delineating pest groups is that this distinction takes the plant response into account, while looking beyond the biological classification of the pest (Higley & Pedigo 1996). Insects often produce acute injury, although small sucking insects such as mites or aphids cause chronic injury; individually the stress caused to the plant by aphids or mites is low, but with many individuals and over a long period of time a much stronger stress response can be produced (Higley & Pedigo 1996).

A further way of searching for commonalities among pest groups is comparing the specific kinds of injuries inflicted, such that insect pests which cause similar physiological responses in their hostplants are grouped together (Hutchins et al. 1988, Higley & Pedigo 1996). Pest species which inflict similar kinds of injury can be grouped into injury types or guilds (Boote 1981). An

injury guild is defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). Guilds are a means of classifying insect groups not taxonomically, but based on niche use; this allows the community structure and interactions between functional groups to be more easily examined (Root 1967). This approach also emphasizes the plant response to insect attack, and incorporates all sympatric species which are involved in competitive interactions in an agricultural environment regardless of their phylogenetic relationship (Root 1967). Furthermore, unrelated or taxonomically-distant species sometimes fill the same ecological niches or perform similar pest behaviors which target the same plant part; in the pest guild arrangement, these species can be treated together as one functional group (Root 1967). The six main injury guilds for pest arthropods are 1) stand reducers, 2) leaf-mass consumers, 3) assimilate sappers, 4) turgor reducers, 5) architecture modifiers, and 6) fruit feeders (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009). These categories group insect pests based on activities or behaviors which are detrimental to a plant's ability to survive, grow, or reproduce. Higley et al. (1993) provide requirements for establishing new injury guilds which are based on homogeneity of the response to plant injury. In order for insect pests to be placed in the same injury guild, the pests need to cause a similar injury within the same phenological time frame of the plant host, produce a similar intensity of injury to the plant, and affect the same plant part (Higley et al. 1993, Higley & Pedigo 1996).

1. Stand reducers produce an immediate loss in biomass that results in decreased photosynthesis for the attacked crop; the severity of these effects depends on the timing, number, and dispersion of the destroyed plants (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009).

2. Leaf-mass consumers are believed to impact absolute photosynthesis of the remaining leaf canopy directly (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009). The resulting damage can be quantified by taking the timing of leaf consumption, consumed leaf mass, and vertical distribution of the consumed leaf mass into account (Pedigo et al. 1986, Pedigo & Rice 2009). However, caution is needed when extrapolating damage from plant parts to determine net photosynthetic activity for the whole plant or stand (Trumble et al. 1993), and plants may employ

compensatory mechanisms, such as increased net photosynthesis, to account for damage by herbivores (Trumble et al. 1993, Agrawal 2000).

3. Assimilate sappers consist mainly of piercing-sucking and rasping insects that remove nutrients from the plant before they can be used for plant tissues, and these insects sometimes inject toxic substances into the plant during the feeding process (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009).

4. Turgor reducers are soil and stem feeders which cause a water or nutrient imbalance at the root or stem sites; these behaviors include root pruning and stem girdling, which limit photosynthesis and decrease plant development (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009).

5. Architecture modifiers cause a physiological change which affects the morphology of the plant and negatively impacts yield; the pest not only destroys some tissue but affects the overall quality of the plant, and the plant's rate and pattern of growth may be drastically changed (Pedigo et al. 1986, Pedigo & Rice 2009).

6. Fruit feeders cause direct damage to fruit, and can affect the quality, yield, or both of harvestable produce (Boote 1981, Pedigo et al. 1986, Boote et al. 1993, Pedigo & Rice 2009). Damage on fruit can sometimes be difficult to relate directly to yield losses because yield loss may not be proportional to loss of reproductive sites, and the compensatory mechanisms of the plant need to be taken into account in order to attribute yield loss to this type of injury (Pedigo et al. 1986, Pedigo & Rice 2009). However, yield losses are easier to attribute to direct damage to fruit in other cases, when reduction in reproductive sites correlates with yield directly. For example, fruit-boring insects may cause reduced yield, such as in processing tomatoes by Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) and Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae) (Zalom et al. 1983), and in cherries by Grapholita packardi (Zeller) (Lepidoptera: Tortricidae) (Howitt 1993). Fruit-piercing moths may also cause reduced yield in fruit orchards because of direct damage to fruit, such as by causing premature fruit drop in citrus resulting from secondary infection by fungi and bacteria at the injury site (e.g., Muniappan et al. 2002).

Yield loss in crops is due not only to the biology of pest injury (which is the pest's pattern of behavior), but also to the plant's biological response to damage (Higley & Pedigo 1996). The timing of an injury during the plant's life cycle is important to the plant's response; for example, seedlings are generally more vulnerable than older plants (Pedigo & Rice 2009). Additionally, the part of the plant that is injured is as important as the pest's mode of injury (Higley et al. 1993, Higley & Pedigo 1996, Pedigo & Rice 2009). A distinction is made between injury to yield-forming organs, which are the harvested portion of the plant (direct injury), and injury to nonyield-forming organs (indirect injury) (Fenemore 1982, Pedigo & Rice 2009). The parts of the plant which are yield-forming depend on the plant species (e.g., leaves of lettuce plants, fruit of fruit trees, roots of carrots, etc.) (Fenemore 1982); this means that depending on the crop involved, any of the injury guilds might be considered to be causing direct or indirect injury based on the injured plant part. Plants are more often able to withstand injuries to nonyield-forming organs (indirect injury) than to yield-forming organs (direct injury) (Fenemore 1982). In the majority of cases, insects cannot simultaneously cause both direct and indirect injury (Pedigo & Rice 2009). Higley and Pedigo (1996) note that when establishing injury guilds, all pest species included in a guild must attack the same or comparable plant tissues.

The environmental conditions in which the insect and crop species are present also greatly contribute to pest impact, affecting both the pest and the plant response while serving as the context for the interaction (Higley & Pedigo 1996, Pedigo & Rice 2009). Environmental conditions are both biotic and abiotic (Higley & Pedigo 1996). Pest numbers can be influenced by environmental conditions, particularly insect pests with short generation times such as mites or aphids (Higley & Pedigo 1996), and factors like weather or the presence of natural enemies can impact aggregation or the ability to cause economic damage (e.g., Pedigo & Rice 2009, Floate 2017). Environmental conditions can also affect the type and robustness of the plant response to pest attack (Higley & Pedigo 1996). Specific types of plant injury may only occur within a given season, while seasonality may also impair a plant's tolerance or compensation for the same level of injury, making the response more or less robust (Higley & Pedigo 1996, Pedigo & Rice 2009). Plants subjected to water stress or multiple biotic stressors such as weeds also have different responses to subsequent stressors than healthy plants (Higley & Pedigo 1996). Because of the effects of the biotic and abiotic environment, it becomes difficult in most cases to

draw a simple relationship between pest numbers and resulting loss in crop yield (Higley & Pedigo 1996). This is one reason for using injury guilds to group pests based on mode of action, which can be helpful in understanding impact on a crop and in determining pest status.

1.4   Economically-significant Lepidoptera

In the vast majority of cases, the larval stage of Lepidoptera pests is the harmful stage. For example, cutworm larvae are the only life stage that causes crop damage, and the rest of the life stages (egg, pupa, adult) have no impact on yield (Floate 2017). This is typical of pest Lepidoptera in agricultural settings (although exceptions exist), and larval feeding is the most common cause of economic damage. The larvae of pest Lepidoptera species may affect yield by causing direct damage to crops, such as by feeding on corn ears or fruit boring, or by causing indirect damage and weakening the plant. Most lepidopterans are phytophagous, and depend on a limited range of plant species (within one or a few plant families) for larval growth (Honda 1995). This plant range is determined most strongly by larval food choice and by female oviposition behaviors (Honda 1995). Because of the more limited mobility of Lepidoptera larvae compared with adults, it has been asserted that oviposition behavior is the most important driving force behind the evolution of plant host range for lepidopteran species (Lederhouse et al. 1992, Honda 1995). The timing of oviposition and feeding by the larvae with respect to the phenology of the host may also contribute to insect speciation, whether on the same host or a novel hostplant (Winkler & Mitter 2008).

In addition to specialization on particular hostplants, most herbivorous insects (including Lepidoptera) specialize in attacking particular plant tissues, such as roots, stems, leaves (young or mature), seeds, fruits, or flowers (Winkler & Mitter 2008). This can allow several different lepidopteran pests to use a hostplant simultaneously because often each pest will occupy a different biological niche (e.g., Schulthess et al. 1991). Moreover, on any one plant part, different species are sometimes specialized for different modes of feeding, such as leaf-rolling, leaf-mining, stalk-boring, or many other behaviors (Winkler & Mitter 2008). These behaviors are helpful to briefly examine when considering lepidopteran pests, within their respective injury categories. As noted by Root (1967), more than one of these behaviors or injury guild functions may be adopted by a single species over the course of its development, and a single species may

be placed in a different injury guild when a different hostplant or plant part is attacked. For example, in *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), young larvae are leaf feeders on corn plants and cause damage by defoliation, and in later instars larvae burrow into stalks and can feed on silks, kernels, and cobs (e.g., Pedigo & Rice 2009). *Xestia c-nigrum* (Linnaeus) (Lepidoptera: Noctuidae) is a gregarious feeder with respect to plant part, and can attack buds and fruit, resulting in direct damage to yield, as well as behaving as defoliators or cutting young plants (Capinera 2001, Floate 2017). Depending on the circumstances, the pest guild of each of these species may be leaf-mass consumer, turgor reducer, fruit feeder, or all three, and *Xestia c-nigrum* may also function as a stand reducer. The same principle applies to many pests within Lepidoptera, although species are used here as examples of a particular pest guild due to specific behaviors. These examples are summarized in Table 1. The functions of economically significant Lepidoptera within each pest injury guild are now briefly reviewed.

Table 1. Summary of Lepidoptera examples given for each pest injury guild. Examples which are not placed in a subcategory are listed first within the injury guild.

Pest injury guild	Subcategory	Lepidoptera examples
Stand reducers		*Crambus praefectellus* Zincken
		Parapediasia teterrellus (Zincken)
	Subterranean	*Apamea devastator* (Brace)
		Agrotis ipsilon (Hufnagel)
		Agrotis venerabilis Walker
	Above-ground	*Euxoa auxiliaris* (Grote)
		Feltia spp. (Walker)
		Xestia c-nigrum (Linnaeus)
		Striacosta albicosta (Smith)
		Lacinipolia renigera (Stephens)
		Mythimna unipuncta (Haworth)
		Euxoa messoria (Harris)
		Nephlodes minians Guenée
		Peridroma saucia (Hübner)
	Climbing	*Egira curialis* (Grote)
Leaf-mass consumers		*Paleacrita vernata* (Peck)
		Pieris brassicae (Linnaeus)
	Leaf-rolling	*Platynota idaeusalis* (Walker)
		Argyrotaenia franciscana (Walsingham)
		Acrobasis tricolorella Grote
		Argyrotaenia velutinana (Walker)
		Platynota flavedana Clemens
		Choristoneura rosaceana (Harris)
		Epiphyas postvittana (Walker)
	Leaf-mining	*Acrolepiopsis assectella* (Zeller)
		Phyllocnistis citrella (Stainton)
		Phyllonorycter blancardella (Fabricius)
Assimilate sappers		*Phyllonorycter blancardella* (Fabricius)
		Other leafminers

Table 1 continued

Pest injury guild	Subcategory	Lepidoptera examples
Turgor reducers		Root-feeding subterranean cutworms (i.e., *Xestia c-nigrum*, *Apamea devastator*) Sod webworms *Chrysoteuchia topiaria* (Zeller)
	Wood-boring	*Synanthedon exitiosa* (Say) *Synanthedon pictipes* (Grote & Robinson) *Synanthedon scitula* (Harris) *Synathedon myopaeformis* (Borkhausen)
Architecture modifiers		*Papaipema nebris* (Guenée)
Fruit feeders		Several cutworm species (*Euxoa messoria*, *Agrotis gladiaria*, *Lacanobia subjuncta*, *Egira curialis*) Many leaf-rolling species (i.e., *Argyrotaenia velutinana*) *Cydia pomonella* (Linnaeus) *Grapholitha molesta* (Busck) *Paralobesia viteana* Clemens *Grapholitha packardi* (Zeller) *Spilonota ocellana* (Denis & Schiffermüller)
	Fruit-piercing	*Eudocima* Billberg (e.g., *Eudocima phalonia* (Linnaeus)) *Gonodonta* Hübner (e.g., *Gonodonta nutrix* (Stoll)) *Plusiodonta* Guenée *Ophiusa* Ochsenheimer (e.g., *Ophiusa tirhaca* (Cramer)) *Oraesia* Guenée *Calyptra* Ochsenheimer *Phyllodes eyndhovii* Vollenhoven *Phyllodes consobrina* Westwood

1.4.1   Stand reducers

Important stand reducers within Lepidoptera pests include several noctuid moth species known as "cutworms" (e.g., Floate 2017). Cutworms cut the stems of young plants at or below the soil level, and certain species of climbing cutworms defoliate plants (Floate 2017, Knodel & Shrestha 2018). Three main feeding behaviors in cutworms have been documented: subterranean, above-ground or surface-feeding, and climbing (Walkden 1950, Floate 2017, Knodel & Shreshtha 2018). Subterranean feeders, such as *Apamea devastator* (Brace) (Lepidoptera: Noctuidae), are active below the soil surface and cut the stems of young plants. Above-ground or surface-feeders feed on foliage above the soil surface during the night and hiding during the day in soil and plant debris; Floate (2017) also categorizes tunneling cutworms such as *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) and *Agrotis venerabilis* Walker (Lepidoptera: Noctuidae), which strip foliage above the surface and carry it back to subterranean tunnels, in this feeding category. Above-ground cutworms are defoliators, but older larvae may feed by stem-cutting young plants at or above the soil surface. Examples include *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae), *Feltia* spp. (Walker) (Lepidoptera: Noctuidae), *Xestia c-nigrum*, *Striacosta albicosta* (Smith) (Lepidoptera: Noctuidae), *Lacinipolia renigera* (Stephens) (Lepidoptera: Noctuidae), *Mythimna unipuncta* (Haworth) (Lepidoptera: Noctuidae), *Euxoa messoria* (Harris) (Lepidoptera: Noctuidae), *Nephelodes minians* Guenée (Lepidoptera: Noctuidae), and *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae) (Floate 2017). Climbing cutworms are primarily defoliators and do not usually damage the main stem of the plant (Floate 2017); however, certain species such as *Egira curialis* (Grote) (Lepidoptera: Noctuidae) are of concern because of direct damage to fruit and not because of defoliation (e.g., Grafton-Cardwell et al. 2001). Of these behaviors, subterranean and surface-feeding cutworms which sever plant stems are considered stand-reducers.

Other stand reducers within Lepidoptera include webworms such as *Crambus praefectellus* Zincken (Lepidoptera: Crambidae) and *Parapediasia teterrellus* (Zincken) (Lepidoptera: Crambidae). Although they are commonly problematic in turfgrass, these species also sever young corn plants and drag them away to feed within silk-lined tunnels in thatch (e.g., Ainslie 1930). This damage is similar to that caused by cutworm species, although it can be distinguished by the amount of plant tissue consumed (Gesell & Calvin 2000)

1.4.2 Leaf-mass consumers

Lepidoptera is arguably the largest single radiation of herbivorous insects (Mitter et al. 2017), and, correspondingly, consumption of leaf mass is by far the most common pest Lepidoptera behavior. Two general hypotheses have been advanced regarding plant response to damage by herbivory: that herbivory is detrimental to plants, or that herbivory produces an overcompensation response which is beneficial to plants (Trumble et al. 1993). Feeding on leaves and foliage has been postulated to decrease the overall photosynthetic ability of the plant (Boote 1981, Pedigo et al. 1986, Pedigo & Rice 2009); however, most measurements of photosynthetic activity are conducted on single leaves, and scaling these measurements to determine the net photosynthetic activity of the whole plant or stand presents challenges (see Trumble et al. 1993). Plant responses such as defense reduce or mitigate damage by herbivores in some plants, usually by means of resistance, tolerance, or phenological escape (Agrawal 2000). Unlike defense, overcompensation is another plant response which results in higher plant fitness after herbivory, resulting in a mutualist relationship between the plant and the herbivore (Agrawal 2000). Therefore, the question of herbivory as harmful or beneficial is not a biological absolute in all plant systems, but varies with different plant responses and compensatory mechanisms, as well as with the environment and particulars of the damage (Trumble et al. 1993). The impact of herbivory is also variable with regard to yield in crops (Trumble et al. 1993), although in cases when plant leaves are the yield-forming organs (lettuce, etc.) the effects of defoliation on yield can be severe. Defoliation involves direct tissue consumption because the plant has already used assimilated nutrients to build tissues (Boote et al. 1993). Straightforward defoliation is a common behavior; some pest species specialize on leaves at a particular stage, such as *Paleacrita vernata* (Peck) (Lepidoptera: Geometridae) on young leaves (Wagner 2005), while other Lepidoptera pests feed in an undifferentiated way on all leaf tissues, almost completely stripping foliage from plants as in the case of *Pieris brassicae* (Linnaeus) (Lepidoptera: Pieridae) on vegetable brassicas (Alford 1999). However, more differentiated feeding behaviors are seen in some Lepidoptera pests in the form of leaf-rolling and leaf-mining, which are both considered here as more specialized subcategories of leaf-mass consumption.

1.4.2.1   Leaf-rolling (Leaf-mass consumption)

Among several moth species which are pests by direct leaf-mass consumption, leaf-rolling larvae feed inside leaf shelters to provide protection from adverse weather conditions and predators (Kadioglu et al. 2012). Included in this group are leaf-tiers, leaf-webbers, and leaf-folders (Kadioglu et al. 2012). Lepidoptera larvae in this group roll, tie, or web one or several leaves together to form a shelter (Kadioglu et al. 2012). In some species such as *Platynota idaeusalis* (Walker) (Lepidoptera: Tortricidae), leaf-rolling on its own is not a damaging pest behavior, but fruit feeding occurs when fruit are webbed in with the leaves and this causes economic damage (Krawczyk 2016). The same is true of *Argyrotaenia franciscana* (Walsingham) (Lepidoptera: Tortricidae) (Grafton-Cardwell et al. 2017a), *Acrobasis tricolorella* Grote (Lepidoptera: Pyralidae) (Howitt 1993), *Argyrotaenia velutinana* (Walker) (Lepidoptera: Tortricidae) (Howitt 1993), *Platynota flavedana* Clemens (Lepidoptera: Tortricidae) (Gilligan & Epstein 2012), *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae) (Howitt 1993), and *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) (Gilligan & Epstein 2012). Therefore, although these species are leaf rollers, their pest guild is fruit feeders (with respect to agriculture - they are also pests as leaf rollers if considering cosmetic damage).

1.4.2.2   Leaf-mining (Leaf-mass consumption)

Another type of defoliation behavior in Lepidoptera is leaf-mining. Leaf-mining insects feed on the inner tissues of a leaf, between the upper and lower leaf surfaces (Johnson & Triplehorn 2005). Like gall-forming in other insects, leaf-mining is considered an "endophagous" form of leaf-mass consumption; however, leaf-mining does not affect plant tissue growth but instead involves consuming already-developed leaf tissue (Connor & Taverner 1997). Larvae feed within the mines after hatching and pupate, and the adult moth must break through the leaf epidermis in order to emerge (Connor & Taverner 1997). Examples of pest leaf-miners within Lepidoptera include *Acrolepiopsis assectella* (Zeller) (Lepidoptera: Glyphipterigidae), *Phyllocnistis citrella* (Stainton) (Lepidoptera: Gracillariidae), and *Phyllonorycter blancardella* (Fabricius) (Lepidoptera: Gracillariidae). Postulated advantages to this lifestyle for phytophagous insects include protection from predators, parasites, and abiotic factors, as well as avoidance of plant defenses (whether structural or chemical) that might come from other tissue layers (Connor & Taverner 1997).

1.4.3   Assimilate sappers

Assimilate sappers feed by removing soluble nutrients from plants before their conversion by the plant into tissue (Boote et al. 1993); examples are often pathogens, nematodes, or small sucking insects such as whiteflies or aphids which tap into the phloem of the plant and extract nutrients (Boote 1981, Boote et al. 1993, Pedigo et al. 1986, Pedigo & Rice 2009). Howitt's (1993) discussion of tree fruit pests which suck sap (from leaves, buds, twigs, branches, trunks, or fruits) centers on mites, aphids, scales, and true bugs. Although no pest Lepidoptera species are known to be assimilate sappers as a primary pest function, this behavior is seen in some species as young larvae. In *Phyllonorycter blancardella*, newly-emerged larvae are sap-feeders inside the leaf, sucking sap from the mesophyll layer until the fourth instar (OMAFRA 2011). At the end of the fourth instar, larvae transition to tissue-feeders on the leaf epidermis (OMAFRA 2011). Other leaf-mining species share this behavioral pattern (see Powell & Opler 2009), and in *Common Tree Fruit Pests*, Howitt (1993) considers pests which suck sap from leaves in the same category as leafminers.

1.4.4   Turgor reducers

Turgor reducers feed upon root and vascular tissue, disrupting water and nutrient uptake and translocation (Boote et al. 1983, Sadras et al. 1999). Like leaf-mass consumption, turgor-reducing pests consume plant tissue directly, and include insects with stem-feeding and root-feeding behaviors. Several species of subterranean cutworms (such as *Xestia c-nigrum* and *Apamea devastator*) and sod webworms attacking corn can also be considered turgor reducers because they sometimes feed directly on root tissues (e.g., Floate 2017). Another example of direct root feeding occurs in larvae of *Chrysoteuchia topiaria* (Zeller) (Lepidoptera: Crambidae), which cause vine death in cranberries by feeding on subterranean vines, girdling and sometimes severing them (Roberts & Mahr 1986). In Lepidoptera, a common functional group of pest turgor reducers includes stalk and wood-borers, which feed upon the plant's vascular or structural tissue. This group of pests all bore into the plant and feed on the tissue within stems or roots. Two subcategories can be considered when dealing with this feeding behavior: stalk-boring, as in vegetables and crops, and wood-boring, as in fruit trees and woody plants.

1.4.4.1 Stalk-boring

In stalk borers, larvae enter the stalk at the base of the plant, causing one of two symptoms depending on plant development (Leuschner 1987): destruction of the apical meristem resulting in a plant condition called dead-heart, or a condition called stem tunneling if the apical meristem has moved upwards (Leuschner 1987). Another stalk-boring behavior involves the larvae entering the stalk from the whorl area and boring downwards (Gesell 2000). Larval tunneling and feeding also cause the stalk to be weakened and prone to wind damage (Leuschner 1987). One generalist stalk-boring species, *Papaipema nebris* (Guenée) (Lepidoptera: Noctuidae), utlilizes plants with smaller stalks earlier in development (e.g., grasses), and moves on to infest corn when the larvae become too large (Gesell 2000). Infestation by this species typically kills grasses and smaller-stemmed plants, while inhibiting yield and growth of larger-stemmed plants like corn (Gesell 2000). Other stalk borers are more specialized; *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidae) only attacks cucurbit plants, preferring plants with large, hollow stems (Kariuki and Gillett-Kaufman 2014). Additional noteworthy stalk borers include *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae) and *Crocidosema aporema* (Walsingham) (Lepidoptera: Tortricidae).

1.4.4.2 Wood-boring

Some lepidopteran pests bore into fruit trees, feeding under the bark or on the cambium layer. Extensive feeding can cause girdling of the trunk, roots, or branches, weakening the tree and ultimately reducing yield. *Synanthedon exitiosa* (Say) (Lepidoptera: Sesiidae), *Synanthedon pictipes* Grote & Robinson) (Lepidoptera: Sesiidae), *Synanthedon scitula* (Harris) (Lepidoptera: Sesiidae), and *Synathedon myopaeformis* (Borkhausen) (Lepidoptera: Sesiidae) are all examples. Boring behavior can be either general or specialized with respect to the tree part; *Synanthedon exitiosa* is a generalist which uses the trunk, roots, and large stems (Strickland 2018), *Synanthedon pictipes* bores into the trunk or scaffold limbs (Shapiro-Ilan et al. 2010), and *Synanthedon scitula* bores into the above-ground portion of the root stock (Leskey et al. 2009).

1.4.5 Architecture modifiers

The defining trait of architecture modifiers is their ability to affect plant morphology. The assignment of an insect pest to the architecture modifier injury guild requires a more in-depth

knowledge of hostplant biology, making this category the most difficult to circumscribe. The example cited in Pedigo & Rice (2009) is *Papaipema nebris*, which bores into young corn stalks and causes tillering. Tillering is one result of dead-heart (i.e., destruction of the apical meristem), because apical dominance has been removed (Leuschner 1987); at the lower five to seven stalk nodes of a corn plant (and sometimes from the roots, see Bailey & Pedigo 1986), auxiliary branches form which are morphologically identical to the main stem (Nielsen 2003). These branches can form their own root system, nodes, internodes, leaves, ears, and tassels (Nielsen 2003), and may develop synchronously with the main stem if formed early enough (Leuschner 1987, Nielsen 2003).

According to Nielsen (2003), most agronomists agree that some tillering, which also occurs in uninfested corn plants, is normal and even an indication of good growing conditions. This is supported by Akman (2002), who found that tiller removal actually decreased ear yield for three varieties of sweet corn. Despite this, tillers can be formed in response to damage and compete for resources with the rest of the plant (Nielsen 2003). During an investigation of stalk borer infestations over the span of several years by Bailey and Pedigo (1986), it was found that rates of tiller formation in *Papaipema nebris*-infested plants with dead-heart damage was ten to twenty-five times higher than in attacked plants that had only foliar feeding damage. Dead-heart damage to corn stalks by *Papaipema nebris* causes corn to produce less tissue (besides stalk weight) and fewer harvestable ears (Bailey and Pedigo 1986). This reduction in yield is likely due to a combination of direct damage to the main stalk (destruction of vascular tissue, i.e., turgor-reducing action), and competition from extensive tiller formation; this latter effect is a result of *Papaipema nebris* acting as an architecture modifier on corn.

1.4.6   Fruit feeders

Fruit-feeding is here considered to be direct damage is caused to the hostplant's reproductive organs, including buds, flowers, and fruits. Some authors (Boote 1981, Boote et al. 1993) categorize these types of feeders as tissue consumers, since the plant has already expended respiration energy converting nutrients into tissue. Damage by these pests directly affects yield-producing and harvestable organs, especially in the case of fruit damage.

The assignment of Lepidoptera pests which directly damage fruit to this category is relatively straightforward. Several cutworm species are fruit feeders; the climbing cutworm *Euxoa messoria* directly damages vine, berry, and tree fruits (Floate 2017), and *Agrotis gladiaria* Morrison (Lepidoptera: Noctuidae) is a pest in berry crops (Floate 2017). *Lacanobia subjuncta* (Grote & Robinson) (Lepidoptera: Noctuidae) can also be problematic in fruit orchards as later larval instars, causing significant fruit injury (Doerr et al. 2002). Larvae of *Egira curialis*, the citrus cutworm, begin feeding on tender leaves of citrus trees during the first instar, and later instars attack the blossoms and young fruit, sometimes boring into mature fruit (Grafton-Cardwell et al. 2001). This pattern is typical of many fruit-feeding moths, which attack fruit during later larval instars and begin by feeding on leaves and/or buds in earlier development. Incidental fruit-feeding occurs among many leaf-rolling species, such as those already mentioned, and can be the main cause of the species' economic significance. Leaf-rolling species typically feed on fruit from the "outside in" on surface tissues; one example is *Argyrotaenia velutinana*, which creates galleries into the fruit surface (Howitt 1993). In contrast, other Lepidoptera feed mainly on the inside of fruits, and are some of the most damaging and costly pests causing direct injury (Howitt 1993). Examples include larvae of the codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae), which enter the blossoms and feed on the fruit internally (Howitt 1993, Alford 1999); this behavior is shared by *Grapholitha molesta* (Busck) (Lepidoptera: Tortricidae) (Howitt 1993, Hasey et al. 2016), *Paralobesia viteana* Clemens (Lepidoptera: Tortricidae) (Isaacs et al. 2012), and *Grapholitha packardi* (Jeger et al. 2018, Wise et al. 2007). Some Lepidoptera species damage buds before the fruit matures, such as *Spilonota ocellana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae), which bores into buds as well as feeding on flowers and leaves (Howitt 1993, Alford 1999, Powell & Opler 2009).

1.4.6.1 Fruit-piercing

Some species of Lepidoptera attack and directly damage fruits as adults, using a specially-adapted proboscis to pierce fruits to suck the juice. Because the mode of damage and methods of control are quite different from other fruit-feeding Lepidoptera, the fruit-piercing habit can be considered a subcategory of fruit-feeding as a pest behavior. Species of *Eudocima* Billberg (Lepidoptera: Erebidae) are common pests of soft or ripening fruits (peaches or plums), with the widespread *Eudocima phalonia* (Linnaeus) (Lepidoptera: Erebidae) considered a serious orchard

pest (e.g., Baptist 1944, Cochereau 1977, Bänziger 1982, Waterhouse & Norris 1987, Waterhouse 1997, Fay 2002, Davis et al. 2005, Astridge 2006, Leong & Kueh 2011, Bhumannavar & Viraktamath 2012). *Gonodonta* Hübner (Lepidoptera: Erebidae) species pierce citrus fruits, including tangerines, grapefruits and oranges, at times causing extensive losses in subtropical and tropical regions (Todd 1959). Serious outbreaks of *Gonodonta* species have occurred in Mexico and Cuba in the 1940's and 1950's, respectively, and one report from the late 1950's stated that 20 percent of the fruit in two orange groves in St. Lucie County, Florida was lost due to attacks by *Gonodonta nutrix* (Stoll) (Lepidoptera: Erebidae) (Todd 1959). *Plusiodonta* Guenée (Lepidoptera: Erebidae) species have been observed feeding on soft-skinned fruits (peaches and plums) in South and Southeast Asia (Zaspel pers. obs. 2005).

1.5   Adult Lepidoptera as pests: fruit-piercing moths

Functionally, fruit-piercing moths are fruit feeders in terms of their injury guild, but their mode of injury is both specialized and unusual compared with other agriculturally-significant pests within Lepidoptera. One important reason is that damage to harvestable yield occurs in the adult stage of the moth's life cycle rather than the larval stage (e.g., Leong & Kueh 2011); this fact separates fruit-piercing moths from the preponderance of Lepidoptera pests. In consequence, the mechanical form of injury by fruit-piercing moths differs from other moth pests in the fruit feeder injury guild. Many other Lepidoptera pests which feed directly on or in fruit do so at later larval instars after eating the plant's leaves or buds, or else (in the case of several leaf-rolling species) feed on fruit when it becomes webbed together with leaves the larva is consuming. Fruit-piercing moths, however, attack only the fruits on a plant and cause no damage to any other plant part. In adults of both sexes, the proboscis is stout and armed with serrated ridges and erectile barbs (Zaspel et al. 2011); piercing is effected using an anti-parallel motion of the proboscis (Bäziger 1982), which the moth uses as a saw or drill to penetrate the skin or rind of a fruit (e.g., Zaspel et al. 2011) to cause direct injury. At certain times of the year in parts of their range, high population densities of fruit-piercing moths appear in fruit orchards, where they can cause severe damage (Bänziger 1982).

Fruit-piercing moths can be grouped into two categories, which are based on the moth's piercing ability. Bänziger (1982) defines fruit-piercing moths as either primary piercers, which can

introduce holes de novo through the rind or skin of fruits, or secondary piercers, which probe or enlarge preexisting wounds in fruits to access the juice. Rather than categorizing a moth as a primary or secondary fruit piercer as a biological absolute, Bänziger (1982) used "primary fruit piercer" and "secondary fruit piercer" with reference to the attacked fruit, such that a moth which is a primary fruit piercer in some fruits is classified as a secondary fruit piercer in other fruits. For instance, *Ophiusa tirhaca* (Cramer) (Lepidoptera: Erebidae) is a primary piercer of peach but a secondary piercer of longan, while *Eudocima phalonia* is a primary piercer of both fruits (Bänziger 1982). For convenience in his study of piercing behavior, Bänziger (1982) categorized attacked fruits into four classes: 1) soft-skinned (e.g., raspberry), 2) soft-skinned (e.g., peach, grape), 3) thick-skinned (citrus), and 4) hard-skinned (longnan, lichi) (Bänziger 1982, Zaspel et al. 2011). The piercing capability of a species therefore determines the plant host range, since fruit-piercing moths which can pierce a variety of fruit thicknesses can damage a larger number of crops. Because of this, the pest status of species capable of piercing hard-skinned fruits is similar to highly polyphagous pests (such as some Lepidoptera larvae) which feed on many plant tissues. Susceptibility for a given crop to damage by fruit-piercing moths should therefore ideally be evaluated based on the thickness of the skin. The distinction between primary and secondary fruit piercers is commonly applied in the literature (e.g., Holloway 2005, Zahiri et al. 2012) without reference to a spectrum of fruit hardness. Rather, moths which habitually pierce fruits with thick or hard skins, such as *Eudocima* spp., are considered primary piercers, while secondary piercers such as species of *Ophiusa* Ochsenheimer (Lepidoptera: Erebidae) commonly probe already-existing holes in thick or hard-skinned fruits to access the juice. Therefore, fruit-piercing moths *per se* are actually habitual primary fruit piercers. The discussion of fruit-piercing moths as pests (and in pest literature) focuses on species which are primary fruit piercers in most systems (e.g., Baptist 1944, Bänziger 1982, Waterhouse & Norris 1987, Waterhouse 1997, Fay 2002, Davis et al. 2005, Astridge 2006, Bhumannavar & Viraktamath 2012).

In many cases where several lepidopteran pest species attack a hostplant simultaneously, each species will usually occupy a different biological niche (leaves, stems, fruit, etc.) (e.g., Schulthess et al. 1991).The presence of multiple pest species on a crop can confound attributing yield loss to a particular species since the effects of each species on the plant's response may not be additive. In the case of fruit-piercing moths, this problem is further complicated when

multiple species are active in the same place, since all primary fruit-piercing moths have the same mode of damage and perform the same ecological function as adults. In field situations involving softer fruits and many fruit-piercing species, damage can be especially difficult to attribute because softer fruits are easier to pierce (more species can act as primary fruit piercers) (e.g., Bänziger 1982). However, in harder fruits, which can only be pierced by a smaller group of moths, species which cause principal damage to the crop can be more easily identified (see Bänziger 1982, Fay & Halfpapp 1999a). Ripe fruit which is still attached to the tree is preferred, especially by primary piercers, to fruit which is picked or has fallen on the ground (Bäziger 1982, Kumar & Lal 1983, Fay 2002, Leong & Kueh 2011). Green or overripe fruit can sometimes be damaged when ripe fruit is not available (Bänziger 1982) or when attacking densities of fruit-piercing moths are high (e.g., Kumar & Lal 1983, Fay 2002). The preference for attached, ripe fruits is one impediment to the effectiveness of fruit baits which are hung up to distract primary-piercing species from the main cultivation (Bänziger 1982). Additionally, the stage of greatest susceptibility (when the fruit is nearly mature prior to harvest) is undesirable for applying pesticides (Bänziger 1982, Leong & Kueh 2011).

The pest status of fruit-piercing moths was first recognized in 1869, when the French botanist Thozet observed species of *Eudocima* injuring orange fruits in Australia (cited in Baptist 1944). In 1892, fruit-piercing moths were receiving increased attention in Thailand due to the introduction of new fruit varieties and more intensive farming practices in orchards, as well as increased destruction of natural forests; these factors combined to lead to heavier outbreaks of fruit-piercing moths, which caused more damage than previously (Bänziger 1982). As the development of fruit cultivation and importation of new fruits increased in various countries, fruit-piercing moths gained in importance as significant fruit pests, especially of citrus and pomegranate (Bhumannavar & Viraktamath 2012). Extensive reviews are provided by Cochereau (1977) detailing the activity of fruit-piercing moths in New Caledonia, Bänziger (1982) on the fruit-piercing moth species in Thailand, and Bhumannavar & Viraktamath (2012) on fruit-piercers in India.

The causes of seasonal fluctuations which lead to outbreaks of fruit-piercing moths are uncertain (Bänziger 1982). In Thailand, populations of primary fruit-piercing species (*Eudocima*) attacking

citrus and longan peak during the rainy season, despite yearlong availability of fruits (Bänziger 1982). It is postulated that this fluctuation is due to the availability of larval hostplants rather than adult hosts, since during the dry season in Thailand leaves are absent on Menispermaceae vines (*Tinospora* spp.), which are used for larval development (Bänziger 1982). In other parts of its range, *Eudocima* outbreaks and piercing activity also coincide with the rainy season; this is the case in many parts of India (Bhumannavar & Viraktamath 2012) and Australia (Sands & Schotz 1989; Fay & Halfpapp 1993a, 1999a). In Sri Lanka, a minor peak in population was recorded by Baptist (1944) in June and July, and a larger peak between November and December; this appears to also coincide with rainfall. In contrast, *Eudocima* populations in Fiji are lowest during the humid rainy season and are prevalent between June and August, peaking in July (Kumar & Lal 1983). The same case is met with in Sierra Leone (Hargreaves 1936) and in Sarawak (Leong & Kueh 2011), where populations were found to be highest during the dry months and lowest during the wet season. Increases in fruit-piercing moth populations and activity might coincide with the main fruiting season where they occur, although the availability of larval hostplants is also a crucial factor (Bänziger 1982, Leong & Kueh 2011).

1.6   Systematics of the fruit-piercing moths

Before molecular evidence became available, the subfamily Calpinae was circumscribed to contain all primary fruit-piercing taxa (Kitching & Rawlins 1998, Fibiger & Lafontaine 2005, Zahiri et al. 2012). Kitching and Rawlins (1998) restricted all primary piercers to Calpinae (then a subfamily of Noctuidae) based on similar armature of the proboscis, as well as similarities in the length of the third labial palp segment. A larval preference for hostplants in the family Menispermaceae was also thought to be apomorphic for tribe Calpini (Kitching & Rawlins 1998). Calpinae retained its subfamily status after the reestablishment of Erebidae, and the restriction to fruit-piercing moths remained (Fibiger & Lafontaine 2005). In this classification Calpinae included tribes Anomini, Calpini, Scolipterygini, and Anobini (Fibiger & Lafontaine 2005). The most current classification of fruit-piercing tribes based on comprehensive sampling of molecular data shows that the piercing behavior and associated proboscis modifications have in reality arisen multiple times, and most primary fruit-piercing moths are found in the revised subfamilies Scoliopteryginae, Calpinae, and frequently in Erebinae (Zahiri et al. 2012).

The current subfamily Calpinae includes numerous high-profile primary fruit piercers which can be damaging pests, and comprises the tribes Calpini, Phyllodini, and Ophiderini (Zahiri et al. 2012). The calpine proboscis is stout and highly modified, with a pointed apex and various serrated ridges, erectile barbs, and tearing hooks present (Zaspel et al. 2011, Zahiri et al. 2012) which enable piercing. Members of all three tribes share taxa with unusual adult feeding behaviors, sometimes in addition to the fruit-piercing habit. Calpini includes primary fruit-piercers such as *Gonodonta* and *Oraesia* Guenée (Lepidoptera: Erebidae), which each can be significant pests (e.g., Todd 1959, Yoon and Lee 1974), as well as facultative blood feeders in the genus *Calyptra* Ochsenheimer (Lepidoptera: Erebidae) which can pierce mammalian skin in addition to thick-skinned fruit (e.g., Bänziger 1982, Zaspel 2008, Zaspel et al. 2011). Phyllodini includes taxa such as *Phyllodes eyndhovii* Vollenhoven (Lepidoptera: Erebidae) and *Phyllodes consobrina* Westwood (Lepidoptera: Erebidae), which were postulated by Bänziger (1982) to be primary piercers of thick-skinned fruit although the precise feeding behavior could not be determined at the time; Zaspel et al. (2011) found in a comparative proboscis survey across Calpinae that the proboscis morphology of *Phyllodes consobrina* suggests an ability to pierce soft or perhaps thick-skinned fruit, but only secondary piercing of hard-skinned fruit. Ophiderini is almost entirely composed of primary piercers of hard-skinned fruits in the pantropical genus *Eudocima*, which are the dominant species of primary fruit-piercing moths in central India (Bhumannavar & Viraktamath 2012), Thailand (Bänziger 1982), Australia (e.g., Fay 2002), and the Pacific (e.g., Cochereau 1977), as well as most of the Old World tropics. An exception within this tribe to primary fruit piercing is the tear-drinking species *Hemiceratoides hieroglyphica* Saalmüller (Lepidoptera: Erebidae). Tear-drinking moths are neither fruit piercing nor skin piercing, but imbibe fluids from the eyes of birds and cattle by inserting the proboscis between the eyelids (e.g., Zaspel et al. 2011). In addition to unusual adult feeding behaviors, all three tribes (Calpini, Phyllodini, and Ophiderini) share larvae which show a preference for Menispermaceae as a food plant in the tropics (e.g., Zahiri et al. 2012).

1.7   Control prospects for fruit-piercing moths

Management efforts adopted to control fruit-piercing moths have largely been ineffective (e.g., Bänziger 1982, Fay 2002, Davis et al. 2005, Bhumannavar & Viraktamath 2012). In addition to the undesirability of applying insecticides on mature fruits, fruit-piercing moths spend very little

time actually on the fruits, rendering control by insecticide application unsuccessful (Bänziger 1982, Fay & Halfpapp 2001, Leong & Kueh 2011). The use of insecticides on larval hosts is also problematic, since larvae of fruit-piercing moths develop on Menispermaceae vines which are often remote from orchards where damage is caused by adults (Bänziger 1982, Fay 1996, Kamala Jayanthi et al. 2009). Methods of control for fruit-piercing moths in orchards (reviewed by Baptist (1944), Bänziger (1982), Fay (2002), Bhumannavar and Viraktamath (2012), and others) can be discussed as either manipulation of the fruit crop to limit susceptibility, or direct measures which are used against the fruit-piercing moths to prevent feeding. In theory, the use of either of these approaches either protects the plant from damage or inhibits injury by fruit-piercers, eliminating or greatly reducing pest behavior (which is dependent on both crop susceptibility and injury by the insect). Suggested economic thresholds by Fay (2002) for fruit-piercing moths in orchards indicate that a tolerable level is one moth per ten-to-fifteen peripheral trees when 50% of the crop is susceptible. Scouting ought to be done over the course of one hour early in the night, and substantial damage would be indicated by finding one moth per tree (Fay 2002).

Methods which involve manipulation of the crop attempt to minimize fruit susceptibility. These include regulating fruiting seasons to avoid times of greatest risk (such as the rainy season in certain areas) by removing blossoms and changing irrigation practices (see Bhumannavar and Viraktamath 2012), early harvest of fruits shortly before peak ripeness (Baptist 1944, Golding 1945, Bänziger 1982, Fay 2002), and using trap crops. Despite the known preference for "living" fruits shown by primary piercing species (see Bänziger 1982), Fay and Halfpapp (2001) were able to successfully attract *Eudocima* adults using fruit baits. This experiment was corroborated by Reddy et al. (2007) and Kamala Jayanthi et al. (2015), who each found banana and guava to be preferable to other fruits. In a study comparing damage to guava and pomegranate in adjacent orchards (Kamala Jayanthi et al. 2009), guava was used as a trap crop to protect commercially-grown pomegranate, which received no piercing damage. The use of physical barriers over the fruit, such as paper or polyethylene bags, leaves, or fine netting, has also been practiced to provide an obstacle to piercing (e.g., Baptist 1944, Bänziger 1982, Yoon & Kim 1977, Fay 2002, Bhumannavar and Viraktamath 2012). Bagging or netting fruits is labor-intensive and costly, and depending on the material may still permit piercing damage (e.g., Yoon & Kim 1977). However,

in Australia this method of control has so far proven most effective (Fay & Halfpapp 2001, Fay 2002). Another cultural practice which may decrease damage by fruit-piercing moths is planting trees in large square blocks rather than rows to limit movement of the moths between trees (Fay 2002).

One example of control measures which are used directly against fruit-piercing moths is baiting adult moths using poisoned fruits (Baptist 1944, Bänziger 1982, Bhumannavar and Viraktamath 2012). Baptist (1944) recommended control of fruit-piercing moth populations in orchards using extracts of ripe or overripe fruits mixed with sodium arsenic in glass bait jars. Later experiments examining attraction to specific fruit volatiles showed that ripe fruit volatiles were preferred by *Eudocima phalonia*, and synthesizing these volatiles in agar baits has potential to be used as a lure-toxicant system for this species (Fay & Halfpapp 1999b, 2001). Other control methods include obscuring olfactory signals from fruits by spraying deterrents (such as fish oil or citronella) or smoking orchards (Baptist 1944, Bänziger 1982, Bhumannavar and Viraktamath 2012). Fruit-piercing moths can also be repelled using light (Nomura et al. 1965, Bänziger 1982, Fay 2002, Bhumannavar and Viraktamath 2012). Yellow wavelengths of light projected around blocks of carambola trees was found to reduce fruit-piercing moth activity by as much as 60-70% (Fay & Halfpapp 1995); however, substantial infrastructure and electricity are needed for this control practice, and illumination has no effect on other fruit pests (Fay 2002). Hand-collection of adult moths in orchards using a flashlight is another recommended method, since adults are heavy fliers and can be netted easily, or captured while on fruits (Baptist 1944, Bänziger 1982, Bhumannavar and Viraktamath 2012). While several parasitoid species are known to attack eggs and caterpillars of *Eudocima* moths across the known range (Waterhouse & Norris 1987), efforts to establish biological control in the Pacific are ongoing (see Sands and Liebregts 2005), and in Australia parasitoid activity during the wet season is insufficient to keep populations of fruit-piercing moths beneath economic injury levels (Fay 1995, Fay 2002). The development of pheromone attractants is another control option which is being explored; long-term monitoring of fruit-piercing moth activity in Australian lychee and carambola orchards indicates that over two thirds of feeding moths are males (Fay & Halfpapp 1999a). Female sex pheromones have been synthesized for *Oraesia excavata* Butler (Lepidoptera: Noctuidae) in Japan (Ohmasa et al. 1991),

but compounds for *Eudocima* spp. which could be used as attractants have not yet been identified (Fay 2002).

A further method intended to reduce populations of active fruit-piercing adults involves targeting larval hostplants. Vines in Menispermaceae can live in a variety of habitats as long as there are trees or bushes to climb, making larval hosts difficult to locate (see Bänziger 1982, Bhumannavar and Viraktamath 2012). Although they can be found in deciduous and evergreen forests, menisperms also favor boundaries between primary and secondary forests, clearings, and disturbed areas (Bänziger 1982); for this reason, it is postulated that the destruction of primary forests in Thailand opens increased habitat for these plants which then leads to higher numbers of fruit-piercing moth larvae (Bänziger 1982). Menisperms are also resistant to mechanical damage (Bänziger 1982) and burning is the only failsafe method of removal (Bhumannavar and Viraktamath 2012). Although destruction of larval hosts has been suggested as a way of controlling populations of adults (see Bhumannavar and Viraktamath 2012), this must be done on a village or community basis for best results and all uprooted vines ought to be burned (Bhumannavar and Viraktamath 2012). Even in this scenario, destruction of all usable larval hostplants within a half-mile radius of orchards still cannot ensure the safety of a crop and is not wholly effective (Bhumannavar and Viraktamath 2012), since primary fruit-piercers such as *Eudocima* are strong fliers and can migrate considerable distances (e.g., Baptist 1944, Waterhouse & Norris 1987, Davis et al. 2005, Bhumannavar and Viraktamath 2012). However, removal of larval hosts around orchards where this is practical can provide some relief from damage (Fay 2002).

1.8   Conclusions and synopsis

- The concept of pest is anthropocentric, and pest status is dependent upon the susceptibility of the crop and the injuring behavior of the insect. The categorization of injuring behaviors into pest injury guilds may be helpful in establishing pest status for insect species, including pests within Lepidoptera.

- Most Lepidoptera pests are economically relevant during the larval stage, and can be classified into each of the pest injury guilds based on their method of injury. Leaf-mining and leaf-rolling are specialized Lepidoptera behaviors within leaf-mass consumers, stalk-

boring and wood-boring are specialized behaviors within turgor reducers, and fruit-piercing is a specialized behavior within fruit feeders.

- An important group of Lepidoptera pests which are agriculturally significant as adults are the fruit-piercing moths, which use a specially-adapted proboscis to pierce fruits and suck the juice. This pest behavior is unique among Lepidoptera in the fruit-feeding injury guild.

- Fruit-piercing moths can be understood generally as primary or secondary piercers of fruit. Primary fruit piercers cause direct damage to fruit and are important as pests in orchards.

- All primary fruit-piercing moths occupy the same ecological niche and were once classified together taxonomically in the same subfamily. Molecular evidence has since revealed that the fruit-piercing habit has evolved several times (Zahiri et al. 2012), and the current classification system places primary fruit piercers into several subfamilies, with many significant pests occurring in the revised subfamily Calpinae (e.g., *Eudocima* spp.).

- Control practices used against fruit-piercing moths have typically been ineffective or labor-intensive, and advances in biological control and pheromone isolation are desirable for protecting susceptible fruit crops.

CHAPTER 2.   CHECKLIST OF AGRICULTURALLY SIGNIFICANT BUTTERFLY AND MOTH SPECIES FOR NORTH AMERICA, WITH NOTES ON NATURAL HISTORY AND GEOGRAPHIC DISTRIBUTIONS (INSECTA: LEPIDOPTERA)

2.1   Abstract

The prevalence of monoculture and landscape simplification is correlated with diminished biodiversity and increased presence of harmful pest species in crop environments. Lepidoptera is the largest clade of herbivorous insects, with many agriculturally significant species. Despite the economic impact of Lepidoptera on agricultural systems, distribution information for many species is lacking. To address this need, we provide the first checklist of pest Lepidoptera for the United States and Canada. Eighty agriculturally significant Lepidoptera species and complexes are listed along with notes on distribution, geographic origin, and establishment in North America. Additionally, information is provided for each species on generations per year, larval hostplants, species delimitation, and economic injury level (where available). This information will have utility as a baseline in both basic and applied research questions.

2.2   Introduction

With human land use and agricultural intensification come the ecological disadvantages of monoculture and landscape simplification (e.g., USDA 1973, Matson et al. 1997, Sánchez-Bayo & Wyckhuys 2019). These adverse effects have led to an overall decline in insect populations and diminishing biodiversity (e.g., Matson et al. 1997, Sánchez-Bayo & Wyckhuys 2019), while allowing some insect species present in the environment to reach high, damaging densities in fields and orchards (e.g., Matson et al. 1997, Sánchez-Bayo & Wyckhuys 2019). In agricultural environments, pest insects are those species that typically reduce crop yield. Within Lepidoptera (i.e., butterflies and moths), one of the largest insect orders with an estimated 350,000 species worldwide (Powell & Opler 2009), many species are agriculturally significant. Pest Risk Analysis (PRA), a suite of methods which allows countries to assess the arrival, establishment, and spread of crop pests likely to cause economic damage, is essential to prioritizing biosecurity threats in agriculture (Baker et al. 2014, Bebber et al. 2019). However, successful PRA is

hampered by incomplete knowledge of current crop pest distributions (Bebber et al. 2019). In recent years, technological advances have enhanced our ability to generate massive amounts of data representing historical records (e.g., museum collections) at an accelerated pace. Despite these advances, resources for efficient aggregation and integration of digitized collections data, especially in the context of established economically important species, are often lacking. To help address this need, we compiled an annotated list of North American Lepidoptera species which are agriculturally significant in food crops. For each listed species, we summarized general distribution information and commonly-utilized larval hostplants, as well as geographic origin, generations per year, establishment in North America, and issues impacting species delineation or complexes. When known, economic injury levels and thresholds are also included. This list will have utility in both basic and applied research, and will improve future research efforts in integrated pest management (IPM), conservation, and community interactions between species.

2.3   Methods

An initial list of 106 important Lepidoptera pests in North America was compiled using Singerland & Crosby (1914), Graham (1952), Fernald & Shephard (1955), Metcalf et al. (1967), Holland (1968), Furniss & Carolin (1977), Rings (1977), Knight & Heikkenen (1980), Davison & Lyon (1987), Johnson & Lyon (1991), Howitt (1993), Higley & Boethel (1994), Solomon (1995), Steffey et al. (1999), Ross (2000), Capinera (2001), Papp (2001), Cranshaw (2004), Wagner (2005), Alford (2007), and Bunten et al. (2007). To emphasize pests harmful to plants people consume, this list was further restricted to exclude pests of ecological importance (i.e., attacking endangered plant species), forest pests, ornamental pests, turfgrass pests, cotton or fiber pests, forage pests, stored grain pests, and pests of apiculture. The resulting checklist represents 80 pest species or complexes that consume human food crops. The most current nomenclature from the literature was applied to each species and verified using the Zoological Record online database (2019).

2.4   Results

To preserve the utility of this list in light of future taxonomic changes, species are presented in alphabetical order and are associated with their common names. Family name is listed after each species name in brackets. Issues affecting species delineation are discussed since they impact correct identification of the species, and therefore may also affect our understanding of range and economic significance. Sixteen families within Lepidoptera, mainly moths, are represented: the most numerous family listed is Noctuidae with 35 species/complexes, and the next most numerous is Tortricidae with 16 species. Six species of moths are listed from Crambidae, 5 from Sesiidae, 4 from Erebidae, 2 each from Pyralidae, Sphingidae, and Gracillariidae, and 1 from Notodontidae, Geometridae, Glyphipterigidae, Argyresthiidae, Lasiocampidae, Cossidae, and Yponomeutidae. Only one butterfly is listed, in the family Pieridae. Additional information on the origin, establishment, and generations per year of each species is summarized in Table 2.

Table 2. Summary of origin, establishment in North America, and generations per year for each species, in conjunction with scientific and common names. For species with ranges limited to North America, North America is listed as the origin of that species even when it is not specified in the literature. For all taxa with North America as the origin, all references which were used for range information are listed. In the cases of species only occurring in North America and not yet established, the origin is not listed since an established population is not yet present.

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Abagrotis alternata (Grote, 1864) [Noctuidae]	Mottled Gray Cutworm	North America	estab.	1	Rings 1971, Pogue 2006
Abagrotis cupida (Grote, 1865) [Noctuidae]	Brown Cutworm	North America	estab.	1	Benjamin 1921, Rings 1972, Pogue 2006
Acrobasis tricolorella Grote, 1878 [Pyralidae]	Mineola Moth, Destructive Prune Worm	North America	estab.	1, partial second	Howitt 1993, Powell & Opler 2009
Acrolepiopsis assectella (Zeller, 1839) [Glyphipterigidae]	Leek Moth	Europe	estab.	2-3 in north, 5-6 in south	Alford 1999, Landry 2007, Mason et al. 2011
Agnorisma badinodis (Grote, 1874) [Noctuidae]	Spotted-sided Cutworm	North America	estab.	1	Walkden 1937, Walkden 1950, Pogue 2006
Agrotis gladiaria Morrison, 1874 [Noctuidae]	Claybacked Cutworm	North America	estab.	1	Walkden 1950, Rings et al. 1976a, Pogue 2006, Floate 2017
Agrotis ipsilon (Hufnagel, 1766) [Noctuidae]	Black Cutworm	North America	estab.	1-2 in north, 2-4 in south	Walkden 1950, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009, Floate 2017
Agrotis venerabilis Walker, [1857] [Noctuidae]	Dusky Cutworm	North America	estab.	1	Walkden 1950, Rings et al. 1976b, Ayre & Lamb 1990, Pogue 2006, Floate 2017
Amorbia cuneana (Walsingham, 1879) [Tortricidae]	Western Avocado Leafroller	North America	estab.	2-3	Powell & Opler 2009, Gilligan & Epstein 2014a, Morse et al. 2016
Amphipyra pyramidoides Guenée, 1852 [Noctuidae]	Pyramidal Fruitworm	Europe	estab.	1	Howitt 1993
Anagrapha falcifera (Kirby, 1837) [Noctuidae]	Celery Looper	North America	estab.	2-3, probably 4	Beirne 1971, Capinera 2001, Powell & Opler 2009

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Apamea devastator (Brace, 1819) [Noctuidae]	Glassy Cutworm	North America	estab.	1	Beirne et al. 1971, Ayer & Lamb 1990, Capinera 2001, Powell & Opler 2009, Floate 2017
Archips podana (Scopoli, 1763) [Tortricidae]	Large Fruit-tree Tortrix	Europe, Asia Minor	estab.	1-2	Cardé & Minks 1995, LaGasa et al. 2003, Stará & Kocourek 2004
Argyresthia pruniella (Clerck, 1759) [Argyresthiidae]	Cherry Blossom Moth, Cherry Fruit Moth	Europe	estab.	1	Looney & LaGasa 2014, Looney et al. 2017
Argyrotaenia franciscana (Walsingham, 1879) [Tortricidae]	Orange Tortrix	North America	estab.	2-4	Landry et al. 1999, Powell & Opler 2009, Grafton-Cardwell et al. 2017a
Argyrotaenia velutinana (Walker, 1863) [Tortricidae]	Red-banded Leafroller	North America	estab.	2-3	Beirne 1971, Cardé & Roelofs 1974, Jubb et al. 1974, Bournier 1976, Howitt 1993, Gilligan & Epstein 2014b
Autographa precationis (Guenée, 1852) [Noctuidae]	Common Looper, Plantain Looper	North America	estab.	likely 2-3	Rings 1977, Khalsa et al. 1979, Capinera 2001
Choristoneura rosaceana (Harris, 1841) [Tortricidae]	Oblique-banded Leafroller	North America	estab.	2	Beirne 1971, Howitt 1993, Ahmad et al. 2002, Powell & Opler 2009
Chrysodeixis chalcites (Esper, 1789) [Noctuidae]	Golden Twin-spot Moth	N/A	occurred	polyvoltine, as many as 8 or 9	Murillo et al. 2013, CAB ISC 2019
Chrysoteuchia topiaria (Zeller, 1866) [Crambidae]	Subterranean Webworm, Cranberry Girdler	Europe	estab.	1	Scammell 1917, Niemczyk et al. 2000
Colias eurytheme Boisduval, 1852 [Pieridae]	Alfalfa Caterpillar	North America	estab.	varies, 2 in north and up to 7 in south	Hovanitz 1950, Beirne 1971, Capinera 2001, Pedigo & Rice 2009
Crambus praefectellus (Zincken, 1821) [Crambidae]	Silver-striped Webworm	North America	estab.	2	Ainslie 1923, Niemczyk et al. 2000
Crocidosema aporema (Walsingham, 1914) [Tortricidae]	Bud Borer, Bean Shoot Moth	N/A	occurred	4-6, at least 2 on soybeans	Pereyra & Sanchez 1998, Gilligan & Epstein 2014c

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Cydia pomonella (Linnaeus, 1758) [Tortricidae]	Codling Moth	Europe, Asia Minor	estab.	2-4 varying with latitude	Howitt 1993, Cardé & Minks 1995, Alford 1999, Pedigo & Rice 2009
Dargida diffusa (Walker, 1856) [Noctuidae]	Wheat Head Armyworm	North America	estab.	1-2 in northern regions	Walkden 1950, Beirne 1971, Reddy & Antwi 2016
Datana ministra (Drury, 1773) [Notodontidae]	Yellow-necked Caterpillar	North America	estab.	1	Katovich 2004, Powell & Opler 2009
Egira curialis (Grote, 1873) [Noctuidae]	Citrus Cutworm	North America	estab.	1	Atkins 1958, Grafton-Cardwell et al. 2017b
Enarmonia formosana (Scopoli, 1763) [Tortricidae]	Cherry Bark Tortrix	N/A	occurred	1	Alford 1999, Breedveld & Tanigoshi 2007
Epiphyas postvittana (Walker, 1863) [Tortricidae]	Light Brown Apple Moth	Australia	estab.	2-4	Danthanarayana 1983, Cardé & Minks 1995, Powell & Opler 2009, Gilligan & Epstein 2014d
Euxoa auxiliaris (Grote, 1873) [Noctuidae]	Army Cutworm	North America	estab.	1	Walkden 1950, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009, Floate 2017
Euxoa detersa (Walker, 1856) [Noctuidae]	Sandhill Cutworm	North America	estab.	1	Walkden 1950, Beirne 1971, Rice et al. 1990
Euxoa messoria (Harris, 1841) [Noctuidae]	Dark-sided Cutworm	North America	estab.	1	Walkden 1950, Capinera 2001, Pogue 2006, Floate 2017
Euxoa scandens (Riley, 1869) [Noctuidae]	White Cutworm	North America	estab.	1	Walkden 1950, Beirne 1971, Lampert 1976, Floate 2017
Euzophera semifuneralis (Walker, 1863) [Pyralidae]	American Plum Borer	North America	estab.	2	Biddinger and Howitt 1992, Powell & Opler 2009, Krawczyk 2017
Feltia jaculifera (Guenée, 1852)**;** *Feltia subgothica* (Haworth, 1809)**;** *Feltia herilis* (Grote, 1873)**;** *Feltia tricosa* (Lintner, 1874) [Noctuidae]	Dingy Cutworm	North America	estab.	1	Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Pogue 2006, Powell & Opler 2009, Floate 2017

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Grapholita molesta (Busck, 1916) [Tortricidae]	Oriental Fruit Moth	China	estab.	3 and a partial 4th in the Midwest, 5-6 in California	Howitt 1993, Cardé & Minks 1995, Gilligan and Epstein 2014e, Hasey et al. 2016
Grapholita packardi (Zeller, 1875) [Tortricidae]	Cherry Fruit Worm	North America	estab.	2-3, 1 in blueberries	Howitt 1993, Gilligan & Epstein 2014f, Jeger et al. 2018, Wise et al. 2007
Helicoverpa armigera (Hübner, [1809]) [Noctuidae]	Old World Bollworm	N/A	occurred	4 in cotton	Reed & Pawar 1982, Cunningham et al. 1999, Liu et al. 2004, Kriticos et al. 2015
Helicoverpa zea (Boddie, 1850) [Noctuidae]	Corn Earworm	North and South America	estab.	1 in north, increases up to year-round in south	Walkden 1950, Beirne 1971, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009
Hypena scabra (Fabricius, 1798) [Erebidae]	Green Cloverworm	North America	estab.	2-3	Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009
Hyphantria cunea (Drury, 1773) [Erebidae]	Fall Webworm	North America	estab.	1-2 in the north, at least 4 in the south	Katovich 2004, Wagner 2005, Powell & Opler 2009
Lacanobia subjuncta (Grote & Robinson, 1868) [Noctuidae]	Speckled Cutworm	North America	estab.	2	Doerr et al. 2002, Powell & Opler 2009
Lacinipolia renigera (Stephens, 1829) [Noctuidae]	Bristly Cutworm	North America	estab.	2, more in the southern US	Walkden 1950, Beirne 1971, Powell & Opler 2009, Floate 2017
Lithophane antennata (Walker, 1858) [Noctuidae]	White-striped Fruitworm, Green Fruitworm	Europe	estab.	1	Rings 1973, Howitt 1993, Wagner 2005
Lobesia botrana (Denis & Schiffermüller, 1775) [Tortricidae]	European Grapevine Moth	N/A	occurred	2-3	Cardé & Minks 1995, Bournier 1976, Alford 1999, Ifoulis & Savopoulou-Soultani 2006, Gilligan et al. 2011
Malacosoma americanum (Fabricius, 1793) [Lasiocampidae]	Eastern Tent Caterpillar	North America	estab.	1	USDA 1985, Costa & Ross 1994, Fitzgerald 1995, Wagner 2005, Pedigo & Rice 2009
Manduca quinquemaculata (Haworth, 1803) [Sphingidae]	Tomato Hornworm	North America	estab.	1-2	Beirne 1971, Capinera 2001, Powell & Opler 2009

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Manduca sexta (Linnaeus, 1763) [Sphingidae]	Tobacco Hornworm	North America	estab.	usually 2, can vary from 1-4	Beirne 1971, Capinera 2001, Powell & Opler 2009
Melanchra picta (Harris, 1841) [Noctuidae]	Zebra Caterpillar	North America	estab.	2	Walkden 1950, Beirne 1971, Capinera 1979, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009
Melittia cucurbitae (Harris, 1828) [Sesiidae]	Squash Vine Borer	North America	estab.	1-2	Beirne 1971, Capinera 2001, Kariuki and Gillett-Kaufman 2014, Krinski 2015
Mythimna unipuncta (Haworth, 1809) [Noctuidae]	Armyworm, Armyworm Cutworm, Rice Armyworm, True Armyworm	North America	estab.	varies by location from 2 to 6	Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009, Floate 2017
Neodactria caliginosellus (Clemens, 1860) [Crambidae]	Corn Root Webworm, Black Grass-veneer	likely North America	estab.	1	Beirne 1971, Gesell & Calvin 2000, McLeod & Austin 2016
Nephelodes minians Guenée, 1852 [Noctuidae]	Bronzed Cutworm	North America	estab.	1	Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009, Floate 2017
Orgyia leucostigma (Smith, 1797) [Erebidae]	White-marked Tussock Moth	North America	estab.	2 or more	Wagner 2005, Powell & Opler 2009
Orthosia hibisci (Guenée, 1852) [Noctuidae]	Speckled Green Fruitworm	Europe	estab.	1	Wagner 2005, Powell & Opler 2009
Ostrinia nubilalis (Hübner, [1796]) [Crambidae]	European Corn Borer	thought to be Europe	estab.	1-4	Alford 1999, Capinera 2001, Powell & Opler 2009
Paleacrita vernata (Peck, 1795) [Geometridae]	Spring Cankerworm	North America	estab.	1	Wagner 2005, Powell & Opler 2009
Papaipema nebris (Guenée, 1852) [Noctuidae]	Stalk Borer	North America	estab.	1	Decker 1930, Walkden 1950, Beirne 1971, Bailey & Pedigo 1986, Gesell & Calvin 2000, Capinera 2001
Paralobesia viteana (Clemens, 1860) [Tortricidae]	Grape Berry Moth	North America	estab.	2-3	Cardé & Minks 1995, Gilligan et al. 2011, Gilligan & Epstein 2014g

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Parapediasia teterrellus (Zincken, 1821) [Crambidae]	Bluegrass Sod Webworm	North America	estab.	2-3	Ainslie 1930, Gesell & Calvin 2000, Powell & Opler 2009
Peridroma saucia (Hübner, [1808]) [Noctuidae]	Variegated Cutworm	thought to be Europe	estab.	2-4	Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009, Floate 2017
Phyllocnistis citrella (Stainton, 1856) [Gracillariidae]	Citrus Leafminer	Asia	estab.	continuous	Heppner & Dixon 1995, Peña et al. 1996, Heppner 1999
Phyllonorycter blancardella (Fabricius, 1781) [Gracillariidae]	European Tentiform Leafminer, Spotted Tentiform Leafminer	Europe	estab.	3	Landry & Wagner 1995, OMAFRA 2011
Platynota flavedana Clemens, 1860 [Tortricidae]	Variegated Leafroller	North America	estab.	2, partial 3rd in the south	Wilde & Semel 1966, Weires & Riedl 1991, Howitt 1993, Gilligan & Epstein 2014h
Platynota idaeusalis (Walker, 1859) [Tortricidae]	Tufted Apple Bud Moth	North America	estab.	2	Weires & Riedl 1991, Howitt 1993, Krawczyk 2016
Prionoxystus robiniae (Peck, 1818) [Cossidae]	Carpenterworm Moth	North America	estab.	at least 4	Burke 1921, Powell & Opler 2009
Spilonota ocellana (Denis & Schiffermüller, 1775) [Tortricidae]	Eyespotted Bud Moth	Europe	estab.	1	Howitt 1993, Powell & Opler 2009, Alford 1999
Spilosoma virginica (Fabricius, 1798) [Erebidae]	Virginia Tiger Moth	North America	estab.	2-3	Capinera 2001, Wagner 2005, Powell & Opler 2009
Spodoptera exigua (Hübner, [1808]) [Noctuidae]	Beet Armyworm	Southeast Asia	estab.	varies by climate, can be continuous	Walkden 1950, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009
Spodoptera frugiperda (Smith, 1797) [Noctuidae]	Fall Armyworm	North and South America	estab.	1-4	Walkden 1950, Capinera 2001, Goergen et al. 2016
Spodoptera ornithogalli (Guenée, 1852) [Noctuidae]	Yellow-striped Armyworm	North and South America	estab.	1-4	Walkden 1950, Capinera 2001, Powell & Opler 2009
Striacosta albicosta (Smith, 1888) [Noctuidae]	Western Bean cutworm	North America	estab.	1	Powell & Opler 2009, Floate 2017

Table 2 continued

Scientific name and family	Common name(s)	Origin	Occurred or established	Generations per year	References
Synanthedon exitiosa (Say, 1823) [Sesiidae]	Peach Tree Borer	North America	estab.	1, partial second brood in the south	Howitt 1993, Powell & Opler 2009, Strickland 2018
Synanthedon myopaeformis (Borkhausen, 1789) [Sesiidae]	Red-belted Clearwing, Apple Clearwing	Europe	estab.	1-2	Cossentine et al. 2010, MSU 2010
Synanthedon pictipes (Grote & Robinson, 1868) [Sesiidae]	Lesser Peachtree Borer	North America	estab.	2	Howitt 1993, McKern & Szalanski 2008, Shapiro-Ilan et al. 2010
Synanthedon scitula (Harris, 1839) [Sesiidae]	Dogwood Borer	North America (Riedl et al. 2012) or Europe (Looney et al. 2012)	estab.	1	Riedl et al. 1985, Bergh et al. 2009, Lesky et al. 2009, Looney et al. 2012
Trichoplusia ni (Hübner, [1803]) [Noctuidae]	Cabbage Looper	uncertain, probably Africa or Central Asia	estab.	2-7	Walkden 1950, Capinera 2001, Powell & Opler 2009
Udea rubigalis (Guenée, 1854) [Crambidae]	Greenhouse Leaftier, Celery Leaftier	North and South America	estab.	5-6	Capinera 2001, Powell & Opler 2009
Xestia c-nigrum (Linnaeus, 1758)**;** *Xestia dolosa* Franclemont, 1980 [Noctuidae]	Spotted Cutworm	North America	estab.	2-3	Walkden 1950, Beirne 1971, Capinera 2001, Pogue 2006, Powell & Opler 2009, Floate 2017
Yponomeuta padella (Linnaeus, 1758) [Yponomeutidae]	Cherry Ermine Moth	Europe	estab.	1	Hoebeke 1987, Mowat & Clawson 1988, Sperling et al. 1995

2.4.1   List of Species

2.4.1.1   *Abagrotis alternata* (Grote, 1864) [Noctuidae]

Common name(s). Mottled Gray Cutworm

Distribution. Widely distributed in North America across southern Canada from Nova Scotia to Alberta (Rings 1971, Pogue 2006). It extends from the eastern United States from Maine south to North Carolina, Tennessee, and Mississippi, and west to Texas, Utah, and Arizona (Rings 1971, Pogue 2006). This species is present in the northern Great Plains in North and South Dakota, Montana, and northeastern Wyoming, and from Colorado, Utah, New Mexico, and central Arizona in the Rocky Mountains (Pogue 2006).

Remarks. Larvae are climbing cutworms (Rings 1971) which feed on buds and new growth of vegetable crops and some fruit trees, including walnut, cabbage, strawberry, apple, cherry, plum, peach, potato and tomato (Rings 1971, Pogue 2006, Beadle & Leckie 2012).

2.4.1.2   *Abagrotis cupida* (Grote, 1865) [Noctuidae]

Common name(s). Brown Cutworm

Distribution. Widely distributed species. Common throughout the northeastern United States and is present northward in Canada to the Northwestern Territories (Rings 1972), occurring from Newfoundland across to British Columbia (Pogue 2006). In the United States, this species occurs from Maine to Tennessee and west to Minnesota; there are scattered records from South Dakota south to Texas and west to Colorado, Utah, and Washington (Rings 1972, Pogue 2006).

Remarks. Climbing cutworm, damages fruit buds of grape, apple, peach, and blueberry (Benjamin 1921, Walkden 1950, Rings 1972, Bournier 1976, Pogue 2006, Beadle & Leckie 2012). Larvae pass the day a few centimeters below the soil at the foot of rootstocks and come out at night to feed on the buds (Walkden 1950, Rings 1972, Bournier 1976, Pogue 2006).

Identification. This species is hard to identify and may form a complex with *Abagrotis brunneipennis* Grote (see Benjamin 1921, Anweiler 2007, Pogue 2006, Pohl et al. 2010). *Abagrotis brunneipennis* was initially separated from *A. cupida* by differences in wing pattern and smaller size (Benjamin 1921), although it is reported by Anweiler (2007) to be somewhat larger than *A. cupida*. The two species are often confused in collections (Pogue 2006), and barcoding for these species is also identical (Anweiler 2007). The relationship between these species needs further investigation.

2.4.1.3   *Acrobasis tricolorella* Grote, 1878 [Pyralidae]

Common name(s). Mineola Moth, Destructive Prune Worm

Distribution. Present in the northern United States up to southern Canada, and in the west across the Rocky Mountains to New Mexico, Arizona, and California (Powell & Opler 2009).

Remarks. Overwintered larval generation attacks the fruit buds and developing flower parts of cherry, plum, apple, and chokecherry (Howitt 1993, Powell & Opler 2009, Beadle & Leckie 2012), later forming nests in leaf terminals in which they continue feeding (Howitt 1993). Early summer larvae directly attack ripe fruits near harvest time and feed around the pits (Howitt 1993).

2.4.1.4   *Acrolepiopsis assectella* (Zeller, 1839) [Glyphipterigidae]

Common name(s). Leek Moth

Distribution. Occurs across almost all of Europe, and is widespread from Scandinavia and western Russia in the north, extending south to northern Africa (Landry 2007, Mason et al. 2011). It is also widely distributed in Asia (Landry 2007, Mason et al. 2011). This species has expanded its range throughout eastern Ontario, southwestern Quebec, and Prince Edward Island in Canada, and to New York in the United States (Landry 2007, Mason et al. 2011).

Remarks. Larvae are leafminers of *Allium* plants, particularly leek, garlic, and onion (Alford 1999, Landry 2007, Mason et al. 2011).

2.4.1.5   *Agnorisma badinodis* (Grote, 1874) [Noctuidae]

Common name(s). Spotted-sided Cutworm

Distribution. Distributed in the northeastern United States and in southern Quebec and Ontario in Canada (Walkden 1937, Walkden 1950, Pogue 2006). It ranges along the Atlantic Coast from New York south to South Carolina and Mississippi, and occurs westward to Iowa, Kansas, Texas, and North Dakota (Walkden 1937, Walkden 1950, Pogue 2006). A larger distribution for this species is probable (Walkden 1937).

Remarks. Larvae attack apple, aster, chickweed, and dock, as well as clover and tobacco (Walkden 1937, Walkden 1950, Pogue 2006, Beadle & Leckie 2012).

2.4.1.6 *Agrotis gladiaria* Morrison, 1874 [Noctuidae]

Common name(s). Claybacked Cutworm

Distribution. Occurs in North America east of the Rocky Mountains, from Nova Scotia across to southern British Columbia at its northernmost extent in Canada, and from southern Quebec to the panhandle of Florida in the United States (Walkden 1950, Rings et al. 1976a, Pogue 2006, Floate 2017). It is most prevalent in the northcentral and northeastern United States and occurs west to eastern Texas, eastern Kansas, eastern Nebraska, southern Wisconsin, and Michigan (Rings et al. 1976a, Pogue 2006).

Remarks. A tunneling cutworm species (Walkden 1950) which feeds on garden, berry, and field crops, including tomato, sweet potato, strawberry, peas, oats, grasses, corn, bean, and cabbage (Walkden 1950, Rings et al. 1976a, Pogue 2006, Beadle & Leckie 2012, Floate 2017).

2.4.1.7 *Agrotis ipsilon* (Hufnagel, 1766) [Noctuidae]

Common name(s). Black Cutworm

Distribution. Cosmopolitan species and one of the most widespread moths in the world (e.g., Pogue 2006, Powell & Opler 2009). Has been recorded from "virtually everywhere" (Powell & Opler 2009), including oceanic islands, with the exception of Antarctica and the Arctic and subarctic portions of North America and Eurasia (Walkden 1950, Odiyo 1975, Capinera 2001, Pogue 2006, Powell & Opler 2009). In North America, this species is wide-ranging and has resident populations in the southern United States, but regularly emigrates northward (Capinera 2001, Powell & Opler 2009, Philip 2015) as far as southern Canada in the spring from Newfoundland to British Columbia (Walkden 1950, Beirne 1971, Antonelli et al. 2000, Capinera 2001, Powell & Opler 2009, Floate 2017).

Remarks. Larvae are highly polyphagous on a wide variety of crops in 20 families (Powell & Opler 2009), including corn, bean, asparagus, cabbage, potato, garden vegetables, berries, grapes, tree fruits, and tobacco (Walkden 1950, Beirne 1971, Alford 1999, Antonelli et al. 2000, Capinera 2001, Pogue 2006, Philip 2015, Floate 2017). This species is an aboveground tunneling cutworm which feeds mainly by severing plants at the soil surface (Walkden 1950, Beirne 1971, Philip 2015, Floate 2017). The economic thresholds cited by Philip (2015) are 3-4 larvae per meter squared in cereals, 25-30% stand reductions in oilseeds, and 2-3 larvae per meter squared in the top 7 cm (3 in.) of soil in peas.

2.4.1.8 *Agrotis venerabilis* Walker, [1857] [Noctuidae]

Common name(s). Dusky Cutworm

Distribution. Widespread in North America from Newfoundland to British Columbia across southern Canada, and throughout the United States from Maine to Florida and the West Coast (Walkden 1950, Rings et al. 1976b, Ayre & Lamb 1990, Pogue 2006, Floate 2017).

Remarks. Aboveground tunneling cutworm; the larvae are defoliators which cut the leaves from plants during the night to consume in their tunnels (Walkden 1950, Rings et al. 1976b, Floate 2017). Attacked plants include corn, tobacco, tomato, and oats, as well as alfalfa, chickweed, dandelion and other roadside weeds (Walkden 1950, Rings et al. 1976b, Pogue 2006, Beadle & Leckie 2012, Floate 2017). No economic thresholds have been developed (Floate 2017).

2.4.1.9 *Amorbia cuneana* (Walsingham, 1879) [Tortricidae]

Common name(s). Western Avocado Leafroller

Distribution. Occurs in British Columbia and along the Pacific Coast to northern Baja California (Powell & Opler 2009, Gilligan & Epstein 2014a), and eastwards to Arizona and Idaho (Gilligan & Epstein 2014a). There is a disjunct population in the mountains of southern Baja California (Powell & Opler 2009).

Remarks. Larvae feed on the leaves of 20 families of broad-leaved trees and shrubs (Powell & Opler 2009), skeletonizing them in early instars and later consuming entire leaves (Gilligan & Epstein 2014a, Morse et al. 2016). Larvae also web leaves to fruit and feed on the skin of fruits in a cluster (Gilligan & Epstein 2014a, Morse et al. 2016). Mature, healthy trees can tolerate a considerable amount of larval feeding on foliage, buds, and blossoms without severely impacting tree growth or yield; however, fruit feeding by larvae causes economic damage (Gilligan & Epstein 2014a, Morse et al. 2016).

2.4.1.10 *Amphipyra pyramidoides* Guenée, 1852 [Noctuidae]

Common name(s). Pyramidal Fruitworm

Distribution. Ranges in North America from British Columbia in Canada east to the Atlantic coast, and south in the United States to central California, southeastern Arizona, and northeastern Colorado (Capinera 2001, Powell & Opler 2009).

Remarks. Larvae are defoliators of many broadleaf plants, including basswood, hawthorn, maple, oak, walnut, raspberry, grape, and greenbrier (Powell & Opler 2009, Beadle & Leckie 2012). Larvae also eat deep holes into apple, peach, pear, cherry, and plum (Howitt 1993).

2.4.1.11 *Anagrapha falcifera* (Kirby, 1837) [Noctuidae]

Common name(s). Celery Looper

Distribution. Occurs in North America throughout Canada from southern British Columbia to the East Coast, with records extending to northern Labrador (Capinera 2001, Powell & Opler 2009). Although this species is scarce or absent in California, Nevada, Arizona, and New Mexico, it is found throughout the rest of the continental United States (Capinera 2001, Powell & Opler 2009).

Remarks. Larvae are defoliators of corn, garden vegetables such as celery, beet, cabbage, carrot, lettuce, and pea, as well as clover, dandelion, and tobacco (Beirne 1971, Capinera 2001, Beadle & Leckie 2012).

2.4.1.12 *Apamea devastator* (Brace, 1819) [Noctuidae]

Common name(s). Glassy Cutworm

Distribution. Occurs in the north from Alaska to across southern Canada to Newfoundland, and south to California, Arizona, Texas, and Mexico (Ayer & Lamb 1990, Powell & Opler 2009). In the United States, it extends east to Virginia and does not occur in the southeastern states (Capinera 2001, Powell & Opler 2009). It is also found in South America (Capinera 2001).

Remarks. Larvae of this species are subterranean (below-ground) cutworms, which feed on roots and stem bases below the soil (Beirne et al. 1971, Ayer & Lamb 1990, Antonelli et al. 2000, Capinera 2001, Philip 2015, Floate 2017). Grasses are the preferred hosts, but this species also attacks corn, cereals, tobacco, and vegetable crops (Beirne et al. 1971, Ayer & Lamb 1990, Antonelli et al. 2000, Capinera 2001, Beadle & Leckie 2012, Philip 2015, Floate 2017). No economic thresholds have been established (Philip 2015, Floate 2017).

2.4.1.13 *Archips podana* (Scopoli, 1763) [Tortricidae]

Common name(s). Large Fruit-tree Tortrix

Distribution. Present in several northern European regions (Cardé & Minks 1995), including northern Ireland and the United Kingdom, Hungary (Cuthbertson & Murchie 2005), and the

Czech Republic (Stará & Kocourek 2004). In North America, occurs in British Columbia and in Washington in the northwestern United States (LaGasa et al. 2003).

Remarks. Larvae are leafrollers, and in addition to defoliation derive their economic importance from causing direct damage to fruit in apple orchards (Cardé & Minks 1995, LaGasa et al. 2003, Stará & Kocourek 2004, Cuthbertson & Murchie 2005).

2.4.1.14 *Argyresthia pruniella* (Clerck, 1759) [Argyresthiidae]

Common name(s). Cherry Blossom Moth, Cherry Fruit Moth

Distribution. In Europe, this species is distributed in the United Kingdom and most of continental Europe, Russia, and Asia Minor (Looney et al. 2017). In North America, this species is also established in British Columbia, Canada and in Washington in the United States (Looney & LaGasa 2014, Looney et al. 2017).

Remarks. Larvae enter the ovaries of flowers or developing fruits to feed, resulting in considerable yield loss in *Prunus* species such as cherry and plum (Alford 1978, Looney & LaGasa 2014, Looney et al. 2017).

2.4.1.15 *Argyrotaenia franciscana* (Walsingham, 1879) [Tortricidae]

Common name(s). Orange Tortrix

Distribution. Occurs along the Pacific Coast of North America from British Columbia to northern Baja California (Landry et al. 1999) and on the California Channel Islands (Landry et al. 1999, Powell & Opler 2009).

Remarks. Larvae of this species are polyphagous (Powell & Opler 2009) and feed within silken webs on outer canopy shoots, green bark, or flowers, although economic importance is derived from feeding on fruits (Morse et al. 2016). Second generation larvae cause superficial scarring on young fruit, while later generations eat holes into the rind, causing early drop and fruit rot (Grafton-Cardwell et al. 2017a). Injured crops include notably citrus (Landry et al. 1999, Powell & Opler 2009), but also grape, strawberry, and sometimes avocado (Morse et al. 2016).

Identification. This species is part of a semi-species complex with *A. citrana*, another Californian species (Landry et al. 1999, Powell & Opler 2009), and voucher specimens show gradual phenotypic change from 1910-1960 in San Francisco which is indicative of hybridization during this time (Powell & Opler 2009). Mating trials between different populations have

produced viable progeny (Powell & Opler 2009) and a phylogeny of populations along the coast based on mitochondrial DNA failed to distinguish between *A. franciscana* and *A. citrana* (Landry et al. 1999). As the older name, *A. fransicana* is here used to represent the complex and to refer to the agricultural pest, the Orange Tortrix (Landry et al. 1999), although further investigations should be made into this group.

2.4.1.16 *Argyrotaenia velutinana* (Walker, 1863) [Tortricidae]

Common name(s). Red-banded Leafroller

Distribution. Occurs in the midwestern and eastern United States and eastern and western Canada (Taschenberg et al. 1974, Jubb & Cox 1974, Bournier 1976, Howitt 1993). It is widely distributed in eastern North America (Gilligan & Epstein 2014b).

Remarks. A leaf-rolling species which is an important pest of apple, grape, and fruit trees (Beirne 1971, Taschenberg et al. 1974, Bournier 1976, Jubb & Cox 1974, Howitt 1993, Gilligan & Epstein 2014b). It has also been found feeding on vegetables, ornamentals, and shrubs (Howitt 1993), as well as cruciferous plants (Beirne 1971). Economic damage is caused when late-instar larvae web leaves onto fruit and feed directly on the fruit surface, causing fruit rot and early fall in apples (Howitt 1993, Gilligan & Epstein 2014b). Larvae will also continue feeding on fallen fruit and can be moved to new areas this way (Gilligan & Epstein 2014b).

Identification. Damage by this species, while similar to damage in fruit orchards by *Platynota flavedana* (Variegated Leafroller) and *Platynota idaeusalis* (Tufted Apple Bud Moth), is continuous across the fruit surface (Howitt 1993). It can be distinguished from feeding by the other two species, which leave separated, peck-like wounds (Howitt 1993).

2.4.1.17 *Autographa precationis* (Guenée, 1852) [Noctuidae]

Common name(s). Common Looper, Plantain Looper

Distribution. Eastern distribution in North America, and is present in Canada from Nova Scotia to Manitoba, occurring widely in the United States east of the Great from Maine south to Georgia (Rings 1977, Khlasa et al. 1979, Capinera 2001). It ranges westward to Nebraska, Kansas, and Wyoming (Rings 1977, Khlasa et al. 1979, Capinera 2001), and is infrequently found in the southernmost states (Capinera 2001).

Remarks. Larvae defoliate plants in Asteraceae, along with cabbage, plantain, clover, and soybean (Rings 1977, Khalsa et al. 1979, Capinera 2001, Beadle & Leckie 2012).

2.4.1.18 *Choristoneura rosaceana* (Harris, 1841) [Tortricidae]

Common name(s). Oblique-banded Leafroller

Distribution. Found throughout the apple-producing areas of the northeastern and Midwestern United States (Howitt 1993), and ranges throughout the North American continent from Newfoundland, northern Alberta, and British Columbia in Canada south to Florida and Texas in the United States (Beirne 1971, Howitt 1993, Powell & Opler 2009). This species is also present in all of the western United States, except at high elevations and deserts (Powell & Opler 2009).

Remarks. Larvae of this species are leaf-rolling, and attack orchard crops and woody plants such as apple, blueberry, pine, and oak (Howitt 1993, Ahmad et al. 2002, Powell & Opler 2009, Beadle & Leckie 2012). The larvae are polyphagous and may feed on the leaves, buds, flowers, and fruits of over 50 plant types (Ahmad et al. 2002). At the early petal-fall stage, screening may be done by examining 20 clusters per tree in five trees per orchard; treatment is recommended if two or more larvae or fresh feeding sites are found per tree (Howitt 1993). Additional screening can be done in the summer by examining ten fruit clusters and ten terminals in five trees per orchard, and if an average of three or more larvae is found per tree treatment is recommended again (Howitt 1993).

2.4.1.19 *Chrysodeixis chalcites* (Esper, 1789) [Noctuidae]

Common name(s). Golden Twin-spot Moth

Distribution. Currently distributed primarily in southern Europe, Mediterranean, the Middle East, and Africa, and extends north to southern Spain and northern Italy (Murillo et al. 2013, CAB ISC 2019). This species has also been recorded in North America from southwestern Ontario since 2008 (Murillo et al. 2013).

Remarks. Larvae are highly polyphagous and defoliate plants in at least 16 plant families, including many fruit and vegetable crops and ornamentals (Murillo et al. 2013, CAB ISC 2019). Young larvae begin by grazing on the underside of leaves and are leafrollers in the second and third instars, while later larval instars eat through and skeletonize leaves (CAB ISC 2019).

2.4.1.20 *Chrysoteuchia topiaria* (Zeller, 1866) [Crambidae]

Common name(s). Subterranean Webworm, Cranberry Girdler

Distribution. Widespread in Canada and the United States (Scammell 1917). This species is often present in bogs, and occurs in the Pacific Northwest and south to central California on both sides of the Sierra Nevada coastal range (Powell & Opler 2009). This species is also transcontinental, and is distributed widely in Europe (Scammell 1917, Powell & Opler 2009).

Remarks. Larvae are problematic in cranberry, blueberry, grass seed, turfgrass, and coniferous nursery stock (Roberts & Mahr 1986, Niemczyk et al. 2000, Powell & Opler 2009). In cranberry, larvae feed on subterranean vines, causing girdling and sometimes severing them completely (Roberts & Mahr 1986).

2.4.1.21 *Colias eurytheme* Boisduval, 1852 [Pieridae]

Common name(s). Alfalfa Caterpillar

Distribution. According to Hovanitz (1950), this species is the most southern of all North American species of *Colias*. It often disperses to southern Canada during the summer, and covers the United States from the Atlantic to the Pacific (Hovanitz 1950, Capinera 2001). To the south, it extends to the southern parts of Lower California and the coastal areas of southern Mexico (Hovanitz 1950). This species was once restricted to central and western North America east of the Appalachian Mountains, although it dispersed eastward in the 1900's and was helped by the clearing of forests and more widespread alfalfa cultivation (Capinera 2001).

Remarks. The larvae are defoliators of alfalfa, clovers, vetch, milkvetch, trefoil, and forage legumes (Capinera 2001, Philip 2015). They are also harmful in peas, soybean, and beans (Beirne 1971, Capinera 2001, Pedigo & Rice 2009). No economic thresholds have been established (Philip 2015).

2.4.1.22 *Crambus praefectellus* (Zincken, 1821) [Crambidae]

Common name(s). Silver-striped Webworm

Distribution. This species appears to be limited to the eastern United States, where it occurs up to the Mississippi River and also in North Dakota, South Dakota, Minnesota, Iowa, Colorado, Missouri, Arkansas, and eastern Texas (Ainslie 1923). In Canada it is reported from Cartwright, Manitoba, and on the southeastern edge (Ainslie 1923).

Remarks. This species is known for damaging grasses and cereal grains such as wheat, rye, and oats (Ainslie 1923, Niemczyk et al. 2000, Beadle & Leckie 2012). The larvae injure plants by cutting holes in the stalks below the ground level and feeding within a spun silk tube (Ainslie 1923).

2.4.1.23 *Crocidosema aporema* (Walsingham, 1914) [Tortricidae]

Common name(s). Bud Borer, Bean Shoot Moth

Distribution. Occurs throughout Central and South America, and is also likely present in southern Mexico and the Caribbean (Gilligan & Epstein 2014c). Although specimens were collected in Brownsville, Texas in the 1940's, there have been no recent United States records for this species as of 2013 (Gilligan & Epstein 2014c).

Remarks. Larvae feed primarily on vegetative buds and can also bore into stems, floral buds, and pods (Pereyra & Sanchez 1998). Hosts include soybean and beans, and also cotton and corn (Pereyra & Sanchez 1998, Gilligan & Epstein 2014c).

2.4.1.24 *Cydia pomonella* (Linnaeus, 1758) [Tortricidae]

Common name(s). Codling Moth

Distribution. This species occurs everywhere apples are grown (Powell & Opler 2009). It has assumed the status of a key pest of orchards in Europe, North and South America, South Africa, and Australia (Cardé & Minks 1995, Powell & Opler 2009).

Remarks. Larvae enter blossoms and feed on the fruit internally around the pit (Howitt 1993, Cardé & Minks 1995, Alford 1999, Pedigo & Rice 2009). They are problematic on apple, pear, peach, apricot, walnut, and other pome fruits (Howitt 1993, Cardé & Minks 1995, Alford 1999, Pedigo & Rice 2009, Beadle & Leckie 2012).

2.4.1.25 *Dargida diffusa* (Walker, 1856) [Noctuidae]

Common name(s). Wheat Head Armyworm

Distribution. This species is widely distributed in North American grasslands from the Atlantic coast west to Utah and Arizona in the United States (Walkden 1950), and is most common on the Great Plains (Reddy & Antwi 2016). In Canada it is found in Saskatchewan and Alberta (Beirne 1971), and is widely distributed from Alberta to Nova Scotia (Walkden 1950). The range also extends south into South America (Walkden 1950).

Remarks. Larvae eat the seed heads of grasses as well as wheat, rye, oats, and barley (Walkden 1950, Beirne 1971, Beadle & Leckie 2012, Philip 2015, Reddy & Antwi 2016). The host range and pest status of this species are not well studied (Reddy & Antwi 2016), and no treatment or management thresholds are currently available (Philip 2015, Reddy & Antwi 2016).

2.4.1.26 *Datana ministra* (Drury, 1773) [Notodontidae]

Common name(s). Yellow-necked Caterpillar

Distribution. Occurs discontinuously in western North America from British Columbia south to central California and Colorado, and ranges east in Canada to Nova Scotia (Powell & Opler 2009).

Remarks. Larvae feed gregariously on a wide variety of woody trees and shrubs and are orchard pests (Powell & Opler 2009, Beadle & Leckie 2012), especially on apple (Powell & Opler 2009) and walnut (Katovich 2004). Early-instar larvae skeletonize young leaves and are defoliators (Powell & Opler 2009).

2.4.1.27 *Egira curialis* (Grote, 1873) [Noctuidae]

Common name(s). Citrus Cutworm

Distribution. This species is distributed in western North America, occurring in British Columbia in Canada and along the Pacific coast of the United States east to Montana and Colorado (Atkins 1958).

 Remarks. A climbing cutworm which feeds on new spring growth as young larvae and on ripening citrus fruits (Atkins 1958, Grafton-Cardwell et al. 2017b), including oranges, grapefruits, lemons, and plums (Atkins 1958). Although larval feeding may occur on leaves or flowers, larvae preferentially feed on fruit (Grafton-Cardwell et al. 2017b). Because citrus trees can tolerate high levels of leaf damage, prebloom treatment thresholds are relatively high (Grafton-Cardwell et al. 2017b), and a similarly high treatment threshold is used by citrus growers before petal fall (15 larvae per 20 net shakes) (Grafton-Cardwell et al. 2001, Grafton-Cardwell et al. 2017b). A more conservative threshold is adopted after petal fall (3-4 larvae per sampling method) because of the greater economic damage this species does to young fruit on the tree (Grafton-Cardwell et al. 2001, Grafton-Cardwell et al. 2017b).

2.4.1.28 *Enarmonia formosana* (Scopoli, 1763) [Tortricidae]

Common name(s). Cherry Bark Tortrix

Distribution. This species is an occasional pest in Europe, and occurs in the Pacific Northwest in North America (Breedveld & Tanigoshi 2007).

Remarks. The larvae attack the trunk and main branches of apple and cherry trees, burrowing into the bark (Alford 1999, Breedveld & Tanigoshi 2007).

2.4.1.29 *Epiphyas postvittana* (Walker, 1863) [Tortricidae]

Common name(s). Light Brown Apple Moth

Distribution. Distributed in Australia, Tanzania, New Wales, and New Zealand (Bournier 1971, Danthanarayana 1983, Cardé & Minks 1995, Powell & Opler 2009, Gilligan & Epstein 2014d), and is established in Hawaii and in California from Napa to Monterey (Powell & Opler 2009, Gilligan & Epstein 2014d).

Remarks. Larvae feed on the leaves, buds, flowers, and fruits of pome fruits, stone fruits, and other horticultural crops (Powell & Opler 2009, Gilligan & Epstein 2014d). This species is a generalist feeder on over 500 plant species, although herbaceous plants are preferred to woody plants (Gilligan & Epstein 2014d), and is a serious pest of apples (Danthanarayana 1983, Cardé & Minks 1995, Powell & Opler 2009, Gilligan & Epstein 2014d). The majority of economic damage is caused by fruit injury, when larvae feed on the surface of fruits under webbed leaves (Gilligan & Epstein 2014d).

2.4.1.30 *Euxoa auxiliaris* (Grote, 1873) [Noctuidae]

Common name(s). Army Cutworm

Distribution. Occurs throughout western North America and is abundant in the Great Plains and Rocky Mountains from the southern part of the Northwest Territories in Canada to northern Mexico (Capinera 2001, Powell & Opler 2009, Floate 2017). It is common east of the Cascade Mountains and throughout the western United States, favoring arid habitats (Antonelli et al. 2000, Capinera 2001, Floate 2017) and ranging east to Kansas (Walkden 1950), Michigan (Floate 2017), Missouri, and Texas (Powell & Opler 2009). It is not found east of the Mississippi River (Walkden 1950, Capinera 2001).

Remarks. Larvae are above-ground cutworms (Walkden 1950, Floate 2017) that defoliate a wide variety of grasses and cereals such as wheat, oat, triticale, barley, canola, mustard, flax, alfalfa, and sweet clover, as well as damaging pea, cabbage, vegetable crops, sugar beet, grapes, strawberries, and even tree fruits (Walkden 1950, Beirne 1971, Antonelli et al. 2000, Philip 2015, Floate 2017). No economic thresholds have yet been established (Philip 2015, Floate 2017).

2.4.1.31 *Euxoa detersa* (Walker, 1856) [Noctuidae]

Common name(s). Sandhill Cutworm

Distribution. Present in eastern Canada (Ontario, Quebec) (Beirne 1971), Nova Scotia, and the northern United States as far west as Nebraska and Colorado (Walkden 1950).

Remarks. Larvae are subterranean cutworms and move below the soil in seedling stands feeding on underground parts of the plant (Walkden 1950, Rice et al. 1990). Problematic in low plants and crops, especially corn (Rice et al. 1990) but also in cranberry and tobacco (Beadle & Leckie 2012).

Identification. This species is part of the Detersa Species Group, a complex which includes 32 species and which is the largest *Euxoa* species complex in North America (Lafontaine 1980, Powell & Opler 2009). According to Lafontaine (1980), all the species in this group have distributions in western North America, with the ranges of four species extending to the eastern part of the continent.

2.4.1.32 *Euxoa messoria* (Harris, 1841) [Noctuidae]

Common name(s). Dark-sided Cutworm

Distribution. Northern distribution in North America from the Atlantic to the Pacific Coast (Walkden 1950, Capinera 2001, Pogue 2006, Floate 2017). Present in Canada from Yukon Territory east to Newfoundland, and south in the United States to southern California, southern Arizona, New Mexico, Missouri, Oklahoma, South Carolina, and Virginia (Capinera 2001, Pogue 2006, Powell & Opler 2009).

Remarks. This above-ground (and climbing) cutworm defoliates a broad range of herbaceous and woody hostplants, including vegetables, cereals, canola, corn, tobacco, flax, sunflower, vine, berry and tree fruits (Walkden 1950, Capinera 2001, Pogue 2006, Beadle & Leckie 2012, Philip 2015, Floate 2017). Cited economic thresholds by Floate (2017) are five to six larvae per square

meter in cereal and oilseed crops, two to three larvae per meter squared in peas, and in dry beans and soybeans, the presence of one small (<2.5 cm long) larva per meter of row or 20% of plants cut. A nominal threshold of five to six larvae per square meter can also be used (Philip 2015).

2.4.1.33 *Euxoa scandens* (Riley, 1869) [Noctuidae]

Common name(s). White Cutworm

Distribution. A northern North American species, distributed from the Rocky Mountains east to the Atlantic Ocean (Floate 2017), and from Nebraska and Colorado in the United States north to the Northwest Territories in Canada (Walkden 1950, Lampert 1976).

Remarks. Larvae of this species are climbing cutworms (Walkden 1950, Rings 1971, Floate 2017) which cause damage to vegetable crops such as onion, corn, tomato, peas, potato, beans, asparagus, carrot, beets, radish, and rhubarb (Beirne 1971, Lampert 1976), as well as fruit trees (Floate 2017). Larvae feed at, above, or just below ground level (Walkden 1950), and on fruit trees feeding occurs on the buds and leaves (Floate 2017).

2.4.1.34 *Euzophera semifuneralis* (Walker, 1863) [Pyralidae]

Common name(s). American Plum Borer

Distribution. Widely distributed throughout the North American continent (Biddinger and Howitt 1992, Powell & Opler 2009) from British Columbia in Canada south to Baja California, Florida, and Texas (Biddinger and Howitt 1992). This species appears to have a disjunct distribution and is absent in both the northcentral United States and the central Canadian provinces, although it is present in southern Canada adjacent to the Great Lakes, southern Quebec, and the Canadian west coast (Biddinger and Howitt 1992, Powell & Opler 2009).

Remarks. In a wide variety of orchard trees, the larvae of this species feed on the cambium of weakened trees, girdling the trunk and the lower scaffold limbs (Biddinger and Howitt 1992, Powell & Opler 2009). Hostplants include apple, walnut, stone fruits, pecan, ginkgo, and persimmon (Powell & Opler 2009, Beadle & Leckie 2012).

2.4.1.35 *Feltia jaculifera* (Guenée, 1852); *Feltia subgothica* (Haworth, 1809); *Feltia herilis* (Grote, 1873); *Feltia tricosa* (Lintner, 1874) [Noctuidae]

Common name(s). Dingy Cutworm

Distribution. The distribution of the species complex as a whole extends from Alaska east across Canada south of the Canadian shield to Nova Scotia, and south throughout most of the United States (Walkden 1950, Capinera 2001, Powell & Opler 2009). According to Floate (2017), both *F. jaculifera* and *F. herilis* have coast-to-coast ranges in the United States and southern Canada, while *F. subgothica* is restricted to east of the Rocky Mountains. *Feltia jaculifera* is reported to have the widest range, extending from Alaska and Yukon south to Sonora, Mexico (Pogue 2006). *Feltia subgothica* is also discussed as a widespread species, extending across southern Canada from Nova Scotia to Saskatchewan and southward in the United States from Maine to the southern Appalachians, and occuring west across the Rocky Mountains and Great Plains to eastern Washington, southern Idaho, Utah, and western Arizona (Walkden 1950, Pogue 2006). *Feltia tricosa* is an eastern North American species, and is distributed from southeastern Canada south to northern Georgia, and west to Kansas, also occurring in central Texas and in the western Great Plains of Montana (Pogue 2006). According to Capinera (2001), members of this complex are absent only from southern Florida and from California, and are not found in adjacent desert areas.

Remarks. Larvae are known to feed on alfalfa, clover, flax, tobacco, raspberry, oats, and wheat, although a much broader host range is expected (Lafontaine, cited in Powell & Opler 2009) and many other vegetable, grass, ornamental, and weed hosts are utilized (Floate 2017). These species are above-ground climbing cutworms which climb up plants and eat the leaves (Walkden 1950, Rings 1971, Floate 2017). Economic thresholds for this group of species are as follows: three to four larvae per square meter in cereals, 25-30% stand reductions in oilseeds, and two to three larvae per square meter in the top 7 cm (3 in.) of soil in peas (Philip 2015, Floate 2017).

Identification. The common name "Dingy Cutworm" has been applied to all four of these closely-related species in North America (Capinera 2001), which together form a species complex (e.g., Pogue 2006). In addition to sharing the same common name, these species have similar life histories, and are typically treated together; as such, they are combined here in one entry (Capinera 2001, Floate 2017). These species are very similar in appearance and are often confused with one another (see Rings et al. 1975, Ayre & Lamb 1990, Pogue 2006, Powell &

Opler 2009), and *F. jaculifera*, the most economically important (Capinera 2001), likely represents at least six "currently inseparable" though separate species (Powell & Opler 2009). Because of the uncertainty in species identifications and confusion in the literature (Rings et al. 1975, Capinera 2001), there is also difficulty in delineating plant host range for each (Pogue 2006, Powell & Opler 2009), and correspondingly, accurately separating range boundaries and apportioning economic damage.

2.4.1.36 *Grapholita molesta* (Busck, 1916) [Tortricidae]

Common name(s). Oriental Fruit Moth

Distribution. Widely distributed across the world wherever stone fruits are grown, including parts of Asia, Europe, South and North America, North Africa, the Middle East, New Zealand, and Australia (Howitt 1993, Cardé & Minks 1995, Gilligan and Epstein 2014e).

Remarks. An important worldwide pest of orchard fruits, including apple, cherry, pear, and peach (Howitt 1993, Cardé & Minks 1995, Gilligan & Epstein 2014e, Hasey et al. 2016). The larvae bore into the terminal of shoots to feed until fruit matures and becomes the preferred site of attack (Hasey et al. 2016). Larvae are internal fruit feeders, and bore immediately into the fruit to feed around the pit (Howitt 1993).

2.4.1.37 *Grapholita packardi* (Zeller, 1875) [Tortricidae]

Common name(s). Cherry Fruit Worm

Distribution. Widely distributed in the eastern United States and in Washington, as well as in British Columbia and southern Ontario in Canada (Gilligan & Epstein 2014f, Jeger et al. 2018). This species has also been recorded from Texas and Colorado, and its range extends from the Pacific Northwest south along the coast to Baja California and Mexico (Jeger et al. 2018).

Remarks. Larvae of this species feed on the fruit or shoots of apple, cherry, pear, blueberry, and peach (Howitt 1993, Wise et al. 2007, Beadle & Leckie 2012, Gilligan & Epstein 2014f, Jeger et al. 2018). On blueberries, feeding on immature green fruit causes premature ripening, i.e., "bluing" (Wise et al. 2007, Jeger et al. 2018). Larvae also bore into cherries and can be stem-borers in apple trees (Howitt 1993, Jeger et al. 2018), rarely causing direct injury to apples (Jeger et al. 2018).

Identification. Differences in feeding behavior exhibited by this species on different hosts might indicate that a species complex is involved (Gilligan & Epstein 2014f).

2.4.1.38 *Helicoverpa armigera* (Hübner, [1809]) [Noctuidae]

Common name(s). Old World Bollworm

Distribution. Found from the Cape Verde islands in the Atlantic through Africa, Asia, and Australasia to the south Pacific Islands, and from Germany in the north to New Zealand in the south (Reed & Pawar 1982, Kriticos et al. 2015). It is a serious pest in China, Australia, India (Liu et al. 2004), and in most of its Old World range (Kriticos et al. 2015), and has also expanded its range into the New World in South and Central America (Kriticos et al. 2015). This species is cited by Walkden (1950) to be distributed throughout the United States; however, prior to the 1950's the name *H. armigera* was also applied to corn earworm (=*Helicoverpa zea* Boddie) populations in the United States, which were thought to belong to the same species as *H. armigera* in the Old World (Reed & Pawar 1982).

Remarks. Larvae of this species are polyphagous and feed on a wide variety of field and garden crops, such as cotton, sorghum, sunflower, chickpeas, tomatoes, lettuce, soybeans, tobacco, maize, and wheat (Cunningham et al. 1999, Kriticos et al. 2015). Leaves may be consumed, but larvae more commonly feed on buds, flowers, and fruit (Kriticos et al. 2015).

Identification. Although *H. armigera* occupies Old World countries and island regions and *H. zea* (Corn Earworm) is a New World species with allegedly no range overlap (although between them they are present around the globe), a complex situation may exist between these two closely-related species (Reed & Pawar 1982). Some authors have suggested that there is only subspecies differentiation between *H. armigera* and *H. zea*, while others have found population-level differences across the wide geographic range which may circumscribe separate species (see Reed & Pawar 1982). *Helicoverpa armigera* and *H. zea* are difficult to distinguish using morphological characters and have a similar ecology (Kriticos et al. 2015); they have also been shown to hybridize in laboratory settings, further complicating the situation (Kriticos et al. 2015). Because of the possibility of hybridization in the field, molecular diagnostic methods are also problematic and could prove inaccurate (see Kriticos et al. 2015).

2.4.1.39 *Helicoverpa zea* (Boddie, 1850) [Noctuidae]

Common name(s). Corn Earworm

Distribution. Present throughout the New World in resident populations where there are no freezing winters, and regularly recolonizes colder areas farther north in the summer (Powell & Opler 2009). It is resident in warmer parts of Latin America and is found south to Chile and Argentina, and also occurs in Hawaii and the Caribbean islands (Capinera 2001, Powell & Opler 2009). It can be found throughout the North American continent and the United States except for northern Canada (although it is damaging in southern Canada from British Columbia to Newfoundland) and Alaska, and this species is resident across the southern United States from southern California east to Florida (Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009). This species tends to be less abundant west of the Rocky Mountains (Capinera 2001).

Remarks. Larvae are generalists and feed on many low plants and crops, including corn, cotton, tomato, lettuce, tobacco, and strawberries, with corn and tomato as the major economic hosts (Walkden 1950, Beirne 1971, Zalom et al. 1983, Hoffmann et al. 1991, Antonelli et al. 2000, Capinera 2001, Pedigo & Rice 2009, Beadle & Leckie 2012, Philip 2015). Powell & Opler (2009) cite this species as the most serious pest of agriculture in the western hemisphere. Like *Helicoverpa armigera*, larvae feed by burrowing into the reproductive parts of the plant to feed (Capinera 2001, Powell & Opler 2009). No economic thresholds have been developed (Philip 2015).

Identification. This species may form a complex with *H. armigera* (Old World Bollworm) (see identification notes on *H. armigera*).

2.4.1.40 *Hypena scabra* (Fabricius, 1798) [Erebidae]

Common name(s). Green cloverworm

Distribution. May be found from western Texas throughout eastern North America to the Atlantic Coast, and colonizes the northeastern United States and southern Canada where it cannot overwinter (Powell & Opler 2009, Philip 2015). Because of this migratory habit it occurs throughout the United States and southern Canada east of the Rocky Mountains (Walkden 1950), and is an occasional pest of beans in southwestern Ontario (Beirne 1971).

Remarks. Larvae are defoliators of soybean and other bean plants, and also accept alfalfa, clover, pea, and a wide range of other plants as hosts (Walkden 1950, Beirne 1971, Powell & Opler

2009, Philip 2015). The larvae feed mainly on upper surface of the leaves on the top one-third of the plants, and sometimes on the buds, flowers, and young pods (Beirne 1971, Philip 2015). When normal to above-average precipitation conditions prevail, an economic threshold of 22.5 per meter of soybean row is used, and a threshold of ten green cloverworms per meter of soybean row is used during drought (Philip 2015).

2.4.1.41 *Hyphantria cunea* (Drury, 1773) [Erebidae]

Common name(s). Fall Webworm

Distribution. Ranges from coast to coast across southern Canada, and southward to central California, the Rocky Mountains, the eastern United States south to Florida and Texas, and much of Mexico (Wagner 2005, Powell & Opler 2009). It is absent from the deserts, much of the Great Basin, and most boreal habitats (Powell & Opler 2009).

Remarks. Larvae of this species make extensive communal silken nests on ornamental shade and orchard trees, especially walnut and pecans (Katovich 2004, Wagner 2005, Powell & Opler 2009, Beadle & Leckie 2012). Sometimes these webs may encase entire trees (Katovich 2004, Wagner 2005). Despite this, defoliation rarely causes growth loss or tree or branch mortality (Katovich 2004).

2.4.1.42 *Lacanobia subjuncta* (Grote & Robinson, 1868) [Noctuidae]

Common name(s). Speckled Cutworm

Distribution. Occurs widely in North America (Doerr et al. 2002) and can be found from British Columbia east across Canada to Nova Scotia and south in the West to California, Arizona, and New Mexico in the United States (Powell & Opler 2009). In the east, this species extends south to Missouri and Virginia (Powell & Opler 2009).

Remarks. Larvae of this cutworm species feed primarily on foliage, although in some orchards, significant fruit injury by late instars also occurs (Doerr et al. 2002). Deciduous trees, shrubs, woody and herbaceous plants, and cultivated crops like corn, asparagus, and strawberries serve as plant hosts (Powell & Opler 2009, Beadle & Leckie 2012).

2.4.1.43 *Lacinipolia renigera* (Stephens, 1829) [Noctuidae]

Common name(s). Bristly Cutworm

Distribution. Ranges from British Columbia and the Northwest Territories east across Ontario (Beirne 1971) and southern Canada to Nova Scotia (Floate 2017). It extends southwards through most of the eastern United States (Walkden 1950, Powell & Opler 2009), occurring south to California, Arizona, Texas, Mississippi, and Georgia (Powell & Opler 2009). Walkden (1950) demarcates the western range extent of the species as North Dakota, Nebraska, Kansas, Colorado, and New Mexico. This species also occurs in Europe (Walkden 1950).

Remarks. Larvae are above-ground (and climbing) cutworms which usually feed near the ground and cling to stems, where they blend in very well with their surroundings (Walkden 1950, Floate 2017). The larvae feed on many wild and cultivated broad-leaved plants (Powell & Opler 2009), including alfalfa, clover, corn, tobacco, turnip, apple, grape, cottonwood, and many other species of herbaceous plants and grasses (Walkden 1950, Beirne 1971, Floate 2017). No economic thresholds have been developed (Floate 2017).

2.4.1.44 *Lithophane antennata* (Walker, 1858) [Noctuidae]

Common name(s). White-striped Fruitworm, Green Fruitworm

Distribution. Ranges in woodland and forest habitats from Nova Scotia westward across southern Canada to California, and extends southward to South Carolina and Mississippi (Rings 1973, Wagner 2005).

Remarks. Larvae of this species defoliate many deciduous trees and other woody plants, including ash, elm, hickory, maple, oak, and willow, as well as feeding directly on apples, pear, blackberry, blueberry, cherry, and plum (Rings 1973, Howitt 1993, Wagner 2005, Beadle & Leckie 2012). Initially young larvae feed on tender foliage, progressing to buds and blooms at later instars (Howitt 1993). Fruit-feeding begins when fruits become available, and feeding causes deep, sunken pits in the fruit (Howitt 1993).

2.4.1.45 *Lobesia botrana* (Denis & Schiffermüller, 1775) [Tortricidae]

Common name(s). European Grapevine Moth

Distribution. This species is a key pest of vineyards in Europe, southern Russia, Japan, the Middle East, Near East, and northern and western Africa (Alford 1999, Ifoulis & Savopoulou-

Soultani 2006, Gilligan et al. 2011, Schartel et al. 2019). Although it was previously not known to be established in the United States (Alford 1999, Ifoulis & Savopoulou-Soultani 2006), it was discovered in California in 2008-2009 (Gilligan et al. 2011, Schartel et al. 2019). In European vineyards this species predominates in warmer southern regions (Cardé & Minks 1995, Alford 1999), and in France it lives mostly in dry areas (Bournier 1976).

Remarks. Larvae attack the reproductive parts of grapevines, feeding on flower buds and later on developing grapes (Alford 1999, Gilligan et al. 2011). The penetration of the larvae into the grape causes *Botrytis* fungus infection by means of the entry site (Bournier 1976, Cardé & Minks 1995, Alford 1999, Ifoulis & Savopoulou-Soultani 2006, Gilligan et al. 2011). Because whole grape bunches can be lost to *Botrytis* rot, action thresholds implemented against *L. botrana* are relatively low (Cardé & Minks 1995). Although grape and olive are the primary hostplants in natural settings, this species can opportunistically utilize berry or berry-like plants in 27 families (Schartel et al. 2019).

Identification. Morphological characters (including wing pattern) are unreliable for separating *L. botrana* from *Paralobesia viteana* (Grape Berry Moth), although some differences are present in the genitalia (Gilligan et al. 2011, Gilligan & Epstein 2014g). If the ranges of these species should overlap (*P. viteana* is an eastern North American species), identifications will need to be made based on molecular information (Gilligan et al. 2011, Gilligan & Epstein 2014g).

2.4.1.46 *Malacosoma americanum* (Fabricius, 1793) [Lasiocampidae]

Common name(s). Eastern Tent Caterpillar

Distribution. Distributed mainly in the eastern United States and southern Canada (USDA 1989, Wagner 2005). From southern Canada this species extends to northern Florida, and from the Atlantic seaboard to west of the Mississippi River and Texas (Costa and Ross 1994, Wagner 2005).

Remarks. Larvae are generalist defoliators of cherry, apple, peach, plum, cherry, and other trees, although apple and cherry trees are the preferred hosts (Costa and Ross 1994, Wagner 2005, Pedigo & Rice 2009, Beadle & Leckie 2012, USDA 1989). During development the larvae move back and forth from tents to feeding areas and use the tents for shelter (USDA 1989, Pedigo & Rice 2009). This species primarily causes aesthetic damage (USDA 1989) and the trees usually refoliate soon after the caterpillars disappear, although the new growth may be more sparse

(Fitzgerald 1995). In serious cases after multiple episodes of defoliation, branch die-back or tree death is possible (Fitzgerald 1995).

2.4.1.47 *Manduca quinquemaculata* (Haworth, 1803) [Sphingidae]

Common name(s). Tomato Hornworm

Distribution. Widely present in the New World (Powell & Opler 2009). In Canada, this species occurs sporadically from southern British Columbia east to Columbia, Saskatchewan, Ontario, and Nova Scotia (Beirne 1971, Powell & Opler 2009). The range extends south through most of the United States, Mexico, and Central America, and to northern South America (Capinera 2001, Powell & Opler 2009). In the western United States, this species is found from southern British Columbia south to southern California and east to Idaho, Utah, and Colorado (Powell & Opler 2009). This species is more commonly encountered in the northern United States and southern Canada, and is uncommon along the Gulf Coast (Capinera 2001).

Remarks. Larvae are serious defoliators of Solanaceous plants, notably tomato, potato, and tobacco (Beirne 1971, Zalom et al. 1983, Capinera 2001, Powell & Opler 2009, Pedigo & Rice 2009, Beadle & Leckie 2012), and occasionally directly feed on fruits (Beirne 1971, Zalom et al. 1983, Capinera 2001).

Identification. This species can be distinguished from *Manduca sexta* (Tobacco Hornworm) by wing patterns (Powell & Opler 2009).

2.4.1.48 *Manduca sexta* (Linnaeus, 1763) [Sphingidae]

Common name(s). Tobacco Hornworm

Distribution. Ranges widely in the United States, Mexico, the Caribbean, and Central America, and ranges south to at least the northern part of South America (Capinera 2001, Powell & Opler 2009). This species has also been recorded from British Columbia, Ontario, and Quebec, although it rarely reaches southern Canada as a vagrant (Beirne 1971, Capinera 2001, Powell & Opler 2009). In the western United States occurrences come from two large regions: the Front Range of Colorado from western Texas to southern New Mexico, southern Arizona, and southwestern Utah; and from southern Nevada to California west of the Sierra Nevada mountains (Powell & Opler 2009). It is sympatric with *Manduca quinquemaculata* (tomato hornworm), but

is encountered more often in the southern United States, especially along the Gulf Coast (Capinera 2001, Powell & Opler 2009).

Remarks. Larvae have similar behavior and plant host range to *M. quinquemaculata* and feed mainly on the leaves of Solanaceous plants, though sometimes direct fruit-feeding may occur (Beirne 1971, Zalom et al. 1983, Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012).

Identification. See identification notes on *Manduca quinquemaculata* (Tomato Hornworm).

2.4.1.49 *Melanchra picta* (Harris, 1841) [Noctuidae]

Common name(s). Zebra Caterpillar

Distribution. Ranges in southern Canada from British Columbia east to Ontario, Quebec, and Newfoundland (Walkden 1950, Beirne 1971, Capinera 1979, Capinera 2001, Powell & Opler 2009) and thrives throughout the northern United States (Antonelli et al. 2000, Capinera 2001). This species occurs from the Atlantic to the Pacific Coast and is present south from Canada to the Great Plains and Mid-Atlantic states (Capinera 2001, Powell & Opler 2009), and west to California, Utah, Wyoming, and Colorado (Walkden 1950, Powell & Opler 2009).

Remarks. Larvae are generalist feeders and defoliate garden crops such as beets, peas, cabbage, potatoes, beans, spinach, asparagus, canola, flax, and tobacco, as well as non-crop plants and cultivated flowers (Walkden 1950, Beirne 1971, Capinera 1979, Antonelli et al. 2000, Capinera 2001).

2.4.1.50 *Melittia cucurbitae* (Harris, 1828) [Sesiidae]

Common name(s). Squash Vine Borer

Distribution. Distributed throughout the United States east of the Rocky Mountains, southern Ontario and southeastern Canada, and south to Mexico, Guatemala, and Brazil in South America (Beirne 1971, Capinera 2001, Beadle & Leckie 2012, Krinski 2015).

Remarks. Larvae of this stem-boring species feed within the plant stems of wild and cultivated Cucurbitaceae, notably squash, gourds, pumpkin, and sometimes cucumbers (Beirne 1971, Capinera 2001, Beadle & Leckie 2012, Kariuki and Gillett-Kaufman 2014, Krinski 2015), and prefer stems with larger diameters (Kariuki and Gillett-Kaufman 2014, Krinski 2015). Up to 142 larvae have been removed from a single plant (Capinera 2001).

2.4.1.51 *Mythimna unipuncta* (Haworth, 1809) [Noctuidae]

Common name(s). Armyworm, Armyworm Cutworm, Rice Armyworm, True Armyworm

Distribution. Globally distributed, and occurs in parts of Europe, Asia, Africa, Mexico and Central America, and northern South America (Walkden 1950, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009, Floate 2017). It migrates north annually and occurs most frequently in Canada in southern Saskatchewan and Manitoba, and eastward in southern Ontario, New Brunswick, and Nova Scotia, with records as far north as James Bay (Beirne 1971). This species is wide-ranging through the United States and is most abundant east of the Rocky Mountains (Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009, Floate 2017).

Remarks. This species is an above-ground climbing cutworm (Walkden 1950, Floate 2017) which preferentially damages grasses and also feeds on cereals like oat, wheat, fall rye, corn, and barley, although bean, cabbage, onion, pea, sugar beet, turnip, and other species may also be attacked (Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009, Pedigo & Rice 2009, Beadle & Leckie 2012, Philip 2015, Gavloski & Olfert 2016, Floate 2017). All larval instars feed on the leaf margins and crown tissues of host plants during the night, and hide near the base of the plant by day (Capinera 2001, Philip 2015, Floate 2017). Feeding occurs during the day when the larvae assume the army habit (Walkden 1950). Economic action thresholds for this species from Floate (2017) are as follows: in cereal crops, 40 small (<2.5 cm long) nonparasitized larvae per square meter prior to heading, and 20 larvae per square meter after heading if the heads are clipped; and in seedling crops, 20-30 small (<2.5 cm long) larvae per square meter. More general thresholds of ten larvae per square meter (Philip 2015) or four unparasitized larvae smaller than one inch (2.5 cm) long per square foot (Gavloski & Olfert 2016) may also be used.

2.4.1.52 *Neodactria caliginosellus* (Clemens, 1860) [Crambidae]

Common name(s). Corn Root Webworm, Black Grass-veneer

Distribution. Occurs to the north in Quebec and Alberta in Canada southwards through New England in the United States to Florida (McLeod & Austin 2016). To the west, this species is present to South Dakota and California (McLeod & Austin 2016).

Remarks. Larvae of this species are ordinarily pests of lawns and grasses, although they can also damage seedlings of corn, tobacco, commercial mint, and the roots of cabbage, especially if those crops were planted in an area which had historically been grassland or sod (Beirne 1971, Gesell & Calvin 2000). Young corn plants are most notably injured (Gesell & Calvin 2000); the larvae live at or near the ground level and cut the plant stems, dragging them back into silk-lined tunnels to feed (Beirne 1971, Gesell & Calvin 2000). The type of injury may often look like cutworm damage, although sod webworms normally eat more of the plant (Gesell & Calvin 2000).

2.4.1.53 *Nephelodes minians* Guenée, 1852 [Noctuidae]

Common name(s). Bronzed Cutworm

Distribution. Ranges across Canada from British Columbia and the Northwest Territories east to New Brunswick, Newfoundland, and the Atlantic provinces, where it can occur in high densities (Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Capinera 2001, Powell & Opler 2009). In the United States this species is distributed from coast to coast (Floate 2017) and is most prevalent throughout the northern part of the country east of the Rocky Mountains (Walkden 1950, Ayre & Lamb 1990, Capinera 2001), occurring to the south in California, Arizona, New Mexico, Texas, Colorado, Kansas, Missouri, Tennessee, and Virginia (Walkden 1950, Powell & Opler 2009). Its eastward extent is to Georgia (Powell & Opler 2009).

Remarks. This species is an above-ground cutworm which can also climb (Walkden 1950, Floate 2017). The larvae are defoliators and primarily feed on grasses and cereal crops (Walkden 1950, Beirne 1971, Ayre & Lamb 1990, Powell & Opler 2009, Beadle & Leckie 2012, Floate 2017), as well as garden vegetables (Capinera 2001). Feeding has also been reported on fruit tree buds and leaves (Walkden 1950, Ayre & Lamb 1990, Floate 2017). No economic thresholds have been developed for this species (Floate 2017).

2.4.1.54 *Orgyia leucostigma* (Smith, 1797) [Erebidae]

Common name(s). White-marked Tussock Moth

Distribution. Occurs primarily in eastern North America (Powell & Opler 2009) and is found in fields, woodlands, and forests from southern Canada west to Alberta (Wagner 2005, Powell &

Opler 2009). In the United States it is distributed south to Florida and Texas (Wagner 2005) and west to Colorado and New Mexico (Powell & Opler 2009).

Remarks. Larvae are widely polyphagous and defoliate various deciduous trees and woody plants, including apple, birch, cherry, elm, hackberry, hickory, oak, rose, willow, fir, hemlock, larch, spruce, and other conifers (Wagner 2005, Beadle & Leckie 2012, Powell & Opler 2009).

2.4.1.55 *Orthosia hibisci* (Guenée, 1852) [Noctuidae]

Common name(s). Speckled Green Fruitworm

Distribution. Is found in southern Canada from British Columbia east to Newfoundland (Wagner 2005, Powell & Opler 2009). The species extends south in woodlands and forests throughout most of the northeastern United States south to Florida and Texas, although it is mostly absent from the Great Plains and the Southeast (Wagner 2005, Powell & Opler 2009). In the west, it extends to California, Arizona, New Mexico, and Texas (Powell & Opler 2009).

Remarks. Larval hosts include many deciduous trees and woody plants, including apple, chokecherry, cherry, gooseberry, elm, hickory, poplar, spruce, and willow (Wagner 2005, Beadle & Leckie 2012). Larvae of this species are pests of rosaceous orchard trees such as apple, crabapple, cherry, and plum (Powell & Opler 2009).

2.4.1.56 *Ostrinia nubilalis* (Hübner, [1796]) [Crambidae]

Common name(s). European Corn Borer

Distribution. Present in continental Europe, northern Africa, and Asia, and in the northern part of North America from Newfoundland and the Atlantic provinces in Canada west to the Prairie provinces and the Rocky Mountains (Beirne 1971, Alford 1999, Capinera 2001, Powell & Opler 2009). This species extends south in the United States to the Gulf Coast, and occurs west to Colorado, Wyoming, Montana, and the eastern foothills of the Rocky Mountains (Capinera 2001, Powell & Opler 2009).

Remarks. Larval feeding can damage all parts of corn plants. Young larvae feed on the leaves and cause shot hole and window pane damage, while older larvae burrow into and feed within the stalks and ears (Beirne 1971, Alford 1999, Capinera 2001, Powell & Opler 2009, Pedigo & Rice 2009, Philip 2015). Larvae also feed on corn silks, kernels, and cobs, often causing the cobs to drop prematurely (Beirne 1971, Alford 1999, Philip 2015). Tomatoes, potatoes, beans, sugar

beets, and many other species of large stemmed flowers and weeds may also serve as plant hosts (Beirne 1971, Alford 1999, Capinera 2001, Beadle & Leckie 2012, Philip 2015). Economic thresholds vary based on the larval feeding behavior (see Gavloski & Olfert 2016), and Phillip (2015) provides tables showing action thresholds for corn at different crop values and chemical control costs.

Identification. This species represents of complex of at least three different strains by DNA and pheromone types, with a range of external phenotypes and hostplant adaptations present across its distribution (Powell & Opler 2009).

2.4.1.57 *Paleacrita vernata* (Peck, 1795) [Geometridae]

Common name(s). Spring Cankerworm

Distribution. Occurs in yards, orchards, woodlands, and forests of Canada from Alberta east to Nova Scotia, and south in the United States to Georgia, Mississippi, and eastern Texas (Wagner 2005, Powell & Opler 2009).

Remarks. Larvae are new-leaf specialists and defoliate apple, cherry, oak, elm, birch, maple, and many other deciduous trees and shrubs (Wagner 2005, Powell & Opler 2009, Beadle & Leckie 2012). Young fruit are also damaged (Powell & Opler 2009).

2.4.1.58 *Papaipema nebris* (Guenée, 1852) [Noctuidae]

Common name(s). Stalk Borer

Distribution. Recorded from New Brunswick, Prince Edward Island, Quebec, Ontario, and Manitoba in Canada, and extends from the Atlantic coast west to the Rocky Mountains (Decker 1930, Walkden 1950, Beirne 1971, Bailey & Pedigo 1986, Capinera 2001). This species ranges from southern Canada throughout New England and the eastern United States west to South Dakota, Nebraska, and Kansas, and south to Georgia, Mississippi, Louisiana, and the Gulf of Mexico (Decker 1930, Walkden 1950, Bailey & Pedigo 1986, Gesell & Calvin 2000). It is rarely abundant in the southern United States or along the western part of its range (Capinera 2001).

Remarks. The larvae of this species bore into stalks and feed within the stems of many grasses and broad-leaved plants, including potato, tobacco, rhubarb, eggplant, pepper, and other thick-stemmed plants, especially corn (Walkden 1950, Beirne 1971, Bailey & Pedigo 1986, Davis & Pedigo 1991, Gesell & Calvin 2000, Capinera 2001, Beadle & Leckie 2012). Grasses are

attacked as the first available hosts and rarely survive boring by the larvae (Walkden 1950, Gesell & Calvin 2000, Capinera 2001). Once grasses are exhausted and the larvae grow too large to feed inside the stems, other hosts with larger stems are utilized (Walkden 1950, Gesell & Calvin 2000). Larvae may also mine leaves, although leaf-mining in young corn plants rarely causes significant damage (Capinera 2001).

2.4.1.59 *Paralobesia viteana* (Clemens, 1860) [Tortricidae]

Common name(s). Grape Berry Moth

Distribution. Occurs in Ontario, Canada and in the eastern United States (Cardé & Minks 1995). It has also been recently recorded in Colorado, although it is absent from grape-producing regions in California and the Pacific Northwest (Gilligan & Epstein 2014g).

Remarks. This species is a pest of grapes in eastern North America (Gilligan & Epstein 2014g). It has a similar life history and mode of injury as *Lobesia botrana* (European grapevine moth) (Cardé & Minks 1995), and feeds on grape blossoms and berries, allowing infection by *Botrytis* fungus (Gilligan et al. 2011).

Identification. See identification notes on *Lobesia botrana* (European grapevine moth).

2.4.1.60 *Parapediasia teterrellus* (Zincken, 1821) [Crambidae]

Common name(s). Bluegrass Sod Webworm

Distribution. Widely distributed throughout the eastern United States, and ranges from the east coast westward across the contiguous states to Texas, Colorado, and Iowa (Ainslie 1930, Powell & Opler 2009). It occurs north to southeast New York, and reaches its southern extent in Florida (Ainslie 1930, Powell & Opler 2009).

Remarks. Larvae most commonly damage Kentucky bluegrass and other grass species, as well as wheat, rye, and corn leaves and silk (Ainslie 1930). Along with *Neodactria caliginosellus* (Corn Root Webworm), this species is one of the main sod webworm species which causes damage to corn in Pennsylvania (Gesell & Calvin 2000). Unlike *N. caliginosellus*, most larval feeding takes place on the plant, although leaves are sometimes dragged into loosely-constructed feeding burrows at the surface (Ainslie 1930). More sturdy silk tunnels are also constructed by larvae of this species as a refuge during the daytime and ecdysis, and are not usually used for feeding (Ainslie 1930).

2.4.1.61 *Peridroma saucia* (Hübner, [1808]) [Noctuidae]

Common name(s). Variegated Cutworm

Distribution. Broad global distribution, and is present throughout North America, Central and South America, Europe, North Africa, Asia, and the Middle East, with scattered reports from Sri Lanka, China, Japan, and Taiwan (Walkden 1950, Antonelli et al. 2000, Capinera 2001, Pogue 2006, Powell & Opler 2009, Floate 2017). It also occurs on midoceanic islands such as Bermuda, Iceland, Gough Island, and Tristan da Cunha in the Atlantic, and Hawaii and the Galapagos Islands in the Pacific (Pogue 2006). In North America, this species occurs from tree line in southern Canada from Newfoundland to British Columbia, throughout the United States, and south to Chile and Argentina (Beirne 1971, Antonelli et al. 2000, Pogue 2006, Powell & Opler 2009, Floate 2017). It is considered one of the most damaging cutworm species of vegetables in the northern United States and southern Canada (Capinera 2001).

Remarks. Larvae are above-ground climbing cutworms (Walkden 1950, Rings 1971, Floate 2017) and attack a wide variety of broad-leaved herbaceous plants, appearing on almost any crop (Antonelli et al. 2000) including corn, bean, alfalfa, cereals, sweet clover, garden crops, orchard trees, vines, grasses, ornamentals, and greenhouse plants (Beirne 1971, Antonelli et al. 2000, Capinera 2001, Pogue 2006, Powell & Opler 2009, Beadle & Leckie 2012, Philip 2015, Floate 2017). According to Lafontaine (cited in Powell & Opler 2009), the most seriously damaged crops are vegetable brassicas, solanaceous plants, beets, lettuce, and artichoke. Damage to hostplants is usually caused by the larvae climbing up to feed on foliage (Beirne 1971), and when larvae are present in high densities they may assume the army habit (Walkden 1950). Feeding also occurs on flowers, buds, and fruits (Powell & Opler 2009, Philip 2015, Floate 2017); larvae do not clip plants off at ground level like other cutworm species, but climb up plants instead to feed (Philip 2015, Floate 2017). No species-specific economic thresholds have been developed (Philip 2015, Floate 2017).

2.4.1.62 *Phyllocnistis citrella* (Stainton, 1856) [Gracillariidae]

Common name(s). Citrus Leafminer

Distribution. An Old World pest which is widespread in southern Asia, including India, southern China, and Japan, as well as Southeast Asia, Australia, New Guinea, and nearby Pacific islands (Heppner & Dixon 1995, Peña 1996, Heppner 1999). It is also distributed in the

Mediterranean and in East and West Africa (Peña 1996, Heppner 1999). In the New World this species is present in much of Central America, and is found in North America throughout Florida in the United States, in the Caribbean region, and in eastern Mexico (Peña 1996, Heppner 1999). It also has reached Louisiana, Alabama, and southern Texas (Heppner 1999).

Remarks. The larvae of this species are leafminers of citrus and other Rutaceae, including grapefruit and pomelo (Heppner & Dixon 1995, Peña 1996, Heppner 1999). Several cases of mining into fruit rinds have also been reported in Florida (Heppner 1999). Larvae specialize on newly-formed leaves, which curl and become chlorotic with heavy infestations (Peña 1996).

2.4.1.63 *Phyllonorycter blancardella* (Fabricius, 1781) [Gracillariidae]

Common name(s). European Tentiform Leafminer, Spotted Tentiform Leafminer

Distribution. Widely distributed in the eastern United States and southeastern Canada (Landry & Wagner 1995). This species is also present in the Pacific Northwest in British Columbia in Canada, and south in Washington and Oregon in the United States (Landry & Wagner 1995).

Remarks. Newly-emerged larvae are sap-feeders on the mesophyll layer of leaves, while later instars are tissue-feeders that mine the leaf epidermis (OMAFRA 2011). When large numbers of larvae feed on a plant, premature leaf drop and the production of undersized fruit may result, and the fruit may also drop prematurely (Pree et al. 1986). Pre-bloom, the economic threshold for this species is three eggs per spur prior to hatching, or one mine per leaf after hatching (OMAFRA 2011). In early to midsummer, the threshold is two mines per leaf on stressed trees and four mines per leaf on healthy trees (OMAFRA 2011).

2.4.1.64 *Platynota flavedana* Clemens, 1860 [Tortricidae]

Common name(s). Variegated Leafroller

Distribution. Widely distributed in the eastern United States, from eastern Massachusetts and southeastern New York in the north along the Atlantic Coast to Florida, Louisiana, and southeastern Texas (Wilde & Semel 1966, Gilligan & Epstein 2014h). To the west, this species extends into Arkansas, Kansas, western Iowa, and is also found north to Illinois, southeastern Michigan, and western Pennsylvania (Wilde & Semel 1966). There are even records of this species as far west as Arizona (Weires & Riedl 1991), although this may be questionable (Gilligan & Epstein 2014h).

Remarks. The larvae of this species feed within a shelter of tied or folded leaves, and will often web leaves together with blossoms and immature fruit (Weires & Riedl 1991, Howitt 1993, Gilligan & Epstein 2014h). Fruit feeding occurs when a leaf becomes attached to the surface of a fruit, or from within the center of a fruit cluster (Weires & Riedl 1991, Howitt 1993, Gilligan & Epstein 2014h). Feeding on fruit and blossoms by this species causes the most economic impact, and fruit feeding by large larvae may be extensive (Weires & Riedl 1991, Howitt 1993, Gilligan & Epstein 2014h). Foliar feeding by the larvae may also greatly weaken plants such as strawberry (Howitt 1993). This species is a general feeder, with prominent economic hosts including strawberry, apple, and peach (Wilde & Semel 1966, Weires & Riedl 1991, Howitt 1993, Gilligan & Epstein 2014h).

Identification. See identification notes for *Argyrotaenia velutiana* (Red-banded Leafroller). Damage by this species is very similar to that caused by *Platynota idaeusalis* (Tufted Apple Bud Moth), but can be distinguished by the absence of cut petioles, which are present in the leaf shelters of *P. idaeusalis* (Howitt 1993).

2.4.1.65 *Platynota idaeusalis* (Walker, 1859) [Tortricidae]

Common name(s). Tufted Apple Bud Moth

Distribution. Wide distribution in the northern United States and in southern Canada from Nova Scotia to British Columbia (Weires & Riedl 1991, Howitt 1993). However, its importance as a fruit pest is limited to the eastern and mid-Atlantic apple-growing regions in the United States, such as the Shenandoah Valley, Pennsylvania, Virginia, and North Carolina (Weires & Riedl 1991, Howitt 1993).

Remarks. Although larvae of this species are leafrollers, leaf-rolling has little physiological impact on the tree and does not affect yield (Krawczyk 2016). Rather, the economic impact of this species is due to fruit feeding, which occurs when leaves are webbed to the surface of fruits (Krawczyk 2016). Larval feeding and fruit injury is similar to *Platynota flavedana* (variegated leafroller) (Howitt 1993). This species is problematic as a pest in apple, cherry, peach, and pear orchards (Krawczyk 2016) and is a generalist feeder (Weires & Riedl 1991, Howitt 1993).

Identification. See identification notes for *Argyrotaenia velutiana* (Red-banded Leafroller) and *Platynota flavedana* (Variegated Leafroller).

2.4.1.66 *Prionoxystus robiniae* (Peck, 1818) [Cossidae]

Common name(s). Carpenterworm Moth

Distribution. Occurs across North America, and in the West is recorded in Colorado, Utah, Nevada, California, and Arizona (Powell & Opler 2009).

Remarks. The larvae of this species are large in size (up to 7.5 cm long), and are live-wood borers which tunnel into a variety of hardwoods, including orchard and ornamental trees (Burke 1921, Powell & Opler 2009). This species is reported to complete its life cycle in three years or more, with several age guilds sometimes infesting the same tree (Burke 1921, Powell & Opler 2009).

Identification. The largest and best-known American goat moth (Powell & Opler 2009).

2.4.1.67 *Spilonota ocellana* (Denis & Schiffermüller, 1775) [Tortricidae]

Common name(s). Eyespotted Bud Moth

Distribution. Widely distributed in northeastern North America and along the Pacific Coast, possibly by separate introduction events (Powell & Opler 2009). In addition to the Northeast, where this species is a destructive pest on apple and cherry trees, it is present in British Columbia in Canada, and in Montana, Idaho, and along the Pacific in the United States (Howitt 1993, Powell & Opler 2009).

Remarks. Larvae feed on apple, tart cherry, and all pome and stone fruits, as well as cane fruits and several forest tree species such as oak and laurel (Howitt 1993, Alford 1999, Powell & Opler 2009). Damage is caused by the larvae boring into buds as well as feeding on blossoms and leaves (Howitt 1993, Alford 1999, Powell & Opler 2009).

2.4.1.68 *Spilosoma virginica* (Fabricius, 1798) [Erebidae]

Common name(s). Virginia Tiger Moth

Distribution. Present in North America across southern Canada and is widespread in the eastern part of the continent, extending south along the Pacific Coast to central California in the United States (Capinera 2001, Powell & Opler 2009). This species also extends south from Canada throughout the United States to Florida and Texas, and is distributed through the Rocky Mountains to Utah, the White Mountains in Arizona, and New Mexico (Capinera 2001, Wagner

2005, Powell & Opler 2009). This species is normally limited as a pest to a region including from the Great Plains to the west coast (Capinera 2001).

Remarks. Larvae are very general feeders (Capinera 2001, Wagner 2005, Powell & Opler 2009) and may damage vegetable crops such as asparagus, bean, brassicas, cruciferous plants, celery, carrots, pea, potato, pumpkin, cabbage, and many others, as well as field and berry crops (Capinera 2001, Beadle & Leckie 2012). Early larval instars feed gregariously and skeletonize the leaf tissue, while older larvae are solitary feeders and create irregular holes in foliage (Capinera 2001, Powell & Opler 2009). Capinera (2001) cites 1.2-2.2 mature larvae per plant as capable of causing 20% defoliation, which may result in yield loss.

2.4.1.69 *Spodoptera exigua* (Hübner, [1808]) [Noctuidae]

Common name(s). Beet Armyworm

Distribution. Found worldwide throughout the world's tropical and subtropical regions, including many oceanic islands, but is absent from South America (Capinera 2001, Powell & Opler 2009). It is also found in the Caribbean and in Mexico (Capinera 2001). In North America, this species is resident in areas where winter freezes are absent or minimal, including southern California, southern Arizona, southern Texas, southern Florida, and the Gulf of Mexico, since it is originally a tropical insect and lacks a diapause mechanism (Walkden 1950, Capinera 2001, Powell & Opler 2009). Despite this, it annually invades the southern half of the United States up to Maryland, Nebraska, Kansas, Colorado, and northern California, and is sometimes found as far north as New York and Maine, or Ontario, Manitoba, and British Columbia in Canada (Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009). This species reaches damaging densities in the southern part of its range in the United States and is often a pest in the west (Antonelli 2000, Capinera 2001, Powell & Opler 2009).

Remarks. A wide variety of plants are attacked by larvae of this species, including beets, apple, tomatoes, corn, peas, peppers, spinach, and many other vegetable, field, and flower crops (Walkden 1950, Beirne 1971, Antonelli 2000, Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012). After hatching, the larvae feed gregariously during the day and skeletonize leaves (Walkden 1950, Antonelli 2000, Capinera 2001, Powell & Opler 2009). Older larvae gradually disperse as they mature and feed solitarily, eating large holes in leaves or burrowing into buds

and low-growing fruits and vegetables such as tomatoes and cabbages (Antonelli 2000, Capinera 2001, Powell & Opler 2009).

Identification. A recent study discovered two putative species clusters for *Spodoptera exigua* using molecular methods (Dumas et al. 2015a).

2.4.1.70 *Spodoptera frugiperda* (Smith, 1797) [Noctuidae]

Common name(s). Fall Armyworm

Distribution. Distributed across the North and South American continents from the United States to Argentina (Capinera 2001, Goergen et al. 2016), and is commonly found in the Caribbean, including Puerto Rico (Capinera 2001, Goergen et al. 2016). In the United States, overwintering usually successfully occurs in southern Florida and southern Texas, although this species can sometimes survive along the Gulf Coast and in southern Arizona (Capinera 2001). Despite this, it disperses long distances annually during the summer months, and is recorded from nearly all of the United States east of the Rocky Mountains (Walkden 1950, Capinera 2001). It is also a migrant to southern Canada, where it causes damage to corn in the west and in the Atlantic provinces (Beirne 1971, Philip 2015), and is an invasive species in West and Central Africa (Goergen et al. 2016).

Remarks. Although grasses are preferred hosts, such as corn, wheat, rice, sorghum, and sugarcane, this species will use a wide plant host range (Walden et al. 1950, Beirne 1971, Capinera 2001, Pedigo & Rice 2009, Beadle & Leckie 2012, Kergoat et al. 2012, Philip 2015, Goergen et al. 2016). In addition to extensive defoliation, which causes a ragged or torn appearance and may only leave the ribs and stalks of corn plants, larvae also burrow into buds, whorls, and through the husk on the side of corn ears to feed on the kernels (Walden et al. 1950, Beirne 1971, Capinera 2001, Pedigo & Rice 2009, Philip 2015, Goergen et al. 2016). No economic thresholds for this species have yet been developed (Philip 2015).

Identification. This species is comprised of two closely related host-races, which are currently called the corn and rice strains (see Kergoat et al. 2012, Dumas et al. 2015b). Although they are indistinguishable by morphology, differences between the two strains are present in mating behavior, pheromone composition, and hostplant use (Dumas et al. 2015b). In a study by Dumas et al. (2015b), these host races were found to have some post-zygotic isolation in laboratory crosses, providing evidence for the hypothesis that the two strains could be sibling species. At

least two distinct haplotypes were collected on corn in Nigeria and São Tome (Goergen et al. 2016).

2.4.1.71 *Spodoptera ornithogalli* (Guenée, 1852) [Noctuidae]

Common name(s). Yellow-striped Armyworm

Distribution. Distributed in Mexico, Central America, South America, and many Caribbean islands, and extends northward in warmer months to California, Arizona, and southern Colorado in the United States, and to Ontario and southeastern Canada (Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009). In the United States, this species is most common in the South and Southwest (Walkden 1950, Powell & Opler 2009), though it is also widely distributed in the eastern United States up to the Rocky Mountains (Capinera 2001).

Remarks. Larvae of this species damage grasses, clover, tobacco, potato, and a wide variety of vegetable, field, and berry crops (Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012). The larvae feed gregariously and skeletonize foliage, also feeding on soybean pods and the fruits of tomatoes, cotton, and other plants (Capinera 2001, Powell & Opler 2009).

2.4.1.72 *Striacosta albicosta* (Smith, 1888) [Noctuidae]

Common name(s). Western Bean Cutworm

Distribution. Distributed from southern Idaho, Colorado, Nebraska, and northwestern Iowa south through Mexico and Central America to Colombia (Powell & Opler 2009). Since about 2000, the range of this species has also rapidly expanded east and north in North America to include the northeastern United States and Canada in southern Ontario, Quebec, and into the Prairie Provinces (see Floate 2017).

Remarks. Larvae are generalist feeders on many herbaceous species with a preference for legumes (although this species is not a soybean pest), and are important as pests of corn (Powell & Opler 2009, Floate 2017). They also feed on tomato, pea, squash, and cucumber (Powell & Opler 2009, Floate 2017). On corn, early larval instars feed on silks and tassels, while older larvae tunnel into the ear to feed on kernels and are commonly found feeding on ear tips (Floate 2017). On beans larvae feed on the reproductive plant structures, tunneling into the pod to feed on the developing beans or feeding on the pod from the outside (Powell & Opler 2009, Floate

2017). The economic threshold in corn is reached if eggs or small larvae are detected on 5% of scouted plants (Floate 2017). If this threshold is met for corn, neighboring dry edible bean fields are also at risk, particularly if the corn has passed the pre-tassel stage (Floate 2017).

2.4.1.73 *Synanthedon exitiosa* (Say, 1823) [Sesiidae]

Common name(s). Peach Tree Borer

Distribution. One of the most widespread sesiids in North America, occurring in the eastern part of the continent through the Rocky Mountains to New Mexico in the United States, and south from Canada along the Pacific Coast to southern California (Powell & Opler 2009, Beadle & Leckie 2012). It has been reported in all of the fruit-growing areas of the United States and Canada (Howitt 1993, Strickland 2018).

Remarks. Larvae of this species bore into the trunk, large roots, or stems of young *Prunus* trees and feed on live cambium, causing significant losses in orchards and plantations (Howitt 1993, Powell & Opler 2009, Strickland 2018). Almond, peach, cherry, plum, prune, nectarine, apricot, chokecherry, and other stone fruit trees are harmed by this species, as well as some ornamental shrubs (Howitt 1993, Powell & Opler 2009, Beadle & Leckie 2012, Strickland 2018).

Identification. See identification notes on *Synanthedon pictipes* (Lesser Peach Tree Borer).

2.4.1.74 *Synanthedon myopaeformis* (Borkhausen, 1789) [Sesiidae]

Common name(s). Red-belted Clearwing, Apple Clearwing

Distribution. Found in Europe and Eurasia, and extends in the North American continent to British Columbia in Canada and Washington in the United States (Cossentine et al. 2010, MSU 2010).

Remarks. This species attacks trees in Rosaceae, including apricots, cherries, crabapples, hawthorn, mountain ash, peaches, pears, plums, and quince, although apple is the primary economic host (MSU 2010). The larvae bore into the tree, normally near the base, and feed within tunnels (Cossentine et al. 2010). Larval development may extend over two years before emergence as adults (Cossentine et al. 2010).

2.4.1.75 *Synanthedon pictipes* (Grote & Robinson, 1868) [Sesiidae]

Common name(s). Lesser Peach Tree Borer

Distribution. Found in North America east of the Great Plains and north into Canada (McKern & Szalanski 2008). It occurs widely in the eastern United States and southeastern Canada, with the southern parts of its range in Texas, Arkansas, Virginia and north to New York, Ohio, and South Dakota (Howitt 1993, McKern & Szalanski 2008, Shapiro-Ilan et al. 2010, Beadle & Leckie 2012).

Remarks. The larvae bore into the inner bark and cambium of *Prunus* trees, including peach, cherry, and plum (McKern & Szalanski 2008, Shapiro-Ilan et al. 2010, Beadle & Leckie 2012).

Identification. Unlike *Synanthedon exitiosa* (peach tree borer), which bores new holes into tree hosts, *S. pictipes* enters the tree at preexisting injury sites in the bark (McKern & Szalanski 2008, Strickland 2018). Additionally, the larvae of this species may bore into the trunk, scaffold limbs, or branches, while *S. exitiosa* only utilizes the trunk (Howitt 1993, Shapiro-Ilan et al. 2010). According to a molecular study using mitochondrial DNA, three genetically distinct but morphologically indistinguishable subspecies are present within *S. pictipes* (McKern & Szalanski 2008).

2.4.1.76 *Synanthedon scitula* (Harris, 1839) [Sesiidae]

Common name(s). Dogwood Borer

Distribution. In eastern North America and the eastern part of the United States, this species is a serious pest of apple (Warner & Hay 1985, Lesky et al. 2009). It has been reported throughout the eastern United States, including New York, West Virginia, Virginia, North Carolina, and Tennessee, and in Ontario in southeastern Canada (Warner & Hay 1985, Bergh et al. 2009, Lesky et al. 2009, Beadle & Leckie 2012).

Remarks. In addition to causing damage to flowering dogwood, this species is a polyphagous wood-boring pest of many deciduous trees and shrubs, including pecan, oak, and apple, with infestations in apple becoming a growing problem (Warner & Hay 1985, Bergh et al. 2009, Lesky et al. 2009, Beadle & Leckie 2012). Feeding larvae are attracted to previous wounds or injury sites on the tree and bore into burr knots on the exposed rootstock (Warner & Hay 1985, Lesky et al. 2009).

2.4.1.77 *Trichoplusia ni* (Hübner, [1803]) [Noctuidae]

Common name(s). Cabbage Looper

Distribution. Widely distributed worldwide and is found in Africa, Asia, Europe, and in North and South America in continental areas (Capinera 2001, Powell & Opler 2009). Overwintering in the United States occurs only in the southernmost states, but adults are highly dispersive and establish temporary populations annually in more northern areas (Capinera 2001, Powell & Opler 2009). In North America, this species may be found throughout the continental United States and across southern Canada from British Columbia to Newfoundland (Walkden 1950, Powell & Opler 2009).

Remarks. Larvae of this species feed on "the widest possible variety of herbaceous plants" (Powell & Opler 2009), but have a preference for crucifers such as broccoli, cabbage, cauliflower, Chinese cabbage, collards, kale, and mustard (Walkden 1950, Capinera 2001, Powell & Opler 2009). This species is especially damaging to cabbage plants, defoliating the wrapper leaves and boring into the cabbage head (Capinera 2001, Powell & Opler 2009). Other field and vegetable crops may also be injured (Capinera 2001).

2.4.1.78 *Udea rubigalis* (Guenée, 1854) [Crambidae]

Common name(s). Greenhouse Leaftier, Celery Leaftier

Distribution. Ranges transcontinetally in Central and South America and can be found throughout North America and the United States (Capinera 2001, Powell & Opler 2009). It can adapt to both indoor and outdoor crop cultivation, a factor which favors its wide distribution (Capinera 2001). As a field pest, this species is destructive in all major celery-growing regions in North America, including California, Florida, Michigan, and New York (Capinera 2001). In Canada it is mostly a greenhouse pest, but causes damage to field crops such as lettuce in southern Ontario (Beirne 1971, Capinera 2001).

Remarks. Larvae are polyphagous on low-growing, herbaceous plants (Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012). In the field, this species is most importantly a pest of celery, but may also feed on sugarbeet, lettuce, bean, beet, cabbage, cauliflower, spinach, and other crops (Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012). In greenhouses the plant host range is even wider, and includes vegetable and horticultural crops that are not attacked in the field (Capinera 2001, Powell & Opler 2009).

Identification. Can be confused with *Udea profundalis* (False Celery Leaftier) (Capinera 2001, Powell & Opler 2009). However, the range of *U. profundalis* is much smaller, occurring only along the Pacific Coast from British Columbia to California (Capinera 2001). According to Powell & Opler (2009), older specimens collected along the Pacific Coast were identified as *U. rubigalis* prior to the 1950s, although afterwards they were identified as *U. profundalis*. *Udea profundalis* also has a larger adult size, and can be distinguished from *U. rubigalis* by small differences in the habitus and genitalia (Powell & Opler 2009). The relationship between these species merits investigation.

2.4.1.79 *Xestia c-nigrum* (Linnaeus, 1758), *Xestia dolosa* Franclemont, 1980 [Noctuidae]

Common name(s). Spotted Cutworm

Distribution. In North America, *Xestia c-nigrum* is the most widespread *Xestia* (Powell & Opler 2009). It ranges throughout Canada and the United States, from Alaska east to James Bay and Newfoundland, and south through Mexico to El Salvador (Walkden 1950, Beirne 1971, Capinera 2001, Pogue 2006, Powell & Opler 2009, Floate 2017). This species has been expanding its range in the east, mostly colonizing disturbed habitats (Powell & Opler 2009). In the United States its distribution is mostly in the north (Walkden 1950, Antonelli et al. 2000); it is widespread south to Virginia, Tennessee, Kansas, and Arizona, and is uncommon or absent in southern states and drier regions (Walkden 1950, Pogue 2006, Floate 2017). It also occurs widely in Eurasia (Walkden 1950, Capinera 2001, Powell & Opler 2009, Landolt et al. 2010). *Xestia dolosa* has a more restricted range and occurs in the northcentral to northeastern United States west to the Rocky Mountains in North Dakota, and in southeastern Canada (Capinera 2001, Floate 2017).

Remarks. Larvae of these species are polyphagous and consume an extremely wide range of broad-leaved trees, shrubs, and herbaceous plants, including flowers, vegetables, fruit trees, and row crops (Walkden 1950, Beirne 1971, Capinera 2001, Powell & Opler 2009, Beadle & Leckie 2012, Floate 2017). The larvae may sever seedlings and young plants at ground level, feed on roots, defoliate plants, burrow into low fruits and vegetables like tomatoes, and climb vines and trees to feed on the buds (Capinera 2001, Landolt et al. 2010, Floate 2017). When high population densities are present, the larvae may also feed gregariously and assume an armyworm

habit (Beirne 1971, Capinera 2001). No economic thresholds have yet been developed (Floate 2017).

Identification. Following Floate (2017), these two species are treated together since they share the same common name, have overlapping distributions, and have similar appearances and lifestyles (Floate 2017). The more widespread of these two species throughout the United States and Canada was once known under the name *Xestia adela* (Ayre & Lamb 1990, Capinera 2001), and was thought to have diverged along with *Xestia dolosa* from Eurasian *Xestia c-nigrum*, possibly following separate introduction events to the North American continent (see Capinera 2001). However, *Xestia adela* was synonomized under *Xestia c-nigrum* by Lafontaine in 1998 (see Lafontaine & Schmidt 2010), and this synonomy was recognized in a more recent checklist (Lafontaine & Schmidt 2010). In the east, *X. c-nigrum* can be confused with *X. dolosa*, but there are no similar western species (Powell & Opler 2009). Additionally, records in the east ascribing damage to crops by *X. c-nigrum* are complicated by its confusion with *X. dolosa* prior to 1980 (Powell & Opler 2009). According to Capinera (2001), these species remain difficult to differentiate from one another and are best considered together, as they are by Floate (2017). Further investigation into their relationship is needed.

2.4.1.80 *Yponomeuta padella* (Linnaeus, 1758) [Yponomeutidae]

Common name(s). Cherry Ermine Moth

Distribution. Present in Europe and the Palearctic (Hoebeke 1987). In North America, this species is established in southern British Columbia and southeast Canada, and has also been recorded in the United States in Washington, Oregon, and New York (Hoebeke 1987, Sperling et al. 1995, Beadle & Leckie 2012).

Remarks. Feeds on the foliage of woody Rosaceae as larvae, including blackthorn, hawthorn, mountain ash, serviceberry, and stone fruits (*Prunus* spp.) such as cherry, peach and plum (Hoebeke 1987, Mowat & Clawson 1988, Sperling et al. 1995, Beadle & Leckie 2012). Larvae have also been found in apple orchards (Hoebeke 1987). This species is economically important on cherry and plum trees (Hoebeke 1987, Sperling et al. 1995). One episode of defoliation is not likely to have much effect on the plant and does not warrant treatment, although treatment of a second attack may be justified (Mowat & Clawson 1988).

Identification. This species is part of a complex with *Yponomeuta malinellus* and *Yponomeuta cagnagella* (Hoebeke 1987, Sperling et al. 1995). Both recently-collected and dried specimens of these three sister species are difficult to identify without host records (Sperling et al. 1995). In a study by Sperling et al. (1995), mitochondrial DNA could not distinguish *Y. padella* and *Y. cagnagella* in North America, although it could distinguish *Y. malinellus*.

2.5   Discussion

This annotated list is the first compilation of pests of food crops in North America within Lepidoptera. Although 80 taxa/groups are included, this list is not comprehensive, and ought to be considered a starting point for continued investigations into North American Lepidoptera of agricultural significance. Despite being one of the most species-rich orders of insects, it is estimated in North America that a third of Lepidoptera species diversity remains unnamed (Powell & Opler 2009). In this list, the lag of taxonomy behind observed diversity is apparent, and many of the included named species comprise complexes or carry taxonomic uncertainty despite their economic importance. This taxonomic deficiency is detrimental to pest management, and further basic research on natural history and species delimitation is necessary for achieving effective control strategies (Debach and Rosen 1991). Additional research into species boundaries and relationships for uncertain taxa is therefore recommended, and taxonomic uncertainty is highlighted for species included in this list when it appears in the literature.

Although taxonomic deficiency is a significant issue, a recent review by Sánchez-Bayo and Wyckhuys (2019) names Lepidoptera as one of the groups most affected by decreasing biodiversity. While many species native to certain environments are experiencing decline, a few species are increasing and experiencing range expansion; the drivers behind these phenomena are the growing intensification of agricultural practices and the increasing prevalence of monoculture (Sánchez-Bayo & Wyckhuys 2019). The increase of a handful of species in simplified landscapes is unsurprising as the environment becomes more and more amenable to their survival, and the corresponding decline in native species can similarly be tied to declining environmental suitability. In order to understand these trends further, compilation of additional and existing baseline data in the form of surveys, monitoring, and historical data available in natural history collections is necessary. Distribution information which extends from a historical

understanding of a species' range (obtained from digitized museum specimens) to the present by means of surveys and monitoring can provide a clearer picture of biodiversity, which is currently only available for charismatic taxa (i.e., monarch butterflies). The range information provided in this list is intended to help address this need, and to provide foundational distribution information for testing hypotheses on dispersal, niche competition and exclusion, community structure, and interspecific interactions. These questions necessitate the examination of comparable species which are active in similar environments. Agricultural environments, especially field and orchard crops intended for human consumption, provide a useful setting for understanding insect interactions given their relative homogeneity and their potential for investigating patterns of insect dispersal across the landscape. This annotated list of Lepidoptera species harmful to food crops will therefore be helpful to researchers formulating and testing distribution-related hypotheses for North American taxa.

CHAPTER 3.   THE FRUIT-PIERCING MOTH GENUS *EUDOCIMA* (LEPIDOPTERA: EREBIDAE: CALPINAE): SYSTEMATICS, MORPHOLOGY, AND BIOGEOGRAPHY

3.1   Abstract

Fruit-piercing moths in the genus *Eudocima* Billberg, 1820 are distinctive due to their bright coloration, large size, and significant pest status. There are at least 48 *Eudocima* species, which can be found throughout the New World tropics, Asia, Africa and Australasia; they have been noted as severely damaging pests in these regions due to their ability to pierce hard-skinned fruits. The current *Eudocima* classification has been considered by some as artificial, and there are many suspected species complexes. Additionally, the area of origin for this group is uncertain, although the Oriental region has been postulated by some authors. Despite this, no comprehensive phylogeny of the genus exists, and evidence for the ancestral origin and patterns of distribution for *Eudocima* is wanting. In this study, a phylogenetic analysis of *Eudocima* is conducted using morphological characters, which are each described and figured, and the resulting data matrix is analyzed using parsimony. Results suggest that *Eudocima* is not monophyletic; strongly-resolved relationships were recovered, although support is not robust for previously-used generic concepts or newly-recovered groupings. The Australian region is recovered as the most parsimonious area of origin for *Eudocima*, and patterns of dispersal, particularly between the Oriental and Australian regions along the Indo-Australian Archipelago, are now better understood. An order of dispersal for *Eudocima* out of the Australian region is also postulated to other biogeographic regions of the world; these dispersal hypotheses are the first of their kind for this economically-important genus, and can provide a basis for future investigation.

3.2   Introduction

Among the most recognized and notorious of the fruit-piercing moths are members of the genus *Eudocima* Billberg, 1820 (Erebidae: Calpinae). A specialized and heavily sclerotized proboscis enables these large-sized moths to pierce through the skin and into the pulp of at least 50 different cultivated fruits and nuts, including valuable commodities such as peaches, citrus, and grapes (Cochereau 1977, Bänziger 1982). Unlike many Lepidoptera, fruit-piercing moths are unique in that they are pests as adults rather than as larvae (Bänziger 1982, Fay & Halfpapp 2006, Bhumannavar & Viraktamath 2012). Members of *Eudocima* are considered to be primary fruit-piercing moths because they are able to introduce new holes into hard-skinned fruits such as pomegranates or lychees, while secondary fruit-piercers utilize already-existing wounds or can only pierce soft-skinned fruits (Bänziger 1982). The introduction of a new hole through the skin of a fruit can result in premature ripening and falling from the tree, as well as invasion by pathogens, making the fruit unmarketable to consumers (Bhumannavar & Viraktamath 2012, Fay & Halfpapp 2006). As larvae, *Eudocima* species feed on numerous vines in the family Menispermaceae, with the notable exception of *E. phalonia* (Linnaeus, 1763), which can also feed and complete its development on coral trees in the genus *Erythrina* in its Pacific range (e.g., Muniappan et al. 1995). In addition to *Erythrina*, oviposition by *E. phalonia* also occurs on Menispermaceae plants where they are present in Africa, Asia, and Australia (Muniappan et al. 1995).

3.2.1   Taxonomy

Despite the economic importance of this group of moths, disagreement about classification and species delineation persists in the literature (Moore 1881, Bänziger 1987, Poole 1989, Zilli & Hogenes 2002, Zaspel & Branham 2008, Zilli et al. 2017). This disagreement is due in part to the high level of external morphological variation present in *Eudocima* as a whole and within certain species, which also often corresponds to variation in the genitalia of males and females. For example, *E. phalonia* is a well-known pest species distributed throughout the Old World and the Pacific that displays a wide range of morphological variation, and as such is strongly suspected to be a species complex. The African species *E. lequeuxi* Brou & Zilli, 2016, and two other related species in the Pacific Islands, *E. oliveri* Zilli & Brou, 2017 and *E. steppingstonia* Brou,

Klem, Zaspel & Zilli, 2017, were recently described using internal and external morphology from within the *E. phalonia*-group (Brou & Zilli 2016, Zilli et al. 2017). *Eudocima materna* (Linnaeus, 1767) is another widely-distributed species, and was considered by many authors to be cosmopolitan (see Zilli & Hogenes 2002) until the status of *E. apta* (Walker, [1858]) (a superficially similar *Eudocima* species in the New World) was resolved by Zilli and Hogenes (2002) as a distinct species based on characters of both the habitus and genitalia of both sexes. Morphological variation has also been noted in *E. tyrannus* (Guenée, 1852) (see Zilli & Hogenes 2002). The species *E. srivijayana* (Bänziger, 1985), *E. talboti* (A. E. Prout, 1922), and *E. cajeta* (Cramer, [1775]) are strikingly similar superficially, making them difficult to distinguish from one another; however, their genitalia configurations show marked differences. Conversely, a new synonymy is pending between *E. cocalus* (Cramer, [1777]) and *E. hypermnestra* (Stoll, [1780]), two species which display notable differences in wing pattern but no meaningful differences in genitalia (Zilli et al. 2017).

Historically, this range of variation was accounted for by placing variants in separate genera, with the names *Othreis* Hübner, [1823], *Adris* Moore, 1881, *Khadira* Moore, 1881, and *Eudocima* s.str. being most commonly employed (Zilli & Hogenes 2002). These names derive from the treatment of the group by Moore (1881), which reflect the more "traditional" understanding of these species (see Holloway 2005). In addition to the above, Moore (1881) split *Ophideres* Boisduval, 1832 (=*Eudocima* s.l.) into *Purbia*, Moore, 1881, *Maenas* Hübner, [1823], *Vandana* Moore, 1881, *Othreis* Hübner, [1823], *Rhytia* Hübner, [1823], and *Argadesa* Moore, 1881. Of these names, *Rhytia*, *Othreis*, *Adris*, *Khadira*, and *Eudocima* were used by both Bänziger (1982) and Fay (1996). Additionally, *Trissophaes* Hübner, [1823] has occasionally been used to circumscribe a subset of Neotropical species, and *Elygea* Billberg, 1820 has been used to relate to the *E. materna*-group (Zilli & Hogenes 2002). Distinctions between these historical generic concepts were based primarily upon diversity in the overall shape of the forewing, the the hindwing markings, and the terminal joint of the palpi in both sexes (Moore 1881). Such features, although useful to visually circumscribe groupings, do not include internal features such as genitalia, differences in which are especially important in accurate species identification.

These historical generic concepts have all since been combined into a single genus by Poole (1989) under the oldest available name, *Eudocima* Billberg, 1820. Poole's (1989) choice "is based in large part on an unpublished manuscript of George Hampson" and relies mainly on the curation of systematists at museum collections such as the U.S. National Museum of Natural History and the Natural History Museum, London (Poole 1989). This treatment has since been preserved and followed by modern workers based on the general appearance of the species and available morphological descriptions (Zilli & Hogenes 2002), although Zilli and Hogenes (2002) also suggest that "some of these generic names circumscribe species groups which somehow could be considered monophyletic groups within *Eudocima* s.l.". Despite these assertions, a phylogenetic reconstruction of the group has not yet been made to test these relationships.

3.2.2 Biogeography

Forty-eight species are currently recognized within *Eudocima* (Zilli & Hogenes 2002, Brou & Zilli 2016, Zilli et al. 2017), and are found in the world's tropics with occasional extension into temperate regions. Waterhouse and Norris (1987) put forth the Indo-Malaysian region (=Oriental region, Müller 1986, Olson et al. 2001, Morrone 2015) as the center of origin, but without giving supporting information for their rationale. A clear geographic disjunction exists between *Eudocima* fauna in the Old World and the New; the bulk of species diversity is present in the Old World (i.e., the African, Australian, Oriental, and Palearctic regions), while 8 species (*E. anguina* (Schaus, 1911), *E. apta*, *E. collusoria* (Cramer), *E. colubra* (Schaus), *E. memorans* (Walker), *E. procus* (Cramer, [1777]), *E. serpentifera* (Walker, [1858]), and *E. toddi* (Zayas, 1965)) are Neotropical (Zilli & Hogenes 2002). The majority of the Old World diversity is in the tropics, with only a handful of species occurring regularly in the East Palearctic (such as *E. tyrannus*, *E. okurai* (Okano), and *E. homaena* (Hübner)) or with occasional extensions into this region (including *E. salaminia* (Cramer), *E. phalonia*, and *E. materna*). The ranges of *E. phalonia* and *E. materna* are the largest, spanning from Africa across Asia and Australia and into the Pacific; the range of *E. salaminia* is similarly large, although its alleged presence in the Afrotropics has never been confirmed (Zilli et al. 2017). Neotropical *Eudocima* (i.e., *E. apta* and *E. serpentifera*) are occasionally also reported in the southern United States, sometimes occurring singly as far north as Canada (Brou 2006, Brou & Águila 2013, Gilligan & Passoa 2016, Reeves et al. 2017).

The Oriental and Australian biogeographic regions are the most species rich in *Eudocima*; the area from Wallace's line eastwards into the central Pacific hosts 21 *Eudocima* species (Zilli et al. 2017), and 22 species are found in the Oriental region. These regions, which intersect at the Indo-Australian Archipelago, have very different faunal compositions, so much so that Wallace (1860) wrote: "South America and Africa, separated by the Atlantic, do not differ so widely as Asia and Australia". This prompted his famous demarcation of Wallace's line, which bisects the Indo-Australian Archipelago between Borneo and Sulawesi in the north and Bali and Lombok in the south. This line coincides with the boundary of the Sunda shelf, and marks an abrupt change in the biotic composition of the islands which are adjacent on either side of the line in many plant and animal species. Wallace's line is also the traditional boundary between the Oriental and Australian regions. However, none of the breaks between the distributions of individual *Eudocima* species occurring in the Australian region were found to correspond perfectly to Wallace's line, and frequently crossed it into the Greater Sunda Islands (Zilli et al. 2017).

The Indo-Australian Archipelago is made up of three main components: two continental shelves, the (Oriental) Sunda shelf in the west and the (Australian) Sahul shelf in the east, and the area of oceanic islands between these two shelves. The Sunda shelf includes the continental islands Borneo, Java, and Sumatra, known as the Greater Sunda Islands; of these, Borneo is termed a "cradle of biodiversity" by Lohman et al. (2011) due to its high level of in situ speciation. *Eudocima kinabaluensis* (Feige, 1976) is a Bornean endemic, and two other uncommon *Eudocima* species, *E. mionopastea* (Hampson, 1926) and *E. smaragdipicta* (Walker, [1858]), also occur there (Zilli & Hogenes 2002, Holloway 2005). Phylogeographic studies (Lohman et al. 2010, 2011) show a greater affinity between the other Greater Sundas (Java and Sumatra) and the southern tip of the Malay Peninsula, than with Borneo. Bali, one of the Lesser Sunda Islands, is also situated on the Sunda Shelf. Papua New Guinea and Australia are situated on the Sahul shelf, and are separate evolutionary centers (e.g., Walker 1972, cited in Heads 2008); Papua New Guinea has its own *Eudocima* endemics, *E. prolai* Zilli & Hogenes, 2002, and *E. nigricilia* (Prout, 1924), and is a distributional center for *E. kuehni* (Pagenstecher, 1886), *E. muscigera* (Butler, 1882), and *E. iridescens* (T.P. Lucas, 1894) (Zilli et al. 2017).

The islands between the Sunda and Sahul shelves, including Sulawesi, the Moluccas, and the Lesser Sunda islands east of Bali, comprise "Wallacea", an area circumscribed by Dickerson (1928) because of both the unique and transitional biotic features which are present between the two adjoining biogeographic regions. Most of these islands have never been connected to a continent (van Oosterzee 1997, Lohman et al. 2011, Stelbrink et al. 2012, Reilly 2016), which accounts for this area's largely endemic fauna (e.g., Mayr 1944, Stelbrink et al. 2012). The combined presence of endemics and shared taxa from either of the adjoining regions has made this area a biodiversity hotspot (Myers et al. 2000). Mayr's (1944) review identifies four different island groups which are considered separate districts and which have been combined with Wallacea at different times: "(1) the Lesser Sunda Islands from Lombok eastward; (2) the Moluccas and other outliers of the Papuan Region (Tenimber, Kei); (3) the Celebes [=Sulawesi] group (with Sula and Talaut); and (4) the Philippines". These four areas are also noted as distinct faunal regions by Stresemann (1939). These regions are unalike except for occurring in the Indo-Australian Archipelago, and do not represent clinal variations of Oriental and Australian taxa, but rather differently-distributed pockets of endemism (Reilly 2016). No *Eudocima* species are known which have ranges restricted to the Lesser Sundas, although certain Oriental *Eudocima* species which are mainly continental (*E. discrepans* (Walker [1858]), *E. homaena*, and *E. srivijayana*) reach their easternmost limits in this island group, and *E. discrepans* has only this extent into Wallacea. This pattern could be consistent with the "stepping stone" hypothesis of dispersal (see Zilli et al. 2017) from the Sunda shelf in the Oriental region to the Sahul shelf in the Australian region (Reilly 2016). The Moluccas island group is a biogeographically independent center, and also represents an area of absence for species with disjunct distributions (see Heads 2008). *Eudocima caesar* (C. Felder, 1861) and *E. talboti* are strictly Moluccan (Zilli et al. 2017). Sulawesi, the largest of the islands in Wallacea, is a complex landmass; it is a composite of continental fragments of Australian and Oriental origin (Müller 1986, Lohman 2011, Stelbrink et al. 2012). Lohman (2011) identifies Sulawesi as a site of extensive in situ speciation, with a unique and highly endemic fauna from the meeting of Asian and Australasian lineages. Another contribution to species richness in Sulawesi comes from more recent dispersal events from the Sunda Islands (e.g., Mayr 1944, Müller 1986, Lohman 2011). For some species of *Eudocima*, Sulawesi represents a range boundary to either the east (*E. homaena*, *E. dividens* (Walker, [1858]), *E. srivijayana*) or the west (*E. jordani* (Holland, 1900)). The Philippines was

originally included in Dickerson's (1928) demarcation of Wallacea, but is now regarded most commonly as a separate biogeographic entity due to its unique fauna (Stelbrink et al. 2012). The Philippines is also a biodiversity hotspot (Myers et al. 2000). Three *Eudocima* endemics are present there: *E. mazzeii* Zilli & Hogenes, 2002; *E. behouneki* Zilli & Hogenes, 2002; and *E. treadawayi* Zilli & Hogenes, 2002.

The Pacific islands east of Papua New Guinea have a posed a problem for many authors in terms of assignment to a broad biogeographic region; they have been assigned to the Oriental region, the Australian region, and as a region unto themselves (see Morrone 2015). To emphasize their affinities to the tropics, Morrone (2015) classifies the Pacific islands as part of the Oriental region in his biogeographic regionalization. Following Zilli et al. (2017), we choose here to assign them to the Australian region. Although they are part of the Australian region, the Solomon Islands, Fiji islands, and French Polynesia have developed strong evolutionary centers of their own due to isolation (e.g., see Triantis et al. 2016), and therefore can equally be considered to have ties to Paleotropic (=African and Oriental regions) as well as Australian fauna (Müller 1986). In the Solomon Archipelago, *E. martini* Zilli & Brou, 2017 is an endemic. Furthermore, differentiation in the external markings and forewing profile is evident in examined specimens of *E. salaminia* and *E. phalonia* from the Solomon Islands; although genitalia dissections do not reveal significant differences, it is likely that these specimens reflect genetic divergence to some extent by the Solomon populations of these two species (Zilli et al. 2017). Other insular endemics of *Eudocima* in the Pacific include *E. oliveri* (Vanuatu), *E. paulii* (Robinson, 1968) (Fiji), and *E. steppingstonia* (Marquesas Islands) (Zilli et al. 2017).

3.2.3   Study objectives

The goal of the present study is to construct a comprehensive phylogenetic hypothesis for *Eudocima* based on morphology to test the monophyly of the genus, as well as to assess the validity of the historical groupings under the names *Adris*, *Othreis*, *Rhytia*, *Trissophaes*, and *Eudocima* s.str, which may circumscribe monophyletic lineages (Zilli et al. 2017, and original observation) but whose mutual relationships are unresolved. This study presents the first phylogenetic tree for *Eudocima*, and the development and description of novel morphological character systems that can be used for future work on the group. The biogeographic region of

origin for *Eudocima* is also investigated. In order to understand the radiation of *Eudocima* between the Oriental and Australian regions and throughout Wallacea into the Pacific, eleven island groups are also examined in a phylogeographical context in order to provide a preliminary hypothesis of differentiation and dispersal for *Eudocima*: (**1**) Sumatra and Java (hereafter called the western Sunda Islands), (**2**) Borneo, (**3**) the Philippines, (**4**) Sulawesi, (**5**) the Lesser Sunda Islands east of Bali, (**6**) the Moluccas, (**7**) Papua New Guinea, (**8**) the Solomon Islands, (**9**) Vanuatu, (**10**) Fiji, and (**11**) the Marquesas Islands.

3.3   Materials and methods

3.3.1   Selection of terminal taxa

Fifty-seven ingroup taxa representing 45 *Eudocima* species (94% taxonomic coverage of the genus) were selected (Table 4), along with six outgroup taxa: four from tribe Calpini (*Oraesia argyrosigna* Moore, [1884]; *Oraesia triobliqua* (Saalmüller, 1880), *Plusiodonta incitans* (Walker, [1858]), and *Gonodonta indentata* (Hampson, 1926)) and 2 from tribe Phyllodini (*Phyllodes consobrina* Westwood, 1848; *Phyllodes verhuelli* Vollenhoven, 1858). Outgroup taxa were selected based on the molecular phylogeny of the subfamily Calpinae proposed by Zaspel et al. (2012). Four *Eudocima* species could not be examined as specimens, and for three of these not enough information was found to allow inclusion in this study. Those for which no data were available are *E. anguina* Schaus, 1911 (Neotropical), for which no pertinent character information was available in the original species description; and *E. formosa* Griveaud & Viette, [1962], an African species which is unlikely to be correctly placed in *Eudocima* (Zilli & Hogenes 2002). For *E. toddi* Zayas, 1965, a rare endemic of Cuba, only wing and antenna data amounting to 6 characters could be found in the literature (Brou & Águila 2013), so this species was also excluded. In the case of *E. splendida*, all available characters were coded from the original species description and physical specimens were not seen; although the holotype is cited by Yoshimoto (1999) to be deposited "in future" at the Natural History Museum, London, the specimen could not be located. Because of the large degree of variation in *Eudocima* as a whole, multiple representatives of each species were included in the study when possible, resulting in multiple terminals for *E. phalonia*, *E. materna, E. tyrannus, E. srivijayana, E. talboti, E.*

homaena and *E. cajeta*. Collections used for included material are listed in Table 3, and ingroup taxa included in this study are summarized in Table 4.

Table 3. Collections which provided loans for this study. The "Coden" column indicates either the four-letter coden of the institution or else the name of the personal collector.

Coden	Institution
FLMNH	Florida Museum of Natural History, Gainesville, Florida, US
H.A.C. Fay	Personal Collection of H.A.C. Fay, Mareeba, Queensland, AU
HNHM	Hungarian Natural History Museum, Budapest, HU
M. Fibiger	M. Fibiger collection, (now in Zoological Museum of the University, Copenhagen, DK)
NHMUK	Natural History Museum, London, UK (historically British Museum of Natural History)
PERC	Purdue Entomological Research Collection, West Lafayette, Indiana, US
USNM	National Museum of Natural History, Washington DC, US

Table 4. Ingroup taxa examined for this study. "Locality" lists the uninterpreted label information for the specimen(s) used, with multiple localities sometimes used for a single species dataset. "PNG" signifies Papua New Guinea. The "Collection" column indicates a loan or a visit to the institution to examine material, which was sometimes supplemented by scoring characters from the literature. Such cases are indicated by the "Figures used" column, if applicable. Genitalia data for males and females are indicated by the "♂" and "♀" columns, respectively. The "Habitus" column incorporates data for both males and females; cases in which data for only one sex was available are noted. Data for the "Labial palp" column was collected from either a male or female of the species, based on availability; taxa for which only incomplete (Inc) palp data was available (due to missing parts) are noted. For *E. splendida*, the only information available was from primary literature.

Taxon	Locality	Collection	Figures used (if applicable)	♂ genitalia	♀ genitalia	Habitus (both)	Proboscis	Labial palp
Eudocima phalonia (Linnaeus, 1763)	Malaysia	NHMUK		X	X	X		
Eudocima phalonia (Linnaeus, 1763)	Ghana	NHMUK		X	X	X		
Eudocima phalonia (Linnaeus, 1763)	Malaysia	NHMUK		X		X		
Eudocima phalonia (Linnaeus, 1763)	Australasia	NHMUK, H.A.C. Fay		X		X		Inc
Eudocima phalonia (Linnaeus, 1763)	Australia	NHMUK, H.A.C. Fay		X	X	X	X	X
Eudocima tyrannus (Guenée, 1852)	China	NHMUK		X		X		
Eudocima tyrannus (Guenée, 1852)	China, Nepal	USNM, M. Fibiger		X	X	X	X	X
Eudocima sikhimensis (Butler, 1895)	Malaysia	NHMUK	Fig. 35, Zilli & Hogenes 2002; Plate 17 no. 7, Holloway 2005	X		X		
Eudocima apta (Walker, [1858])	Brazil	NHMUK		X	X	X		

Table 4 continued

Taxon	Locality	Collection	Figures used (if applicable)	♂ genitalia	♀ genitalia	Habitus (both)	Proboscis	Labial palp
Eudocima bathyglypta (A.E. Prout, 1928)	Sumatra	NHMUK	Figs. 8, 9, Zilli & Hogenes 2002	X	X	X		
Eudocima okurai (Okano, 1964)	Malaysia	NHMUK	Plate 5 no. 6, Kononenko & Pinratana 2005	X		X		
Eudocima cocalus (Cramer, [1777])	Australia	FLMNH		X	X	X	X	X
Eudocima cocalus (Cramer, [1777])	PNG	NHMUK		X		X		
Eudocima srivijayana (Bänziger, 1985)	Malaysia	NHMUK	Plate 18 no. 2, 6, Holloway 2005	X		X		
Eudocima srivijayana (Bänziger, 1985)	Philippines, Celebes, Timor	NHMUK		X	X	X		
Eudocima srivijayana (Bänziger, 1985)	Indonesia	NHMUK		X				
Eudocima salaminia (Cramer, [1777])	Java	NHMUK, USNM	Fig. 480, Holloway 2005	X	X	X		
Eudocima nigricilia (A.E. Prout, 1924)	New Guinea	NHMUK, USNM			X	X		Inc
Eudocima materna (Linnaeus, 1767)	Nyasaland	USNM		X	X	X	X	X
Eudocima materna (Linnaeus, 1767)	Cameroon, Ghana	NHMUK		X	X	X		
Eudocima aurantia (Moore, 1877)	Queensland	FLMNH		X	X	X	X	X

Table 4 continued

Taxon	Locality	Collection	Figures used (if applicable)	♂ genitalia	♀ genitalia	Habitus (both)	Proboscis	Labial palp
Eudocima jordani (Holland, 1900)	Australia	PERC		X	X	X	X	Inc
Eudocima homaena (Hübner, [1823])	Taiwan	PERC		X	X	X	X	X
Eudocima homaena (Hübner, [1823])	Indonesia, Philippines	NHMUK, USNM		X	X	X	X	X
Eudocima dividens (Walker, [1858])	Philippines	NHMUK, USNM		X	X	X	X	X
Eudocima boseae (Saalmüller, 1880)	Madagascar	NHMUK		X	X	X		
Eudocima procus (Cramer, [1777])	Costa Rica, Peru	NHMUK, HNHM		X	X	♀ only		
Eudocima discrepans (Walker, [1858])	Indonesia	NHMUK	Plate 5 no. 1-3, Kononenko & Pinratana 2005	X		X		
Eudocima caesar (C. Felder, 1861)	Amboina, Ceram	NHMUK		X		X		
Eudocima imperator (Boisduval, 1833)	Madagascar	NHMUK, USNM		X		X		
Eudocima muscigera (Butler, 1881)	Trobriand Is.	NHMUK		X		X		
Eudocima kuehni (Pagenstecher, 1886)	Indonesia	NHMUK		X	X	X		
Eudocima iridescens (T.P. Lucas, 1894)	New Guinea	NHMUK		X		X		

Table 4 continued

Taxon	Locality	Collection	Figures used (if applicable)	♂ genitalia	♀ genitalia	Habitus (both)	Proboscis	Labial palp
Eudocima talboti (A.E. Prout, 1922)	New Guinea	NHMUK	Figs. 5A, 5B, 6A, 6B in Zilli et al. 2017	X				
Eudocima talboti (A.E. Prout, 1922)	Indonesia	NHMUK						
Eudocima mionopastea (Hampson, 1926)	unknown	NHMUK	Fig. 22, Zilli & Hogenes 2002; Plate 18 no. 3, Kononenko & Pinratana 2005	X		♀ only		
Eudocima paulii (Robinson, 1968)	Fiji	NHMUK		X	X	X		
Eudocima cajeta (Cramer, [1775])	Ceylon	NHMUK		X	X	X		
Eudocima cajeta (Cramer, [1775])	unknown	NHMUK	Figs. 33, 34, Zilli et al. 2017	X	X	X		
Eudocima euryzona (Hampson, 1926)	Madagascar	NHMUK	Figs. 26, 27, Zilli & Hogenes 2002	X	X	X		
Eudocima divitiosa (Walker, 1869)	Lagos, Liberia	NHMUK, USNM		X	X	X		
Eudocima hypermnestra (Stoll, 1780)	Andamans	NHMUK		X	X	X		
Eudocima collusoria (Cramer, [1777])	Venezuela	NHMUK		X				
Eudocima colubra (Schaus, 1911)	Venezuela	NHMUK		X		X		
Eudocima memorans (Walker, [1858])	Venezuela	NHMUK, USNM		X		♂ only		

Table 4 continued

Taxon	Locality	Collection	Figures used (if applicable)	♂ genitalia	♀ genitalia	Habitus (both)	Proboscis	Labial palp
Eudocima serpentifera (Walker, [1858])	Chiriqui, Columbia	NHMUK, USNM		X		X		
Eudocima smaragdipicta (Walker, [1858])	Borneo	NHMUK	Plate 17 no. 4, Holloway 2005	X	X	♂ only		
Eudocima mazzeii Zilli & Hogenes, 2002	Philippines	NHMUK	Figs. 1, 2, 29-31, 34, Zilli & Hogenes 2002	X	X	X		
Eudocima behouneki Zilli & Hogenes, 2002	Philippines	NHMUK	Figs. 6, 7, 36-37, 38, 39, Zilli & Hogenes 2005	X	X	X		
Eudocima prolai Zilli & Hogenes, 2002	PNG	NHMUK	Figs. 10, 11, 40, 42-45, Zilli & Hogenes 2002	X	X	X		
Eudocima treadawayi Zilli & Hogenes, 2002	Phillippines, Leyte I.	NHMUK	Figs. 28, 49, 51, Zilli & Hogenes 2002	X	X	♀ only		
Eudocima steppingstonia Brou, Klem, Zaspel, & Zilli 2017	Marquesas	USNM	Figs. 4A, 4B, Zilli et al. 2017	X	X	X		
Eudocima lequeuxi Brou & Zilli, 2016	Rwanda	NHMUK	Figs. 1-8, 9-12, 17, 21, Brou & Zilli 2016	X	X	X		
Eudocima oliveri Zilli & Brou, 2017	New Hebrides	NHMUK		X	X	X		
Eudocima martini Zilli & Brou, 2017	Guadalcanal	NHMUK		X	X	X		
Eudocima kinabaluensis (Feige, 1976)	PNG* (*probably error)	NHMUK	Fig. 469, Holloway 2005	X		♀ only		
Eudocima splendida (Yoshimoto, 1999)	north Myanmar	N/A	Figs. 1, 3, Yoshimoto 1999	X		♂ only		

3.3.2 Assignment of historical generic names

Historical genera were assigned using to each included species using Moore (1881), Bänziger (1982), Schaus (1911), Draudt & Gaede (1944), Barlow (1982), Fay (1996), Zilli & Hogenes (2002), Leong (2009), and Zilli et al. (2017), with preference given to more recently acknowledged groupings in hopes of utilizing the most complete understanding of these groups to date. An attempt was made to associate each *Eudocima* species in the phylogeny with a historical designation (in a manner similar to character assignment) such that comparisons between previously-recognized genera could still be made in the event that *Eudocima* was recovered as monophyletic. Zilli & Hogenes (2002) and Zilli et al. (2017) discuss some of the species, such as *E. mazzeii* and *E. behouneki*, as belonging to one or another of the historical classifications, e.g., "the *tyrannus*-group (=Adris Moore, 1881)" (Zilli & Hogenes 2002). In these cases, the historical designation was accepted.

For a few taxa, a reliable historical generic designation was unable to be found; this happened because the species was described under a different moniker than those being analyzed here, which did not lend itself to testing. This occurred for one of two reasons: (1) the historical name was too general, as in the case of species described under the name *Ophideres* (*E. boseae*, *E. imperator*) for which a later paper was not found that split the species into a narrower group; and recently-described species (*E. martini*, *E. treadawayi*, *E. kuehni*, *E. prolai*, *E. oliveri*, *E. lequeuxi*, *E. steppingstonia*) which were not explicitly discussed as having a probable affiliation with a previously-recognized generic group (i.e. referenced specifically under a previous generic name, such as *Adris*). Or, (2) the generic name assigned to the species was too specific, and was not applied to enough other taxa to investigate meaningful groupings. This was the case for *E. muscigera*, which was described by Butler (1882) in the genus *Purbia*, (a genus only shared historically with *E. discrepans*) and for *E. euryzona* (Hampson), which was described as *Khadira euryzona* by Hampson (1926). *Khadira* is only used by other authors for *E. aurantia*, which belongs in the *Adris* group. While both Fay (1996) and Bänziger (1982) refer to this species under the name *Khadira* (likely in reference to the concept in Moore (1881)), *E. aurantia* is also referenced in Zilli & Hogenes (2002) as a synonym of *Adris rutilis* Moore, 1881; therefore, *E. aurantia* must be considered a species in the *Adris* group of *Eudocima*.

3.3.3 Morphological characters

This study used 82 adult morphological characters (Table 5), including 12 characters of the head, 4 thoracic characters, 48 characters from male genitalia, and 18 characters from female genitalia. Seventy-eight characters are newly circumscribed for *Eudocima*, and all characters are figured. Dissections of male and female genitalia, and labial palps were visualized using Leica Application Suite v.4.2.0, and photographs were taken with a Leica DFC450 camera mounted on a Leica M165 C stereomicroscope. Proboscides were viewed using an Olympus BX41 histology microscope fitted with an Olympus DP72 camera. The software cellSens Dimension v.1.8 was used for image capture. Previously mounted genitalia slides from NHMUK were also examined and photographed using a ZEISS Stemi SV 11 Apo stereomicroscope, fitted with objective Plan Apochromat 1.0x and a Canon Eos 550D camera. The software Eos Utility for 550D was used for capturing these images.

3.3.4 Character coding

A morphological data matrix with 41 binary characters and 41 multistate characters was scored, for a total of 272 coded character states. Missing and inapplicable data were both coded as "?" (Strong & Lipscomb 1999) and are present in the interest of including as many observations in the analysis as possible (Kearney & Clark 2003). Characters that were indiscernible in photographs and drawings in publications were also coded as "?" to preserve objectivity. In males, characters were assessed using a spread, ventral view of the genital capsule, as is usual in Lepidoptera taxonomy. In cases where certain characters could not be directly examined due to rarity or inaccessibility of material, characters were also coded from the original species descriptions or plates in the literature (see Table 4). Morphological terminology follows Klots (1970), Scoble (1995), Zilli & Hogenes (2002), Goater et al. (2003), and Zaspel et al. (2011). Taxa with multiple replicates (i.e. *E. srivijayana*) are distinguished by listing the specimen locality following the species name, and taxa with multiple localities listed (i.e. *E. homaena* Indonesia + Philippines) indicate that data were used from specimens from the given localities. A summary of all included characters may be found in Table 5.

Table 5. Summary of characters used in this study. Includes character number, descriptive name, number of states, figure number, consistency index (CI) value, retention index (RI) value, ancestral state(s) calculated for the majority of *Eudocima* (recovered in the E s.l. clade from *E. nigricilia* to *E. cajeta* Ceylon), and the number of steps for the maximum parsimony calculation of ancestral states. State number indicates the number of states actually observed, so characters with one state are considered binary (the observed state, and any alternatives to that state). More than one most parsimonious ancestral state was occasionally calculated for certain characters; in these cases, all equally parsimonious states are listed.

Character	Description	States	Figure	CI	RI	Ancestral state(s) for *Eudocima*	Steps, parsimony reconstruction of ancestral states
1	Surface microstructure of proximal region of proboscis	1	2	0	0	0	0
2	Ribs of surface microstructure of proximal region of proboscis	2	3	1	1	0	1
3	Surface microstructure of apical region of proboscis	1	4	0	0	0	0
4	Apex of proboscis	2	5	1	1	0	1
5	Proboscis apical region sclerotization	3	6	1	1	1	2
6	Erectile barbs occurring below junction of ribbed and smooth regions of apical region of proboscis	3	7	1	1	1	1
7	Tearing hooks occurring in apical region of proboscis	3	8	1	1	0	2
8	Number of serrated ridges present in apical region of proboscis	2	9	1	1	0	1
9	Male antenna	2	11	1	1	0	1
10	Female antenna	1	12	0	0	0	0
11	Length of labial palp third segment	3	13	1	1	1	2
12	Shape of labial palp second segment	2	14	1	1	0	1
13	Shape of anal margin of forewing	5	16	0.29	0.44	1	15
14	Shape of male termen	2	17	0.25	0.57	0	5
15	Shape of female termen	2	18	0.13	0.65	0	7
16	Apical process of forewing	2	19	0.25	0.67	0	3
17	Sacculus attached with cucullus	2	22	0.5	0	0	2
18	Sacculus extended beyond cucullus	2	23	0.5	0	0	3
19	Saccular process	4	24	0.67	0.5	0	4
20	Sacculus notched	2	25	0.08	0.45	1	12
21	Saccular notch shape	9	26	0.5	0.62	3	16
22	Valve shape	13	27	0.41	0.43	4	27
23	Cucullus	2	28	0.33	0.5	0	3
24	Valve inner margin	5	29	0.2	0.41	2	20
25	Valve tip shape	3	30	0.17	0.41	0	12

Table 5 continued

Character	Description	States	Figure	CI	RI	Ancestral state(s) for *Eudocima*	Steps, parsimony reconstruction of ancestral states
26	Distal cucullus process	2	31	0.1	0.47	0	10
27	Shape of distal cucullus process	6	32	0.63	0.63	2	8
28	Proximal cucullus process shape	2	33	1	1	1	1
29	Tegumen process	2	34	1	0	0	1
30	Saccus shape	7	35	0.25	0.53	2	24
31	Uncus length	3	36	0.33	0.75	0	7
32	Uncus shape	5	37	0.29	0.38	0	14
33	Uncus hook	1	38	0	0	1	0
34	Aedeagus shape	3	39	0.18	0.64	0	11
35	Spines of carina	3	40	0.2	0.43	0	11
36	Vesica texture	2	41	0.33	0.6	0	3
37	Cornuti coverage	5	42	0.5	0.87	0,1,3	10
38	Multiple types of cornuti	2	43	0.14	0.7	0	7
39	Deciduous cornuti	2	44	0.33	0.91	0	2
40	Stout spike(s) on body of vesica	3	45	0.67	0.89	0	6
41	Apical spike of vesica	2	46	0.25	0.8	0	3
42	Curved stout spike	2	47	0.25	0	0	4
43	Medium-size, non-deciduous cornuti	2	48	0.25	0.87	1	5
44	Dense spiculi	2	49	0.25	0.7	0	4
45	Spiculi placement	2	50	0.33	0	1	2
46	Jaculiferous cornuti	2	51	0.5	0.5	0	2
47	Scobinate patch	3	52	0.33	0	0	6
48	Vesica lobe number	4	53	0.21	0.52	0	15
49	Shape of vesica	6	54	0.29	0.65	0,4,5	17
50	Vesica length	3	55	0.2	0.69	1	12
51	Juxta length	3	56	0.33	0.85	1	6
52	Juxta base shape	5	57	0.17	0.33	1	22
53	Lateral processi off juxta base	2	58	0.11	0.58	1	8
54	Juxta body shape	12	59	0.5	0.66	9	21
55	Tips of juxta processi	3	60	0.25	0.33	0	9
56	Texture of juxta	2	61	0.25	0.4	0	4
57	Space between juxta processi, general category	3	62	0.14	0.64	2	14
58	Vase-shaped space in juxta processi	5	63	0.57	0.5	2	6
59	"V"-shaped space in juxta processi	4	64	0.67	0.75	0	5
60	Notch-shaped space in juxta process	6	65	0.63	0.57	5	7
61	Curve of juxta processi, full length	5	66	0.4	0.4	0	11
62	Curve of juxta processi tips	4	67	0.19	0.52	0	16
63	Bulge on inner margins of juxta	2	68	0.2	0.67	0	6

Table 5 continued

Character	Description	States	Figure	CI	RI	Ancestral state(s) for *Eudocima*	Steps, parsimony reconstruction of ancestral states
64	Antevaginal spine	2	70	0.33	0.8	0	3
65	Bifurcate antevaginal spine	2	71	0.5	0.67	1	1
66	Antevaginal spine texture	4	72	0.75	0.5	0,1,2,3	5
67	Antevaginal spine shape	4	73	0.75	0.5	1,3	4
68	Anterior sclerotization of segment 8	2	74	0.17	0.58	0	5
69	Shape of anterior sclerotization of segment 8	7	75	1	1	1	6
70	Lobes of segment 8 prolonging into pouch	2	76	1	0	0	1
71	Apophyses posteriores	1	77	0	0	0	0
72	Apophyses anteriores	2	78	0.2	0.56	1	4
73	Ductus bursae length	3	79	0.2	0	0	10
74	Ductus bursae shape	4	80	0.23	0.29	1	12
75	Ductus bursae sclerotization	3	81	0.25	0.5	0	8
76	Corpus bursae connected directly to ostium	2	82	1	0	0	1
77	Corpus bursae shape	11	83	0.56	0.3	0	17
78	Corpus bursae texture	3	84	0.18	0.4	0	11
79	Cervical sclerites	2	85	0.5	0.67	0	2
80	Appendix bursae	2	86	0.33	0	0	3
81	Ductus seminalis position	2	87	1	1	0	0
82	Ductus seminalis shape	4	88	0.33	0.14	0	1

3.3.5   Area of origin and distribution

Species distribution information from Zilli & Hogenes (2002), Brou & Zilli (2016), and Zilli et al. (2017) was used to assign species to six biogeographic regions (Nearctic, Palearctic, Neotropical, African, Oriental, and Australian) (see Table 6). Biogeographic regions and their boundaries are taken from Morrone (2015), with the exception of the African region (=Ethiopian region of Morrone (2015)), and the tropical Pacific islands, which we associate with the Australian region in conformity with Zilli et al. (2017). Wallace's line is used as the eastern boundary of the Oriental region and the western boundary of the Australian region.

For *Eudocima* species occurring in the Indo-Australian Archipelago, range information from Zilli & Hogenes (2002), Brou & Zilli (2016), and Zilli et al. (2017), as well as Holloway (2005) and original species descriptions (e.g., Yoshimoto 1999), was used to code presence and absence in the western Greater Sundas, Borneo, the Philippines, Sulawesi, the Lesser Sundas, the Moluccas, Papua New Guinea, the Solomons, Vanuatu, Fiji, and the Marquesas (see Table 6). Species not occurring in the Australian or Oriental regions, as well as Oriental species found only on the continent (*E. hypermnestra*, *E. cajeta*, etc.), were omitted from the analysis.

Table 6. Summary of known range information for ingroup taxa and assignments for biogeographic regions and for the Indo-Australian Archipelago. *Eudocima smaragdipicta* also present in Borneo (Holloway 2005).

Species	Zilli & Hogenes 2002	Brou & Zilli 2016	Zilli et al. 2017	Regions Coded
E. phalonia	African; East-Palaearctic; Indoaustralian		From the African tropics across the Oriental, SE Palaearctic (but up to the NE as a stray) and Australian regions well into the Pacific.	Palearctic, African, Oriental, Australian
E. tyrannus	East-Palaearctic; Oriental			Palearctic, Oriental
E. sikhimensis	Oriental; Himalayas to lesser Sunda Is. (Bänziger 1989)			Oriental
E. apta	South-Nearctic; Neotropical; Southern Atlantic Islands			Nearctic, Neotropical
E. bathyglypta	Oriental			Oriental
E. okurai	East-Palaearctic; Oriental			Palearctic, Oriental
E. cocalus	Indoaustralian		SE Asia (Sunda Islands, Philippines) across Wallacea to New Guinea, Australia (Western Australia, Queensland), the Bismarck archipelago (New Britain, New Ireland, St. Matthias, St. Aignan), Nissan I. and the Solomon Islands (Santa Isabel, Florida Is).	Oriental, Australian
E. srivijayana	Oriental; Wallacea?		Peninsular Malaysia, Singapore, Nias, Sumatra, Borneo, Java, Bali, Lombok, Sumbawa, Sumba, Flores, Timor, Celebes, Philippines (Panay, Negros, Leyte, Samar, Mindanao).	Oriental, Australian
E. salaminia	African (Malagasy); East-Palaearctic; Indoaustralian		Widespread all over the Indoaustralian region from India and Ceylon to the Central Pacific (Fiji, Samoa and Tonga) (Viette 1948, and original observation) and in the Eastern sector of the Palaeartic, as far north as Korea and Japan, it also been recorded from Madagascar (e.g., Hampson, 1894), likely on the basis of strays or spurious specimens and not confirmed from that island anymore (cf. Viette, 1990).	Palearctic, Oriental, Australian
E. nigricilia	Australian (Papuan)		New Guinea	Australian

Table 6 continued

Species	Zilli & Hogenes 2002	Brou & Zilli 2016	Zilli et al. 2017	Regions Coded
E. materna	African; South-Palaearctic; Indoaustralian		Widespread in the African, S-Palaearctic and Indoaustralian regions up to the Central Pacific, in some areas of its vast range the species seems quite scarcer than in others, so there is a particular paucity of records from east of the Indian subcontinent to the Philippines in the north and New Guinea in the east, whereas the species seems to become more common in Australia and the Pacific. This species is replaced in the Americas by the vicariant *Eudocima apta*.	Palearctic, African, Oriental, Australian
E. aurantia	Indoaustralian		Widespread in the SE Palaearctic, Oriental and Australian regions, in the latter it extends from Wallacea across New Guinea and Northern Australia (Queensland) to east of the Sahul shelf in the Bismarck Archipelago (New Britain, New Ireland) and the Solomon Archipelago (Bougainville, Florida Is.).	Oriental, Australian
E. jordani	Australian		From Celebes, the Moluccas (Halmahera, Buru, Ceram) and Kei Is eastwards to New Guinea, NE Australia (Queensland), the Bismarck archipelago (Rook I., New Britain, New Ireland, New Hannover), Nissan I. and New Caledonia.	Australian
E. homaena	East-Palaearctic; Oriental; Wallacea		Widespread in the E Palaearctic and Oriental regions from India and Ceylon eastwards, its range extends also in Wallacea, precisely in Celebes, Lombok, Flores and Timor.	Palearctic, Oriental, Australian
E. dividens	Oriental; Wallacea		A SW Asian element occurring in the Philippines and in Sundaland from Peninsular Malaysia to Java whose distribution extends in Wallacea to the island of Celebes.	Oriental, Australian
E. boseae	African			African
E. procus	Neotropical			Neotropical

Table 6 continued

Species	Zilli & Hogenes 2002	Brou & Zilli 2016	Zilli et al. 2017	Regions Coded
E. discrepans	Oriental; East-Palaearctic; Wallacea		Widespread in the SE Palaearctic and Oriental regions from India eastwards, its range also partly extends in Wallacea, precisely in the lesser Sunda Islands up to Flores.	Palearctic, Oriental, Australian
E. caesar	Wallacea		A strictly Moluccan species so far known exclusively from Halmahera, Buru, Ambon and Ceram, with possible intermediate populations with the preceding species in the Sula group.	Australian
E. imperator	African (Malagasy)			African
E. muscigera	Australian		An eastern vicariant of *Eudocima* discrepans; So far known from Aru Is, Dampier Strait group, New Guinea, Japen I., Fergusson I. and the Bismarck archipelago (New Britain, New Ireand, Mioko I.).	Australian
E. kuehni	Australian (Papuan)		Moluccas (Ceram), Kei Is, New Guinea, Supiori I., Rook I., Goodenough I., Fergusson I., Rook I. and New Britain.	Australian
E. iridescens	Australian		Most eastern member of homaena-group; Known so far from Mysol (= Misool), Kei Is, New Guinea, Cenderawasih Bay islands (Moor I.), Bismarck Archipelago (St. Aignan, New Britain, New Ireland), Fergusson I., Sudest I., Rossell I., Woodlark I. (= Muyua I.), Australia (Western Australia, Queensland).	Australian
E. talboti	Wallacea		Most eastern member of cajeta-group; Indoaustralian region; Moluccas (Ceram, Halmahera), Waigeo, Numfoor.	Australian
E. mionopastea	Oriental; seems exceptionally rare; hitherto known from Peninsular Malaysia and Borneo (Hampson, 1926; Holloway, 1976), it can be also recorded for Sumatra, on basis of a male specimen preserved in the Zoologische Staatssamlung of Munich.			Oriental

Table 6 continued

Species	Zilli & Hogenes 2002	Brou & Zilli 2016	Zilli et al. 2017	Regions Coded
E. paulii	Australian (Fiji)		Endemic to Fiji Islands (Viti Levu and Vanua Levu).	Australian
E. cajeta	Oriental; Wallacea?		Exclusively Oriental species; most western species of cajeta-group; India, Ceylon, Bhutan, Southern China, Burma, Thailand, Vietnam, Andamans.	Oriental
E. euryzona	African (Malagasy); Madagascan endemic			African
E. divitiosa	African			African
E. hypermnestra	Oriental		Essentially a continental species ranging from India and Ceylon to Southern China and whole Indochina; it is also present in the Andaman and Nicobar Islands.	Oriental
E. collusoria	Neotropical			Neotropical
E. colubra	Neotropical			Neotropical
E. memorans	Neotropical			Neotropical
E. serpentifera	Neotropical			Neotropical
E. smaragdipicta	Oriental			Oriental
E. mazzeii	Oriental (Northern Philippines)			Oriental
E. behouneki	Central-Southern Philippines			Oriental
E. prolai	Australian (Papuan)		New Guinea	Australian
E. treadawayi	Oriental (Philippines)			Oriental
E. steppingstonia			Fatu Hiva in the Southern Marquesas Islands	Australian
E. lequeuxi		Central-Eastern and Southeastern African		African
E. oliveri			New Hebrides (= Vanuatu)	Australian
E. martini			Solomon Archipelago	Australian
E. kinabaluensis	Oriental			Oriental
E. splendida	Oriental			Oriental

3.3.6 Phylogenetic and biogeographic analysis

Morphological characters were coded into a data matrix (Appendix A) using Mesquite v.3.04 (Maddison & Maddison 2017), which was exported to TNT v.1.5 (Goloboff et al. 2008). Maximum parsimony trees were constructed using the heuristic "traditional search" algorithm with 10000 replicates, tree bisection and reconnection (TBR) branch swapping, and holding 10 trees per replication. *Gonodonta indentata* was used to root the phylogeny. A strict consensus tree was calculated from all retained trees, and jacknife supports were determined. Character state reconstruction of parsimony ancestral states was accomplished using Mesquite.

Biogeographic regions were coded for each ingroup species into the data matrix according to Table 6, and character state reconstruction of parsimony ancestral states was implemented in Mesquite to ascertain the most parsimonious area of origin. For a separate analysis of ancestral presence of *Eudocima* in the western Greater Sunda Is., Borneo, the Philippines, Sulawesi, the Lesser Sunda Is., the Moluccas, Papua New Guinea, the Solomon Is., Vanuatu, Fiji, and the Marquesas Is., presence and absence of each species was coded into a separate data matrix from that used to test the region of origin, and the same analysis was perfomed.

3.4 Character commentary

3.4.1 Head
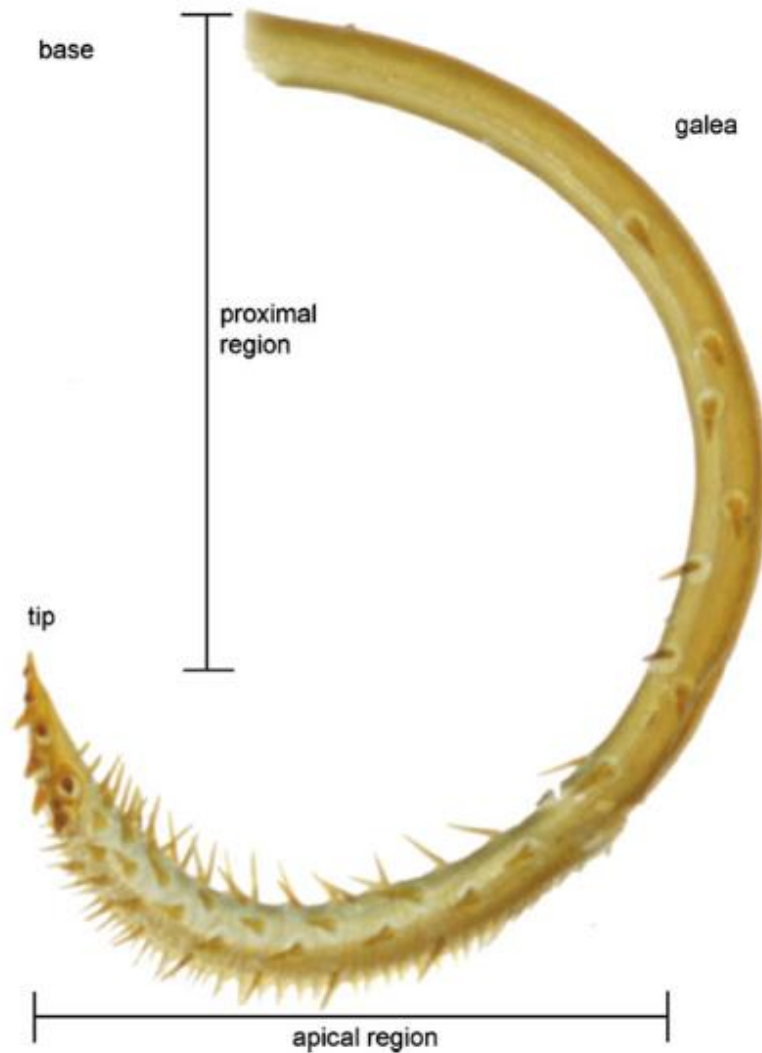
Figure 1. Regions of the proboscis, *Oraesia rectistria* Guenée. Reprinted by permission (Appendix B) from Springer Nature: Springer Zoomorphology. Jennifer M. Zaspel, S. J. Weller, and M. A. Branham. 2011. A comparative survey of proboscis morphology and associated structures in fruit-piercing, tear-feeding, and blood-feeding moths in Calpinae (Lepidoptera: Erebidae). Zoomorphology. 130: 203–225. Copyright 2011.

3.4.1.1 Character 1. *Surface microstructure of proximal region of proboscis, Fig. 2*: (0) simple and smooth, Fig. 2; (1) other (not shown).
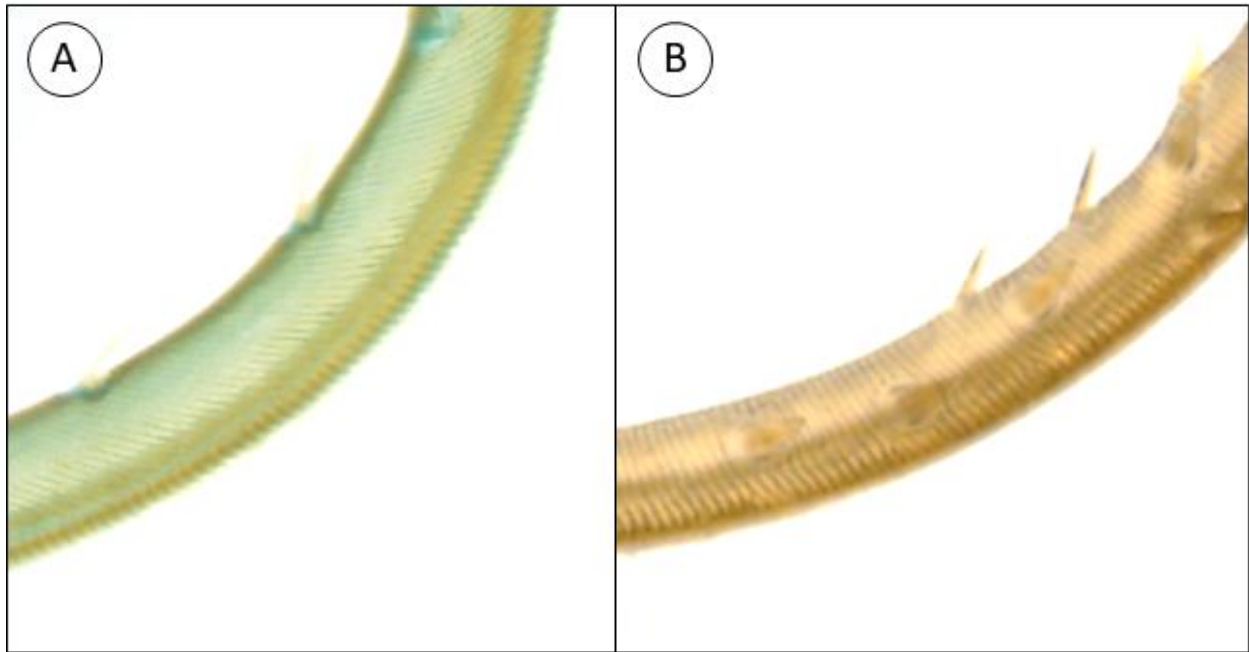
Figure 2. Surface microstructure of proximal region of proboscis, Character 1 (state, condition): **A)** *Eudocima salaminia*, **B)** *Gonodonta indentata* (0, simple and smooth).

This character is taken from Zaspel et al. (2011). Species which pierce fruits display a smooth, unfluted proximal proboscis region. All of the terminal taxa are fruit piercers. Following Bänziger's (1982) classification of piercing ability, Zaspel (2011) categorizes members of the genera *Plusiodonta*, *Oraesia*, and *Gonodonta* as primary piercers of thick-skinned fruit but secondary piercers of hard-skinned fruit, members of *Eudocima* as primary piercers of hard-skinned fruit, and *Phyllodes consobrina* as unknown in its piercing habits but displaying characteristics similar to primary piercers of soft-skinned fruits (Zaspel et al. 2011). As such, all taxa examined showed the same condition for this character and were coded as (0) (Figs. 2A, 2B), while any observed deviations from this condition would have been coded as (1).

3.4.1.2   Character 2. *Ribs of surface microstructure of proximal region of proboscis, Fig. 3* (0) with diagonal semi-circular ribs, Fig. 3A; (1) with circular ribs, Fig. 3B.
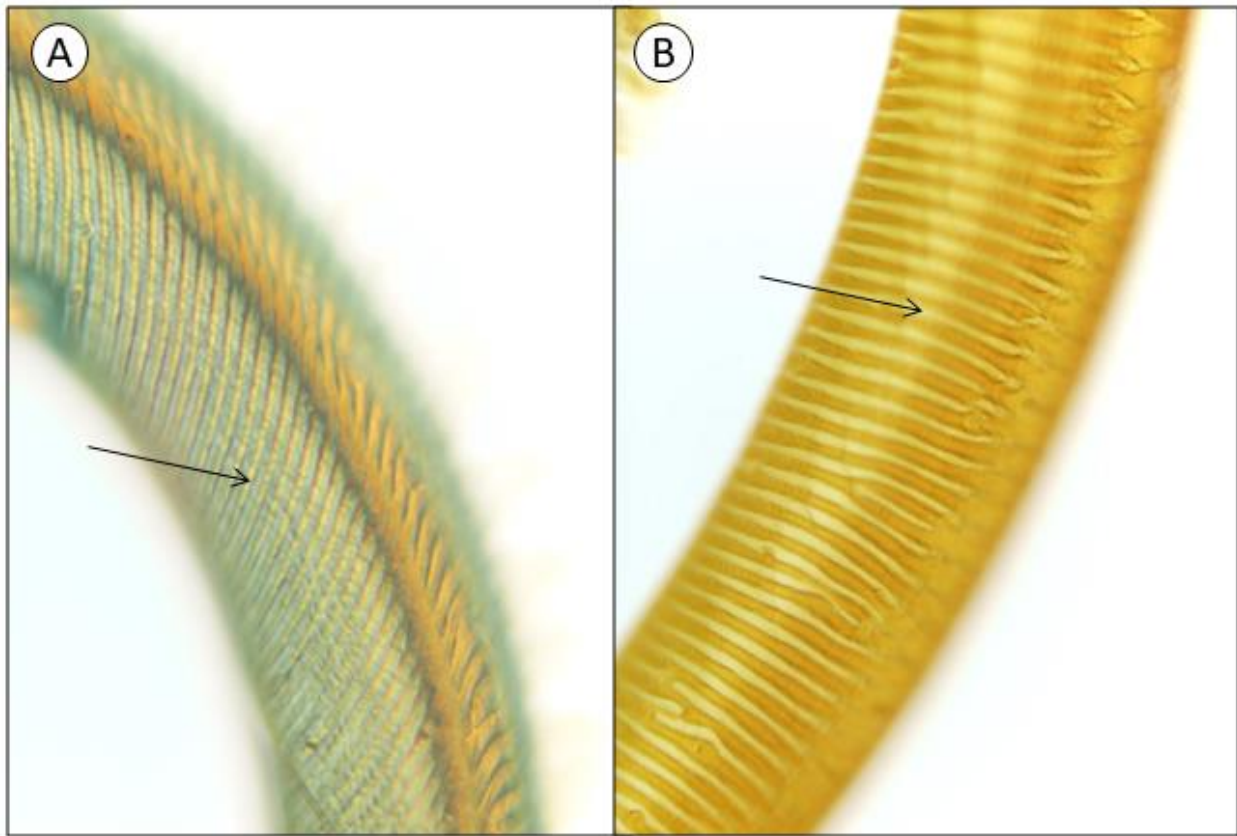
Figure 3. Surface microstructure of the proximal region of the proboscis, diagonal or circular ribs, Character 2 (state, condition): **A)** *E. salaminia* (0, with diagonal semi-circular ribs); **B)** *Phyllodes consobrina* (1, with circular ribs). Rib indicated by arrow.

This character is also based on Zaspel et al. (2011). All piercing species have circular or semi-circular ribs without longitudinal depressions (Zaspel et al. 2011), so in order to make the character informative at a lower taxonomic level, the orientation of the ribs was observed for each taxon. Zaspel et al. (2011) postulated that diagonal semi-circular ribs were characteristic of *Eudocima* species that pierce hard-skinned fruits, but noted that the distribution of this trait needed to be examined further. In this analysis, all examined *Eudocima* species were found to possess diagonal ribs (Fig. 3A), while the outgroup species possessed circular ribs (Fig. 3B). The diagonal trait can therefore be considered diagnostic for *Eudocima*.

3.4.1.3 Character 3. *Surface microstructure of apical region of proboscis, Fig. 4*: (0) smooth, Fig. 4; (1) other (not shown).

Figure 4. Surface microstructure of the apical region of the proboscis, Character 3 (state, condition): *Phyllodes consobrina* (0, smooth). Surface microstructure indicated by arrow.

This character is from Zaspel et al. (2011). In non-piercing species, the apical region of the proboscis is densely nodulose. However, as all taxa examined for this study are piercing species, the apical region in all examined specimens was found to be smooth (Fig. 4).

3.4.1.4 Character 4. *Apex of proboscis, Fig. 5*: (0) serrate, Fig. 5A; (1) smooth, Fig. 5B.
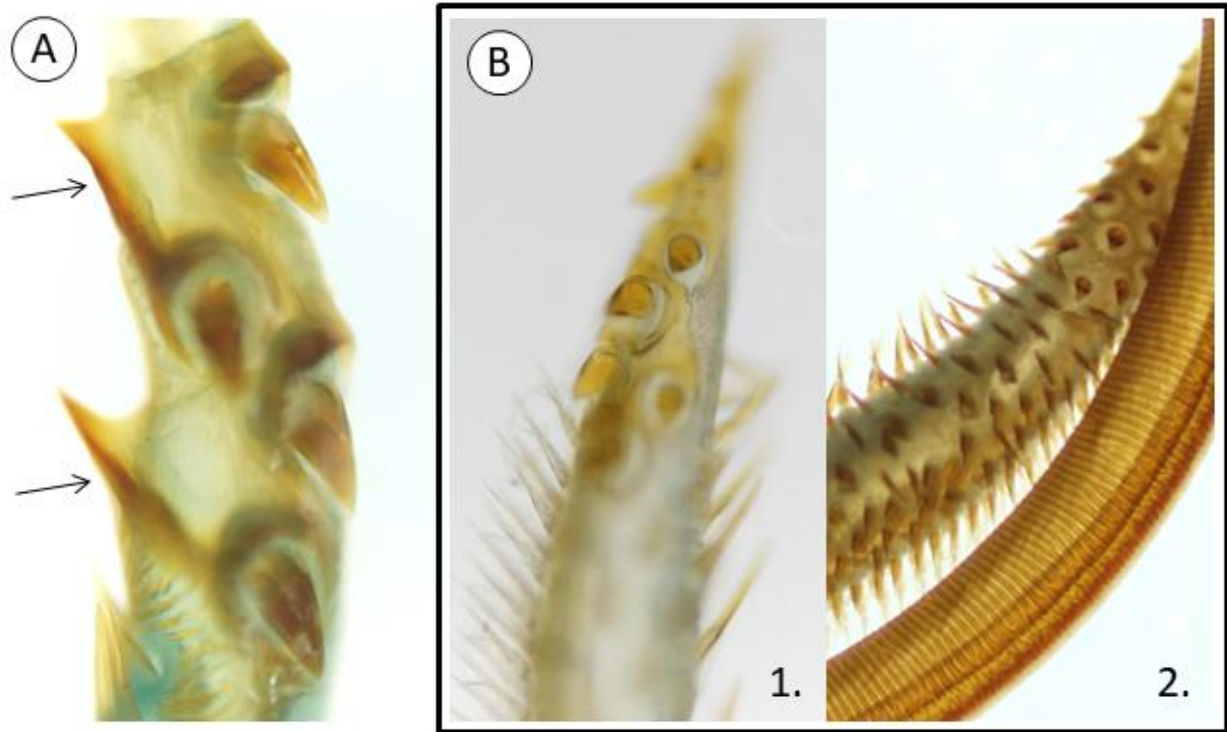
Figure 5. Apex of proboscis, Character 4 (state, condition): **A)** *E. salaminia* (0, serrate); **B)** *Oraesia triobliqua* (B1) and *Phyllodes consobrina* (B2) (1, smooth). Serrated ridges indicated by arrows.

This character is also based on Zaspel et al. (2011) and was modified to apply to only piercing species. All of the taxa included in this study are piercers of thick-skinned fruits (with the possible exception of *Phyllodes consobrina*), so only two character states were employed: the serrate condition with sharp ridges indicated by arrows (Fig. 5A), which is present in all examined *Eudocima* species; and the smooth condition of the proboscis tip (Fig. 5B), which is present in all examined outgroups and is therefore plesiomorphic.

3.4.1.5   Character 5. *Proboscis apical region sclerotization, Fig. 6*: (0) absent, Fig. 6A; (1) present, complete, Fig. 6B; (2) present, partial, Fig. 6C.
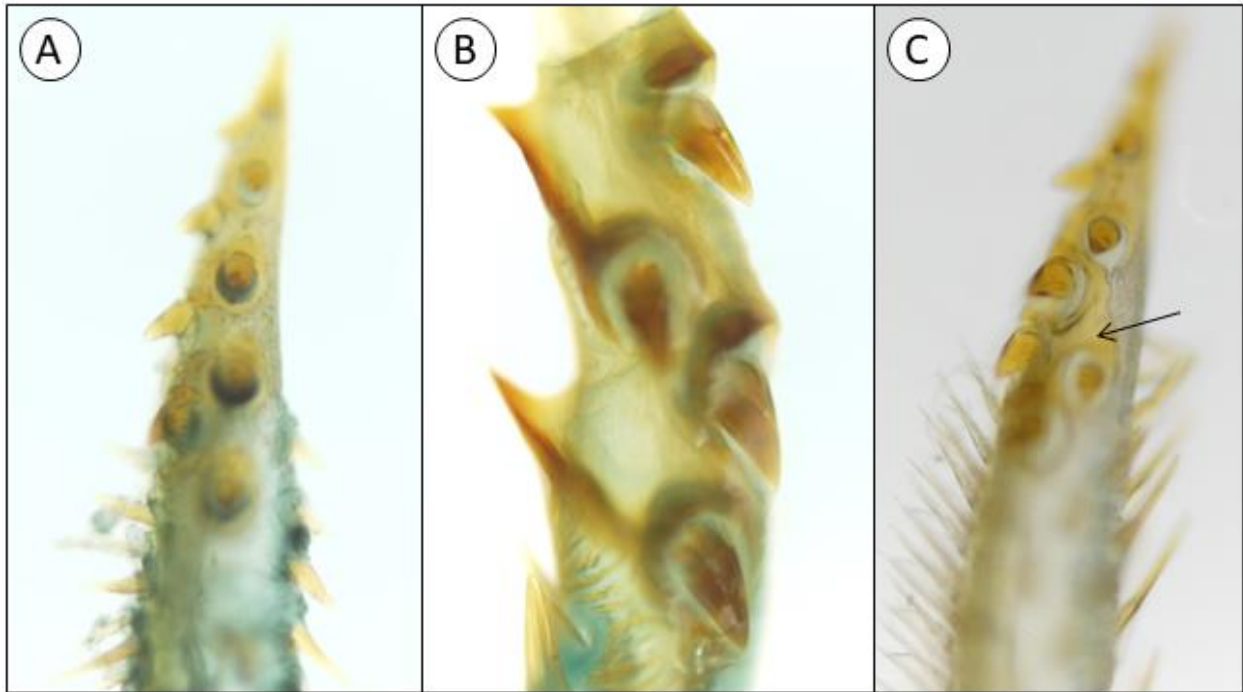
Figure 6. Proboscis apical region sclerotization, Character 5 (state, condition): **A)** *Plusiodonta incitans* (0, absent); **B)** *E. salaminia* (1, present, complete); **C)** *Oraesia triobliqua* (2, present, partial). Sclerotization on *Oraesia triobliqua* indicated by arrow.

In the apical region of the proboscis, complete sclerotization (Fig. 6B) is present for all of the *Eudocima* species examined as well as for *Phyllodes consobrina*. Sclerotization is not present (Fig. 6A) for *Plusiodonta incitans* or *Gonodonta indentata*. Both examined species of *Oraesia* display a condition in which only the distal half of the apical region is sclerotized (indicated by the arrow) where it becomes smooth (Fig. 6C), which is also the area with socketed tearing hooks.

3.4.1.6   Character 6. *Erectile barbs occurring below junction of ribbed and smooth regions of apical region of proboscis, Fig. 7*: (0) absent (not shown); (1) row of erectile barbs present, Fig. 7.

Figure 7. Erectile barbs occurring below the junction of the ribbed and smooth regions of the apical region of the proboscis, Character 6 (state, condition): *E. salaminia* (1, row of erectile barbs present). Erectile barbs indicated by dashed lines.

In Zaspel et al. (2011), the presence of a row of erectile barbs in this location on the proboscis was suggested to be a possible synapomorphy uniting the species of *Eudocima*. The number of barbs was also investigated to determine diagnostic value, but there was no effect on the resulting phylogeny. All *Eudocima* species were found to possess erectile barbs in this area, varying between a line of three barbs along the junction of the two regions and a line of four barbs (Fig. 7). This erectile barb placement was not observed in any of the outgroup species.

3.4.1.7 Character 7. *Tearing hooks occurring in apical region of proboscis, Fig. 8*: (0) four tearing hooks, Fig. 8A; (1) more than four and less than nine (inclusive) tearing hooks, Fig. 8B; (2) more than nine tearing hooks, Fig. 8C.
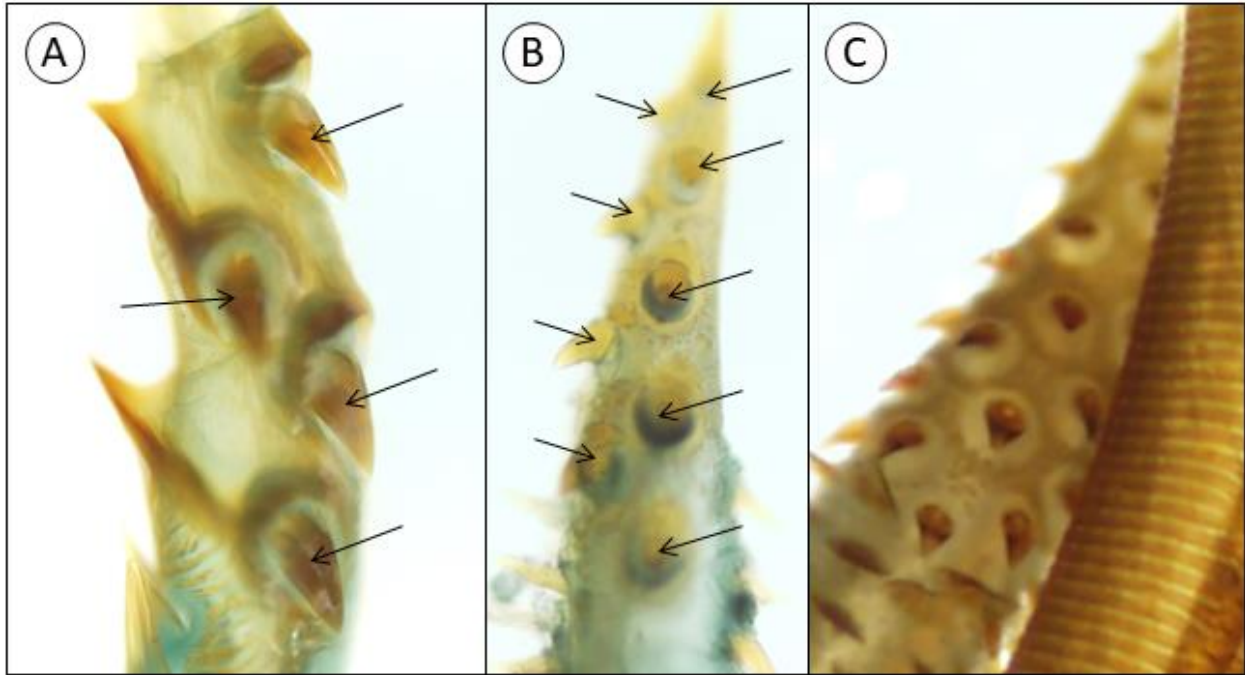
Figure 8. Tearing hooks occurring in apical region of proboscis, Character 7 (state, condition): **A)** *E. salaminia* (0, four tearing hooks); **B)** *Plusiodonta incitans* (1, more than four and less than nine (inclusive) tearing hooks); **C)** *Phyllodes consobrina* (2, more than nine tearing hooks). Number of tearing hooks indicated by arrows except where more than nine are present.

All of the taxa examined had tearing hooks present, so the number for each taxon was investigated. In all examined *Eudocima* species four tearing hooks were present in the smooth apical region of the proboscis (Fig. 8A). In *Plusiodonta incitans*, *Gonodonta indentata*, and both *Oraesia* species, nine or fewer tearing hooks were present but the number observed always exceeded four (Fig. 8B). In *Phyllodes consobrina*, many more than nine hooks were observed (Fig. 8C).

3.4.1.8   Character 8. *Number of serrated ridges present in apical region of proboscis, Fig. 9*: (0) two, Fig. 9A; (1) none, Fig. 9B.
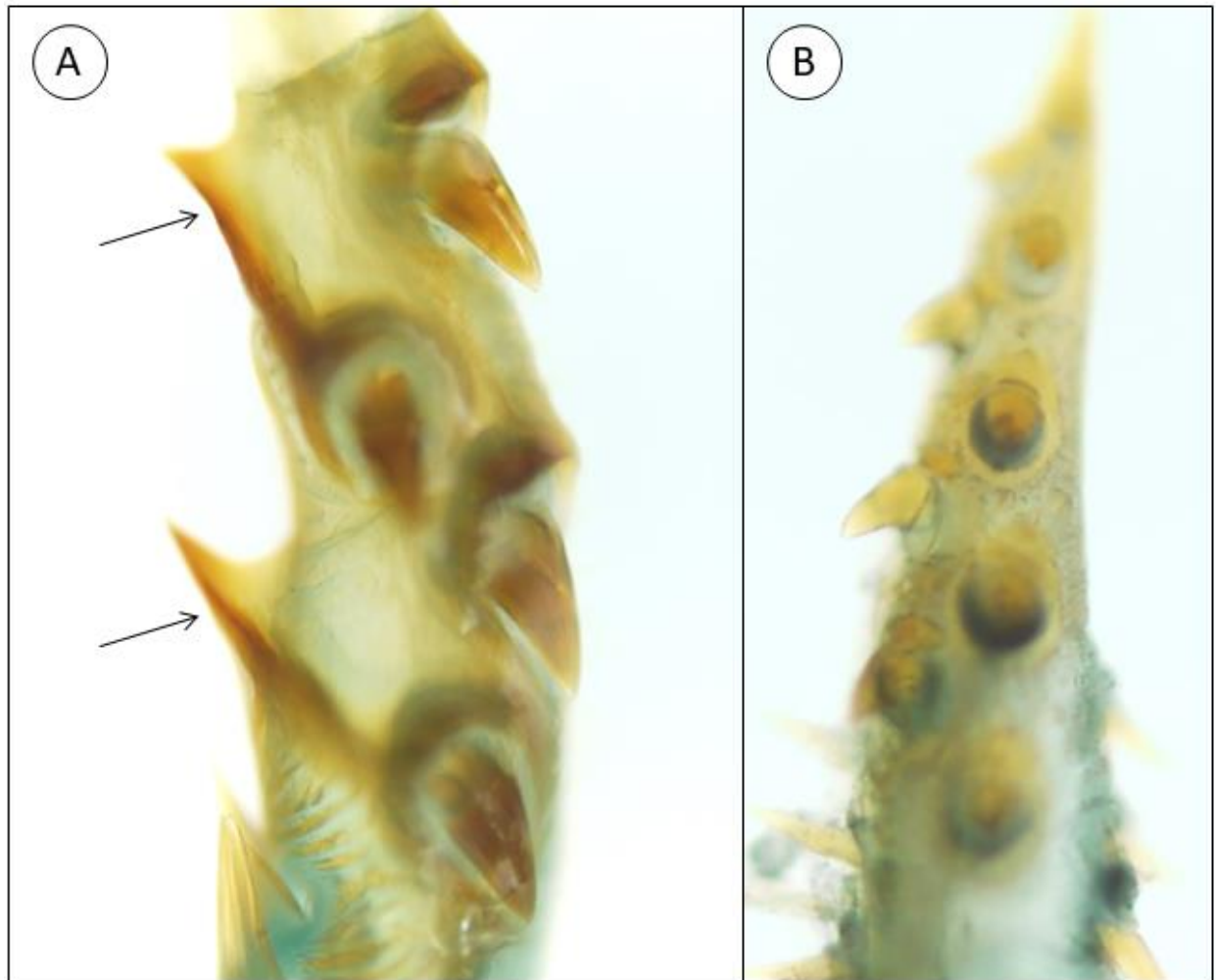
Figure 9. Serrated ridges, Character 8 (state, condition): **A)** *E. salaminia* (0, two); **B)** *Plusiodonta incitans* (1, none). Serrated ridges indicated by arrows.

Serrated ridges were only observed in *Eudocima* species in the smooth apical region of the proboscis, and two ridges were always present (Fig. 9A). Serrated ridges were not observed in the outgroups (Fig. 9B).
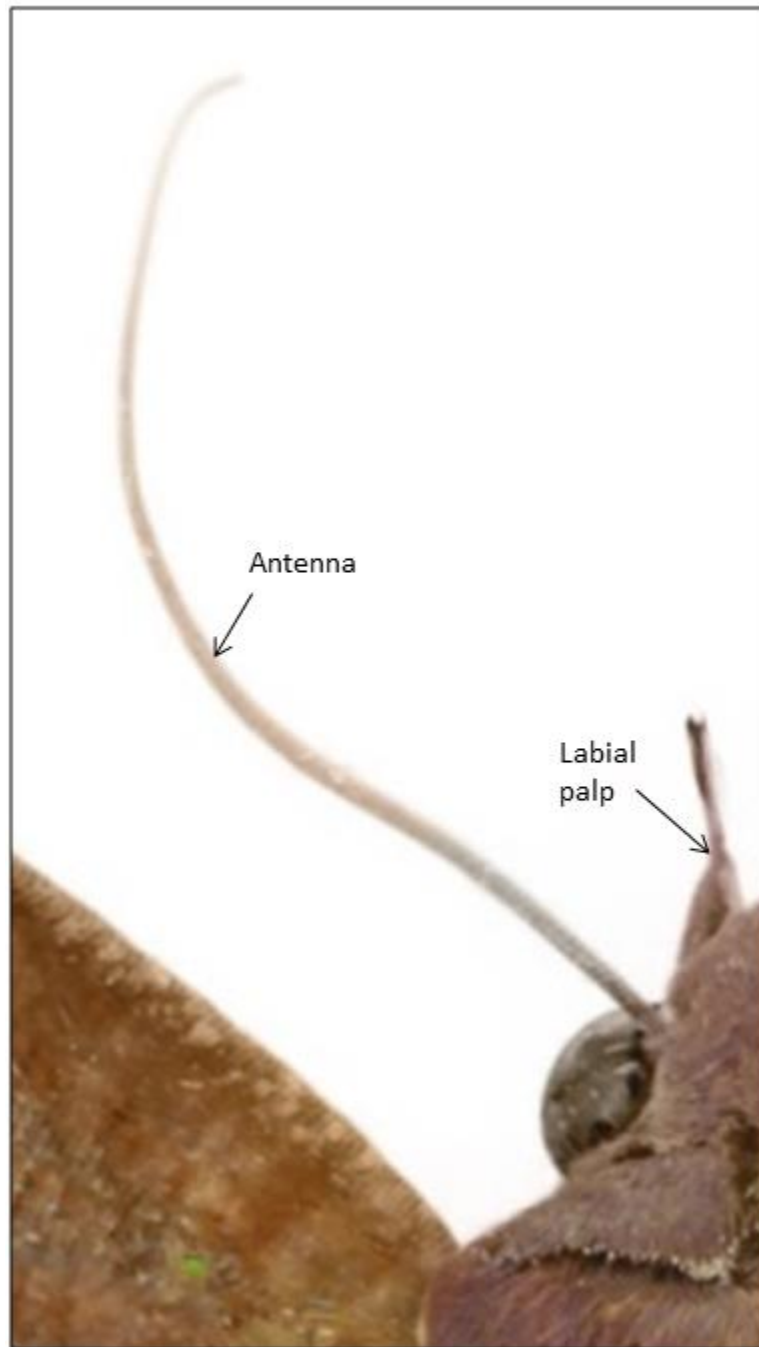
Figure 10. *Eudocima phalonia*, features of the head used for scoring characters, labelled with arrows.

3.4.1.9   Character 9. *Male antenna, Fig. 11*: (0) filiform, Fig. 11A; (1) pectinate, Fig. 11B.
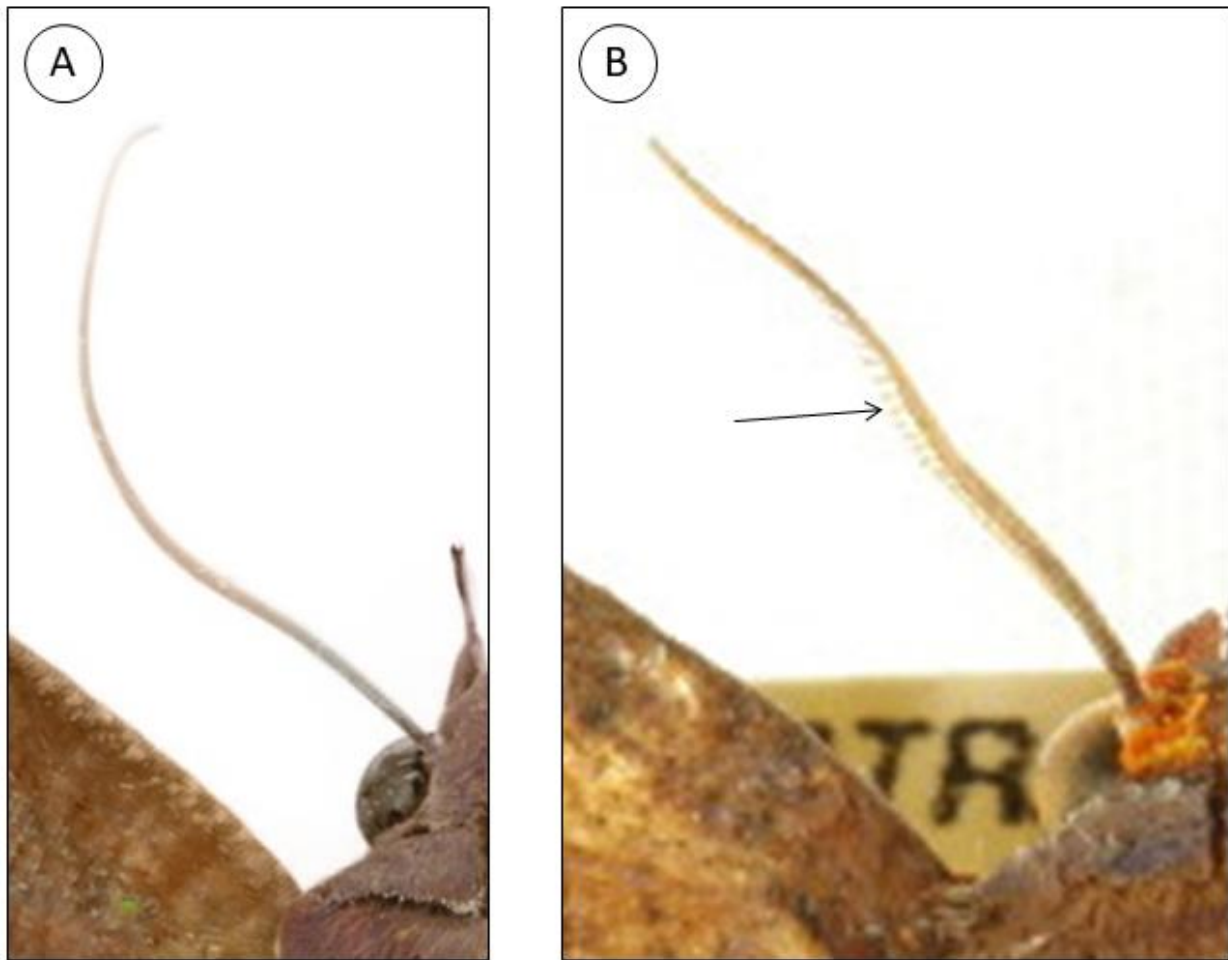
Figure 11. Male antenna, Character 9 (state, condition): **A)** *E. phalonia* (0, filiform); **B)** *Oraesia argyrosigna* (1, pectinate). Pectinate condition of antenna indicated by arrow. Fig. 11B adapted from record ANIAF903-11 (CSIRO/BIO Photography Group, Centre for Biodiversity Genomics), BOLD Systems (Ratnasingham & Hebert 2007).

In all the taxa observed with the exception of the *Oraesia* species, the male antennal type was filiform (Fig. 11A). According to Scoble (1995), most noctuoid moths (then Noctuidae) have filiform or serrated antennae, with pectinate antennae (Fig. 11B) sometimes occurring.

3.4.1.10 Character 10. *Female antenna, Fig. 12*: (0) filiform, Fig. 12; (1) other (not shown).

Figure 12. Female antenna, Character 10 (state, condition): *E. aurantia* (0, filiform).

All female specimens observed in this study had a filiform antennal type (Fig. 12).

3.4.1.11 Character 11. *Length of labial palp third segment, Fig. 13*: (0) short, less than half the length of second segment, Fig. 13A; (1) medium, roughly half the length of second segment, Fig. 13B; (2) long, as long or longer than the second segment, Fig. 13C.
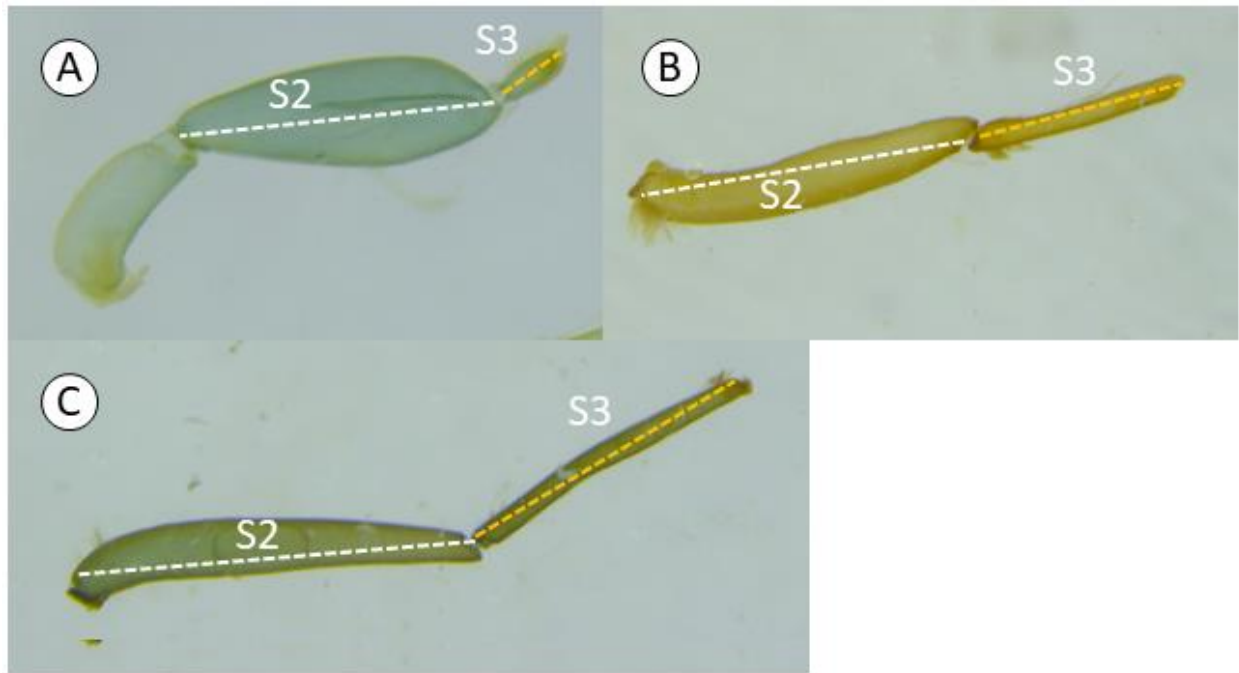
Figure 13. Length of labial palp third segment, Character 11 (state, condition): **A)** *Oraesia argyrosigna* (0, "short"); **B)** *E. materna* (1, "medium"); **C)** *E. tyrannus* (2, "long"). Approximate length of segment 2 (S2) indicated by white dashed line, and approximate length of segment 3 (S3) indicated by orange dashed line.

In species of *Eudocima*, the third segment of the labial palp is normally either roughly half the length of the second segment (Fig. 13B) or nearly the same length (Fig. 13C). In *Phyllodes consobrina* and both species of *Oraesia*, the third segment is much reduced and never reaches half the length of the second segment (Fig. 13A). The third labial palp segment is an important characteristic in Moore's (1881) splitting of *Ophideres* Boisduval, 1832. Moore (1881) notes that species of *Maenas* (=*E. salaminia*) have short labial palpi with a "small, very short, and conical" third segment. This character was not coded for *E. salaminia* in this study due to missing data, but superficial observation of labial palpi on pinned specimens lends credence to Moore's (1881) description. Furthermore, although labial palp data could only be coded here for a female specimen of *E. dividens*, pinned male specimens appear to have a short third segment in the manner of *E. salaminia*. This is the only known example of sexual dimorphism in labial palpi for

Eudocima, and is worth investigating further; for this study, labial palp data for each species is recorded using both males and females as representatives, since sex-based variation is not normally apparent.

3.4.1.12 Character 12. *Shape of labial palp second segment, Fig. 14*: (0) elongated, slightly bent, Fig 14A; (1) ovate, Fig. 14B.
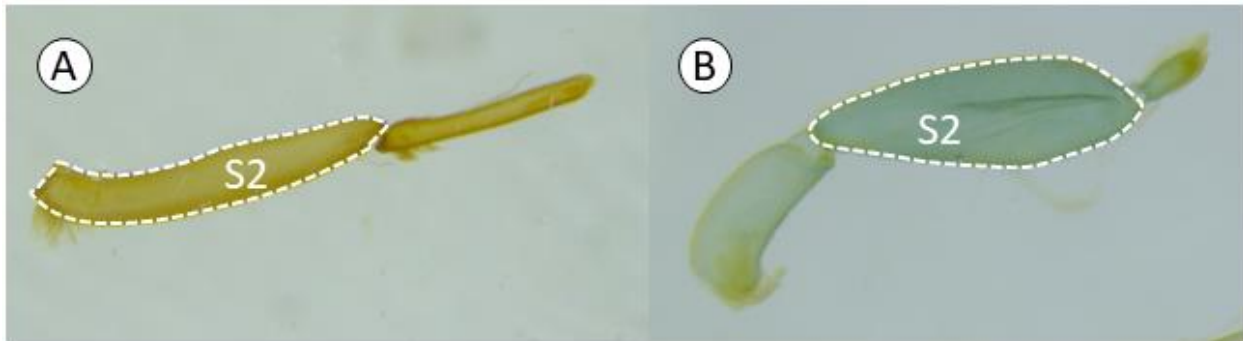
Figure 14. Shape of labial palp second segment, Character 12 (state, condition): **A)** *E. materna* (0, elongated, slightly bent); **B)** *Oraesia argyrosigna* (1, ovate). Dashed line indicates shape of second segment (S2).

The elongated trait was shared by the examined *Eudocima* species and *Phyllodes coansobrina* (Fig. 14A), while the ovate character was common to both species of *Oraesia* (Fig. 14B). While differences in the shape of the palpi and the second segment are noted by Moore (1881) in his generic distinctions, no major differences in the shape of the second segment within *Eudocima* were noted with the scales removed.

3.4.2 Thorax, wings

Figure 15. *Eudocima phalonia*, wing characters. Solid blue line indicates termen, and dashed white line indicates anal margin of forewing. Structural characters were chosen rather than wing patterns to preserve homology in comparisons.

3.4.2.1 Character 13. *Shape of anal margin of forewing, Fig. 16*: (0) straight across or slight anterior indentation, Fig. 16A; (1) anteriorly indented with discernable tornal projection or hook and rounded subbasal projection, Fig. 16B; (2) sharply curved and pronounced tornal hook, rounded or pointed subbasal extension, Fig. 16C; (3) smooth and convex, Fig. 16D; (4) sharply curved tornal hook, subbasal extension slight or absent, Fig. 16E.
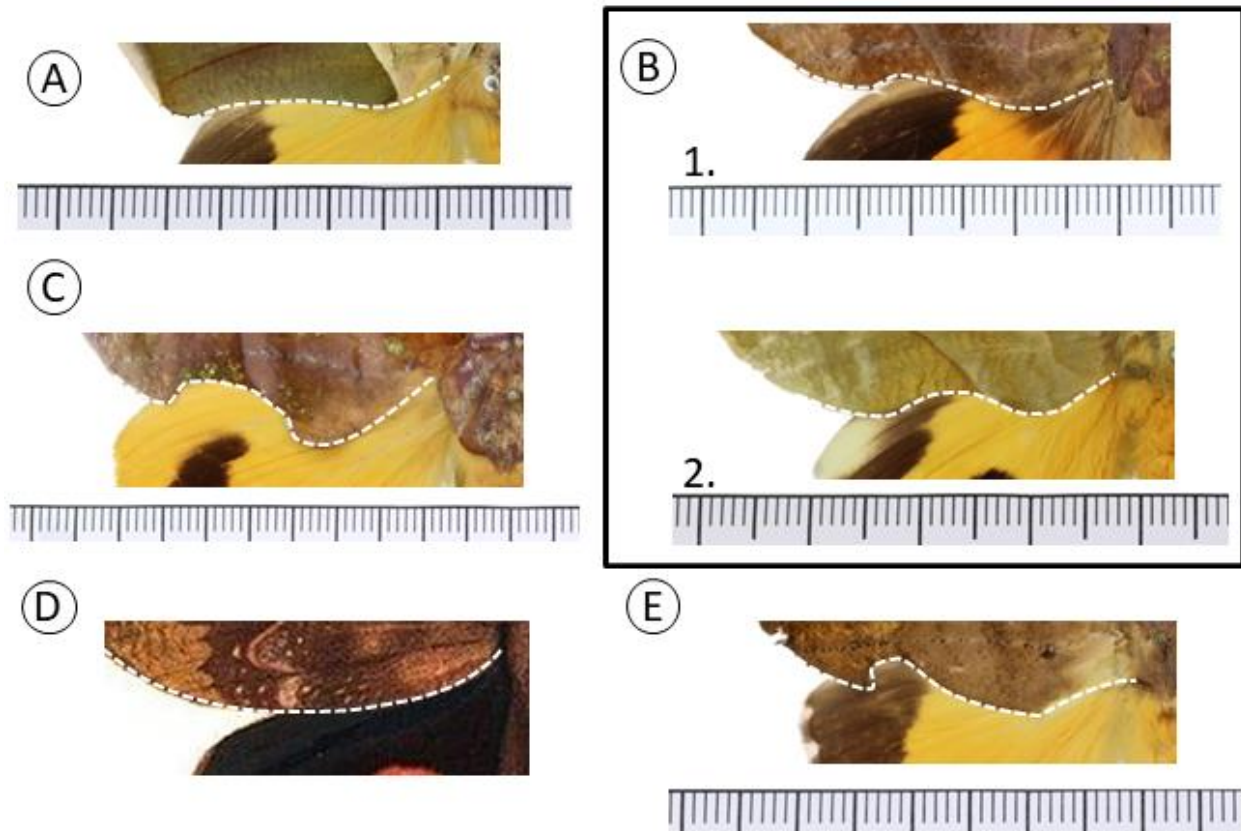
Figure 16. Shape of the anal margin of the forewing, Character 13 (state, condition): **A)** *E. salaminia* (0, straight across or slight anterior indentation); **B)** *E. phalonia* (B1) and *E. hypermnestra* (B2) (1, anteriorly indented with discernable tornal projection or hook and rounded subbasal projection); **C)** *E. aurantia* (2, sharply curved and pronounced tornal hook, rounded or pointed subbasal extension); **D)** *Phyllodes consobrina* (3, smooth and convex); **E)** *E. muscigera* (4, sharply curved tornal hook, subbasal extension slight or absent). Dashed line indicates anal margin shape. Fig. 13D adapted from wikimedia.org.

Most taxa examined possess an anal forewing margin which curves up anteriorly toward the head; this curve is caused by the posterior projection of both the tornus and subbasal extension of the forewing (Fig. 16B). In the most commonly observed condition (1), the curve caused by these posterior projections may be slight, as in the cases of *E. memorans* or *E. smaragdipicta* (Fig. 16B, 1)*,* or more pronounced, as in *E. cocalus* or *E. phalonia* (Fig. 16B, 2)*. Gonodonta indentata* was

scored for this condition but displayed a much more prominent tornal hook than subbasal projection; however, the shape appeared similar enough to discourage the inclusion of a separate character state. Generally, both the tornal and subbasal extensions are discernable and gentle, forming a broad and relatively shallow indentation into the forewing above. In another condition shared by species such as *E. aurantia* and *E. boseae*, the tornal hook is clearly pronounced and pointed back toward the body, while the subbasal extension also clearly projects from the margin (Fig. 16C). The effect on the margin is as if a semi-ovate circle has been cut out, leaving a marked indentation. This distinction in the anal margin of the forewing is also noted in Moore (1881), and is used as a means of separating *Othreis* (i.e. *E. phalonia, E. homaena*) from *Khadira* (=*E. aurantia*): "differs from *Othreis* in the forewing… hind margin with shorter and more deeply excavated space between the angles" (Moore 1881). Species such as *E. dividens* and *E. salaminia* have an anal wing margin without noticeable projections, such that the margin appears nearly level across its extent (Fig. 16A). The smooth and posteriorly convex condition of this character is represented by *Phyllodes consobrina* (Fig. 16D). In *E. muscigera* and *E. discrepans*, the subbasal projection is very slight or absent, while the tornal hook is abruptly pointed and curved (Fig. 16E). Moore's (1881) description of this feature in *Purbia* (=*E. discrepans*) is "lobe of hind margin very broad, more so than in any other of the group, the excavation being also very concave".

3.4.2.2   Character 14. *Shape of male termen, Fig. 17*: (0) smooth, Fig. 17A; (1) dentate, Fig. 17B.
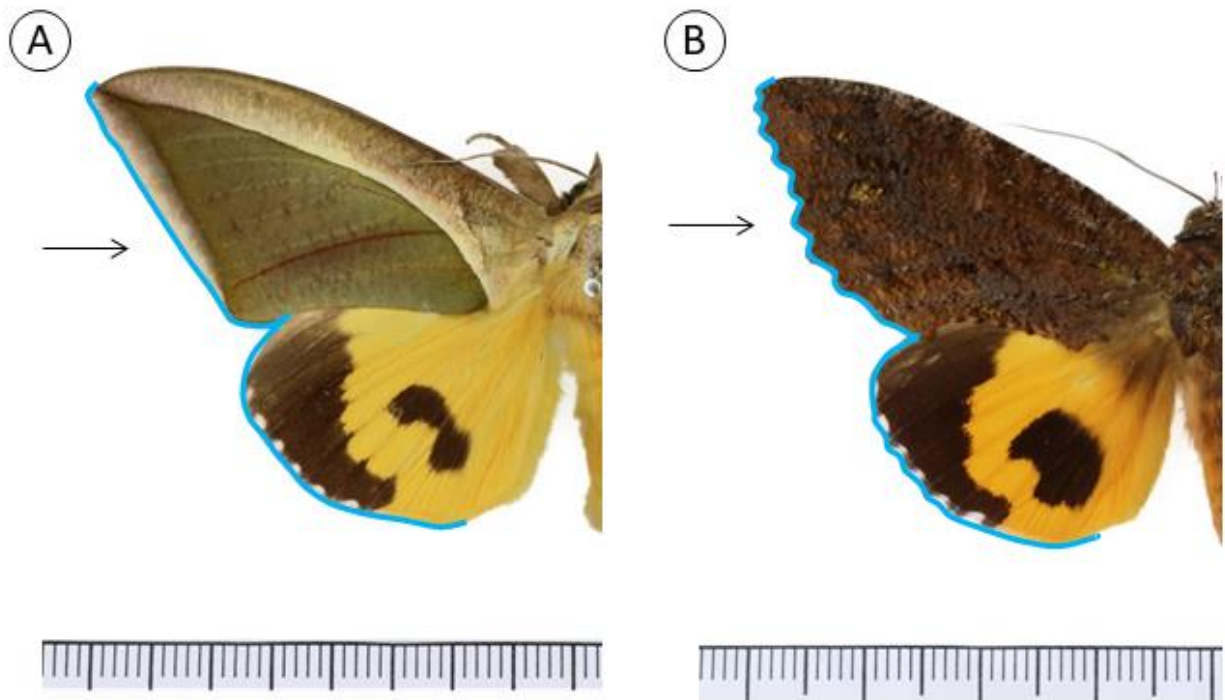
Figure 17. Shape of the male termen, Character 14 (state, condition): **A)** *E. salaminia* (0, smooth); **B)** *E. jordani* (1, dentate). Solid line and arrow indicate male termen.

This character refers to the condition of the outer margins of both forewings and hindwings. In order to be scored as dentate (Fig. 17B), both forewing and hindwing margins needed to display discernable crenellation; in cases where only the hindwing margins showed slight crenellation, the character was scored as smooth (Fig. 17A). In both *E. hypermnestra* and *E. cocalus*, the margins of both sets of wings displayed slight crenellations which were not as pronounced as the dentate condition observed in other taxa (e.g., *E. jordani* at the most extreme, *E. apta* at the least extreme). It was determined to code *E. hypermnestra* and *E. cocalus* as possessing the smooth character state.

3.4.2.3   Character 15. *Shape of female termen, Fig. 18*: (0) smooth, Fig. 18A; (1) dentate, Fig. 18B.
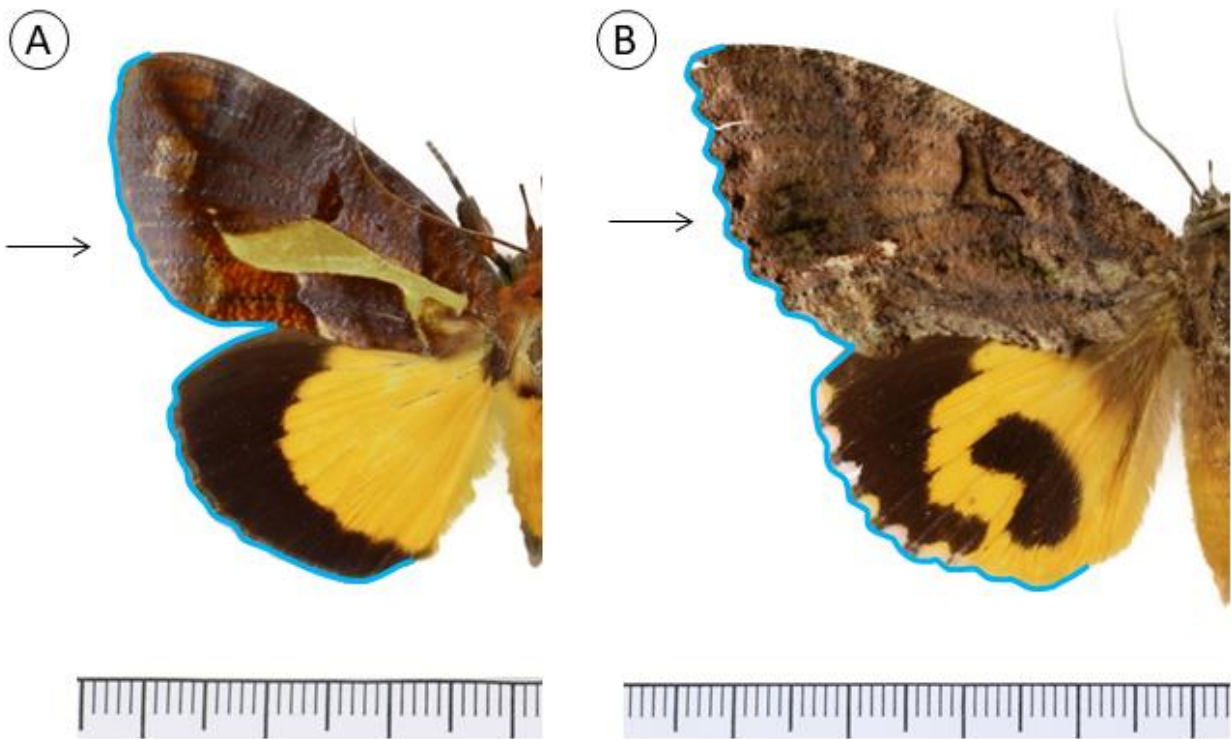
Figure 18. Shape of female termen, Character 15 (state, condition): **A)** *E. iridescens* (0, smooth); **B)** *E. srivijayana* (1, dentate). Solid line and arrow indicate female termen.

The dentate condition (Fig. 18B) is more widely seen in female *Eudocima* species than in males. In both *E. hypermnestra* and *E. cocalus*, the observed crenellation was more apparent in the females than the males (although still slight), and the dentate condition was scored.

3.4.2.4 Character 16. *Apical process of forewing, Fig. 19*: (0) absent, Fig. 19A; (1) present, Fig. 19B.

Figure 19. Apical process of forewing, Character 16 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. aurantia* (1, present). Process indicated by arrow.

An apical forewing process (Fig. 19B) is diagnostic of *Adris* (Moore 1881), and of the *tyrannus*-group of *Eudocima* (*E. tyrannus, E. okurai, E. sikhimensis, E. behouneki,* and *E. mazzeii*, Zilli & Hogenes 2002) with *E. aurantia*. A lengthened apical process was also observed for *E. prolai*, as well as for *Phyllodes consobrina*. Moore (1881) describes members of *Khadira* (=*E. aurantia*) with forewings "having a decided falcate apex" and members of *Adris* with "the apex being produced into a lengthened point". This is likely a means of distinguishing between the shapes of the processi, but although variation in shape was noted, it did not display utility in the phylogenetic analysis. The apical forewing process of *Phyllodes courebrina* also has a different shape, and has a downward bend not seen in the *Eudocima* species.

3.4.3 Abdomen, male genitalia
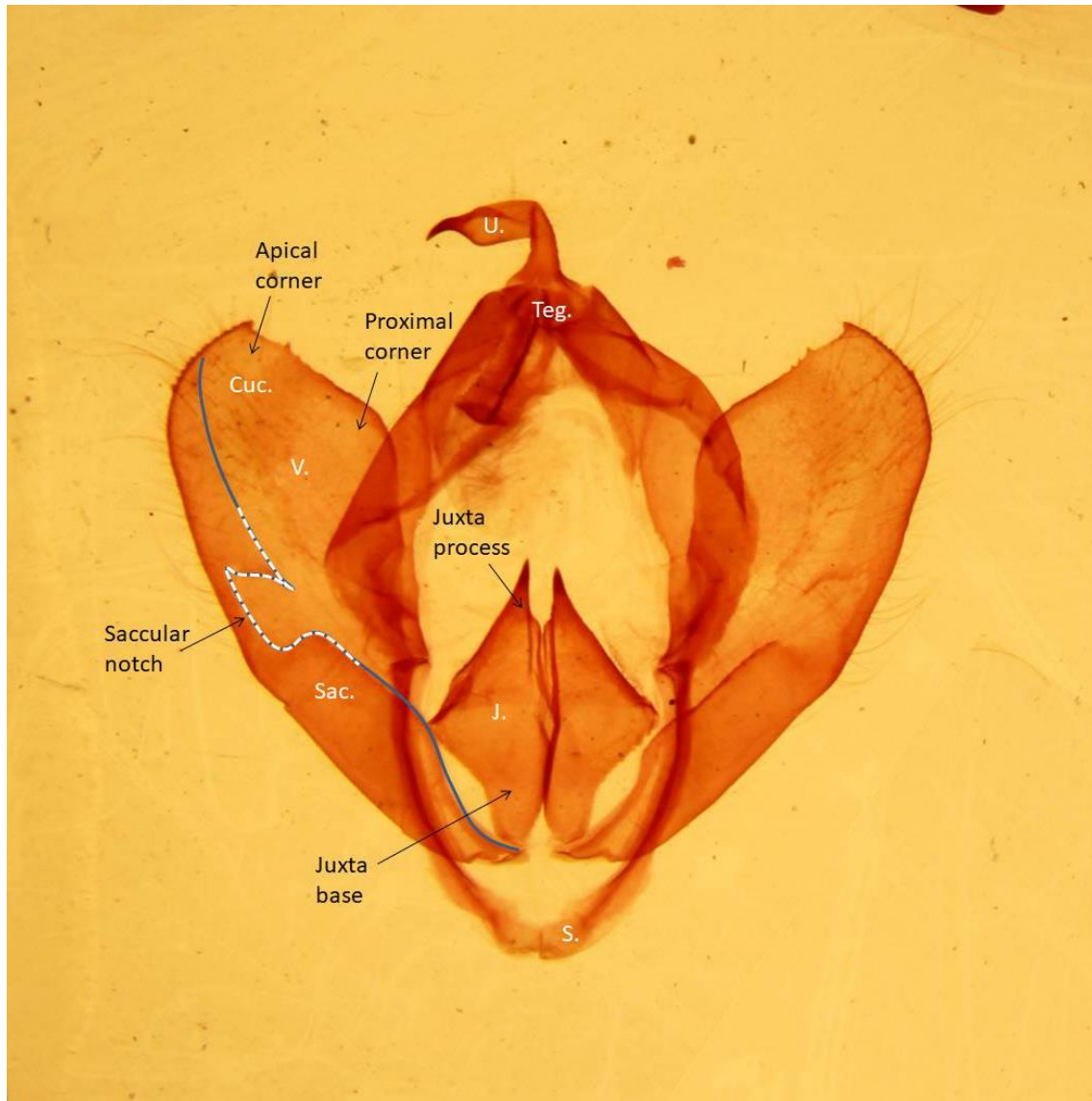
Figure 20. *E. tyrannus*, male genital capsule with labelled parts used for character coding. U. = uncus, Teg. = tegumen, J. = juxta, S. = saccus, V. = valve, Sac. = sacculus, Cuc. = cucullus. Edge of sacculus (Sac.) further defined by blue line, and saccular notch indicated by dashed white line. Additional features labelled and indicated by arrows.

Figure 21. A) *E. jordani*; **B)** *E. materna*. Male phallus (two examples) with labelled parts used for character coding. Ae. = aedeagus, Ves. = vesica. Additional features labelled and indicated by arrows.

3.4.3.1 Character 17. *Sacculus attached with cucullus, Fig. 22*: (0) yes, Fig. 22A; (1) no, Fig. 22B.

Figure 22. Sacculus attached with cucullus, Character 17 (state, condition): **A)** *E. aurantia*, r. valve (0, yes); **B)** *E. kuehni*, r. valve (1, no). Dashed line extends along edge of distal part of sacculus (Sac.) to its tip, indicating attachment with cucullus (Cuc.).

The majority of *Eudocima* species have no separation present between the sacculus and cucullus, which are smoothly joined along the length of the valve (Fig. 22A). In *E. kuehni*, which is atypical of the rest of the genus in many respects, the sacculus splits from the cucullus (Fig. 22B). This condition is also present in *Plusiodonta incitans* and *Gonodonta indentata*.

3.4.3.2 Character 18. *Sacculus extended beyond cucullus, Fig. 23*: (0) no, Fig. 23A; (1) yes, Fig. 23B.
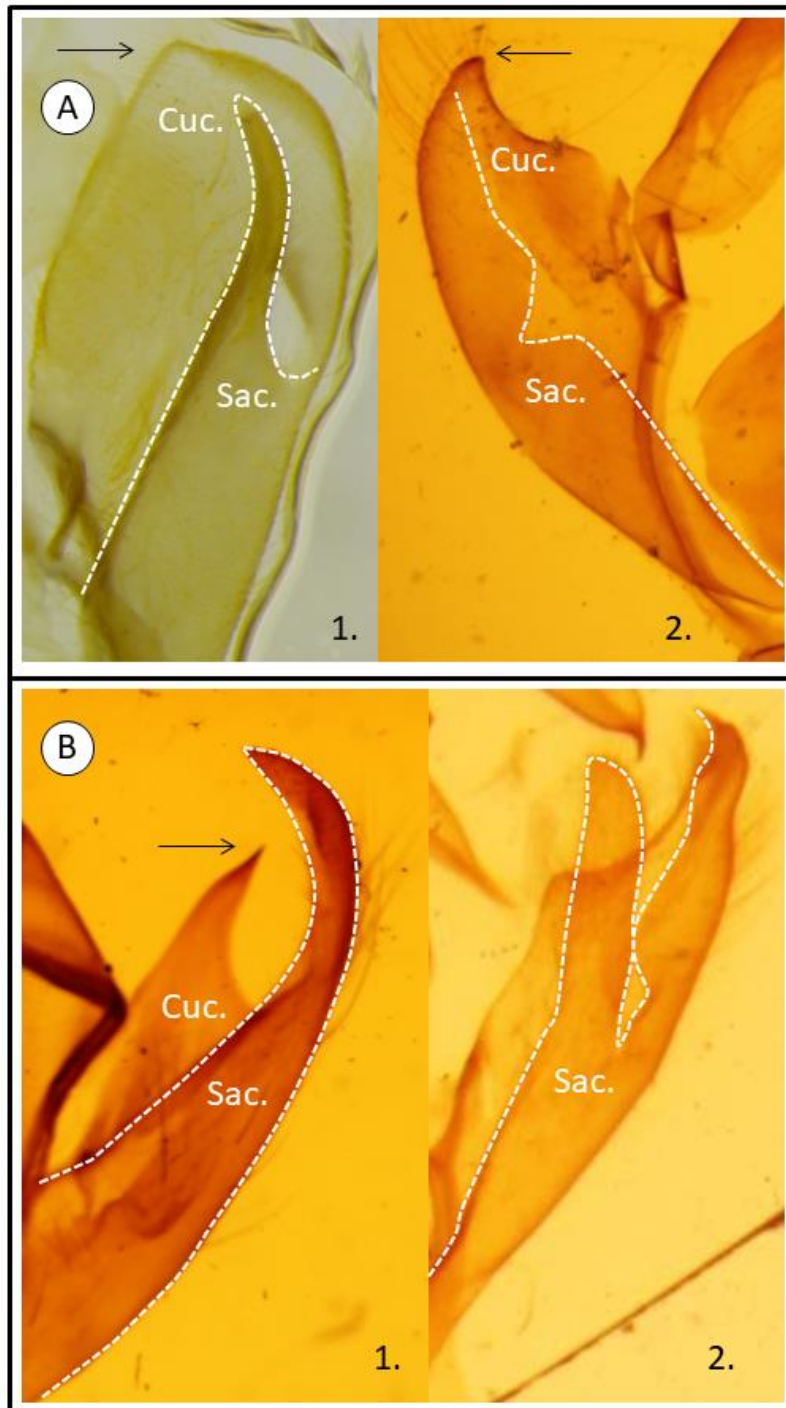
Figure 23. Sacculus extended beyond cucullus, Character 18 (state, condition): **A)** *Gonodonta indentata*, r. valve (A1) and *E. imperator*, l. valve (A2) (0, no); **B)** *E. kuehni*, r. valve (B1) and *E. procus*, r. valve (B2) (1, yes). Dashed line outlines sacculus (Sac.), and arrow indicates tip of cucullus (Cuc.).

In most *Eudocima* (which have an attached sacculus and cucullus), the sacculus does not extend beyond the cucullus, and this character is coded as (0) (Fig. 23A, 2). An exception is *E. procus* (Fig. 23B, 2), in which the sacculus is attached and yet extends past the cucullus tip, obscuring it. The saccular process in this species (character 19) should not be confused with the tip of the sacculus, which can be seen to continue past the attachment of the process. This character is more apparent to distinguish in species which have a detached sacculus. In *E. kuehni* and *Plusiodonta incitans*, the tip of the sacculus extends beyond the tip of the cucullus such that the sacculus is longer (Fig. 23B, 1). In *Gonodonta indentata* the sacculus tip does not extend past the cucullus (Fig. 23A, 1).

3.4.3.3 Character 19. *Saccular process, Fig. 24*: (0) absent, Fig. 24A; (1) one present, uniform in width, Fig. 24B; (2) one present, broader at base and sharply pointed at tip, Fig. 24C; (3) two present, slim and sharply pointed, Fig. 24D.
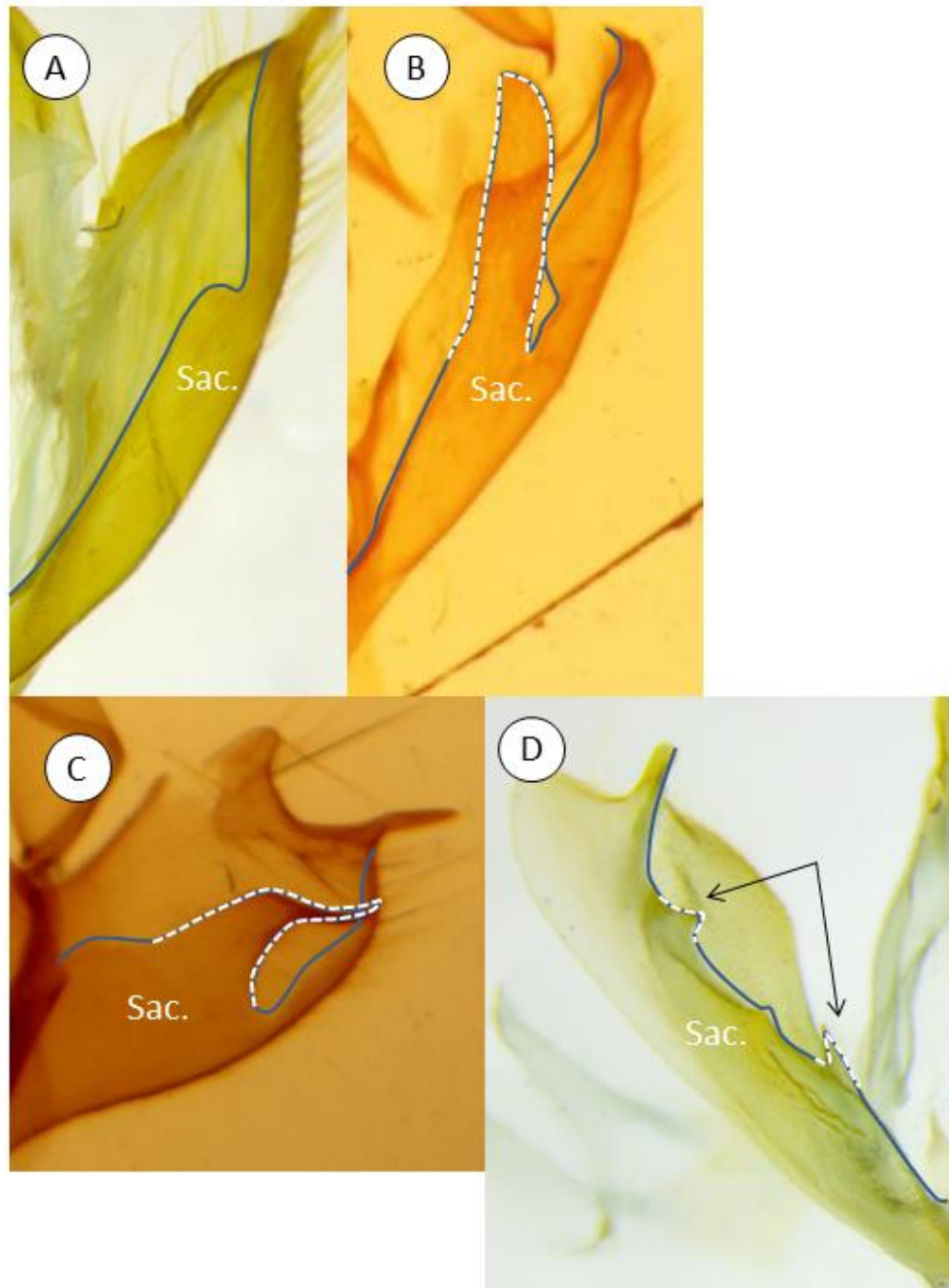
Figure 24. Saccular process, Character 19 (state, condition): **A)** *E. jordani*, r. valve (0, absent); **B)** *E. procus*, r. valve (1, one present, uniform in width); **C)** *E. serpentifera*, r. valve (2, one present, broader at base and sharply pointed at tip); **D)** *Plusiodonta incitans*, l. valve (3, two present, slim and sharply pointed). Proximal edge of sacculus (Sac.) delineated in blue, saccular process indicated by dashed white line (and arrows for *Plusiodonta incitans*, Fig. 19D).

The saccular process is distinct from the attachment of the sacculus and the cucullus; the saccular process originates from the body of the sacculus, and after the separation of the process the rest of the sacculus can be seen continuing upward. In contrast, attachment between the tip of the sacculus and the cucullus can be observed at the valve tip. Most *Eudocima* do not have saccular processi (Fig. 24A), with two exceptions. In *E. procus*, the saccular process is fingerlike and uniform in width with a rounded tip (Fig. 24B). In *E. serpentifera*, the process is roughly triangular, with a broadened base tapering sharply to a thin and pointed tip (Fig. 24C). *Plusiodonta incitans* displays two saccular processi, which are each slim, sharp-pointed, and occur at different locations on the sacculus (Fig. 24D). Due to an artifact from flattening the valvae for photography, the saccular processi of *Plusiodonta incitans* appear smaller and less pronounced than they are in life.

3.4.3.4   Character 20. *Sacculus notched, Fig. 25*: (0) absent, Fig. 25A; (1) present, Fig. 25B.
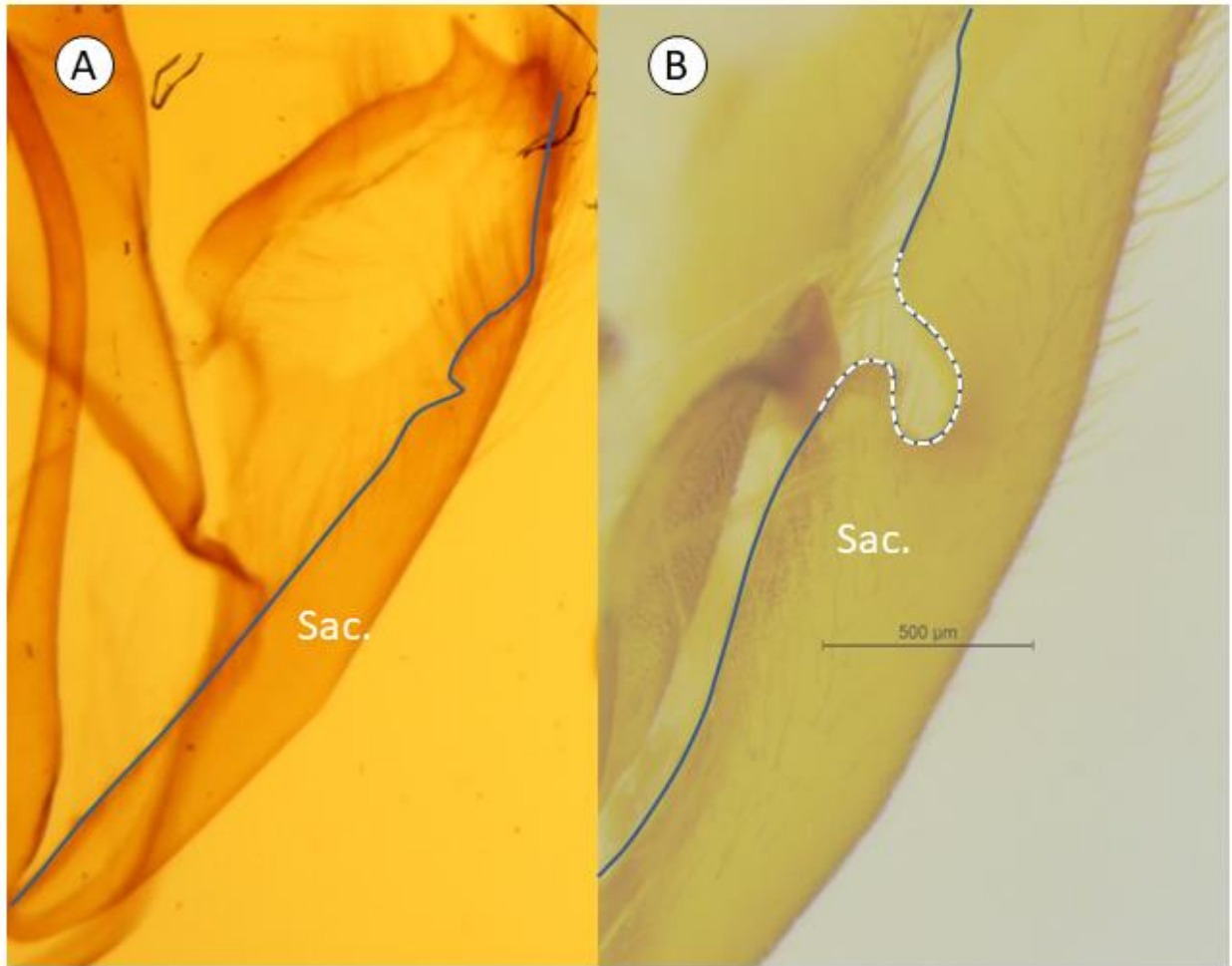
Figure 25. Sacculus notched, Character 20 (state, condition): **A)** *E. cajeta*, r. valve (0, absent); **B)** *E. cocalus*, r. valve (1, present). Inner margin of sacculus (Sac.) delineated in blue, and dashed white line indicates notch.

In ~65% of the taxa examined, the sacculus has a notch or depression of varying shape along the inner margin occurring somewhere along its length (Fig. 25B). In the remaining taxa, the sacculus is smooth and uninterrupted along its extent (Fig. 25A). Taxa without an apparent saccular notch include *E. tyrannus*, *E. boseae*, *E. homaena*, *E. kuehni*, *E. talboti*, *E. discrepans*, *E. cocalus*, *E. hypermnestra*, *E. cajeta*, *E. serpentifera*, *E. sikhimensis*, *E. mazzeii*, *E. behouneki*, *E. martini*, *E. materna*, *Gonodonta indentata*, and both species of *Oraesia*. This character was sometimes difficult to score because of the positioning of the valvae.

3.4.3.5 Character 21. *Saccular notch shape, Fig. 26*: (0) V-shape, narrow in diameter, Fig. 26A; (1) circular, with incurved points on each side, Fig. 26B; (2) narrow, rectangular and deep, Fig. 26C; (3) triangular, broad, Fig. 26D; (4) ovate, broad, distal side (in reference to the valve) with an incurved point, Fig. 26E; (5) defined by projecting proximal side, then continuing diminished to tip of cucullus, Fig. 26F; (6) broad, with intermediate point in the center, Fig. 26G; (7) proximal side projects inwards and notch extends beneath, Fig. 26H; (8) broad half-crescent (not shown, Fig. 11 Brou & Zilli 2016).

Figure 26. Saccular notch shape, Character 21 (state, condition): **A)** *E. phalonia*, r. valve (0, V-shape, narrow in diameter); **B)** *E. materna*, r. valve (1, circular, with incurved points on each side); **C)** *E. aurantia*, l. valve (2, narrow, rectangular and deep); **D)** *E. imperator*, l. valve (3, triangular, broad); **E)** *E. dividens*, l. valve (4, ovate, broad, distal side (in reference to the valve) with an incurved point); **F)** *E. srivijayana*, l. valve (5, defined by projecting proximal side, then continuing to tip of cucullus); **G)** *E. steppingstonia*, l. valve (6, broad, with intermediate point in the center); **H)** *E. mionopastea*, r. valve (7, proximal side projects inwards and notch extends beneath). Inner margin of sacculus (Sac.) delineated in blue, and notch indicated by dashed white line.
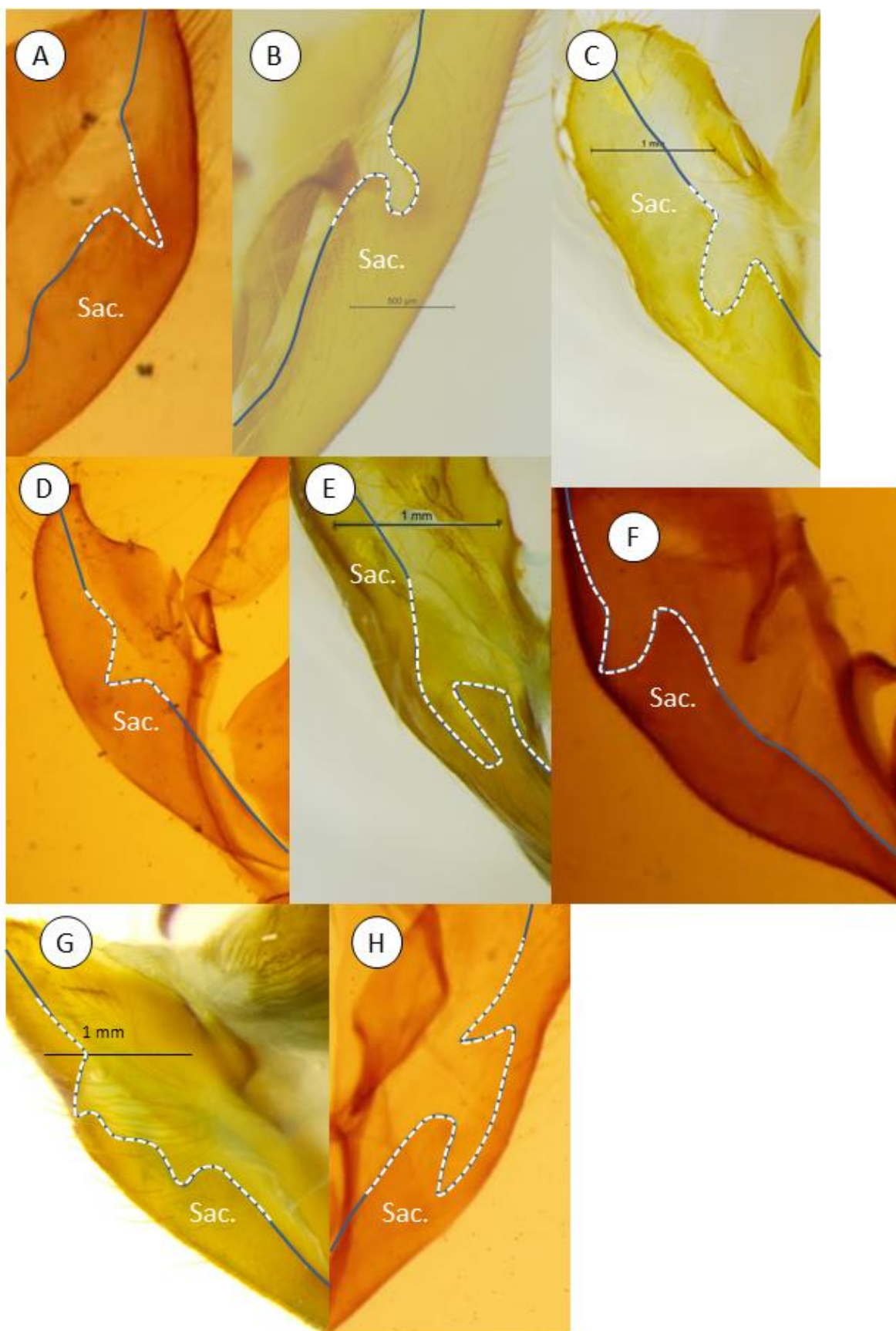
In taxa with a saccular notch, the notch morphology displays considerable variation. Examined *E. phalonia*, *E. euryzona*, *E. collusoria*, and *E. oliveri* were observed to have a narrow V-shaped notch (Fig. 26A), while a circular notch with pointed edges was characteristic of *E. materna* and *E. apta* (Fig. 26B). In *E. caesar*, *E. jordani*, *E. bathyglypta*, *E. aurantia*, and *E. memorans*, the notch is deep and narrow with parallel sides (Fig. 26C). The saccular notch is triangular with a broad base in *E. imperator*, *E. muscigera*, *E. salaminia*, *E. divitiosa*, and *E. iridescens*. *E. dividens*, and *E. okurai* all share a saccular notch which is shaped like an oval depression with the distal side of the notch curving back inwards into a point (Fig. 26D). In *E. treadawayi*, *E. colubra*, and *E. srivijayana*, the "notch" begins in the upper half of the sacculus and the depression continues upwards to the tip of the valve (Fig. 26F). *Eudocima procus*, *E. smaragdipicta*, *E. steppingstonia*, *E. kinabaluensis*, and *Plusiodonta incitans* display a saccular notch that has an intermediate projecting point or knob in the center (Fig. 26G). In *Plusiodonta incitans*, at least two smaller intermediate points are seen between the two saccular processi on either side of the notch, but the condition was deemed similar enough to not warrant a new character state. In *E. mionopastea* and *E. paulii*, the proximal side of the notch extends into the notch as a rounded lobe (Fig. 26H). This causes the notch to be shaped like a boot. The saccular notch in *E. lequeuxi* is similar to the trait seen in *E. phalonia*, but is distinctly broader and more excavated (Brou & Zilli 2016). The shape is similar to a half-crescent. Scoring difficulties arose for the same reason as for character 20.

3.4.3.6 Character 22. *Valve shape, Fig. 27*: (0) wedge shape with rounded tip, Fig. 27A; (1) narrow half-crescent with pointed cucullus and angular proximal corner, Fig. 27B; (2) broad with two rounded prominences on apex, Fig. 27C; (3) ovoid to broadly triangular with rounded margins, Fig. 27D; (4) wedge shape with rectangular prominence and flat upper margin, Fig. 27E; (5) triangular with level upper margin, Fig. 27F; (6) sharply pointed inner corner, tapering down to lower cucullus, Fig. 27G; (7) half-crescent shape with distinct triangular prominence at apex, Fig. 27H; (8) wedge shape with projecting rectangle at apex, Fig. 27I; (9) broadly rectangular with convex margins, level upper margin, and small hook-like protuberance at distal apical corner (not shown, Plate 469 Holloway 2005); (A) narrow ovoid tapering to apex, Fig. 27J; (B) paddle-like (not shown, Plate 477 Holloway 2005); (C) ovate, with two prominent processi along proximal valve margin (not shown, Fig. 3 Yoshimoto 1999).

Figure 27. Valve shape, Character 22 (state, condition): **A)** *E. euryzona*, r. valve (0, wedge shape with rounded tip); **B)** *E. procus*, r. valve (1, narrow half-crescent with pointed cucullus and angular proximal corner); **C)** *E. materna*, r. valve (2, broad with two rounded prominences on apex); **D)** *E. colubra*, r. valve (3, ovoid to broadly triangular with rounded margins); **E)** *E. tyrannus*, l. valve (4, wedge shape with rectangular prominence and flat upper margin); **F)** *E. jordani*, r. valve (5, triangular with level upper margin); **G)** *E. kuehni*, r. valve (6, sharply pointed inner corner, tapering down to lower cucullus); **H)** *E. phalonia*, r. valve (7, half-crescent shape with distinct triangular prominence at apex); **I)** *Plusiodonta incitans*, l. valve (8, wedge shape with projecting rectangle at apex); **J)** *Oraesia argyrosigna*, l. valve (A, narrow ovoid tapering to apex). Valve (V.) shape indicated by dashed line. Processi from valve excluded from overall shape.
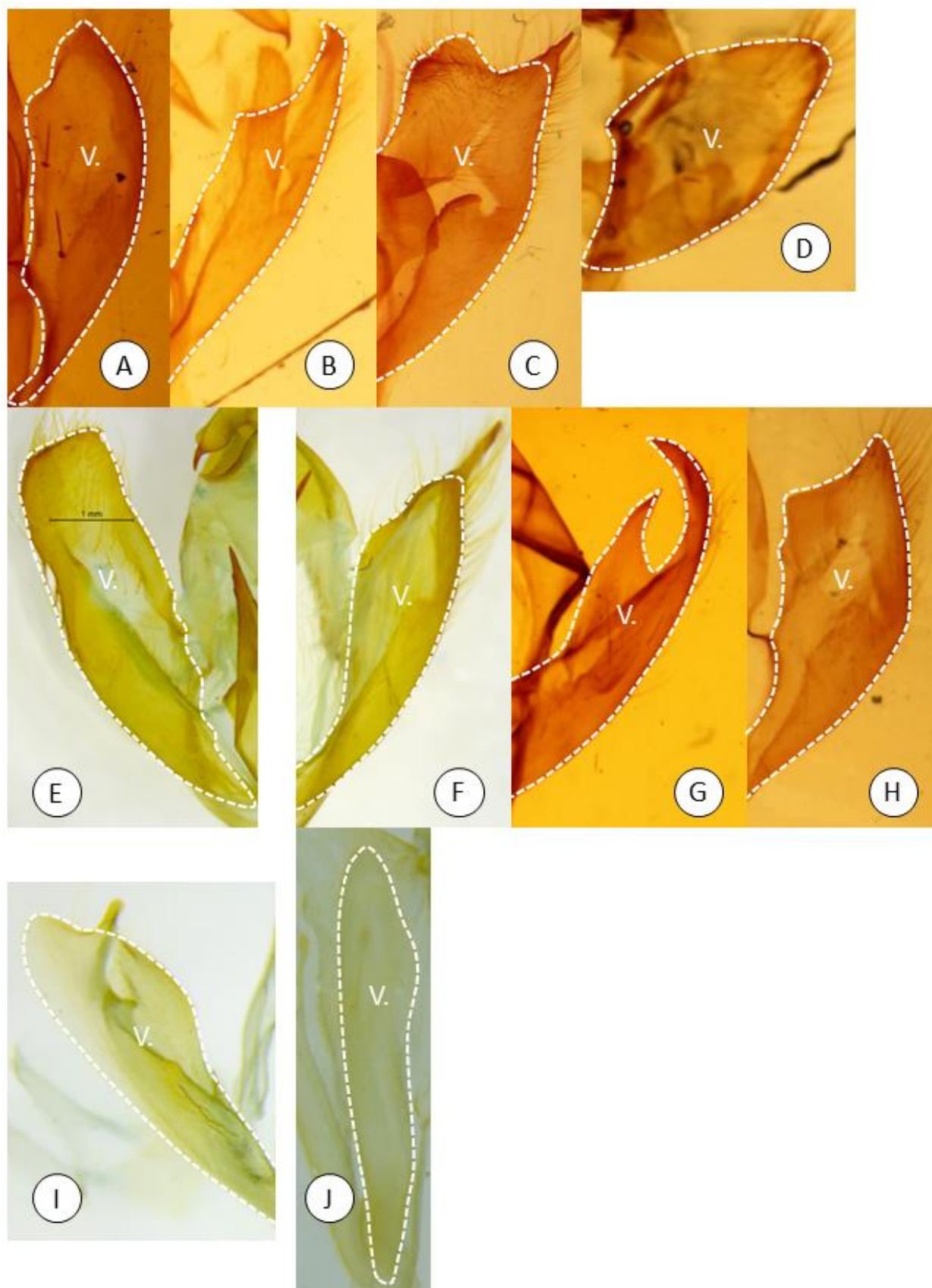
Like saccular notch shape, this trait varies widely among the taxa studied. *Eudocima caesar*, *E. dividens*, the *E. phalonia* specimen from Ghana*, E. paulii*, *E. euryzona*, *E. divitiosa*, *E. steppingstonia*, and *E. martini* have wedge-shaped valvae that feature a rounded tip at the apex and a slightly lower proximal corner (the upper corner of the valve nearest to the body) (Fig. 27A). *Eudocima procus* represents the valve trait which is a narrow half-crescent shape with a pointed apex and pointed proximal corner (Fig. 27B). *Eudocima apta*, *E. materna*, and *E. serpentifera* all share a similar valve shape, which is broadened distally and has two rounded prominences on the apical margin (Fig. 27C). These prominences make this valve shape unmistakable. The valve shape condition present in *E. memorans*, *E. colubra*, *E. collusoria*, *E. cajeta* and *E. prolai* is ranges from broadly ovoid with a tapered apex to triangular with rounded corners and smooth margins (Fig. 27D). In *E. iridescens*, *E. talboti*, *E. mionopastea*, *E. lequeuxi*, *E. oliveri*, *E. mazzeii*, *E. behouneki*, *E. hypermnestra*, *E. homaena*, *E. salaminia*, *E. cocalus*, *E. okurai*, *E. sikhimensis*, *E. tyrannus*, and *Gonodonta indentata*, the valve shape can be characterized by the blunt and level apex, which projects as a rectangle from the body of the valve (Fig. 27E). In *E. jordani*, *E. srivijayana*, and *E. boseae*, the valve shape is triangular (Fig. 27F). The valve condition in *E. kuehni* is markedly different from the rest of the taxa examined, because the cucullus is at a lower level than the proximal corner, which is sharply pointed (Fig. 27G). The tip of the cucullus is difficult to see as it is obscured by the sacculus, which lies above it. The other *E. phalonia* specimens, *E. discrepans*, *E. muscigera*, *E. imperator*, and *E. smaragdipicta* have valvae that are crescent-shaped with a distinct triangular projection on the distal tip of the apex (Fig. 27H). This triangle forms an almost square-shaped indentation between the distal and proximal corners of the apical margin of the valve. The valve condition in *E. bathyglypta* and *Plusiodonta incitans* is similar, except that the projection on the distal apical corner is square or rectangular (Fig. 27I). *Eudocima kinabaluensis*, the Papuan endemic, displays a unique valve shape which is similar to the condition present in *E. colubra* but is broadly rectangular with convex margins; the apical margin is level (Holloway 2005). In *E. splendida* (which shares similarities with *E. kinabaluensis* both in habitus and general configuration of male genitalia), the valvae are ovate and display two very large processi along the inner margin which are easily recognizable (Yoshimoto 1999). The valve conditions in both species of *Oraesia* are also distinctive; both have valvae which are long, slender and ovate, tapering to a

smooth point at the apex (Fig. 27J). The valve shape in *Phyllodes verhuelli* is paddle-like, with an unmistakable bulbous apical margin (Holloway 2005).

3.4.3.7 Character 23. *Cucullus, Fig. 28*: (0) entire, Fig. 28A; (1) separated or split, bifid, Fig. 28B.
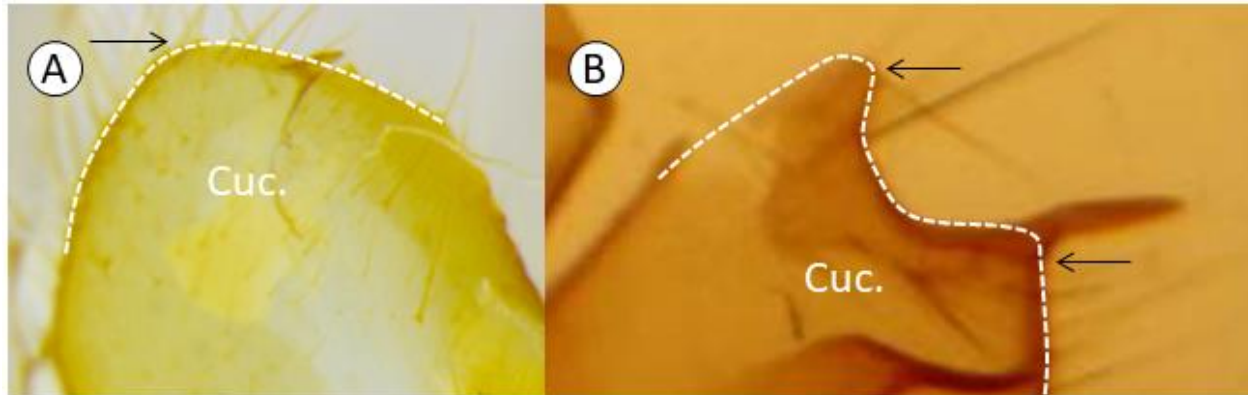
Figure 28. Cucullus, Character 23 (state, condition): **A)** *E. aurantia*, l. valve (0, entire); **B)** *E. serpentifera*, r. valve (1, separated or split, bifid). Margin of cucullus (Cuc.) indicated by dashed line, prominence(s) indicated by arrow(s). Processi from valve excluded from cucullus margin.

The split condition of the cucullus is present in *E. serpentifera*, *E. treadawayi*, *E. materna*, and *E. apta*. In these species, the cucullus is not uniform but divides into two prominences with space between them (Fig. 28B). Because of this, the true "apex" of the valve is difficult to distinguish. In the rest of the species examined, the cucullus is not split (Fig. 28A). *Eudocima kuehni* was coded as unknown (?), as the proximal part of the cucullus could not be seen under the sacculus.

3.4.3.8   Character 24. *Valve inner margin, Fig. 29*: (0) convex, Fig. 29A; (1) concave, Fig. 29B; (2) with protruding proximal corner at apex and projecting distal apical corner, Fig. 29C; (3) straight, Fig. 29D; (4) with protruding proximal corner at apex and no projection at distal apical corner, Fig. 29E.
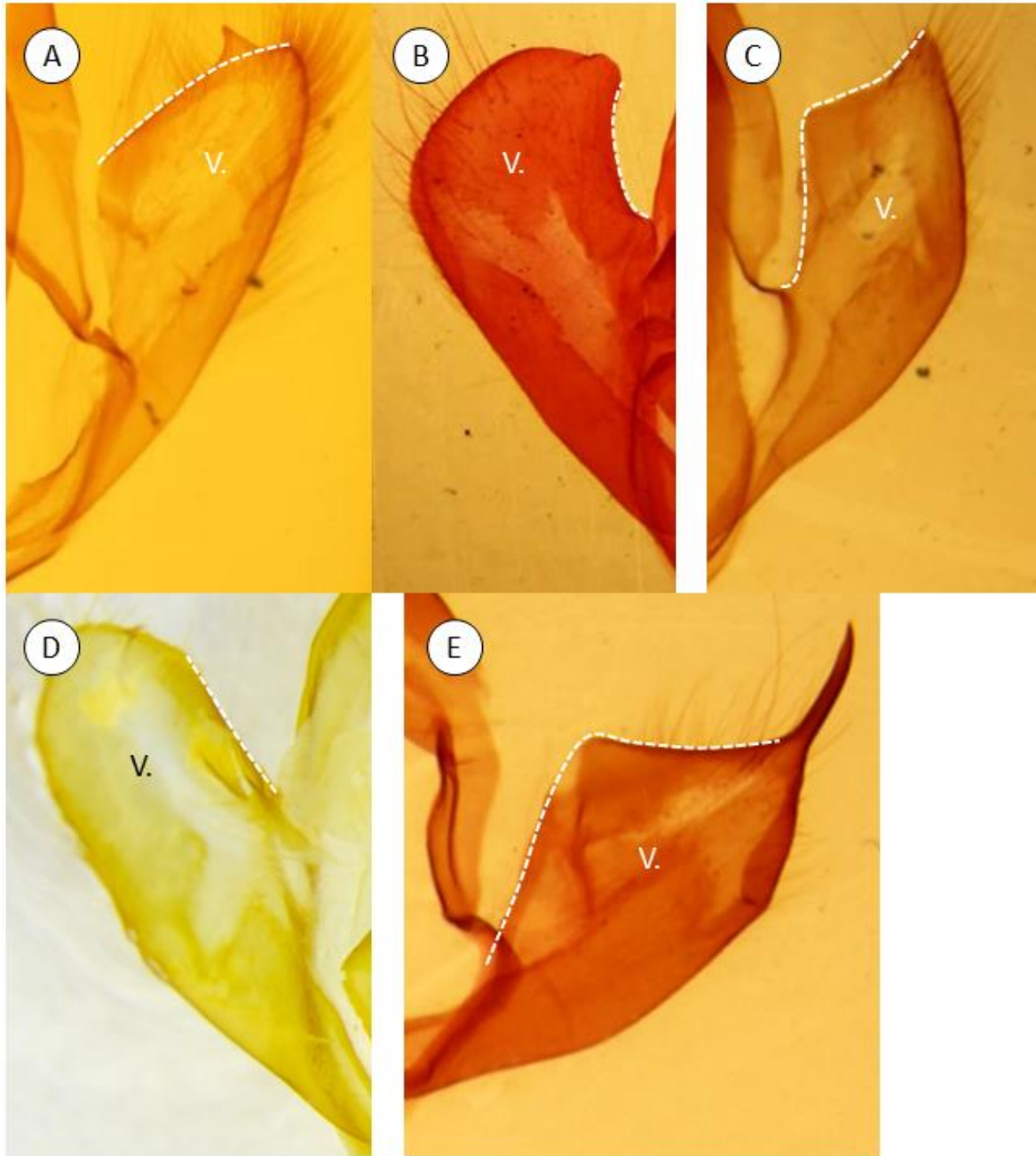
Figure 29. Valve inner margin, Character 24 (state, condition): A) E. cajeta, r. valve (0, convex); B) E. sikhimensis, l. valve (1, concave); C) E. phalonia, r. valve (2, with protruding proximal corner at apex and projecting distal apical corner); D) E. aurantia, l. valve (3, straight); E) E. srivijayana, r. valve (4, with protruding proximal corner at apex and no projection at distal apical corner). Dashed line indicates inner margin of valve (V.).

The inner margin of the valve is defined as the valve margin proximal to the midline in a spread, ventral view of the male genital capsule. In *E. cajeta*, *E. salaminia*, Indonesian *E. talboti*, *E. colubra*, *E. oliveri*, and *Oraesia triobliqua*, this margin is convex (Fig. 29A). The opposite is true of *E. sikhimensis* and *E. behouneki*, which have a uniformly concave margin (Fig. 29B). Most commonly, the valve inner margin is characterized by the proximal corner near the apex of the valve protruding inwards, and a projecting distal corner at the apex (Fig. 29C). This condition is present in ~42% of the taxa examined. In *E. tyrannus*, *E. cocalus*, *E. boseae*, *E. mionopastea*, *E. hypermnestra*, *E. steppingstonia*, *E. kinabaluensis*, and *Gonodonta indentata*, the inner margin of the valve is very nearly straight, without being markedly convex or concave (Fig. 29D). The condition in *E. iridescens*, *E. srivijayana*, *E. talboti* from New Guinea, *E. caesar*, *E. collusoria*, and *E. memorans* is similar to that found in character state (2) because of the protruding proximal corner of the apex, but it can be distinguished by the absence of a projecting distal corner (Fig. 29E). In these taxa, the distal corner is roughly on a level with the proximal corner.

3.4.3.9   Character 25. *Valve tip shape, Fig. 30*: (0) curved point, simple, Fig. 30A; (1) projecting triangle (not shown, Figs. 5A, 6A in Zilli et al. 2017); (2) blunt, rectangular, Fig. 30B.
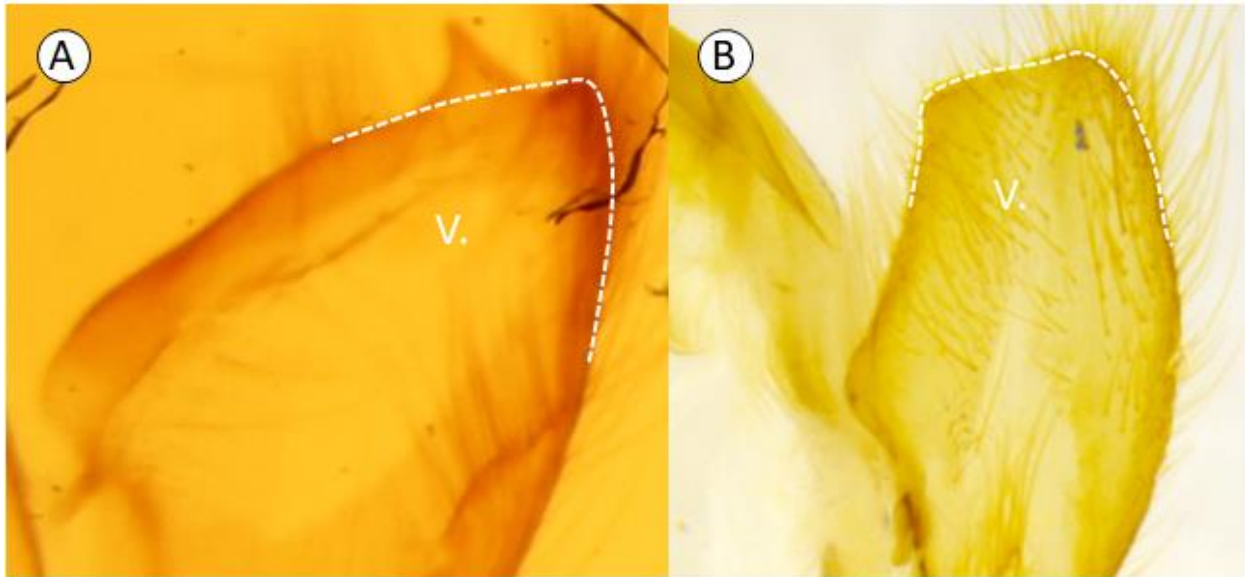
Figure 30. Valve tip shape, Character 25 (state, condition): **A)** *E. cajeta*, r. valve (0, curved point, simple); **B)** *E. cocalus*, r. valve (2, blunt, rectangular). Tip of valve (V.) indicated by dashed line.

In most *Eudocima*, as well as in the outgroups (~65% of taxa examined), the valve tip is a simple, curved point (Fig. 30A). In *E. talboti* from New Guinea, *E. oliveri*, *E. divitiosa*, and *E. collusoria*, the tip of the valve is a distinct triangular projection which gives a sinuous quality to the outer margin of the valve. *Eudocima tyrannus*, *E. sikhimensis*, *E. bathyglypta*, *E. okurai*, *E. cocalus*, *E. homaena* from Indonesia and the Philippines, *E. mionopastea*, *E. hypermnestra*, *E. mazzeii*, *E. behouneki*, *E. kinabaluensis*, and *E. lequeuxi* all have a blunt, rectangular valve tip (Fig. 30B).

3.4.3.10 Character 26. *Distal cucullus process, Fig. 31*: (0) absent, Fig. 31A; (1) present, Fig. 31B.

Figure 31. Distal cucullus process, Character 26 (state, condition): **A)** *E. cocalus*, r. valve (0, absent); **B)** *E. jordani*, r. valve (1, present). Distal process from cucullus (Cuc.) indicated by arrow.

The distal cucullus process refers to the process present on the distal corner of the apical margin of the valve (Fig. 31B). The distal process is specified in order to avoid confusion with species such as *E. serpentifera* which exhibit a split cucullus (see character 23). A distal cucullus process is present in *E. apta*, *E. srivijayana*, *E. materna*, *E. jordani*, *E. homaena*, *E. boseae*, *E. caesar*, *E. iridescens*, *E. cajeta*, *E. divitiosa*, *E. collusoria*, *E. splendida*, *E. memorans*, *E. serpentifera*, and *Phyllodes verhuelli*. No distal cucullus process is present (Fig. 31A) in the other taxa examined.

3.4.3.11 Character 27. *Shape of distal cucullus process, Fig. 32*: (0) sharply pointed, base broad to form shallow triangle, Fig. 32A; (1) long and filiform, Fig. 32B; (2) thin with a sharp point, Fig. 32C; (3) double points, split into two tips, Fig. 32D; (4) cone shape with a sharp point, Fig. 32E; (5) recurved, pointed triangle (not shown, Plate 447 in Holloway 2005).
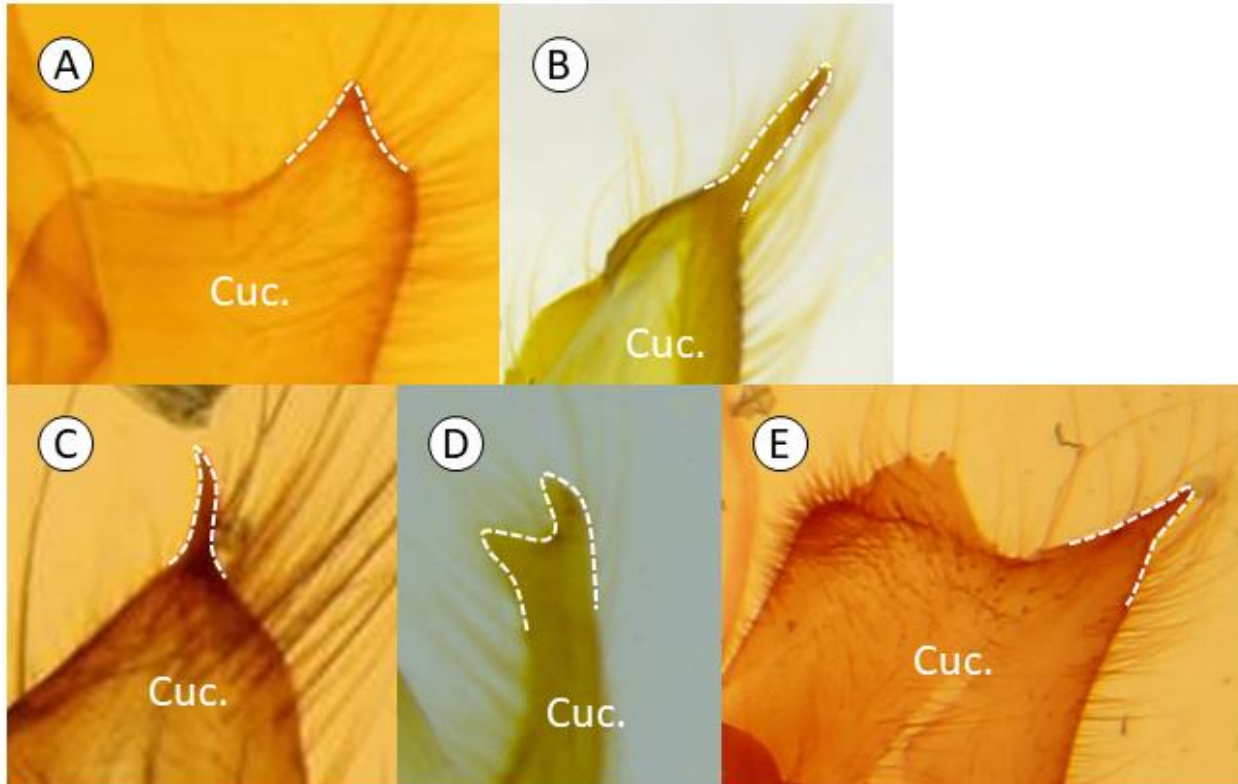
Figure 32. Distal cucullus process shape, Character 27 (state, condition): **A)** *E. divitiosa*, r. valve (0, sharply pointed, base broad to form shallow triangle); **B)** *E. jordani*, r. valve (1, long and filiform); **C)** *E. boseae*, r. valve (2, thin with a sharp point); **D)** *E. homaena*, r. valve (3, double points, split into two tips); **E)** *E. materna*, r. valve (4, cone shape with a sharp point). Distal process of cucullus (Cuc.) indicated by dashed line.

The distal process of the cucullus in *E. cajeta*, *E. caesar*, and *E. divitiosa* is sharply pointed with a broad base where it joins the cucullus (Fig. 32A); in *E. cajeta* and *E. divitiosa* a triangle shape is formed, while in *E. caesar* the process joins so smoothly with the cucullus that the transition is less apparent. The long and filiform condition (Fig. 32B) is present in *E. jordani*, *E. srivijayana*, and *E. serpentifera*. In *E. boseae*, *E. splendida*, and *E. memorans*, the distal cucullus process is slim and sharply pointed (Fig. 32C). The double-pointed condition of the process (Fig. 32D) is represented by *E. iridescens, E. collusoria,* and *E. homaena*. In *E. materna* and *E. apta*, the distal

process of the cucullus is prominent, conical, and narrows abruptly toward its tip into a sharp point (Fig. 32E). For *Phyllodes verhuelli* (Holloway 2005), the distal process is sharply pointed, triangular, and distinctively recurved such that the tip of the process is on the same level as the valve tip without rising above it.

3.4.3.12 Character 28. *Proximal cucullus process shape, Fig. 33*: (0) rounded hump, Fig. 33A; (1) projecting triangle, Fig. 33B.
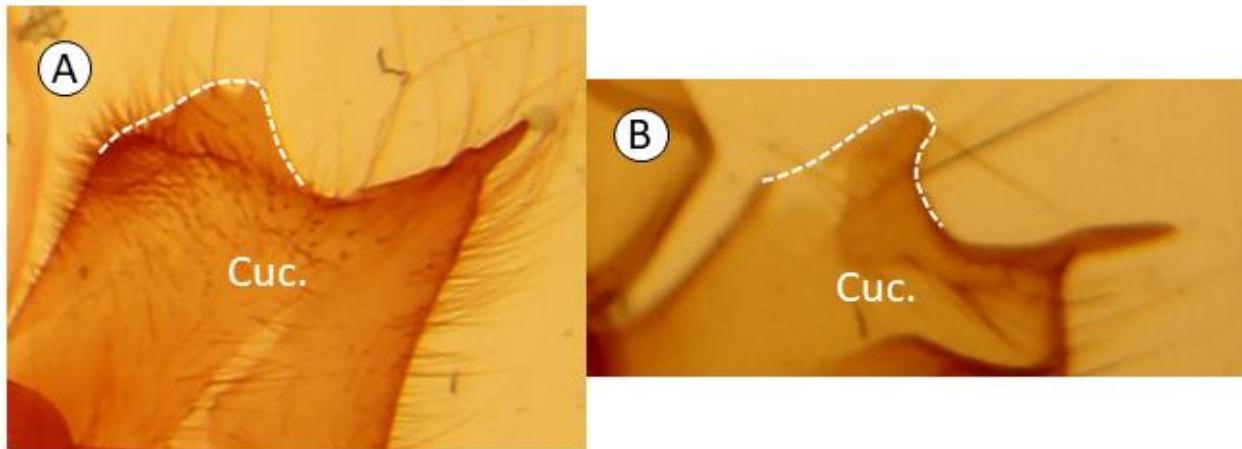
Figure 33. Proximal cucullus process shape, Character 28 (state, condition): **A)** *E. materna*, r. valve (0, rounded hump); **B)** *E. serpentifera*, r. valve (1, projecting triangle). Proximal process of cucullus (Cuc.) indicated by dashed line.

Few taxa in this study exhibit a proximal cucullus process; it is unnecessary to characterize in most *Eudocima* because only a few show a split cucullus. However, of the taxa with a split cucullus, *E. materna* and *E. apta* have a rounded process at the proximal point of the cucullus (Fig. 33A), while *E. serpentifera* has a triangular projection with a rounded point (Fig. 33B). Two other *Eudocima* without a split cucullus were also coded for this character, namely *E. kuehni* and *E. kinabaluensis*, which were given the same condition as *E. serpentifera*. In *E. kuehni*, although the distal portion of the cucullus is obscured by the sacculus, the visible proximal portion is pointed and triangular in a manner similar to *E. serpentifera*, though with a sharper point. *Eudocima kinabaluensis* is interesting because while other *Eudocima* with a cucullus process (without a split cucullus) express the process distally, *E. kinabaluensis* has a cucullus process on the proximal corner of the valve's apical margin (Holloway 2005). This process is triangular and sharp, and while it is smaller than those present in *E. serpentifera* and *E. kuehni*, it was coded as the same character state. For *E. splendida*, it was not clear whether the large process in the distal position on the valve is a homologous structure to the one characterized here, since the valve in *E. splendida* does not appear to be split (Yoshimoto 1999); therefore, *E. splendida* was coded as uncertain (?) for this character.

3.4.3.13 Character 29. *Tegumen process, Fig. 34*: (0) absent, Fig. 234A; (1) present, Fig. 34B.
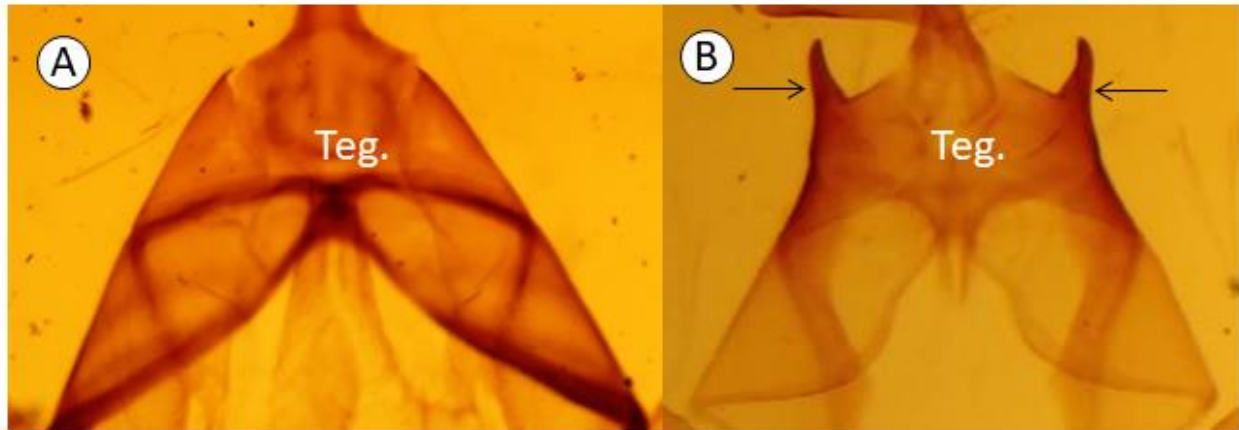
Figure 34. Tegumen process, Character 29 (state, condition): **A)** *E. kuehni* (0, absent); **B)** *E. smaragdipicta* (1, present). Processi from tegumen (Teg.) indicated by arrows.

This character represents *E. smaragdipicta*, which alone among the *Eudocima* examined exhibits paired processi arising from the tegumen on either side of the uncus (Fig. 34B).

3.4.3.14 Character 30. *Saccus shape, Fig. 35*: (0) shallow "U" shape with slim arms, Fig. 35A; (1) pointed "V" shape with stout arms, Fig. 35B; (2) stirrup-shaped with arms that widen toward the base at their junction, Fig. 35C; (3) similar to state (0), but extends deeper into a "V" or cup shape with slim arms and small notch at center, Fig. 35D; (4) broad inverted triangle surrounded by membranous outer layer, stout vinculum arms, Fig. 35E; (5) arms narrow at their juncture, with broad flaps anteriorly, Fig. 35F; (6) long, half as deep as valvae are long, narrow, Fig. 35G.
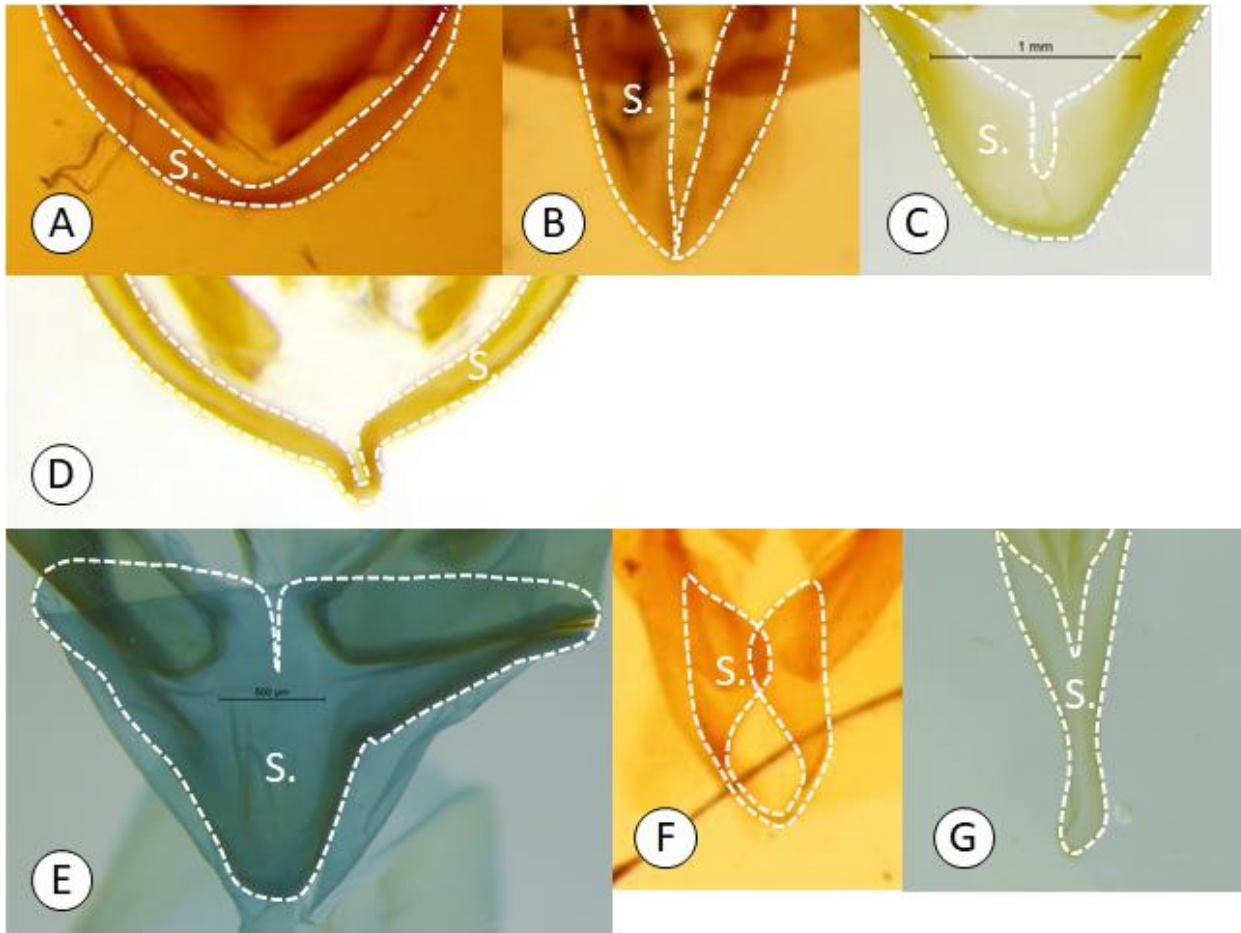
Figure 35. Saccus shape, Character 30 (state, condition): **A)** *E. euryzona* (0, shallow "U" shape with slim arms); **B)** *E. colubra* (1, pointed "V" shape with stout arms); **C)** *E. materna* (2, stirrup-shaped with arms that widen toward the base at their junction); **D)** *E. cocalus* (3, similar to state 0 but extends deeper into a "V" or cup shape with slim arms and small notch at tip); **E)** *E. salaminia* (4, broad inverted triangle surrounded by membranous outer layer, stout vinculum arms); **F)** *E. procus* (5, arms narrow at their juncture, with broad flaps anteriorly); **G)** *Oraesia argyrosigna* (6, long, half as deep as valvae are long, narrow). Saccus (S.) shape indicated by dashed line.

The shallow "U"-shaped condition of the saccus is shared by *E. phalonia*, *E. okurai*, *E. srivijayana*, *E. jordani*, *E. imperator*, *E. cajeta*, and *E. euryzona* (Fig. 35A). For these taxa,

the arms of the vinculum are slim and uniform in thickness, and the saccus is shallow in depth. In *E. colubra*, *E. memorans*, and *E. apta*, the arms are thicker, and meet at the base of the saccus in a point (Fig. 35B). The diameter between the two arms is also more constricted than in state (0), lending the whole structure to a "V" shape. *Eudocima bathyglypta*, *E. srivijayana*, *E. materna*, *E. caesar*, the *E. homaena* from Taiwan, *E. caesar*, *E. talboti*, *E. serpentifera*, *E. smaragdipicta*, *E. martini*, *E. kinabaluensis*, *E. splendida*, *Plusiodonta incitans*, *Phyllodes consobrina*, and *Gonodonta indentata* share a stirrup-shaped saccus characterized by arms that widen gradually until they meet at the saccus base (Fig. 35C). In *E. tyrannus*, *E. cocalus*, *E. homaena* from Indonesia and the Philippines, *E. dividens*, *E. boseae*, *E. muscigera*, *E. iridescens*, *E. mionopastea*, *E. hypermnestra*, *E. prolai*, *E. treadawayi*, *E. steppingstonia*, and *E. oliveri* the arms of the vinculum are slim as in *E. phalonia*, but the saccus is deeper and meets in a "V" shape at the saccus base (Fig. 35D). This state can be distinguished from state (1) by the thinner diameter of the vinculum arms and the small dip or notch usually present where the arms meet. In *E. salaminia*, *E. dividens*, *E. aurantia*, *E. paulii*, *E. divitiosa*, *E. lequeuxi*, *E. sikhimensis*, *E. mazzeii*, and *E. behouneki*, the saccus is a broad inverted triangle formed by the stout arms of the vinculus, which meet under the valves and extend downward to a point (Fig. 35E). The space between where the arms come together and the base of the valvae is not very wide. The saccus is also surrounded by a membranous layer which contributes to holding the genital capsule in a tight three-dimensional shape. *Eudocima procus* and *E. collusoria* have a saccus with vincular arms which bulge into flaps, and then narrow abruptly to where they meet at the saccus base (Fig. 35F). In both *Oraesia* species, the saccus is narrow and twice as deep as seen in species of *Eudocima* (Fig. 35G).

3.4.3.15 Character 31. *Uncus length, Fig. 36*: (0) medium, thumb-like, Fig. 36A; (1) short, knob-like, Fig. 36B; (2) long, similar in length to tegumen arms, Fig. 36C.
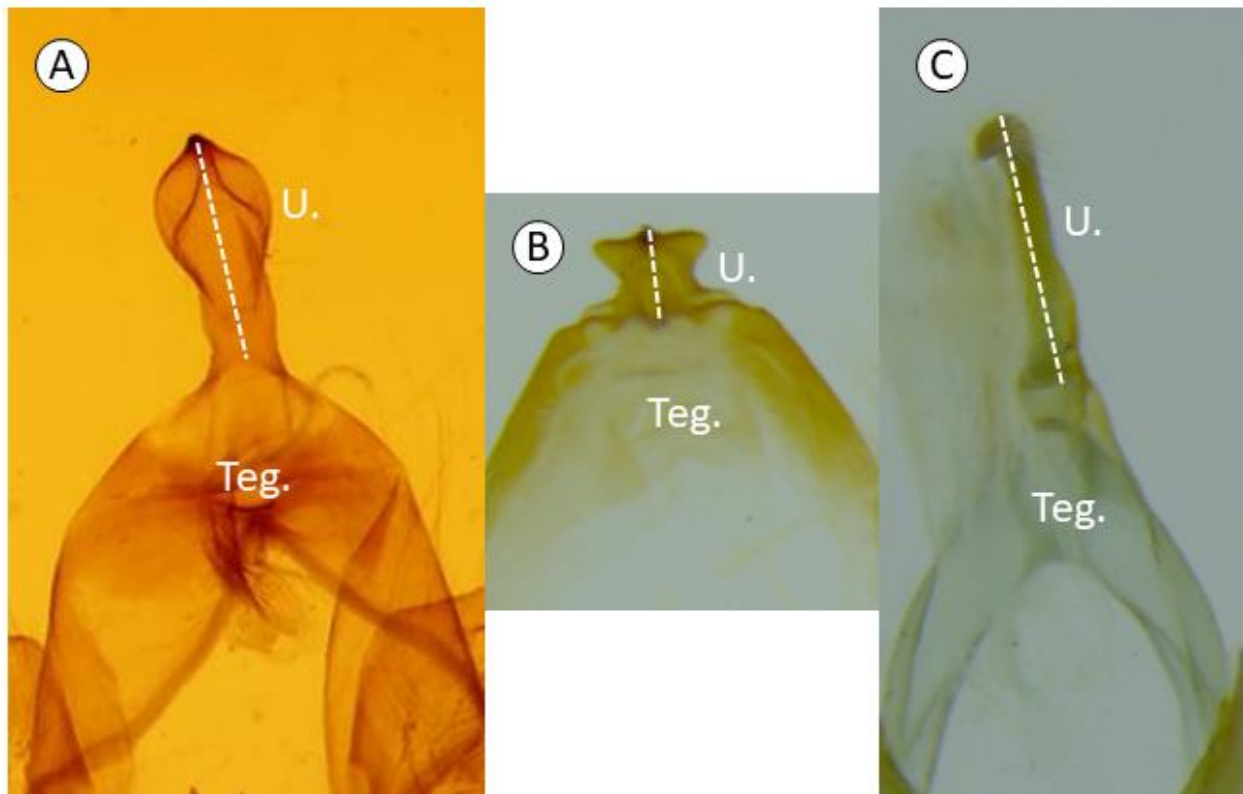
Figure 36. Uncus length, Character 31 (state, condition): **A)** *E. paulii* (0, medium, thumb-like); **B)** *E. homaena* (1, short, knob-like); **C)** *Plusiodonta incitans* (2, long, similar in length to tegumen arms). Approximate uncus (U.) length shown by dashed line, with tegumen (Teg.) below for reference.

The medium, thumb-like condition (Fig. 36A) is most common in *Eudocima*. The short, knob-like condition (Fig. 36B) is shared by *E. srivijayana*, *E. homaena*, *E. caesar*, and *E. iridescens*. The long condition, in which the uncus is nearly as long as the arms of the tegumen (Fig. 36C), is present in *Plusiodonta incitans*, *Gonodonta indentata*, and both *Oraesia* species, as well as in *E. kuehni*, *E. procus*, *E. colubra*, *E. memorans*, *E. steppingstonia*, *E. splendida*, *E. oliveri*, and *E. martini* among the *Eudocima*.

3.4.3.16 Character 32. *Uncus shape, Fig. 37*: (0) clavate, with a hooded apex, Fig. 37A; (1) thick, without apical swelling, Fig. 37B; (2) slender, with slight swelling near apex, Fig. 37C; (3) slender, attenuate, Fig. 37D; (4) clavate, with fingerlike projections extending from the hood of the apex, Fig. 37E.
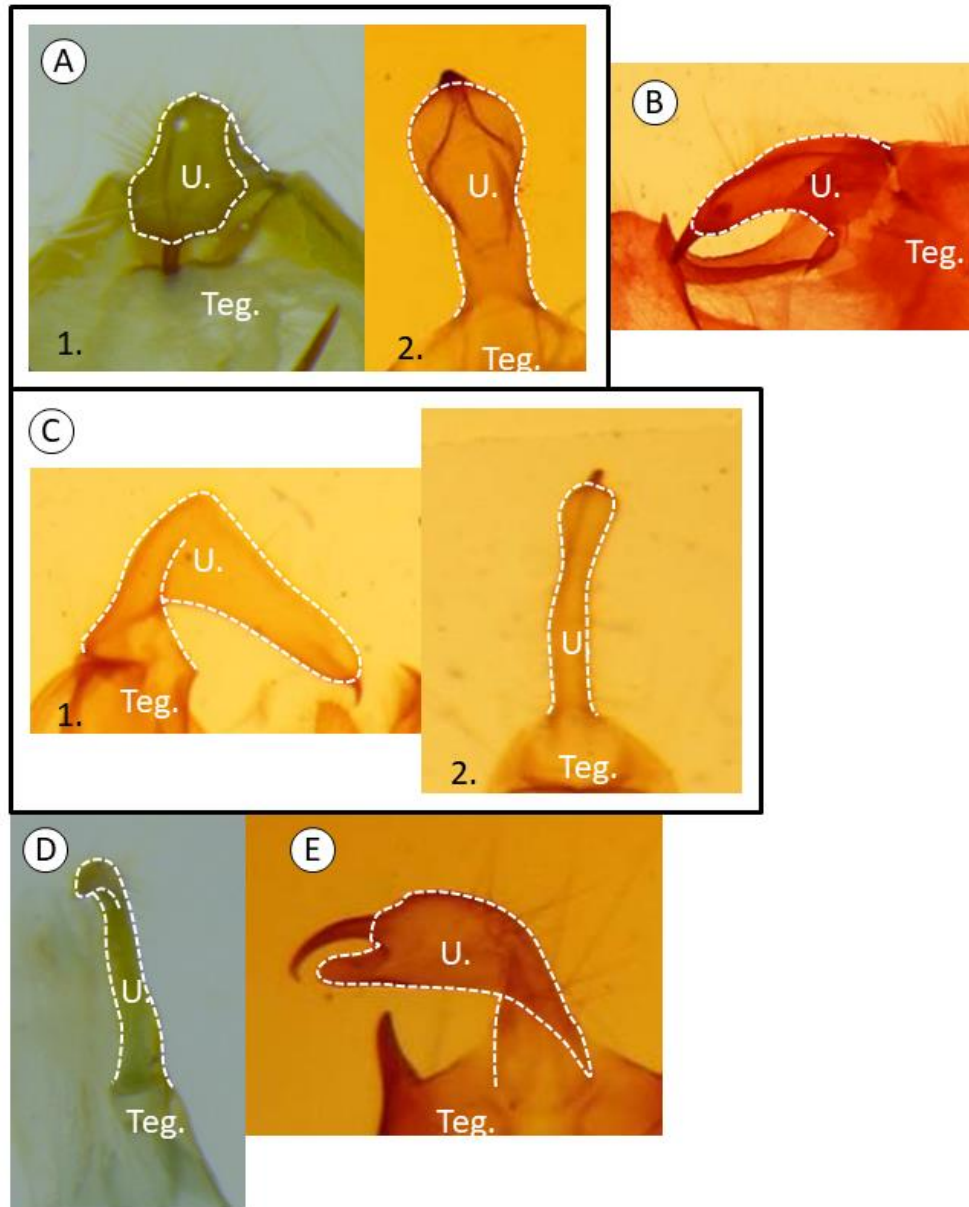
Figure 37. Uncus length, Character 32 (state, condition): **A)** *E. jordani* (A1) and *E. phalonia* (A2) (0, clavate, with a hooded apex); **B)** *E. bathyglypta* (1, thick, without apical swelling); **C)** *E. procus* (C1) and *E. memorans* (C2) (2, slender, with slight swelling near apex); **D)** *Plusiodonta incitans* (3, slender, attenuate); **E)** *E. smaragdipicta* (4, clavate, with fingerlike projections extending from the hood of the apex). Uncus (U.) shape indicated by dashed line (some examples folded over). Uncus hook not included in outlined shape. Tegumen (Teg.) labelled for reference.

The clavate, hooded condition (Fig. 37A) is most prevalent, and was observed in more than half of the *Eudocima* examined (~60%). The thick, tapering uncus condition is representative of *E. mazzeii*, *E. oliveri*, *E. colubra*, *E. okurai*, and *E. bathyglypta*, and does not show any swelling at the uncus apex (Fig. 37B). In *E. procus* and *E. muscigera*, the uncus is more slender, and is uniformly thick or somewhat capitate at the apex without being dramatically hooded (Fig. 37C). The slender and attenuate condition (Fig. 37D), found in *E. kuehni*, *E. memorans*, *E. prolai*, and *E. martini*, is also shared by *Plusiodonta incitans*, *Gonodonta indentata*, and both species of *Oraesia* among the outgroups. A long, slender uncus without apical swelling is symplesiomorphic. In *E. imperator,* one of the *E. cajeta* specimens without locality data, *E. smaragdipicta*, *E. splendida*, *E. kinabaluensis*, and *E. aurantia*, the uncus is clavate and hooded, but also possesses paired fingerlike extensions which extend on either side of the hook at the uncus apex and appear under the apical hook when the hood is folded over (Fig. 37E).

3.4.3.17 Character 33. *Uncus hook, Fig. 38*: (0) absent (not shown); (1) present, Fig. 38.
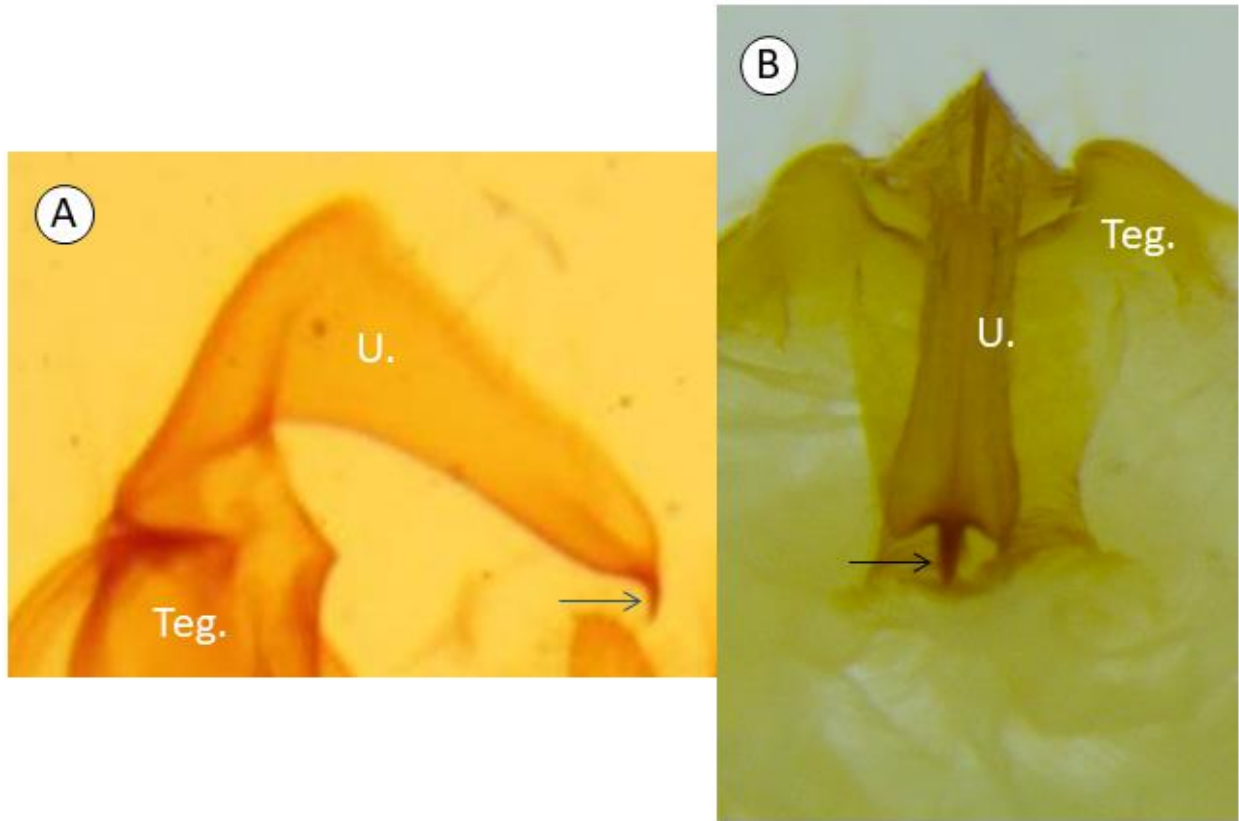
Figure 38. Uncus hook, Character 33 (state, condition): **A)** *E*. procus, **B)** *E. aurantia* (1, present). Uncus (U.) hook indicated by arrow. Tegumen (Teg.) labelled for reference.

A hook at the tip of the uncus (Figs. 38A, 38B) was present in all observed taxa.

3.4.3.18 Character 34. *Aedeagus shape, Fig. 39*: (0) thick, thumb-like, Fig. 39A; (1) thinner than (0), finger-like, Fig. 39B; (2) very thin, rod-like, Fig. 39C.

Figure 39. Aedeagus shape, Character 34 (state, condition): A) E. materna (0, thick, thumb-like); B) E. cocalus (1, thinner than (0), finger-like); C) Oraesia argyrosigna (2, very thin, rod-like). Shape of aedeagus (Ae.) indicated by dashed line.

In *Eudocima*, the aedeagus is typically either stout and thumb-like (Fig. 39A), or slightly longer and more slender (finger-like) (Fig. 39B). The thin and rod-like condition (Fig. 39C) is restricted

to the two examined *Oraesia* species. In *Oraesia argyrosigna*, the condition is particularly pronounced, and although the aedeagus in *O. triobliqua* is comparatively thicker, it was still considered more slender than the finger-like condition in some *Eudocima* and coded as the same state. The aedeagus is compact and stout in ~55% of included taxa. The more slender condition was present in *E. tyrannus*, *E. okurai*, *E. cocalus*, *E. srivijayana*, *E. salaminia*, *E. kuehni*, *E. talboti*, *E. mionopastea*, *E. paulii*, *E. cajeta*, *E. euryzona*, *E. hypermnestra*, *E. serpentifera*, *E. prolai*, and *E. martini*. In *E. caesar* and *E. homaena*, the aedeagus is only slightly more slender than *E. iridescens*, but in these species it is still scored as finger-like.

3.4.3.19 Character 35. *Spines of carina, Fig. 40*: (0) absent, Fig. 40A; (1) present, extending completely around the phallobase, Fig. 40B; (2) present, not extending around the phallobase, Fig. 40C.
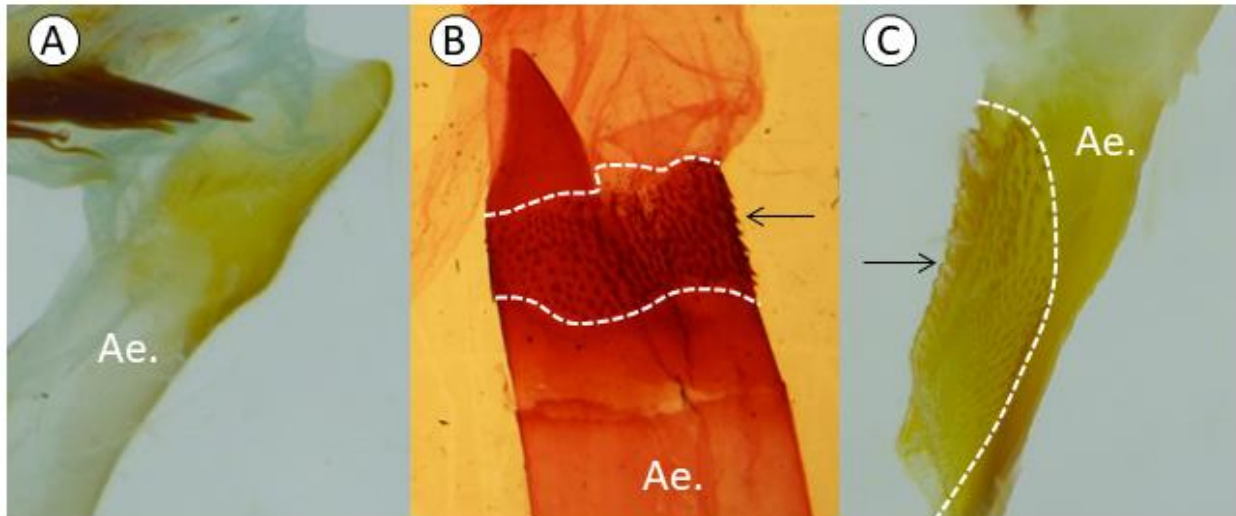
Figure 40. Spines of carina, Character 35 (state, condition): **A)** *E. jordani* (0, absent); **B)** *E. sikhimensis* (1, present, extending completely around the phallobase); **C)** *E. aurantia* (2, present, not extending around the phallobase). Margin of region with carina spines indicated by dashed line, region of carina spines indicated by arrow. Aedeagus (Ae.) labelled for reference.

In most *Eudocima* species (~70%), the tip of the aedeagus from which the vesica emerges is smooth and uniform. However, in *E. tyrannus*, *E. sikhimensis*, *E. okurai*, *E. materna*, *E. paulii*, *E. behouneki*, and *E. martini*, a region of small, rough spines forms a muricate band around the aedeagus tip (Fig. 40B). In *E. apta*, the *E. cocalus* specimen from Papua, *E. aurantia*, *E. dividens*, *E. kuehni*, *E. mionopastea*, and *E. mazzeii*, this muricate region does not extend all the way around the phallobase, but instead forms a rough patch (Fig. 40C).

3.4.3.20 Character 36. *Vesica texture, Fig. 41*: (0) smooth, Fig. 41A; (1) rugose, Fig. 41B.

Figure 41. Vesica texture, Character 36 (state, condition): **A)** *E. cocalus* (0, smooth); **B)** *E. materna* (1, rugose). Patch of vesica (Ves.) showing texture indicated by arrow. Aedeagus (Ae.) labelled for reference.

The majority (~80%) of *Eudocima* examined have a smooth vesica membrane (Fig. 41A), while in *E. apta*, *E. salaminia*, *E. materna*, *E. kuehni*, *E. divitiosa* the vesica surface is wrinkled or corrugated (Fig. 41B). The smooth condition also prevails in the examined outgroup taxa. This character was difficult at times to score because of incomplete eversion of the vesica or wrinkling of the vesica membrane due to slide mounting.

3.4.3.21 Character 37. *Cornuti coverage, Fig. 42*: (0) absent from vesica body, Fig. 42A; (1) present, one patch, Fig. 42B; (2) present, two patches, Fig. 42C; (3) present, three or more patches, Fig. 42D; (4) present, dispersed over vesica, Fig. 42E.

Figure 42. Cornuti coverage, Character 37 (state, condition): **A)** *E. kuehni* (A1) and *E. tyrannus* (A2) (0, absent from vesica body); **B)** *E. phalonia* (1, present, one patch); **C)** *E. jordani* (2, present, two patches); **D)** *E. divitiosa* (D1) and *E. salaminia* (D2) (3, present, three or more patches); **E)** *E. collusoria* (4, present, dispersed over vesica). Cornuti patches (when present) indicated by arrows. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.
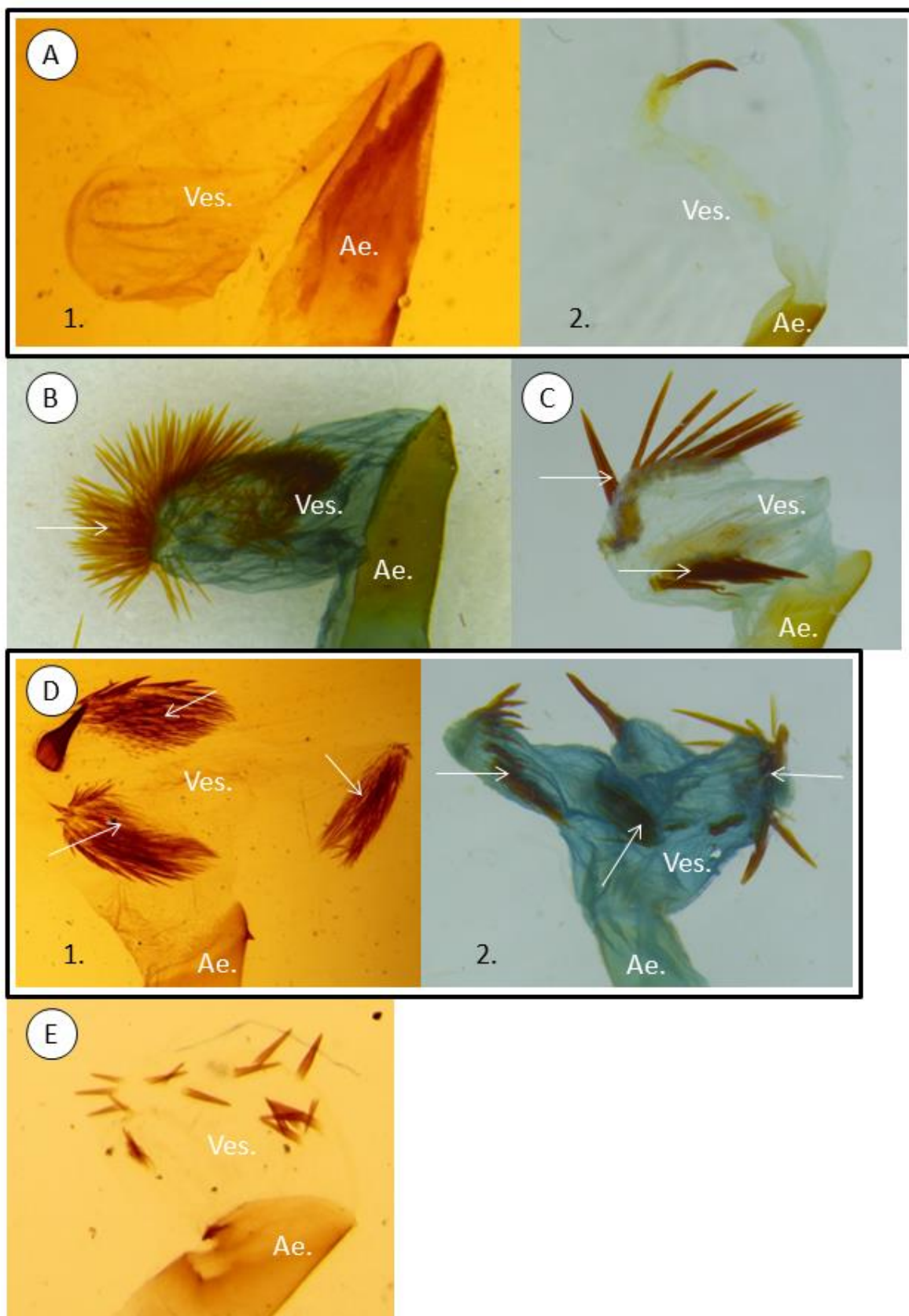
Cornuti was coded as absent from the body (Fig. 42A) either if no cornuti of any kind was present (as in *E. kuehni*) (Fig. 42A, 1), or if only a single stout spine was observed (as in *E. tyrannus*) (Fig. 42A, 2). This is because typically the single spine occurs at the vesica apex, and it seemed unjustifiable to categorize a single spine as an entire patch. This condition includes *E. tyrannus*, *E. bathyglypta*, *E. sikhimensis*, *E. okurai*, *E. kuehni*, *E. mionopastea*, *E. smaragdipicta*, *E. mazzeii*, *E. behouneki*, *E. prolai*, *E. splendida*, *E. kinabaluensis*, and *Phyllodes verhuelli*. In *E. phalonia*, *E. homaena*, *E. procus*, *E. iridescens*, *E. talboti*, *E. caesar*, *E. paulii*, *E. cajeta*, *E. euryzona*, *E. steppingstonia*, *E. lequeuxi*, *E. oliveri*, and *Oraesia triobliqua*, a single cornuti patch was present on the vesica (Fig. 42B). Two separate cornuti patches (Fig. 42C) were observed in *E. cocalus*, *E. srivijayana*, *E. jordani*, *E. boseae*, *E. discrepans*, *E. muscigera*, *E. hypermnestra*, and *E. treadawayi*. Three or more cornuti patches (Fig. 42D) are present in *E. serpentifera*, *E. divitiosa*, *E. imperator*, *E. materna*, *E. salaminia*, *E. apta*, and *Gondonta indentata*. In *E. collusoria* and *E. memorans*, the cornuti are not arranged in distinct patches but are distributed evenly across the surface of the vesica (Fig. 42E).

3.4.3.22 Character 38. *Multiple types of cornuti, Fig. 43*: (0) absent, Fig. 43A; (1) present, Fig. 43B.

Figure 43. Multiple types of cornuti, Character 38 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. materna* (1, present). Different types of cornuti indicated by arrows. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

This character refers to whether a taxon has only a single morphological form of cornuti (Fig. 43A), or whether multiple forms are present together (Fig. 43B). Taxa with various forms of cornuti present include *E. sikhimensis*, *E. apta*, *E. cocalus*, *E. srivijayana*, *E. materna*, *E. dividens*, *E. imperator*, *E. talboti*, *E. paulii*, *E. cajeta*, *E. divitiosa*, *E. hypermnestra*, *E. serpentifera*, *E. mazzeii*, and *E. treadawayi*. *Gonodonta indentata* also has multiple cornuti types. The rest of *Eudocima* (~62%) have only a single type of cornuti.

3.4.3.23 Character 39. *Deciduous cornuti, Fig. 44*: (0) absent, Fig. 44A; (1) present, Fig. 44B.
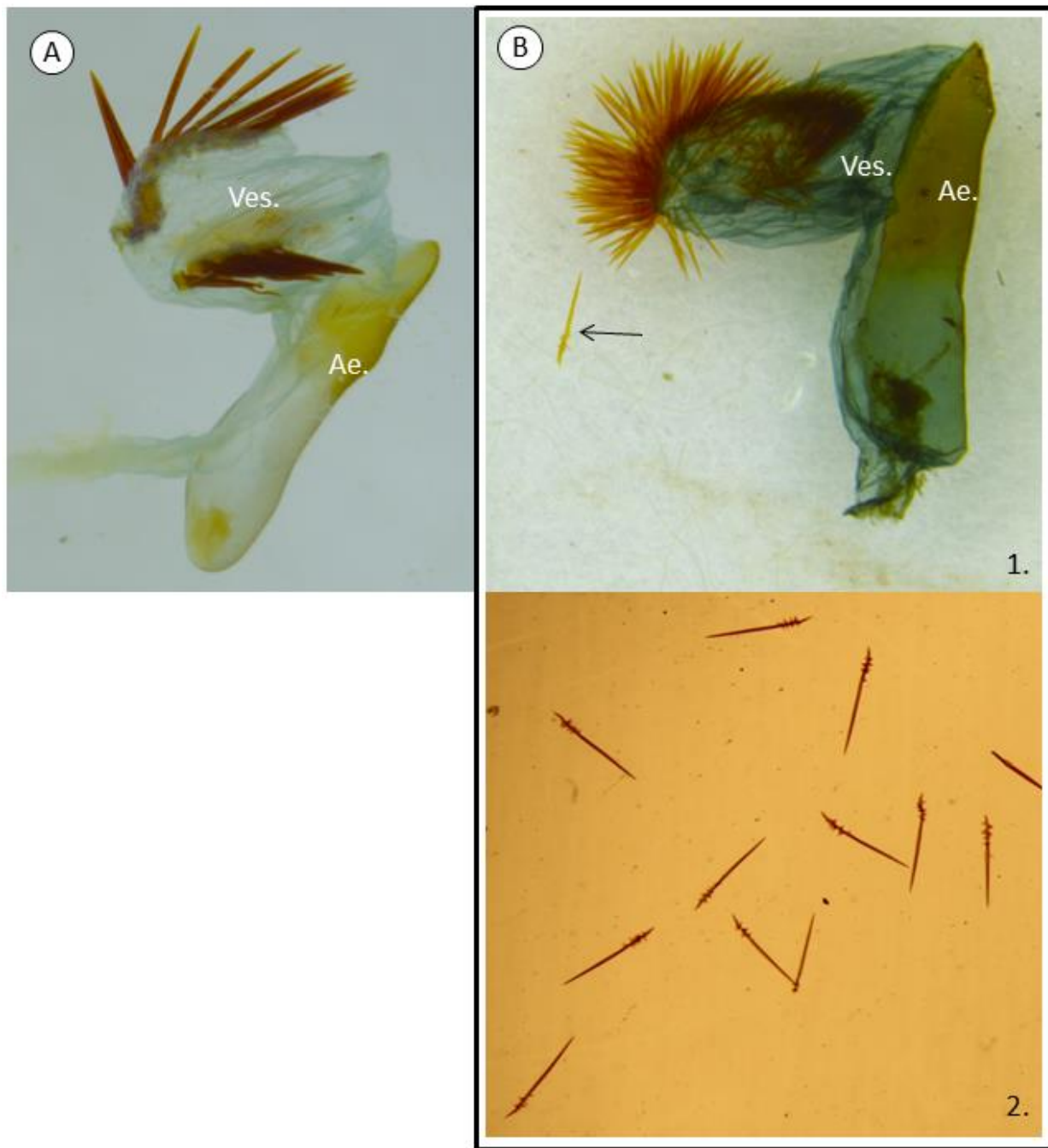
Figure 44. Multiple types of cornuti, Character 39 (state, condition): **A)** *E. jordani* (0, absent); **B)** *E. phalonia*, deciduous cornutus indicated by arrow (B1) and detached *E. phalonia* deciduous cornuti (B2) (1, present). Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

Cornuti that are able to detach from the vesica and remain in the female copulatory tract (Fig. 44B) can be found in males of *E. phalonia*, *E. cocalus*, *E. hypermnestra*, *E. srivijayana*, *E. jordani*, *E. homaena*, *E. caesar*, *E. iridescens*, *E. talboti*, *E. cajeta*, and *E. euryzona*. These cornuti may become detached from the vesica during dissections or examination of previously dissected material, and can also be observed as detached on previously mounted genitalia slides or inside the bursae copulatrix of females. Deciduous cornuti in *Eudocima* are always in the form of thin straight spines, which are also distinguished by a series of barbs projecting laterally near the base; this allows deciduous cornuti to be identified while still attached to the vesica membrane. Some *Eudocima* species have only deciduous cornuti, while others possess both deciduous and non-deciduous types. Hypothesized functions of deciduous cornuti are discussed in Cordero (2010); these include possible utility in breaking apart the spermatophore, damaging or interfering with the positioning of the spermatophores of other males inside the corpus bursae, stimulating the female reproductive tract post-copulation, or damaging the copulatory tract to prevent further matings (Cordero 2010). Because more morphological variety can be observed in non-deciduous cornuti, it is hypothesized that differences in form are more strongly influenced by sexual selection in cornuti which remain attached (Cordero 2010).

3.4.3.24 Character 40. *Stout spike(s) on body of vesica, Fig. 45*: (0) absent, Fig. 45A; (1) one present, Fig. 45B; (2) multiple present, Fig. 45C.
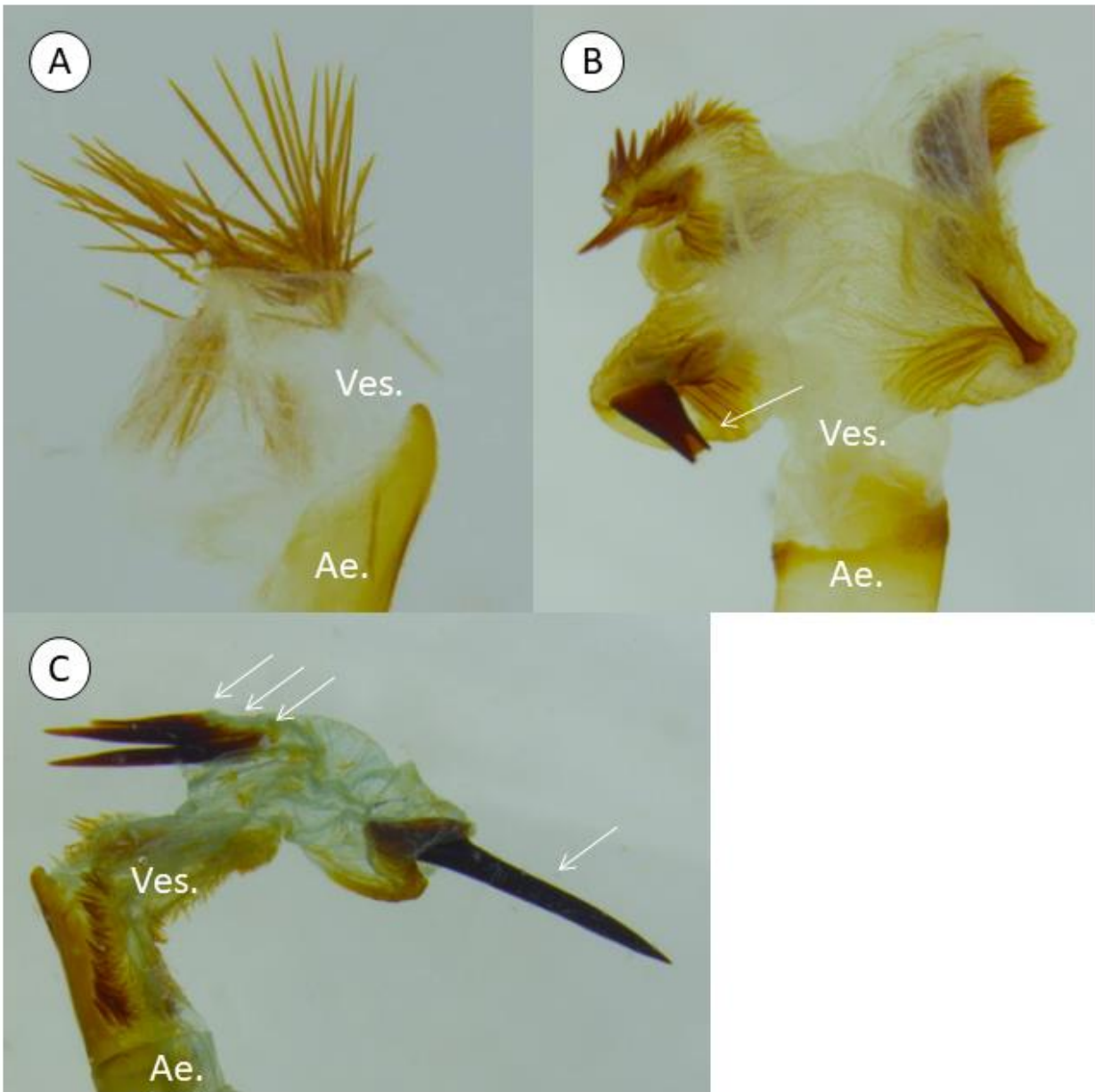
Figure 45. Stout spikes present on body of vesica, Character 40 (state, condition): **A)** *E. homaena* (0, absent); **B)** *E. materna* (1, one present); **C)** *E. dividens* (2, multiple present). Stout spikes indicated by arrows. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

Stout spikes are distinguishable by their wide bases, large size, and heavy sclerotization. This character describes species with stout spikes on the vesica body, rather than the vesica apex. Stout spikes, while always large, may be any length, and can be separated from other cornuti by

the wide base (Figs. 45B, 45C). In some *Eudocima* species, the vesica is multilobed without a clear apex, and in these cases any stout spikes present were coded under this character. Taxa with a single spike (Fig. 45B) include *E. materna*, *E. salaminia*, *E. imperator*, *E. divitiosa*, *E. splendida*, and *E. serpentifera*, while *E. apta* and *E. dividens* have multiple stout spikes (Fig. 45C).

3.4.3.25 Character 41. *Apical spike of vesica, Fig. 46*: (0) absent, Fig. 46A; (1) present, Fig. 46B.
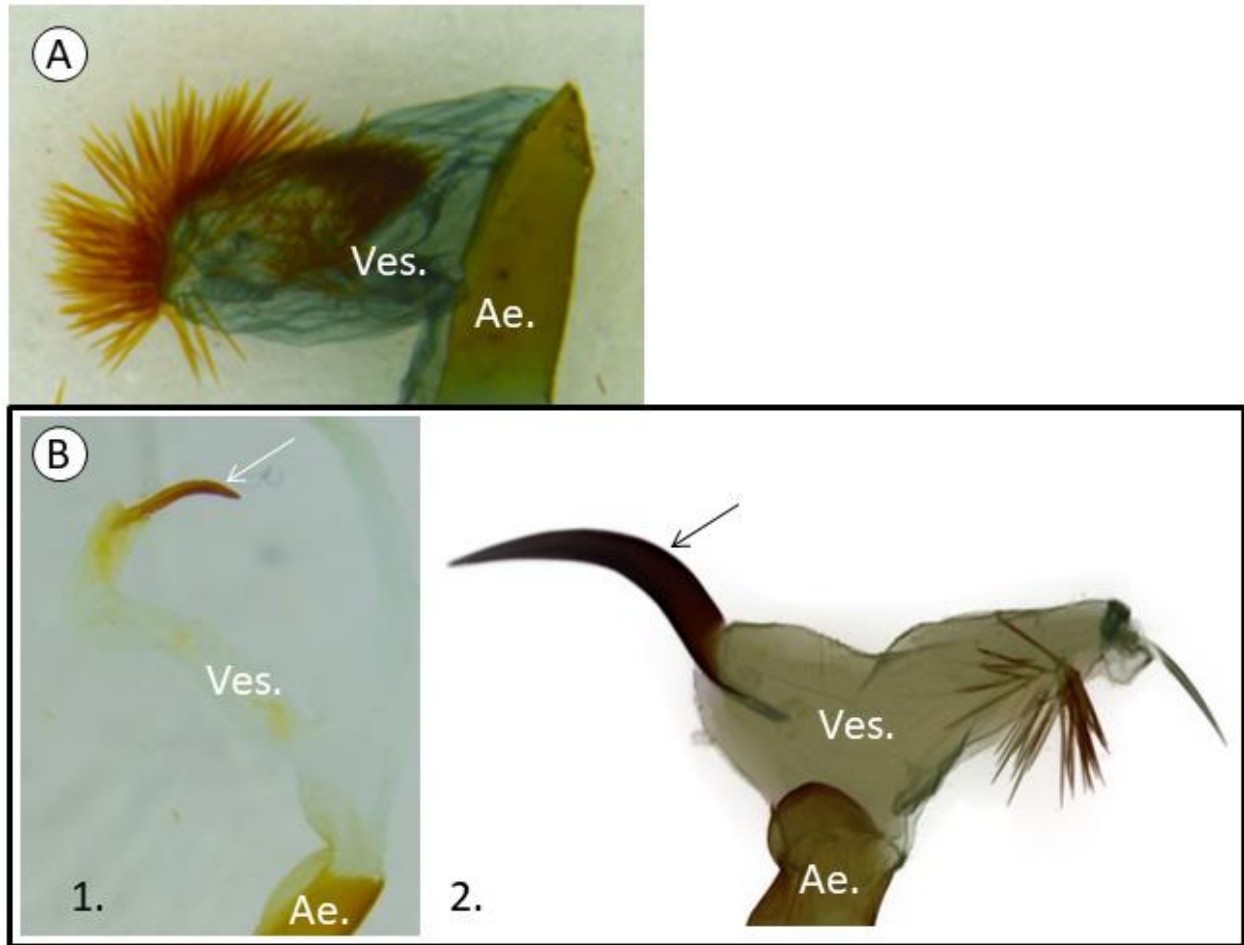
Figure 46. Apical spike of vesica, Character 41 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. tyrannus* (B1) and *E. talboti* (B2) (1, present). Apical spike of vesica (Ves.) indicated by arrow. Aedeagus (Ae.) labelled for reference.

The vesica apex is here defined in *Eudocima* as the tip of the longest lobe (see character 40). In some *Eudocima* species, a stout spike is present at the apex of the vesica, which is termed an apical spike (Fig. 46B). These species include *E. tyrannus*, *E. sikhimensis*, *E. bathyglypta*, *E. okurai*, *E. salaminia*, *E. aurantia*, *E. talboti*, *E. mionopastea*, *E. paulii*, *E. cajeta*, *E. smaragdipicta*, *E. kinabaluensis*, *E. mazzeii*, *E. behouneki*, and *E. prolai*. In *E. talboti*, the longest lobe of the vesica was ambiguous; however, the stout spike was scored as apical (Fig. 46B, 2) because of the similarity of genital configuration to males of *E. cajeta*, and due to the possibility of the ductus ejaculatoris becoming everted during eversion of the vesica.

3.4.3.26 Character 42. *Curved stout spike, Fig. 47*: (0) absent, Fig. 47A; (1) present, Fig. 47B.
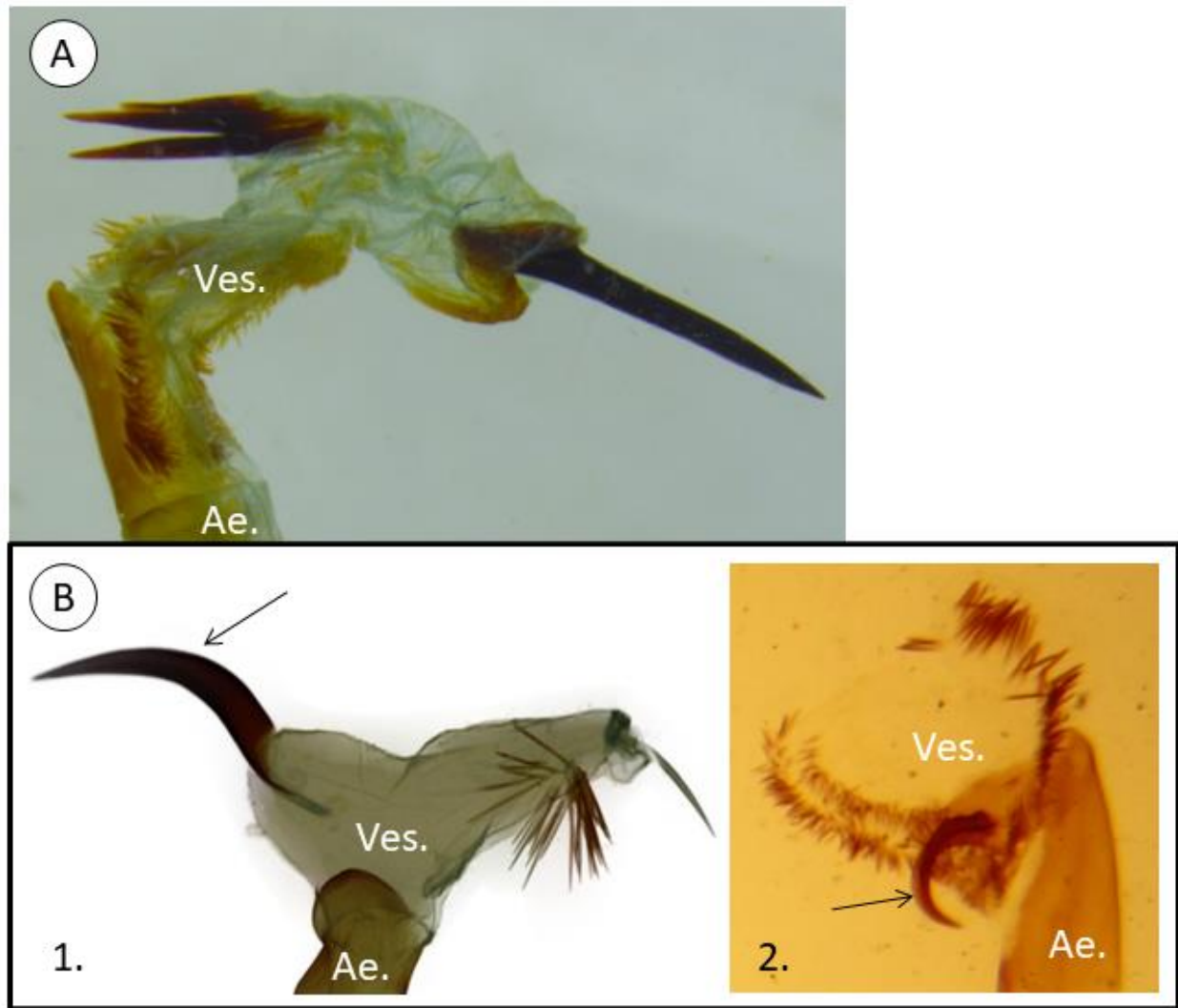
Figure 47. Curved stout spike, Character 42 (state, condition): **A)** *E. dividens* (0, absent); **B)** *E. talboti* (B1) and *E. serpentifera* (B2) (1, present). Curved stout spike indicated by arrow. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

This character describes the condition of any stout spike present on the vesica, whether on the vesica body or on the apex. In *E. talboti*, *E. serpentifera*, *E. smaragdipicta*, and the Chinese replicate of *E. tyrannus*, the stout spike present is curved or hooked (Fig. 47B). The curve may be slight, or very pronounced as in *E. serpentifera* (Fig. 47B, 2).

3.4.3.27 Character 43. *Medium-size, non-deciduous cornuti, Fig. 48* (0) absent, Fig. 48A; (1) present, Fig. 48B.
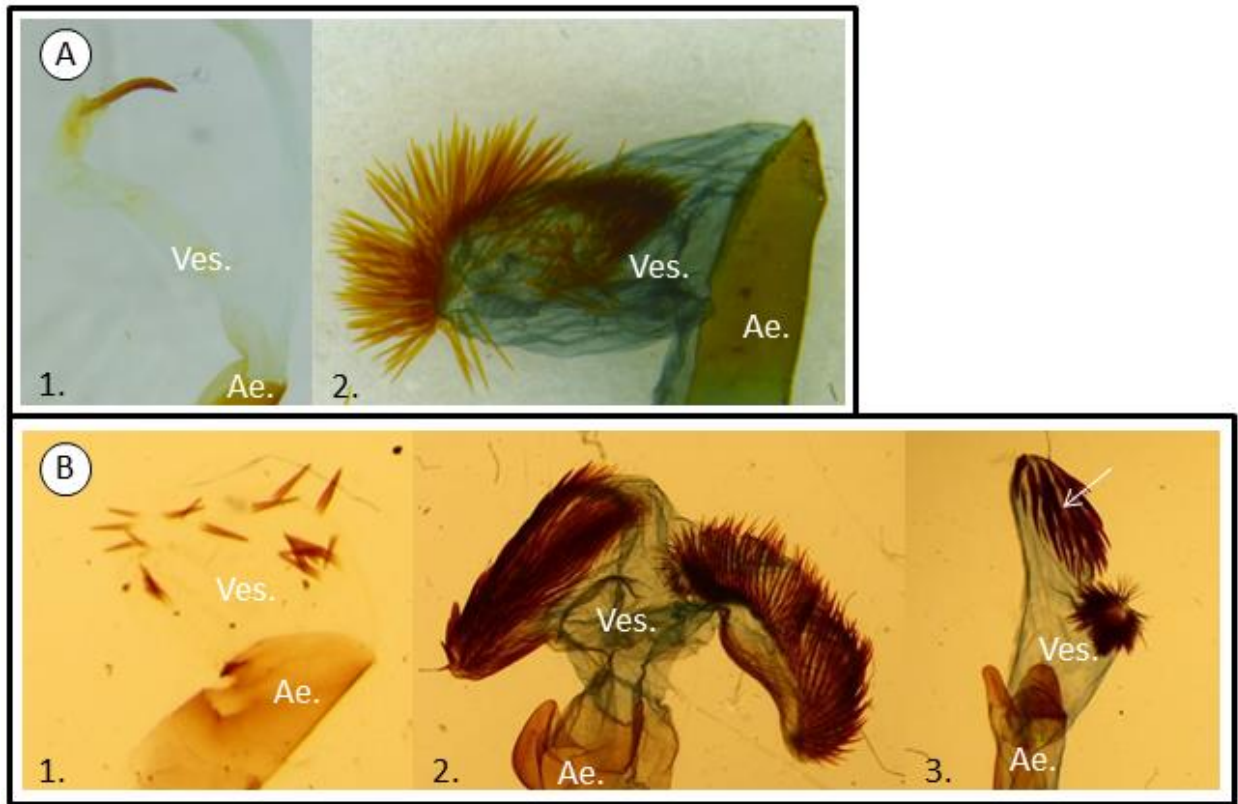
Figure 48. Medium-size, non-deciduous cornuti, Character 43 (state, condition): **A)** *E. tyrannus* (A1) and *E. phalonia* (A2) (0, absent); **B)** *E. collusoria* (B1), *E. boseae* (B2), and *E. cocalus* (B3) (1, present). Medium, non-deciduous cornuti in Fig. 48B, 3 indicated by arrow. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

This character encompasses all non-deciduous cornuti morphologies which are too small to be stout spikes (Fig. 48B), except the scobinate patch (see character 47). Medium, non-deciduous cornuti are present in *E. apta*, *E. cocalus*, *E. srivijayana*, *E. salaminia*, *E. materna*, *E. jordani*, *E. dividens*, *E. boseae*, *E. procus*, *E. discrepans*, *E. imperator*, *E. muscigera*, *E. divitiosa*, *E. hypermnestra*, *E. collusoria*, *E. memorans*, *E. serpentifera*, *E. treadawayi*, *Gonodonta indentata*, and *Oraesia triobliqua*.

3.4.3.28 Character 44. *Dense spiculi, Fig. 49*: (0) absent, Fig. 49A; (1) present, Fig. 49B.

Figure 49. Dense spiculi, Character 44 (state, condition): **A)** *E. jordani* (0, absent); **B)** *E. boseae* (1, present). Areas with dense spiculi indicated by arrows. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

In *E. apta*, *E. materna*, *E. dividens*, *E. boseae*, *E. discrepans*, *E. imperator*, *E. muscigera*, *E. divitiosa*, *E. serpentifera*, and *Gonodonta indentata*, cornuti are present in the form of dense spines that thickly clothe the area on the vesica where they are found (Fig. 49B). These spines can be distinguished by their uniform, tapering shape, and the way they lie closely along the vesica surface. Here they are referred to as dense spiculi.

3.4.3.29 Character 45. *Dense spiculi placement, Fig. 50*: (0) in patches on vesica, Fig. 50A; (1) along creases in vesica, Fig. 50B.
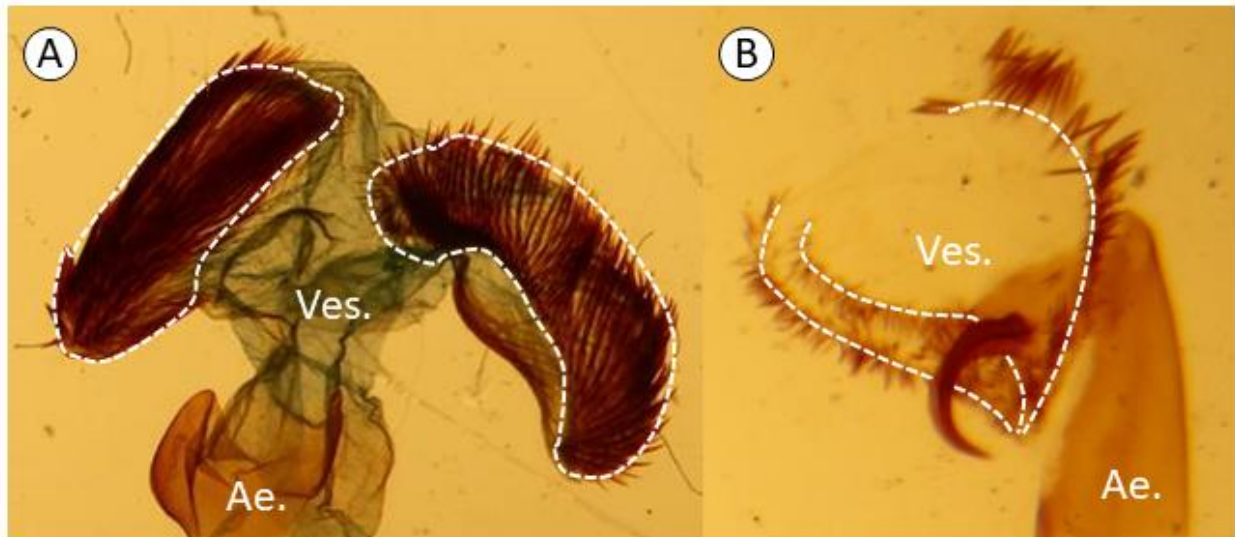
Figure 50. Dense spiculi placement, Character 45 (state, condition): **A)** *E. boseae* (0, in patches on vesica); **B)** *E. serpentifera* (1, along creases in vesica). Areas with dense spiculi indicated by dashed white lines. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

In cases among *Eudocima* where dense spiculi are present, it is most common to find the spiculi in patches on the vesica lobes (Fig. 50A). However, in *E. serpentifera* and *E. dividens*, as well as in *Gonodonta indentata*, spiculi are arranges in rows along creases in the surface of the vesica and not on the lobes (Fig. 50B). The spiculi found in rows on the vesica are shorter and finer than the dense spiculi found in patches, and the two cornuti arrangements may not represent homologous kinds. The presence of spiculi in rows in *Gonodonta indentata* suggests that this trait could be ancestral.

3.4.3.30 Character 46. *Jaculiferous cornuti, Fig. 51*: (0) absent, Fig. 51A; (1) present, Fig 51B.
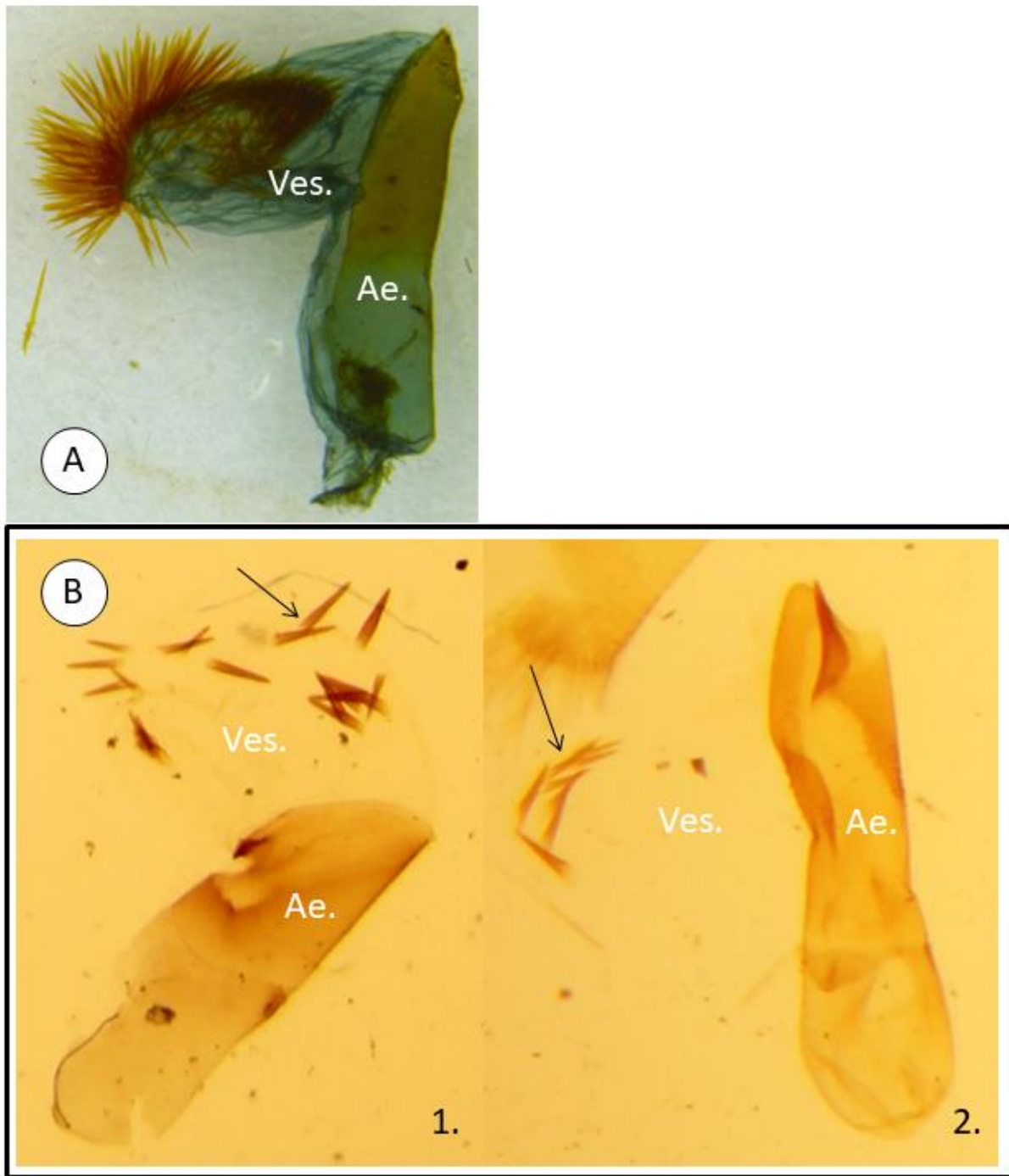
Figure 51. Jaculiferous cornuti, Character 46 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. collusoria* (B1) and *E. procus* (B2) (1, present). Jaculiferous cornuti indicated by arrow. Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

The ingroup species *E. procus*, *E. collusoria*, and *E. memorans* possess cornuti shaped like smooth needles, here referred to as jaculiferous cornuti (Fig. 51B). These spines are shorter and slightly thicker than deciduous cornuti, and can be easily distinguished. In the examined species where they occur, jaculiferous cornuti are the only kind of cornuti present.

3.4.3.31 Character 47. *Scobinate patch, Fig. 52*: (0) absent (not shown); (1) one present, Fig. 52; (2) multiple present (not shown, Plate 477 in Holloway 2005).

Figure 52. Scobinate patch, Character 47 (state, condition): *E. sikhimensis* (1, one present). Scobinate patch(es) indicated by arrow(s). Vesica (Ves.) and aedeagus (Ae.) labelled for reference.

In *E. dividens*, *E. sikhimensis*, *E. mazzeii*, and *Gonodonta indentata*, a small rounded patch is present on the vesica with a densely nodulose surface (Fig. 52). Several of these patches are present on the vesica of *Phyllodes verhuelli* (Holloway 2005). According to Cordero (2010), not all light sclerotizations of the vesica are considered cornuti, so it is unclear whether this structure

is a cornuti patch or not. In *Calyptra minuticornis,* such patches are present and are termed ornamentations of the vesica rather than cornuti (Snyder 2016). When present, the scobinate patch was not included in the character for cornuti coverage (see character 37) or in the character for medium-sized deciduous cornuti (character 43). However, the presence of a scobinate patch was included in the character for multiple cornuti types present (character 38) because it still represents a unique form of scerlotization on the vesica membrane.

3.4.3.32 Character 48. *Vesica lobe number, Fig. 53*: (0) one, Fig. 53A; (1) two, Fig. 53B; (2) three, Fig. 53C; (3) four, Fig. 53D.
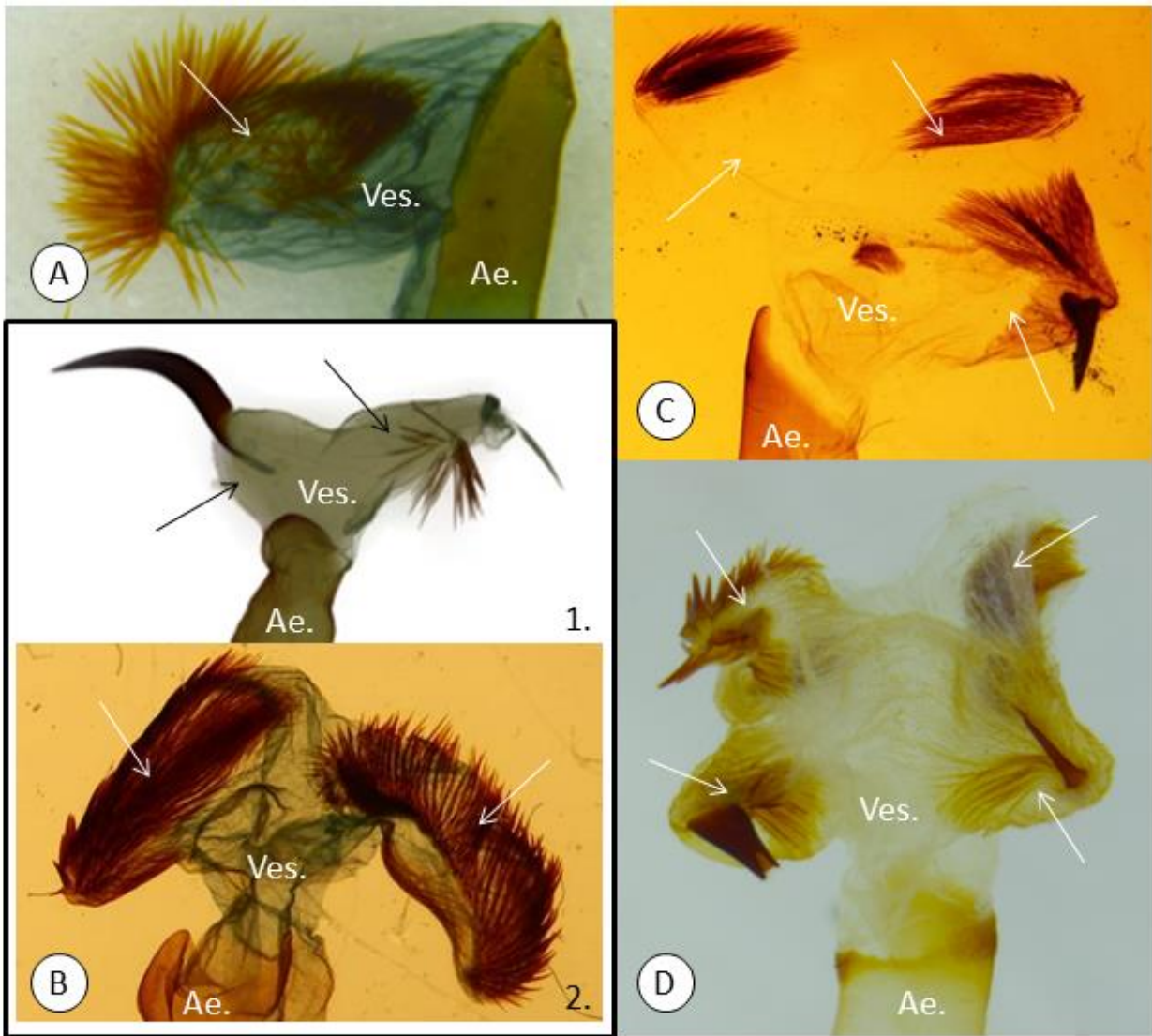
Figure 53. Vesica lobe number, Character 48 (state, condition): **A)** *E. phalonia* (0, one); **B)** *E. talboti* (B1) and *E. boseae* (B2) (1, two); **C)** *E. imperator* (2, three); **D)** *E. materna* (3, four). Lobes of vesica (Ves.) indicated by arrows. Aedeagus (Ae.) labelled for reference.

The vesica in *Eudocima* can be in multiple configurations, with varying numbers of lobes. This character describes the "main" or "primary" lobe number, not including smaller projections or nubs which are less significant in size (these are taken into account in the character for vesica shape, character 49). In *E. phalonia*, *E. tyrannus*, *E. sikhimensis*, *E. bathyglypta*, *E. okurai*, *E. jordani*, *E. caesar*, *E. kuehni*, *E. iridescens*, *E. mionopastea*, *E. paulii*, *E. cajeta*, *E. euryzona*, *E.*

collusoria, *E. memorans*, *E. serpentifera*, *E. smaragdipicta*, *E. prolai*, *E. steppingstonia*, *E. lequeuxi*, *E. oliveri*, *E. splendida*, and *E. kinabaluensis*, only one lobe is present (Fig. 53A). Two lobes (Fig. 53B) are present in *E. cocalus*, *E. homaena*, *E. dividens*, *E. talboti*, *E. hypermnestra*, *E. treadawayi*, *Phyllodes verhuelli*, and *Oraesia triobliqua*. Taxa with three lobes (Fig. 53C) include *E. behouneki*, *E. mazzeii*, *E. imperator*, *E. boseae*, and *E. srivijayana*, and taxa with four lobes (Fig. 53D) include *E. apta*, *E. materna*, *E. salaminia*, *E. discrepans*, *E. muscigera*, *E. divitiosa*, and *Gonodonta indentata*. It is important when numbering the lobes of the vesica not to include the ductus ejaculatoris, which can be pushed inside out through the ejaculatory opening when the vesica is everted.

3.4.3.33 Character 49. *Shape of vesica, Fig. 54*: (0) ovate, Fig. 54A; (1) thick and rhizome-like, with a lobe near the base of the vesica and lobes ascending to near the top of the vesica, Fig. 54B; (2) slender, tube-like or fingerlike, Fig. 54C; (3) thick and box-like, lobes arranged radially near top, Fig. 54D; (4) tripodal or bifurcate with balanced lobe size, Fig. 54E; (5) main lobe with much smaller lobes or nubs budding out, Fig. 54F.

Figure 54. Vesica lobe shape, Character 49 (state, condition): **A)** *E. phalonia* (0, ovate); **B)** *E. apta* (1, thick and rhizome-like, with a lobe near the base of the vesica and lobes ascending to near the top of the vesica); **C)** *E. tyrannus* (2, slender, tube-like or fingerlike); **D)** *E. materna* (3, thick and box-like, lobes arranged radially near top); **E)** *E. talboti* (E1), *E. srivijayana* (E2), and *E. boseae* (E3) (4, tripodal or bifurcate with balanced lobe size); **F)** *E. cocalus* (F1) and *E. muscigera* (F2) (5, main lobe with much smaller lobes or nubs budding out). Shape of vesica (Ves.) indicated by dashed white line. Aedeagus (Ae.) labelled for reference.
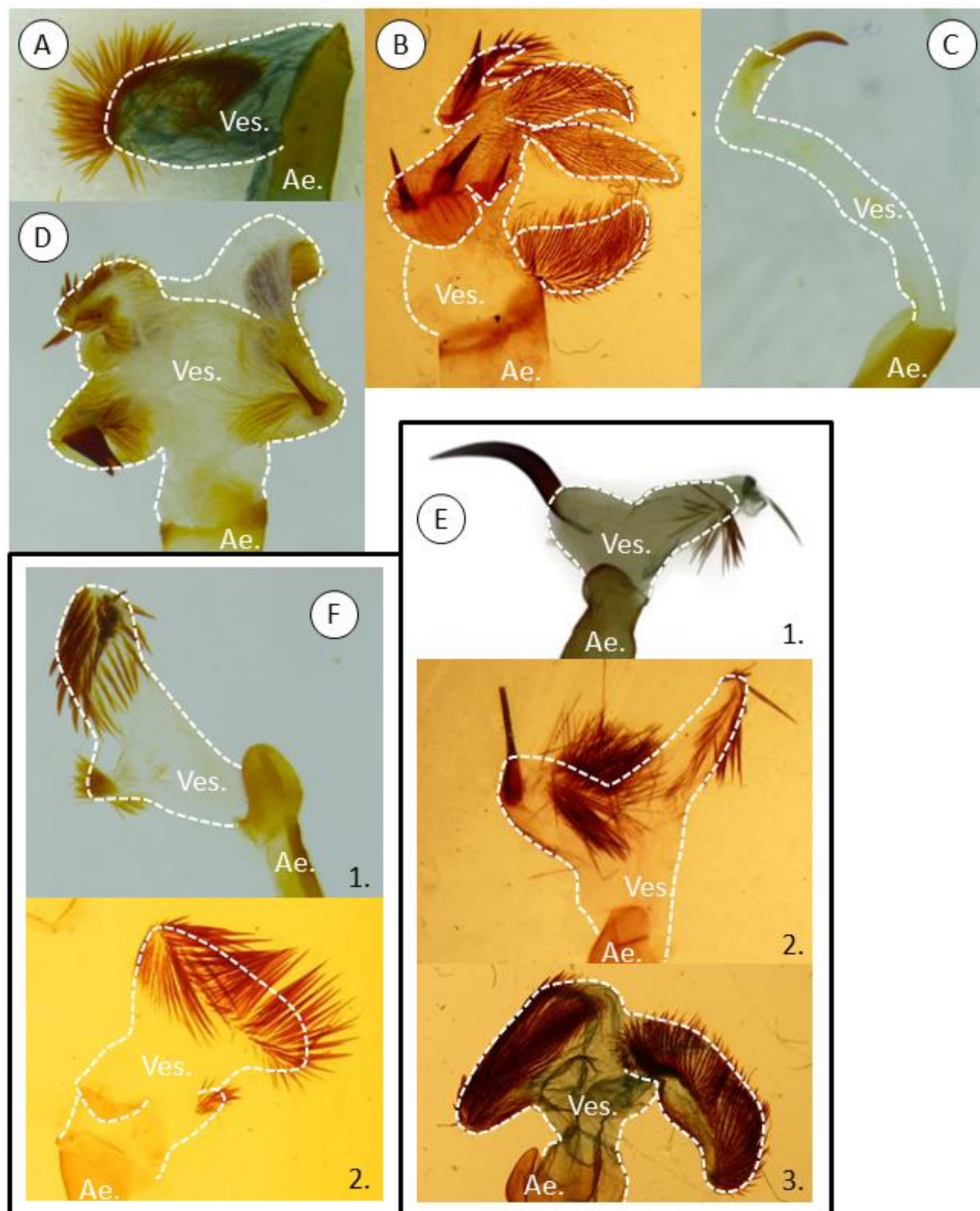
A simple, ovate vesica (Fig. 54A) is found in *E. phalonia*, *E. sikhimensis*, *E. procus*, *E. kuehni*, *E. talboti*, *E. euryzona*, *E. smaragdipicta*, *E. lequeuxi*, *E. oliveri*, *E. kinabaluensis*, and *Oraesia triobliqua*. In *E. apta*, the vesica is thick, with diverticula arising from the base of the vesica, the middle, and toward the apex (Fig. 54B). The overall appearance is similar to a ginger root, which is the reason the shape is described as rhizome-like. A slender, tube-like vesica (Fig. 54C) is present in *E. tyrannus*, *E. bathyglypta*, *E. okurai*, *E. iridescens*, *E. caesar*, *E. mionopastea*, *E. paulii*, *E. cajeta*, and *E. prolai*. *Eudocima materna*, *E. divitiosa*, and *Gonodonta indentata* feature a stout, box-like vesica with numerous shorter diverticula arising somewhat radially near the apex (Fig. 54D). In *E. steppingstonia*, *E. behouneki*, *E. talboti*, *E. imperator*, *E. boseae*, *E. dividens*, and *E. srivijayana*, the vesica lobes are of similar length and emerge radially from the vesica apex (Fig. 54E). The vesica present in *E. cocalus*, *E. jordani*, *E. homaena*, *E. discrepans*, *E. muscigera*, *E. hypermnestra*, *E. collusoria*, *E. memorans*, *E. serpentifera*, *E. mazzeii*, and *E. treadawayi* can be similar in form to that present in *E. phalonia*, although it is set apart by the presence of one or more small, nub-like diverticula arising from the main lobe (Fig. 54F).

3.4.3.34 Character 50. *Vesica length, Fig. 55*: (0) shorter than aedeagus, Fig. 55A; (1) about as long as aedeagus, Fig. 55B; (2) much longer than aedeagus, Fig. 55C.
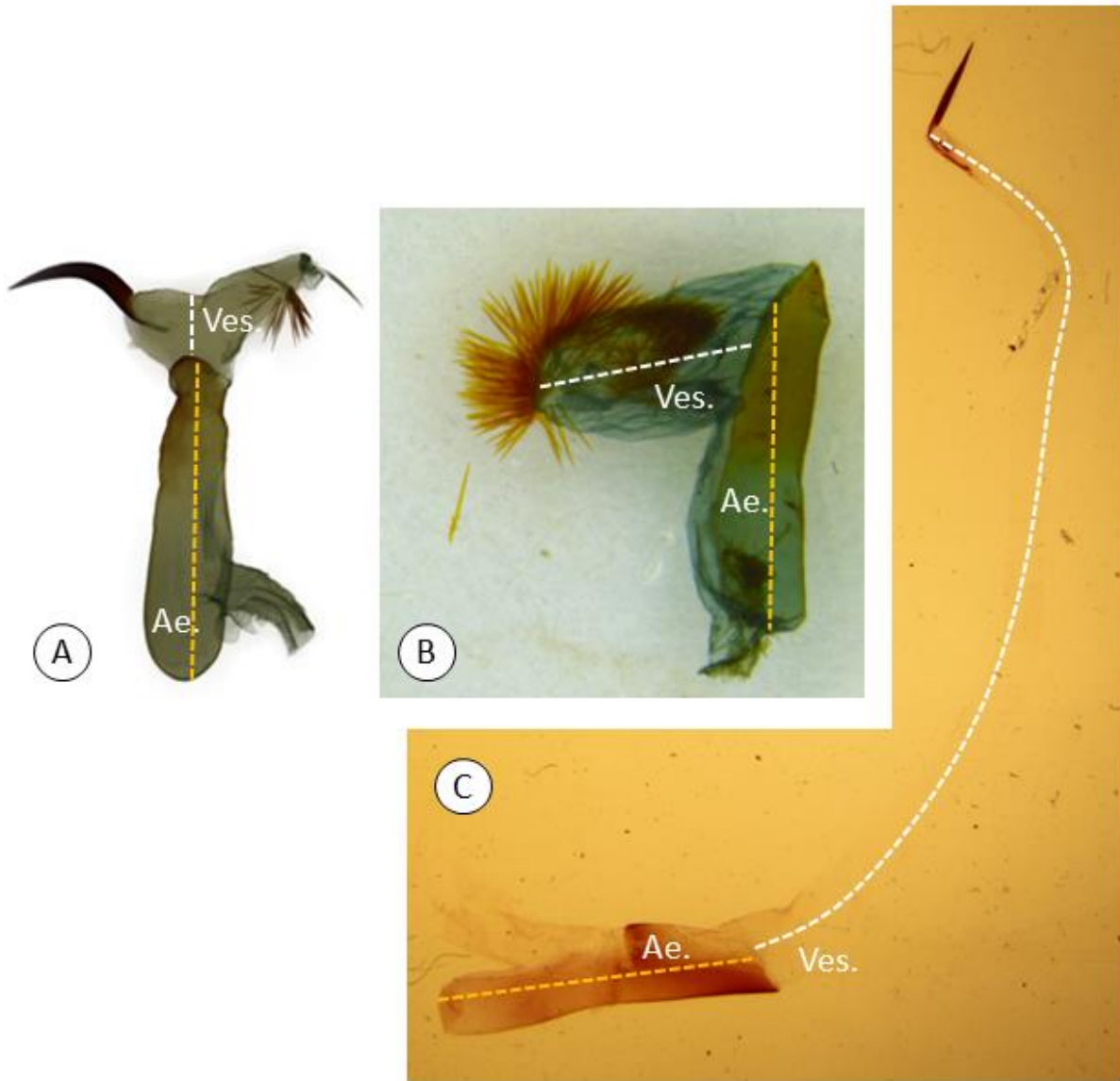
Figure 55. Vesica length, Character 50 (state, condition): **A)** *E. talboti* (0, shorter than aedeagus); **B)** *E. phalonia* (1, about as long as aedeagus); **C)** *E. tyrannus* (2, much longer than aedeagus). Approximate length of vesica (Ves.) indicated by dashed white line, approximate length of aedeagus (Ae.) indicated by dashed orange line.

This character describes the length of the vesica relative to the aedeagus. In *E. oliveri*, *E. lequeuxi*, *E. steppingstonia*, *E. prolai*, *E. mazzeii*, *E. behouneki*, *E. serpentifera*, *E. memorans*, *E. collusoria*, *E. hypermnestra*, *E. euryzona*, *E. cajeta*, *E. talboti*, *E. iridescens*, *E. kuehni*, *E. caesar*, *E. homaena*, *E. srivijayana*, *E. cocalus*, *E. sikhimensis*, and *Oraesia triobliqua*, the vesica is

shorter than the aedeagus (Fig. 55A). Taxa were scored in this category if the vesica was less than proportional to the aedeagus, whether significantly so (as in *E. talboti*) or less dramatically. In *E. phalonia*, *E. apta*, *E. materna*, *E. bathyglypta*, the *E. srivijayana* holotype from Indonesia, *E. jordani*, *E. dividens*, *E. boseae*, *E. procus*, *E. discrepans*, *E. imperator*, *E. muscigera*, *E. mionopastea*, *E. paulii*, *E. divitiosa*, *E. smaragdipicta*, *E. treadawayi*, *E. kinabaluensis*, and *Gonodonta indentata*, the vesica is roughly the same length as the aedeagus and the two are proportional to one another (Fig. 55B). The vesica is significantly longer than the aedeagus (Fig. 55C) in *E. tyrannus* and *E. okurai*, extending about twice the length of the aedeagus in both species.

3.4.3.35 Character 51. *Juxta length, Fig. 56*: (0) less than half as long as valvae, Fig. 56A; (1) about half as long as valvae, Fig. 56B; (2) as long or longer than valvae, Fig. 56C.
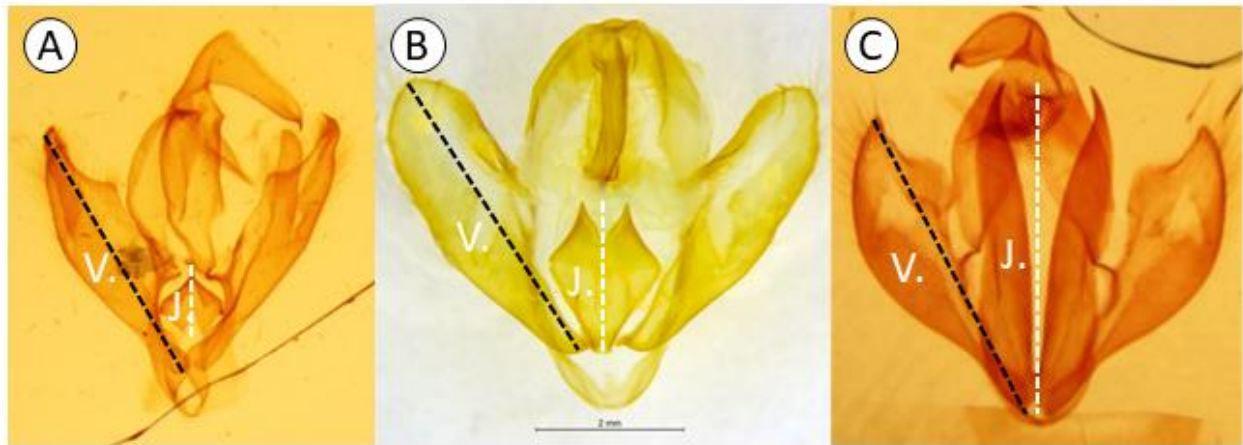
Figure 56. Juxta length, Character 51 (state, condition): **A)** *E. procus* (0, less than half as long as valvae); **B)** *E. aurantia* (1, about half as long as valvae); **C)** *E. phalonia* (2, as long or longer than valvae). Approximate length of valve (V.) indicated by dashed black line, approximate length of juxta (J.) indicated by dashed white line.

In *Eudocima*, the typical condition of this character involves the juxta extending about half as long as the valvae (~50% of examined *Eudocima*) (Fig. 56B). This character state is also shared with *Phyllodes verhuelli*. Species with a shorter juxta (Fig. 56A) include *E. procus*, *E. martini*, *E. kinabaluensis*, *E. smaragdipicta*, and *Plusiodonta incitans*, *Gonodonta indentata*, and both *Oraesia* species in the outgroup taxa. Some species presented a juxta that was as long or longer than the valvae (Fig. 56C); these include *E. phalonia*, *E. cocalus*, *E. jordani*, *E. boseae*, *E. discrepans*, *E. muscigera*, *E. imperator*, *E. talboti*, *E. cajeta*, *E. euryzona*, *E. hypermnestra*, *E. treadawayi*, *E. steppingstonia*, *E. lequeuxi*, and *E. oliveri*.

3.4.3.36 Character 52. *Juxta base shape, Fig. 57*: (0) round and notched, Fig. 57A; (1) small dimple or base uninterrupted, Fig. 57B; (2) deep cleft between rounded points, Fig. 57C; (3) "W"-shaped with pointed triangular notch, Fig. 57D; (4) compressed "W" with small sharp notch and points, Fig. 57E.
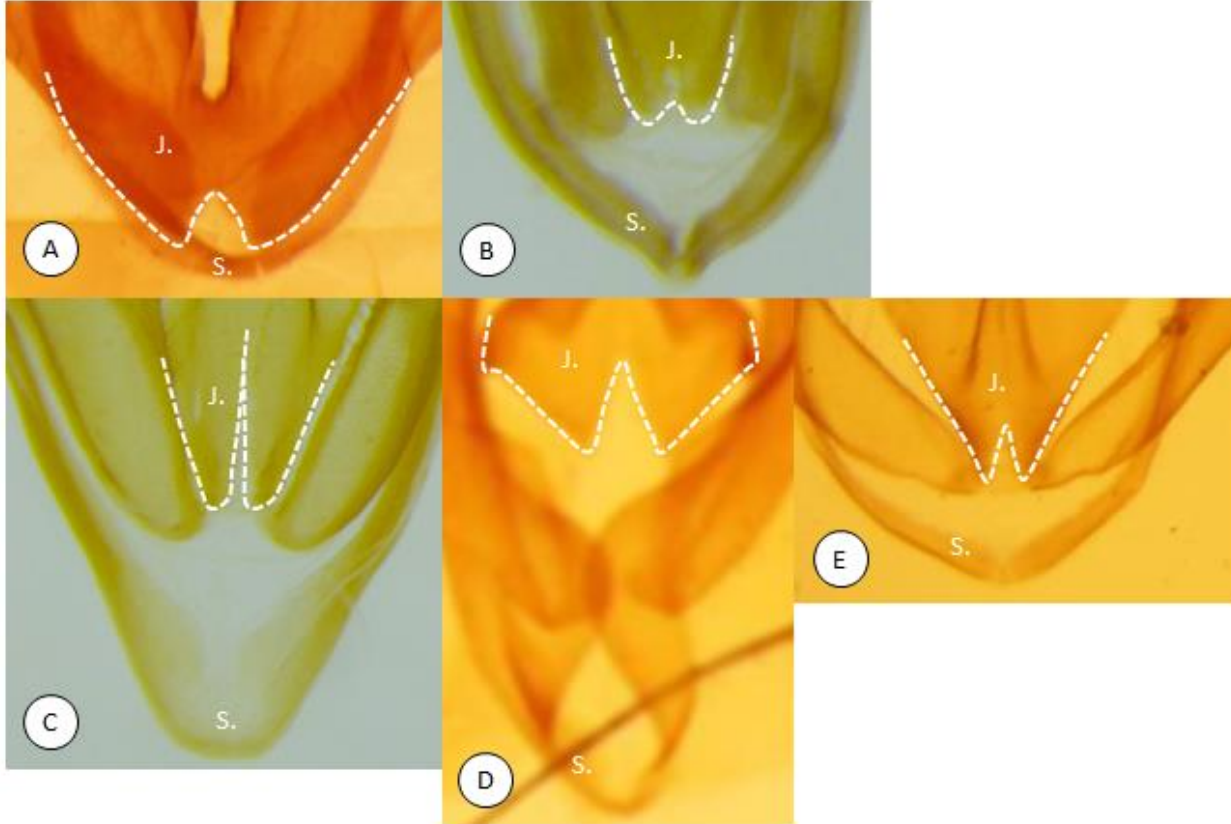
Figure 57. Juxta base shape, Character 52 (state, condition): **A)** *E. phalonia* (0, round and notched; **B)** *E. cocalus* (1, small dimple or base uninterrupted); **C)** *E. materna* (2, deep cleft between rounded points); **D)** *E. procus* (3, "W"-shaped with pointed triangular notch); **E)** *E. muscigera* (4, compressed "W" with small sharp notch and points). Juxta (J.) base shape indicated by dashed white line. Saccus (S.) labelled for reference.

In *E. colubra*, *E. steppingstonia*, *E. lequeuxi*, and *E. oliveri*, the juxta base is rounded with a wedge-like notch (Fig. 57A). Among the taxa scored for this character state, some species showed inconsistency during examination of duplicate specimens. In *E. phalonia*, some specimens from Malaysia and Australia presented a rounded base with a notch, while other specimens from Malaysia, Ghana, and Australia presented a rounded base with a slight dimple or no notch (Fig. 57B). Therefore, this character is likely plastic within *E. phalonia* populations and ought to be looked into further for diagnostic utility among regional groups. The same variability

was observed in *E. srivijayana*; two examined specimens from Indonesia had no notch (Fig. 57B), while another Panay specimen had a rounded notch (Fig. 57A). For *E. cajeta*, *E. homaena*, and Indonesian specimens of *E. talboti*, one notched form (Fig. 57A) and one uninterrupted form (Fig. 57B) was also observed. The uninterrupted or slightly indented character trait (Fig. 57B) is constant in *E. cocalus*, *E. salaminia*, *E. aurantia*, *E. boseae*, *E. kuehni*, *E. euryzona*, *E. hypermnestra*, *E. collusoria*, *E. mazzeii*, *E. behouneki*, *E. prolai*, *E. martini*, *Gonodonta indentata*, and both *Oraesia* species. In *E. paulii*, *E. imperator*, *E. serpentifera*, *E. dividens*, *E. materna*, *E. apta*, *E. okurai*, *E. bathyglypta*, and one *E. tyrannus* specimen from China, the base of the juxta is deeply clefted, and each of the two points created at the base are rounded rather than sharp (Fig. 57C). This cleft may entirely separate the juxta base into two halves or leave the halves attached at the top. The other Chinese *E. tyrannus*, *E. sikhimensis*, *E. jordani*, *E. caesar*, *E. iridescens*, *E. mionopastea*, *E. divitiosa*, *E. memorans*, and *E. procus* all display a juxta base which is "W"-shaped with two widely-seperated pointed triangles (Fig. 57D). In *E. smaragdipicta*, *E. discrepans*, *E. muscigera*, and *E. treadawayi*, the juxta base is shaped like a "V" with a small triangular notch (Fig. 57E). The effect is similar to the juxta condition present in *E. procus*, but the two points at the juxta base are closer together and the notch is smaller.

3.4.3.37 Character 53. *Lateral processi off juxta base, Fig. 58*: (0) absent, Fig. 58A; (1) present, Fig. 58B.
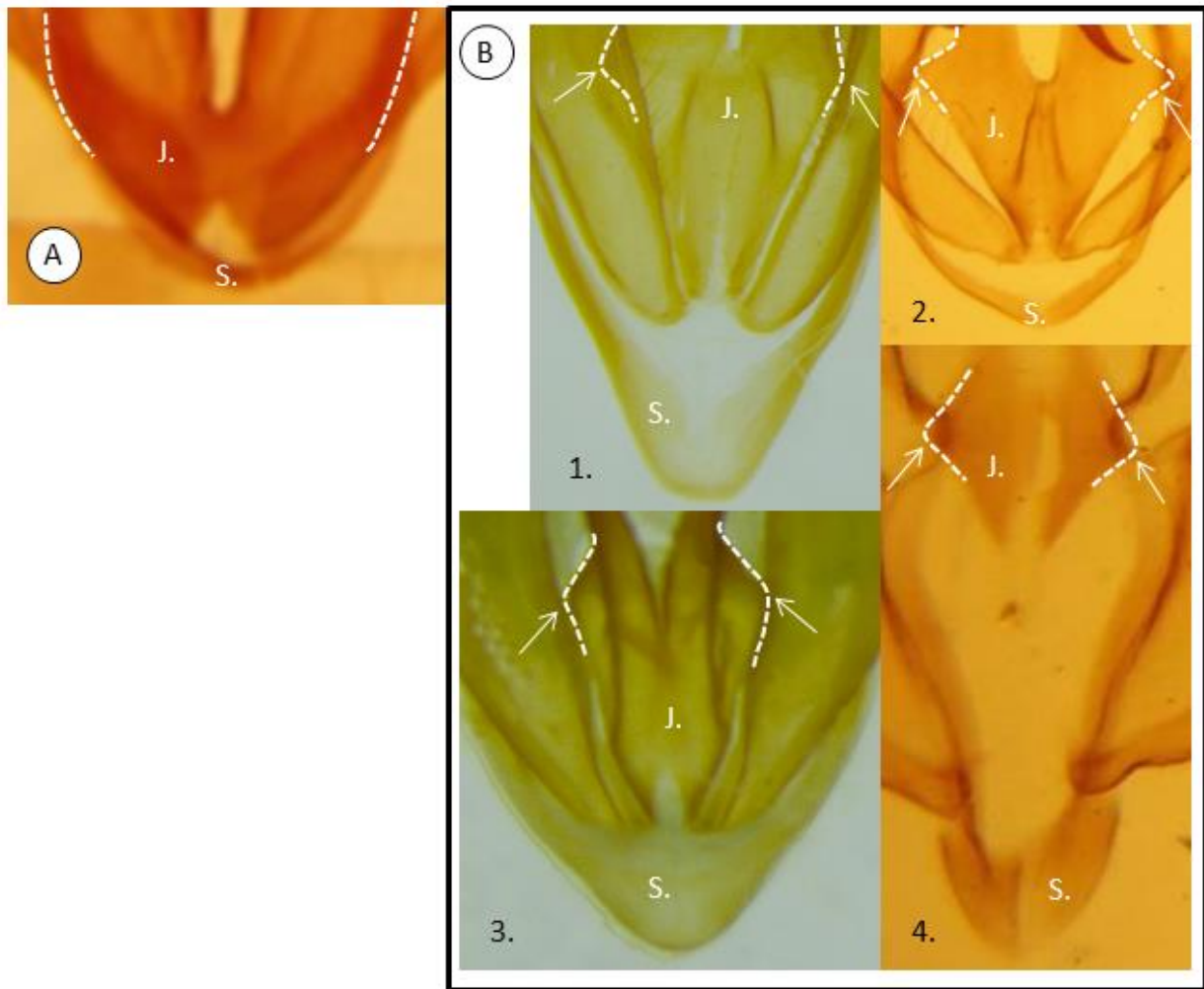
Figure 58. Lateral processi off juxta base, Character 53 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. materna* (B1), *E. muscigera* (B2), *E. tyrannus* (B3), and *E. smaragdipicta* (B4) (1, present). Sides of juxta (J.) emphasized with dashed white lines, lateral processi off juxta indicated by arrows. Saccus (S.) labelled for reference.

The species *E. tyrannus*, *E. apta*, *E. okurai*, *E. salaminia*, *E. dividens*, *E. materna*, *E. aurantia*, *E. boseae*, *E. discrepans*, *E. muscigera*, *E. smaragdipicta*, *E. splendida*, *E. kuehni*, *E. mazzeii*, *E. behouneki*, *E. prolai*, *E. treadawayi*, and *E. martini* possess lateral projections arising from each side of the juxta midway between the base and the body (normally a pair of processi arising from the base) (Fig. 58B). Roughly 70% of the *Eudocima* examined did not have these processi (Fig. 58A), which were also absent in the outgroups except for *Phyllodes verhuelli*. In species such as

E. muscigera and *E. discrepans*, the lateral processi are obvious and unmistakable (Fig. 58B, 2); in other species the condition, while still present, is much less pronounced and appears as a triangular swelling or dilation of the juxta (i.e. *E. materna*, Fig. 58B, 1; *E. smaragdipicta*, Fig. 58B, 4).

3.4.3.38 Character 54. *Juxta body shape, Fig. 59*: (0) flame-like, Fig. 59A; (1) broad triangles with blunt projecting tips, Fig. 59B; (2) broad triangles, Fig. 59C; (3) tweezer-like, Fig. 59D; (4) paired triangles with extended projections at tips, Fig. 59E; (5) broad with short incurved arms, Fig. 59F; (6) upright triangle, no arms and single spike, Fig. 59G; (7) two rounded prominences, Fig. 59H; (8) trough-like, widely spaced arms, Fig. 59I; (9) plate-like with dip or indentation in middle, or small bumps for processi, Fig. 59J; (A) broad and plate-like with two small points, Fig. 59K; (B) slim incurving arms that project away from one another distally at 90 degree angles (not shown, Fig. 3 in Yoshimoto 1999).

Figure 59. Juxta body shape, Character 54 (state, condition): **A)** *E. euryzona* (A1) and *E. cocalus* (A2) (0, flame-like); **B)** *E. materna* (1, broad triangles with blunt projecting tips); **C)** *E. homaena* (2, broad triangles); **D)** *E. smaragdipicta* (3, tweezer-like); **E)** *E. aurantia* (4, paired triangles with extended projections at tips); **F)** *E. colubra* (5, broad with short incurved arms); **G)** *E. procus* (upright triangle, no arms and single spike); **H)** *E. serpentifera* (7, two rounded prominences); **I)** *E. divitiosa* (8, trough-like, widely spaced arms); **J)** *E. caesar* (J1) and *E. salaminia* (J2) (9, plate-like with dip or indentation in middle or small bumps); **K)** *E. dividens* (A, broad and plate-like with two small points). Shape of body of juxta (J.) indicated by dashed white line.
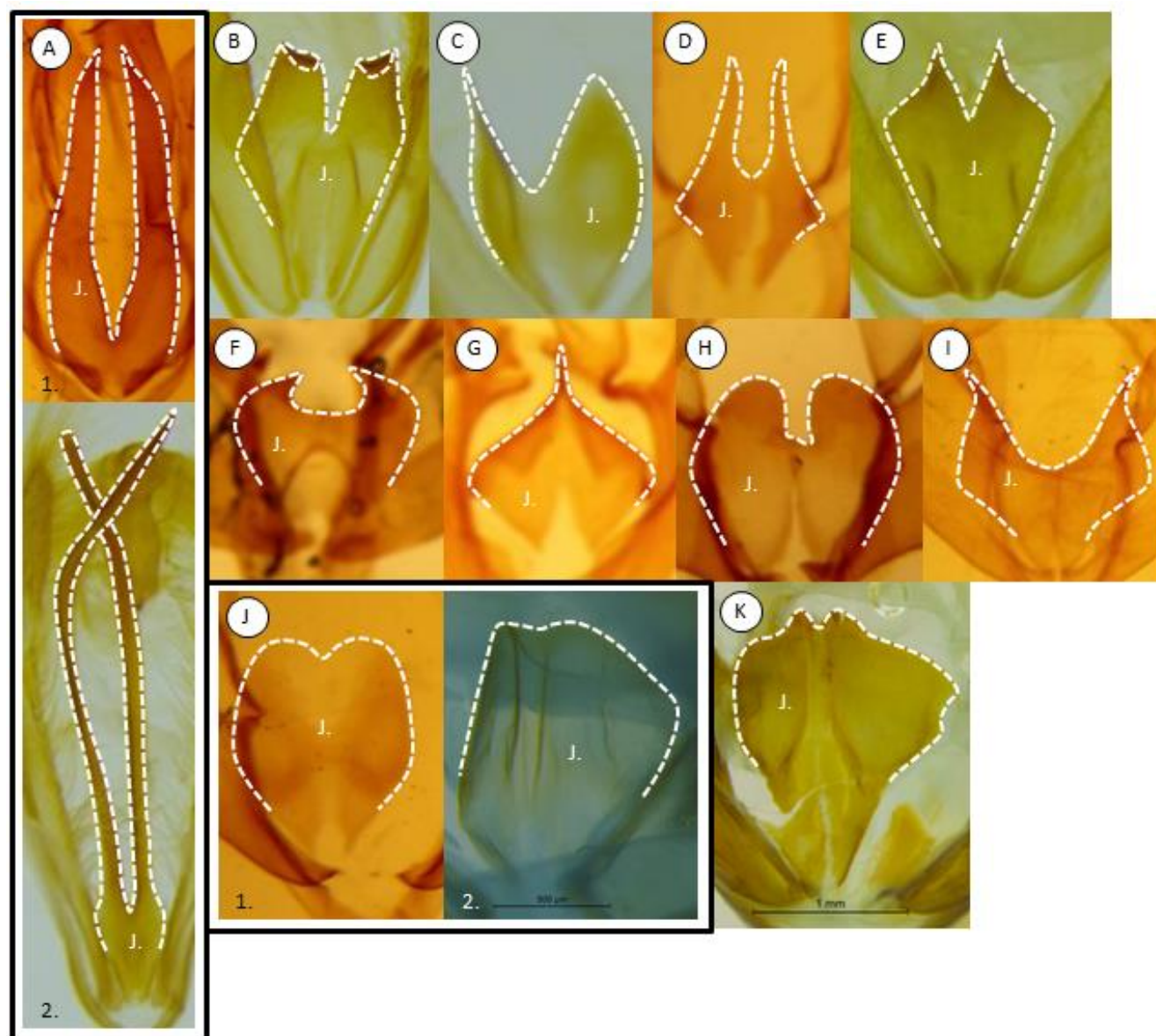
The shape of the juxta in *Eudocima* is one of the most variable characters in the male genitalia. Nearly all *Eudocima* species have a juxta with two paired processi of varying shape and length; even if the "processi" are very shallow, a dent or indentation is still present in the middle of the juxta apex (Fig. 59J), as seen in *E. iridescens*, *E. caesar*, *E. homaena* from Taiwan (in which species shallow bumps on either side of the depression are distinguishable), and *E. salaminia*. A plate-like juxta is also present in *Gonodonta indentata* among the outgroups. The exception to the occurrence of paired juxta processi in *Eudocima* is *E. procus*, which has an undivided juxta with a single spike arising from the center of an upright triangular body (Fig. 59G). This trait is also seen in both *Oraesia* species, neither of which have a divided juxta. The species *E. phalonia*, *E. cocalus*, *E. jordani*, *E. discrepans*, *E. muscigera*, *E. talboti*, *E. cajeta*, *E. euryzona*, *E. boseae*, *E. hypermnestra*, *E. steppingstonia*, *E. lequeuxi*, and *E. oliveri* have paired juxta processi which are long and tapering (Fig. 59A), similar in shape to a flame (Zilli & Hogenes 2002). In *E. materna* and *E. apta*, the processi are broad and triangular, with flat, blunt tips (Fig. 59B). In *E. sikhimensis*, *E. bathyglypta*, *E. homaena* from Indonesia and the Philippines, *E. kuehni*, *E. mazzeii*, *E. behouneki*, and *E. prolai* the triangular processi are smaller than in *E. materna* or *E. apta*, but are still broad at their bases and continue to smooth points (Fig. 59C). *Eudocima martini*, *E. kinabaluensis*, *E. treadawayi*, *E. mionopastea*, *E. paulii*, one of the *E. srivijayana* from Indonesia, *E. okurai*, and *E. smaragdipicta* have a smaller juxta body with sharp points, reminiscent of a pair of tweezers (Fig. 59D). In *E. aurantia*, *E. tyrannus*, the other two specimens of *E. srivijayana*, *E. imperator*, and *E. collusoria*, the juxta processi are triangular with broad bases and tips with extended projections, causing the portion of the juxta beneath the processi to appear to bulge out on either side (Fig. 59E). *Eudocima colubra* and *E. memorans* both have short juxta processi angled inwards on a wide base (Fig. 59F). In *E. serpentifera*, the processi are rounded and semi-ovate (Fig. 59H). *Eudocima divitiosa* is characterized by a very broad juxta with slender processi, which form a trough-shape (Fig. 59I). *Eudocima dividens* has a broad, plate-like juxta similar to *E. salaminia*, but with two short, triangular processi (Fig. 59K). The juxta in *E. splendida* is distinctive, with two arms which curve inward along two thirds of their length in smooth arcs, then project outwards from one another at abrupt 90 degree angles (Yoshimoto 1999).

3.4.3.39 Character 55. *Tips of juxta processi, Fig. 60*: (0) pointed, Fig. 60A; (1) rounded, Fig. 60B; (2) true tips of processi faint or not present, Fig. 60C.

Figure 60. Tips of juxta processi, Character 55 (state, condition): **A)** *E. aurantia* (0, pointed); **B)** *E. bathyglypta* (1, rounded); **C)** *E. salaminia* (2, true tips of processi faint or not present). Tips of juxta (J.) processi indicated by dashed white lines.

In roughly 80% of *Eudocima*, the paired processi of the juxta are sharply pointed at their tips (Fig. 60A). However, in *E. serpentifera*, *E. mionopastea*, *E. iridescens*, *E. caesar*, the *E. homaena* from Taiwan, and *E. bathyglypta*, the tips of the juxta processi are rounded and smooth (Fig. 60B). In some species with a plate-like juxta body, the shallow bumps present on either side of the indentation were enough separated to allow coding of the tips as rounded, as in *E. iridescens*, *E. caesar*, and the Taiwan *E. homaena*. In *E. salaminia*, only the slight indentation in the center denotes splitting of the juxta, and no true processi tips are present (Fig. 60C); this condition also prevails in *Gonodonta indentata*. In taxa without a divided juxta, this character was coded as inapplicable (?).

3.4.3.40 Character 56. *Texture of juxta, Fig. 61*: (0) smooth, Fig. 61A; (1) serrate, Fig. 61B.
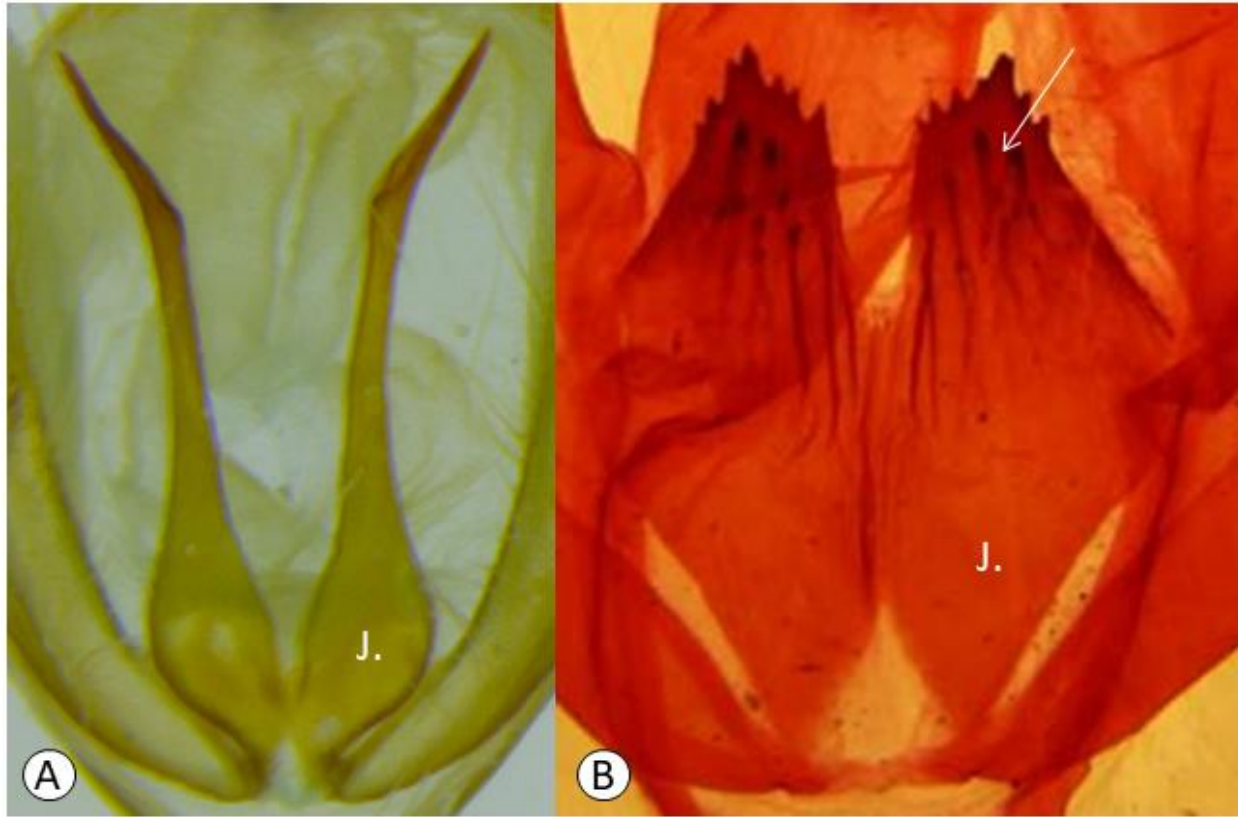
Figure 61. Juxta texture, Character 56 (state, condition): **A)** *E. jordani* (0, smooth); **B)** *E. sikhimensis* (1, serrate). Serrations on juxta (J.) indicated by arrow.

In the vast majority of taxa examined (~90%), the surface and margins of the juxta are smooth and uniform (Fig. 61A). However, in *E. mazzeii*, *E. behouneki*, *E. sikihimensis*, and *E. kuehni*, the juxta body and the inner margins of the juxta processi are serrated with small teeth (Fig. 61B). In *E. lequeuxi*, teeth are also present along the inner margins of the juxta processi (Brou & Zilli 2016), but do not appear elsewhere; despite this, *E. lequeuxi* was also coded as having the serrate condition.

3.4.3.41 Character 57. *Space between juxta processi, general category, Fig. 62*: (0) vase-shaped, Fig. 62A; (1) "V"-shaped, Fig. 62B; (2) notch-shaped, Fig. 62C.

Figure 62. Space between juxta processi, general category, Character 57 (state, condition): **A)** *E. imperator* (A1), *E. boseae* (A2), *E. divitiosa* (A3), *E. phaloia* (A4), and *E. cocalus* (A5) (0, vase-shaped); **B)** *E. tyrannus* (B1), *E. srivijayana* (B2), and *E. jordani* (B3) (1, "V"-shaped); **C)** *E. materna* (C1), *E. smaragdipicta* (C2), *E. colubra* (C3), *E. steppingstonia* (C4), *E. serpentifera* (C5), and *E. salaminia* (C6). Space between processi of juxta (J.) indicated by dashed white line.
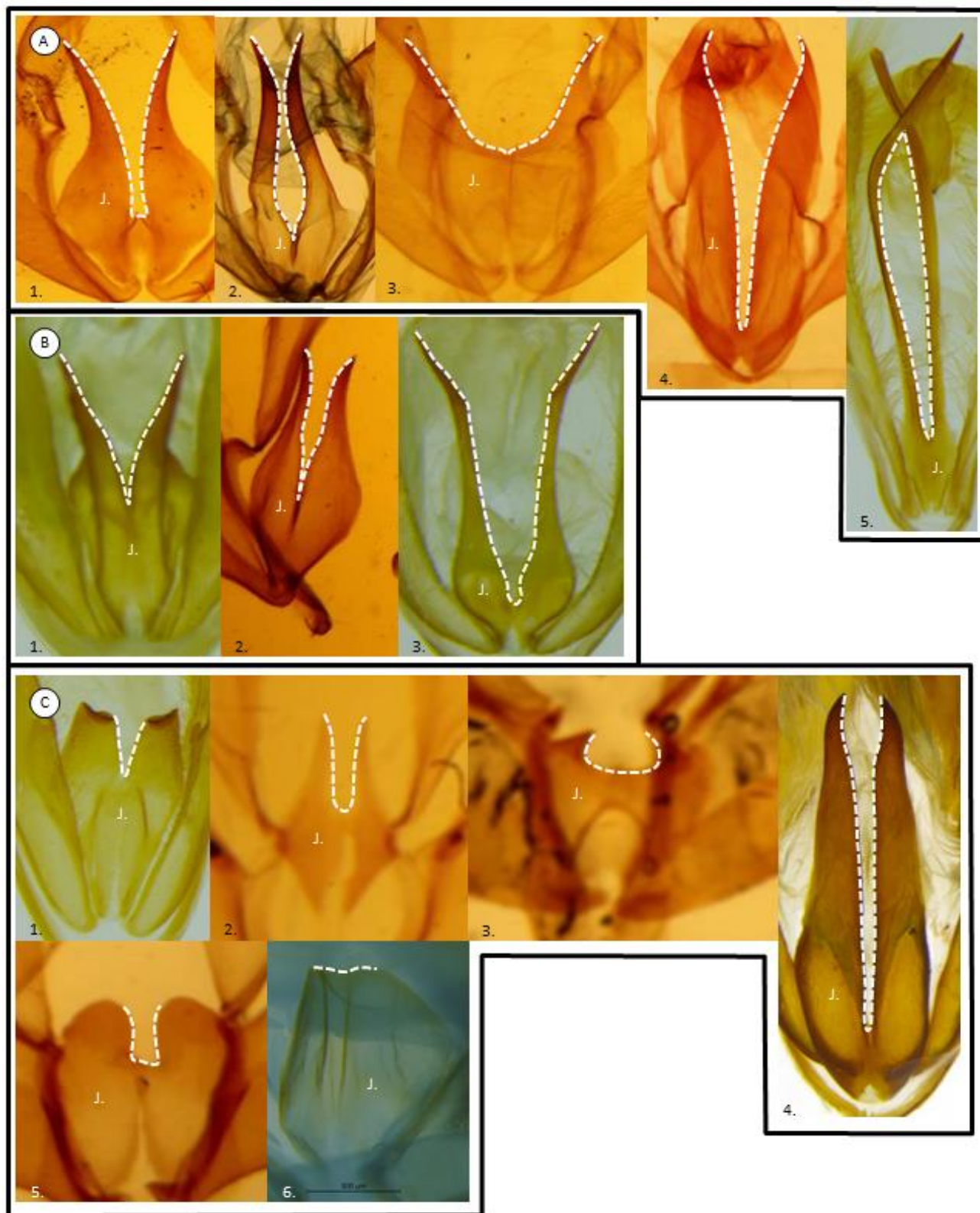
The shape of the space between the two processi of the juxta was observed in addition to the juxta processi themselves because this space seems likely to have biological relevance, since the function of the juxta is to act as a support for the aedeagus (Klots, 1970). In an attempt to characterize the variety of spaces present, a system of three general categories was used, and additional characters created for the states present in each of the categories. Each specimen was first scored for the general category they belonged to as a character condition (character 57), and then the specimen was scored for its condition within that category in a separate character (character 58, 59, or 60). For the characters representing more specific states within the other two general categories that were not coded, the specimen was scored as inapplicable (?). The three general shape categories present for the taxa examined include vase-shaped (~38%), "V"-shaped (~25%), and notch-shaped (~36%). In vase-shaped taxa, the space between the processi is generally as large or larger than the processi themselves, and there are no sharp articulations or bends; rather, the sides of the inner space are smoothly curved or undulating (Fig. 62A). For taxa in the "V"-shaped category, the space between the juxta processi is roughly proportional to the processi in size in most cases, and the sides of the space may either be curved (as in *E. tyrannus*) or articulated (as in *E. jordani*) (Fig. 62B). For taxa with the notch-shaped condition, the juxta processi and the juxta body as a whole are often larger than the gap created between the processi (Fig. 62C).

3.4.3.42 Character 58. *Vase-shaped space in juxta processi, Fig. 63*: (0) narrow at base and dilating upwards, Fig. 63A; (1) dilating smoothly upwards, then forming a closed space where the tips cross, Fig. 63B; (2) narrow at base then dilating rapidly upwards, more compressed and less elongate than (0), Fig. 63C; (3) lower part dilated, then constricting toward top before dilating once more, undulating, Fig. 63D; (4) broad "U"-shape or trough shape, Fig. 63E.
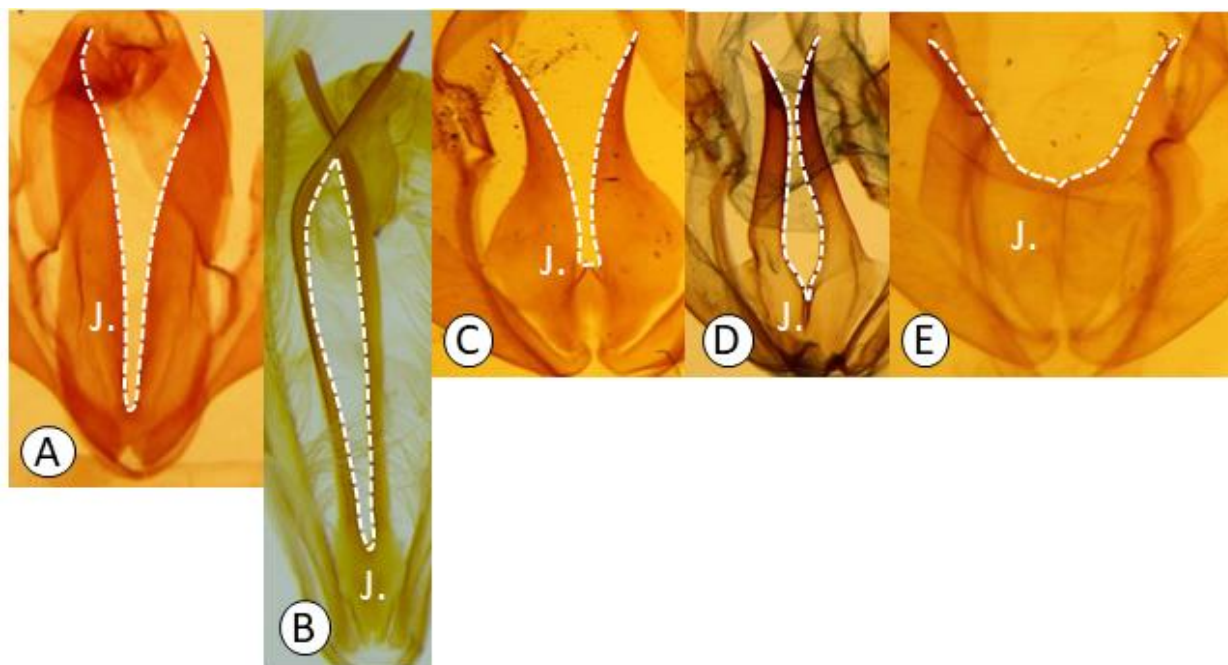
Figure 63. Vase-shaped space in juxta processi, Character 58 (state, condition): **A)** *E. phalonia* (0, narrow at base and dilating upwards); **B)** *E. cocalus* (1, dilating smoothly upwards, then forming a closed space where the tips cross); **C)** *E. imperator* (2, narrow at base then dilating rapidly upwards, more compressed and less elongate than 0); **D)** *E. boseae* (3, lower part dilated, then constricting toward top before dilating once more, undulating); **E)** *E. divitiosa* (4, broad "U"-shape or trough shape). Space between juxta (J.) processi indicated by dashed white line.

Among the taxa with a vase-shaped juxta space, *E. phalonia*, one of the *E. tyrannus* specimens from China, the *E. srivijayana* specimen from Indonesia, *E. talboti*, *E. hypermnestra*, *E. lequeuxi*, and *E. oliveri* have an elongated space which begins narrowly at the base, then flares outward and upward to become widest near the top before curving in slightly (Fig. 63A). The shape in *E. cocalus* is similar, although the curve in the juxta tips occurs earlier in the processi such that the tips cross to form a closed space between them (Fig. 63B). The same condition occurs in *E. cajeta*, although the processi do not extend greatly beyond crossing. In slide preparations of these species, the tips of the processi may become flattened such that they are pointing away from each other. In *E. euryzona*, which is also scored for this condition, the tips of the juxta processi do not

touch, but the inward curve of the tips create a shape similar enough to warrant the same classification. In *E. discrepans*, *E. muscigera*, and *E. imperator*, the space between the processi is uniformly narrow at the base for a distance before widening dramatically near the top (Fig. 63C). The shape is more compact and less elongate than that formed in *E. phalonia*. The shape present in *E. boseae* is more undulating than the others, and is widest near the base (Fig. 63D). It narrows abruptly as it ascends before widening once more at the top. In *E. divitiosa*, the space is a broad, unmistakable "U"-shape or trough shape (Fig. 63E).

3.4.3.43 Character 59.*"V"-shaped space in juxta processi, Fig. 64*: (0) uniform "V", Fig. 64A; (1) laterally compressed "V", Fig. 64B; (2) large, vase-like "V" with sharp, articulated widening near top, Fig. 64C; (3) bubble-like base under widely spread "V", inverted "keyhole" shape (not shown, Fig. 3 in Yoshimoto 1999).
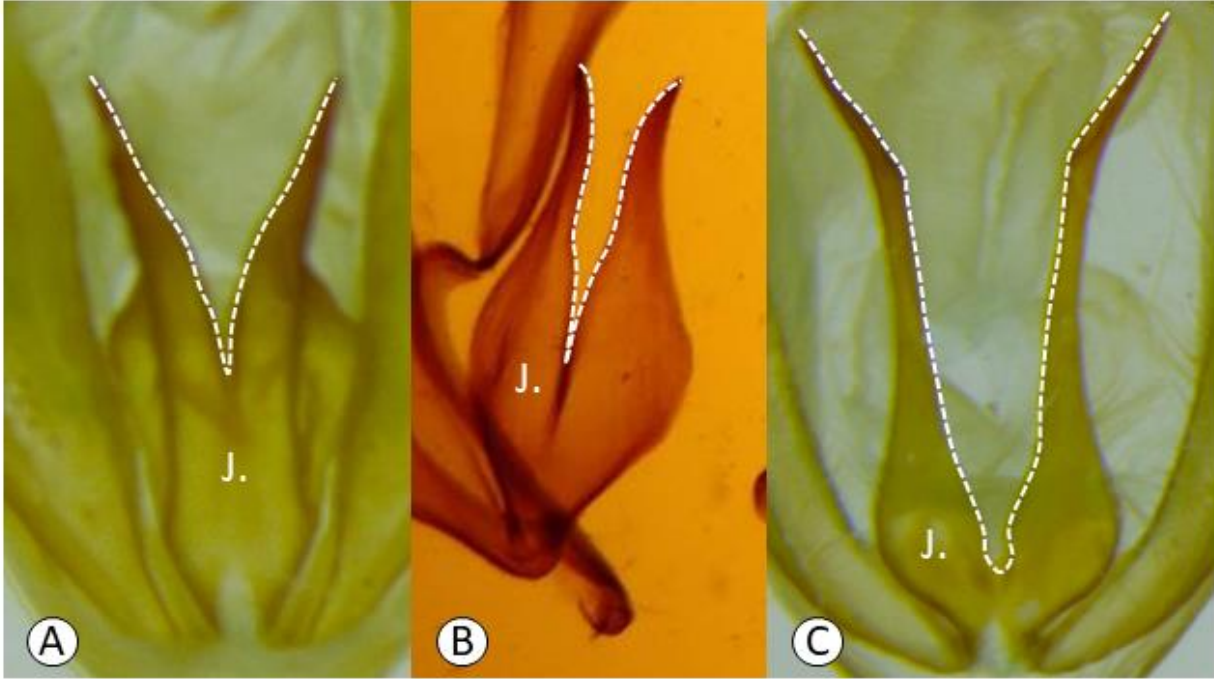
Figure 64. "V"-shaped space in juxta processi, Character 59 (state, condition): **A)** *E. tyrannus* (0, uniform "V"); **B)** *E. srivijayana* (1, laterally compressed "V"); **C)** *E. jordani* (2, large, vase-like "V" with sharp, articulated widening near top). Space between juxta (J.) processi indicated by dashed white line.

In *E. tyrannus*, *E. bathyglypta*, *E. aurantia*, the *E. homaena* from Indonesia and the Philippines, *E. kuehni*, *E. collusoria*, *E. prolai*, and *E. treadawayi*, the shape between the juxta processi is a fairly uniform "V" shape (Fig. 64A). In *E. srivijayana*, *E. paulii*, and *E. mionopastea*, the inverted triangle is laterally compressed and comparatively narrow (Fig. 64B). For *E. paulii*, the gap between the juxta processi is smaller than other members of the group, but the similarity of shape prompted its inclusion in this character state. In *E. jordani*, the "V" is larger than commonly seen in this category, but the uniform widening and distinct articulation near the top (Fig. 64C) separated it from the taxa in the vase-shaped category. The juxta space in *E. splendida* is unlike any of these, and is categorized as "V"-shaped due to the sharp articulation of its paired processi. The rounded base and widely-separated "V"-shape above it are reminiscent of a classic "keyhole" shape which has been inverted.

3.4.3.44 Character 60. *Notch-shaped space in juxta processi, Fig. 65*: (0) "V"-shaped, Fig. 65A; (1) narrow with parallel sides, Fig. 65B; (2) wide, ovate, Fig. 65C; (3) rectangular, wider than (0), Fig. 65D; (4) long and narrow, slight apical widening, Fig. 65E; (5) shallow indentation or depression, Fig. 65F.
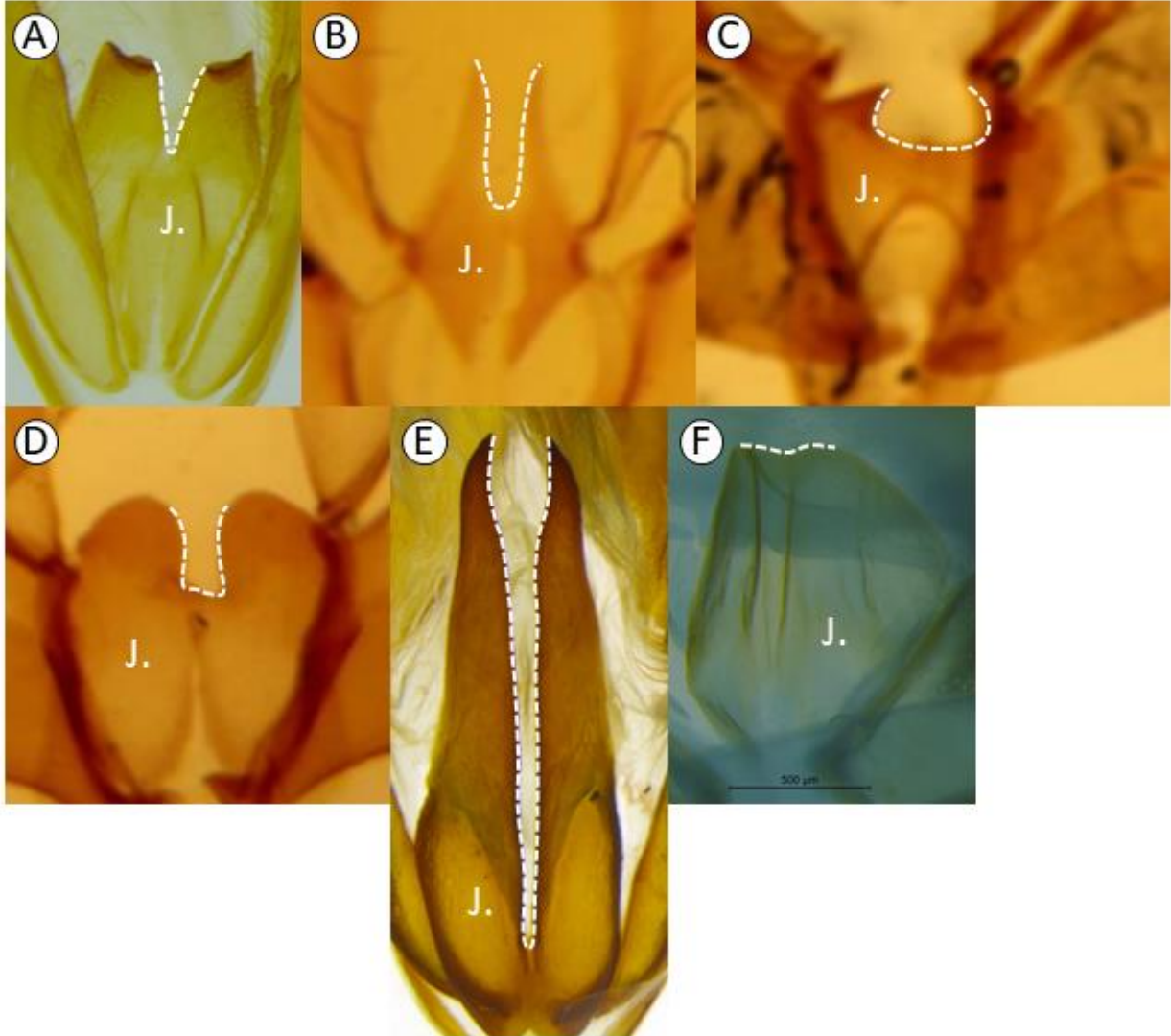
Figure 65. Notch-shaped space in juxta processi, Character 60 (state, condition): **A)** *E. materna* (0, "V"-shaped); **B)** *E. smaragdipicta* (1, narrow with parallel sides); **C)** *E. colubra* (2, wide, ovate); **D)** *E. serpentifera* (3, rectangular, wider than 0); **E)** *E. steppingstonia* (4, long and narrow, slight apical widening); **F)** *E. salaminia* (5, shallow indentation or depression). Space between juxta (J.) processi indicated by dashed white line.

The "V"-shaped notch condition (Fig. 65A) can be distinguished from spaces in the "V"-shaped group by the size of the notch relative to the juxta body as a whole. If the size is equivalent or somewhat larger, the taxon belongs in the "V"-shaped group; if the gap is smaller, it is scored as

a notch. The "V"-shaped notch condition is present in *E. materna*, *E. apta*, E. *homaena* from Taiwan, *E. memorans*, *E. mazzeii*, *E. behouneki*, *E. dividens*, and *E. sikhimensis*. The narrow condition with parallel sides (Fig. 65B) is present in *E. okurai*, *E. smaragdipicta*, *E. kinabaluensis*, and *E. martini*. In *E. colubra*, the notch is relatively wide and ovate lengthways (Fig. 65C), and the condition is apomorphic. Likewise in *E. serpentifera*, although the notch has parallel sides similar to *E. smaragdipicta*, the greater width of the notch disqualified it from the same condition, and the rectangular shape present (Fig. 65D) is apomorphic to this species. In *E. steppingstonia*, the notch is elongated and narrow throughout its extent, and widens slightly at the top into a cup-like depression (Fig. 65E). In *E. caesar*, *E. iridescens*, *E. salaminia*, and *Gonodonta indentata*, the "notch" is really a small indentation or depression in the juxta corresponding with the position of the notch or gap common to other taxa (65F). This condition is symplesiomorphic.

3.4.3.45 Character 61. *Curve of juxta processi, full length, Fig. 66*: (0) straight, uncurved, Fig. 66A; (1) outward toward valvae, Fig. 66B; (2) inward toward each other, Fig. 66C; (3) outward toward valvae, then recurved inward toward each other, Fig. 66D; (4) inward toward each other, then recurved outward toward valvae, Fig. 66E.
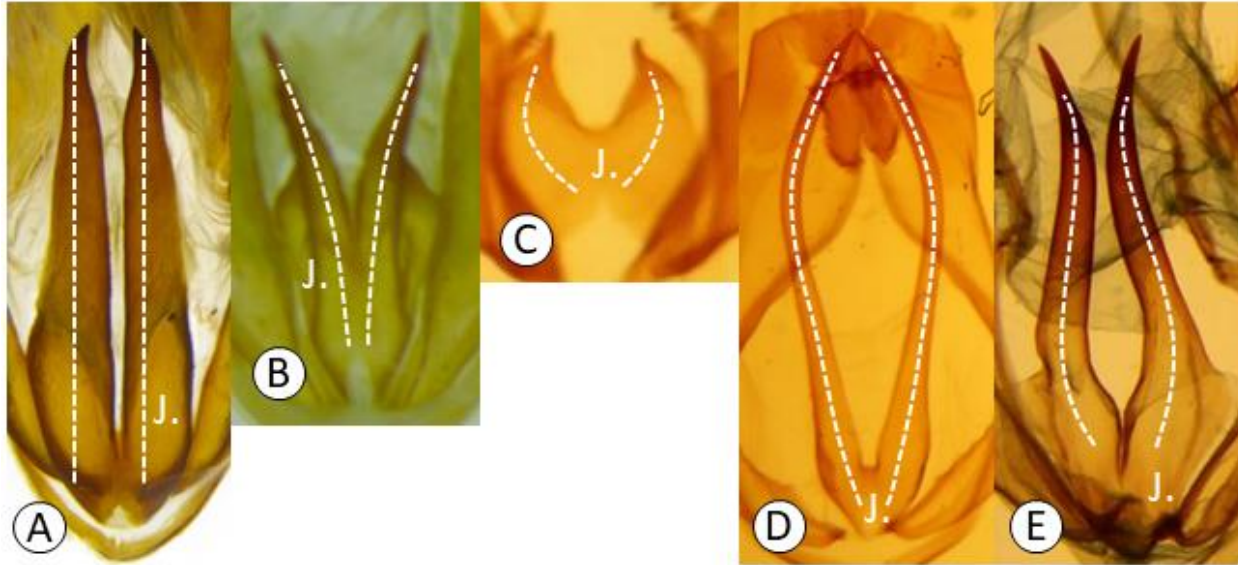
Figure 66. Curve of juxta processi, full length, Character 60 (state, condition): **A)** *E. steppingstonia* (0, straight, uncurved); **B)** *E. tyrannus* (1, outward toward valvae); **C)** *E. memorans* (2, inward toward each other); **D)** *E. cajeta* (3, outward toward valvae, then recurved inward toward each other); **E)** *E. boseae* (4, inward toward each other, then recurved outward toward valvae). Curve of juxta (J.) processi indicated by dashed white line.

In about 70% of *Eudocima* (as well as in *Phyllodes verhuelli* and *Gonodonta indentata*), the full length of both juxta processi is relatively uncurved and forms a straight line between the valvae (Fig. 66A). In *E. tyrannus*, *E. homaena* from Indonesia and the Philippines, *E. imperator*, *E. divitiosa*, and *E. collusoria*, the juxta processi are curved outwards toward the valvae, away from each other (Fig. 66B). *Eudocima martini*, *E. colubra*, and *E. memorans* have juxta processi that curve inwards towards each other (Fig. 66C). In other *Eudocima* species, the situation is more complex; rather than curving uniformly in one direction, the directionality of the curve changes along the length of the juxta. In *E. cajeta* and *E. cocalus*, the juxta processi curve outward, then bend inwards two thirds of the way along their length until the tips meet (Fig. 66D). This condition is also present in *E. cocalus*. In *E. boseae* and *E. splendida* the condition is reversed; the juxta processi first curve inwards before recurving away from each other (Fig. 66E).

3.4.3.46 Character 62. *Curve of juxta processi tips, Fig. 67*: (0) straight, uncurved, Fig. 67A; (1) outward toward valvae, Fig. 67B; (2) inward toward each other, Fig. 67C; (3) projecting toward viewer, Fig. 67D.
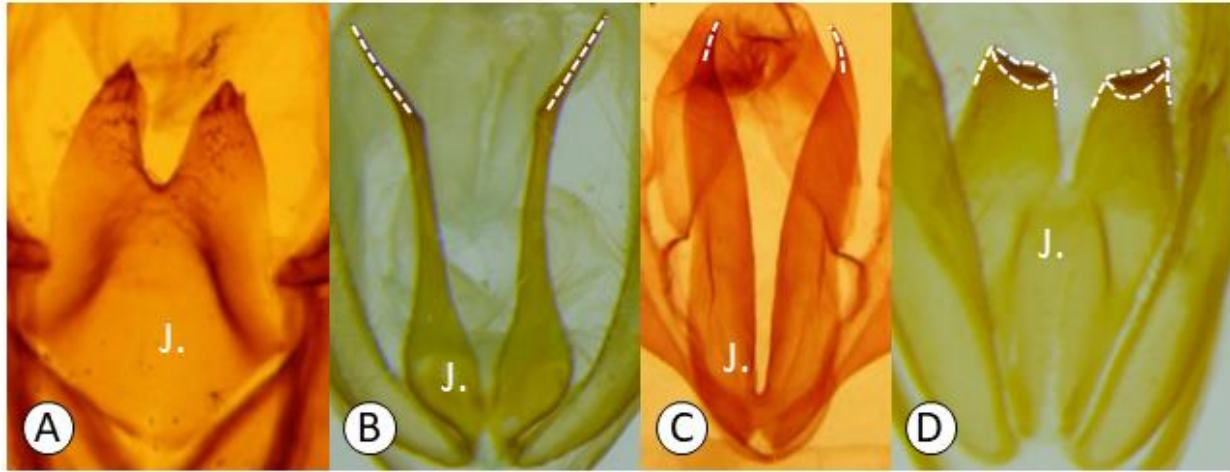
Figure 67. Curve of juxta processi tips, Character 62 (state, condition): **A)** *E. kuehni* (0, straight, uncurved); **B)** *E. jordani* (1, outward toward valvae); **C)** *E. phalonia* (2, inward toward each other); **D)** *E. materna* (3, projecting toward viewer). Curve of tips of juxta (J.) processi indicated by dashed white lines where present; in Fig. 67D, tips are outlined to show projecting condition.

In many *Eudocima* species, a difference was seen between the curvature of the full length of the juxta processi and the curvature at the very tips. For species with tips that align with the curve of the rest of the length of the processi, scoring was the same for the tip as for the process (i.e. an outward-curving process with an outward-curving tip). Straight tips (Fig. 67A) always concurred in this dataset with the presence of straight juxta processi, although not all taxa with straight juxta processi have straight tips. Taxa with straight tips include *E. kinabaluensis*, *E. lequeuxi*, *E. mazzeii*, *E. caesar*, *E. kuehni*, *E. iridescens*, *E. dividens*, *E. homaena* from Taiwan*, E. salaminia*, an Indonesian *E. srivijayana* specimen, *E. okurai*, and *E. sikhimensis*. *Phyllodes verhuelli* and *Gonodonta indentata* were also found to have straight tips. The most common condition in *Eudocima* is for the tips to be curved outward (~45%) (Fig. 67B). Taxa with inward-curving tips (Fig. 67C) include *E. oliveri*, *E. steppingstonia*, *E. colubra*, *E. behouneki*, *E. euryzona*, *E. cajeta*, Australian *E. cocalus*, and *E. phalonia*. *Eudocima apta* and *E. materna* present a condition which is unique; in these species, the tips of the juxta processi are curved outward on the plane of the viewer, pointing away from the genital capsule (Fig. 67D).

3.4.3.47 Character 63. *Bulge on inner margins of juxta processi, Fig. 68*: (0) absent, Fig. 68A; (1) present, Fig. 68B.
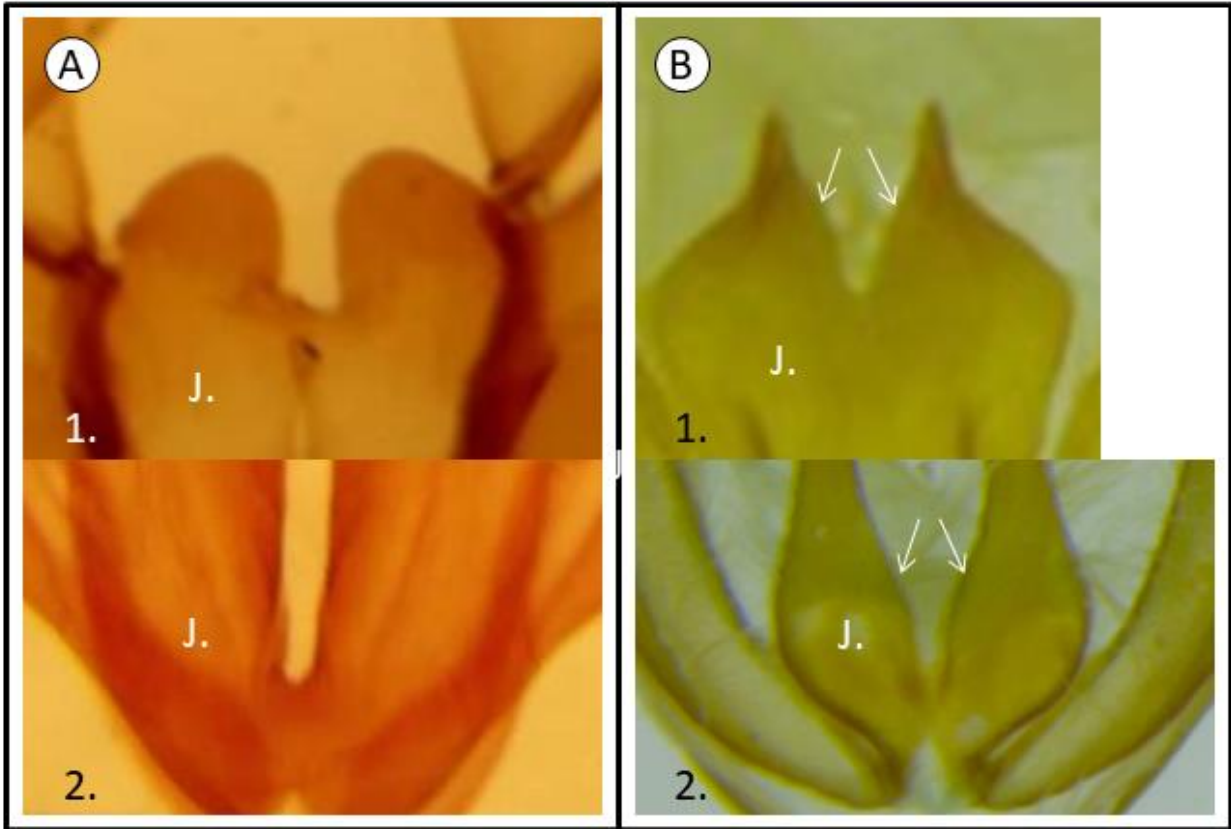
Figure 68. Bulge on inner margins of juxta processi, Character 63 (state, condition): **A)** *E. serpentifera* (A1) and *E. phalonia* (A2) (0, absent); **B)** *E. aurantia* (B1) and *E. jordani* (B2) (1, present). Bulges on juxta (J.) inner margins indicated by arrows.

In *E. tyrannus*, *E. bathyglypta*, *E. okurai*, the *E. srivijayana* specimens from Indonesia and Malaysia, *E. aurantia*, *E. jordani*, *E. paulii*, *E. euryzona*, *E. mazzeii*, *E. behouneki*, and *E. sikhimensis*, a slight bulge is present on the inner margin of each juxta process near the base (Fig. 68B). This bulge is sometimes difficult to discern, as in *E. sikhimensis*, *E. mazzeii*, and *E. behouneki*. In most *Eudocima* (~78%), the condition is absent (Fig. 68A).

3.4.4 Abdomen, female genitalia
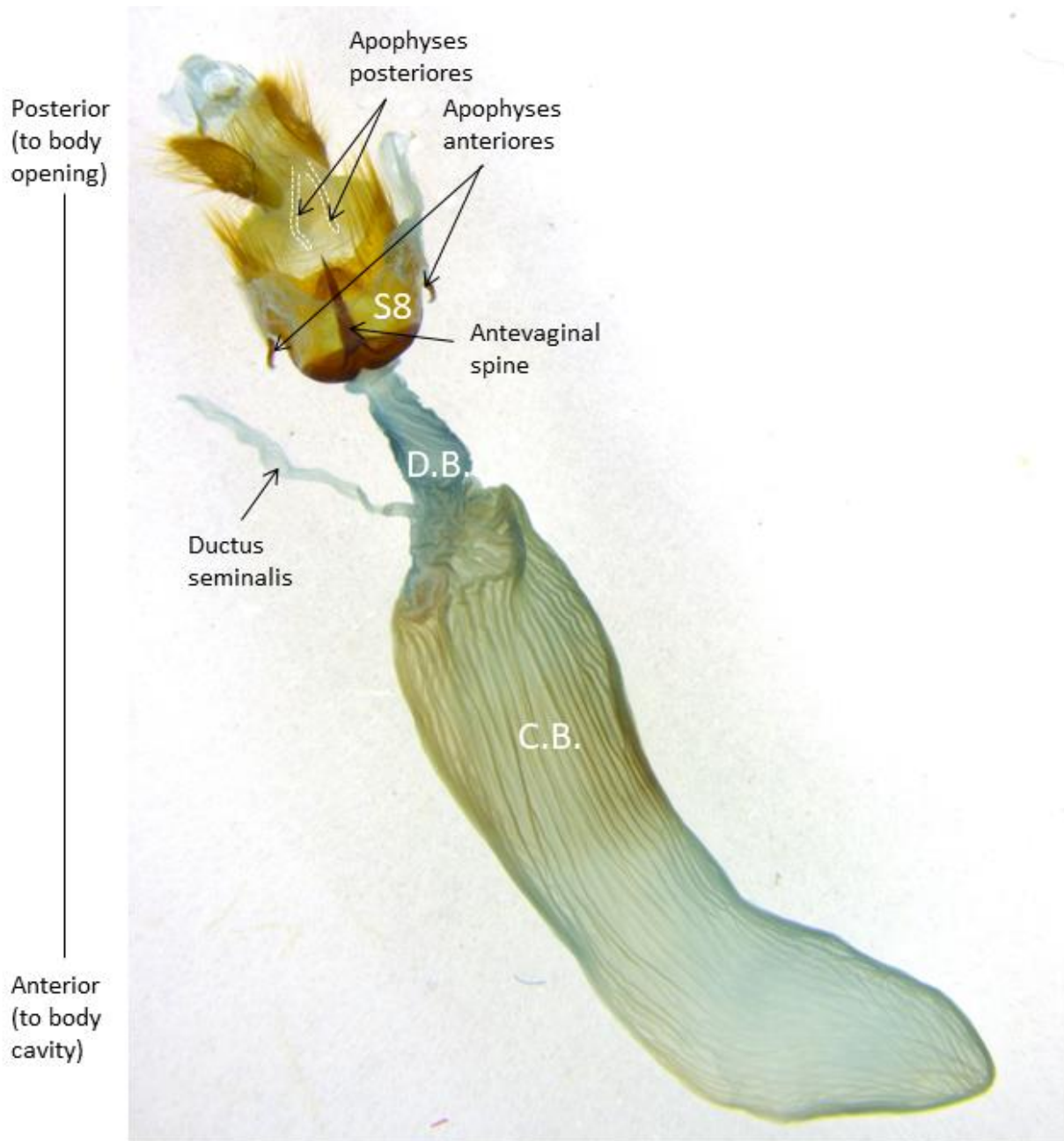
Figure 69. *Eudocima steppingstonia*, female genitalia with labelled parts used for character coding. S8 = segment 8, D.B. = ductus bursae, C.B. = corpus bursae. Additional features labelled and indicated by arrows. Apophyses posteriores further defined by dashed lines.

3.4.4.1   Character 64. *Antevaginal spine, Fig. 70*: (0) absent, Fig. 70A; (1) present, Fig. 70B.
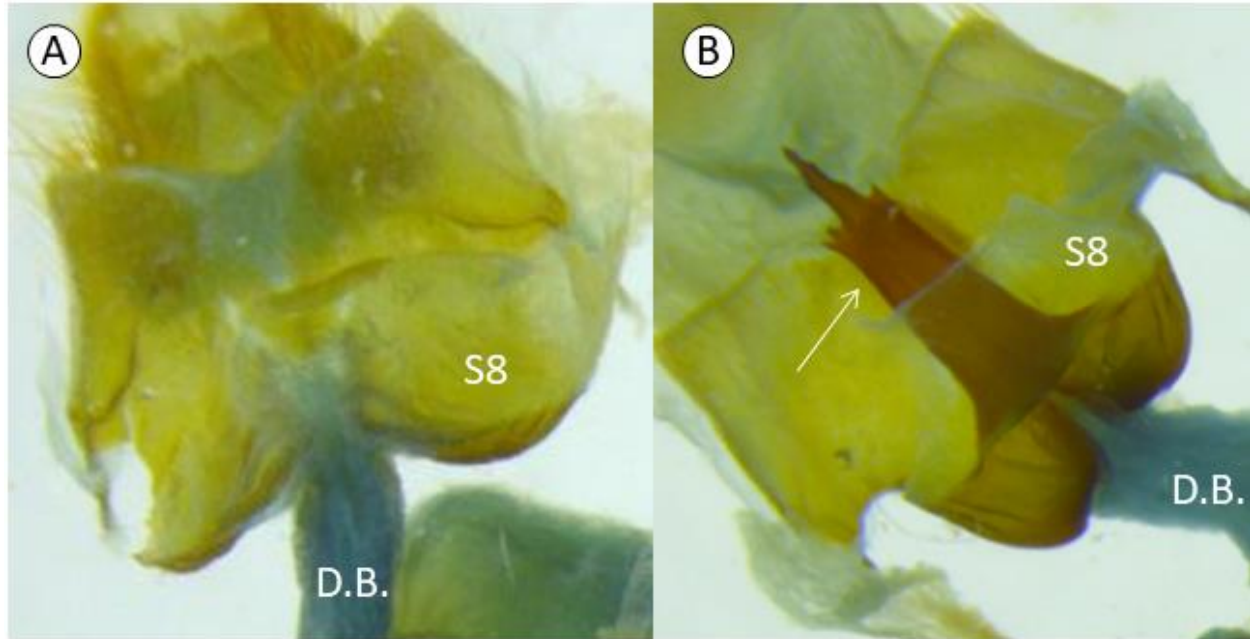
Figure 70. Antevaginal spine, Character 64 (state, condition): **A)** *E. dividens* (0, absent); **B)** *E. phalonia* (1, present). Antevaginal spine indicated by arrow. Segment 8 (S8) and ductus bursae (D.B.) labelled for reference.

A sclerotized antevaginal spine is present arising from the eighth abdominal segment (Fig. 70B) in *E. phalonia*, *E. tyrannus*, *E. jordani*, *E. cajeta*, *E. euryzona*, *E. oliveri*, *E. steppingstonia*, and *E. lequeuxi*. In the majority of *Eudocima* (~73%) this spine is absent (Fig. 70A).

3.4.4.2 Character 65. *Bifurcate antevaginal spine, Fig. 71*: (0) absent, Fig. 71A; (1) present, Fig. 715B.
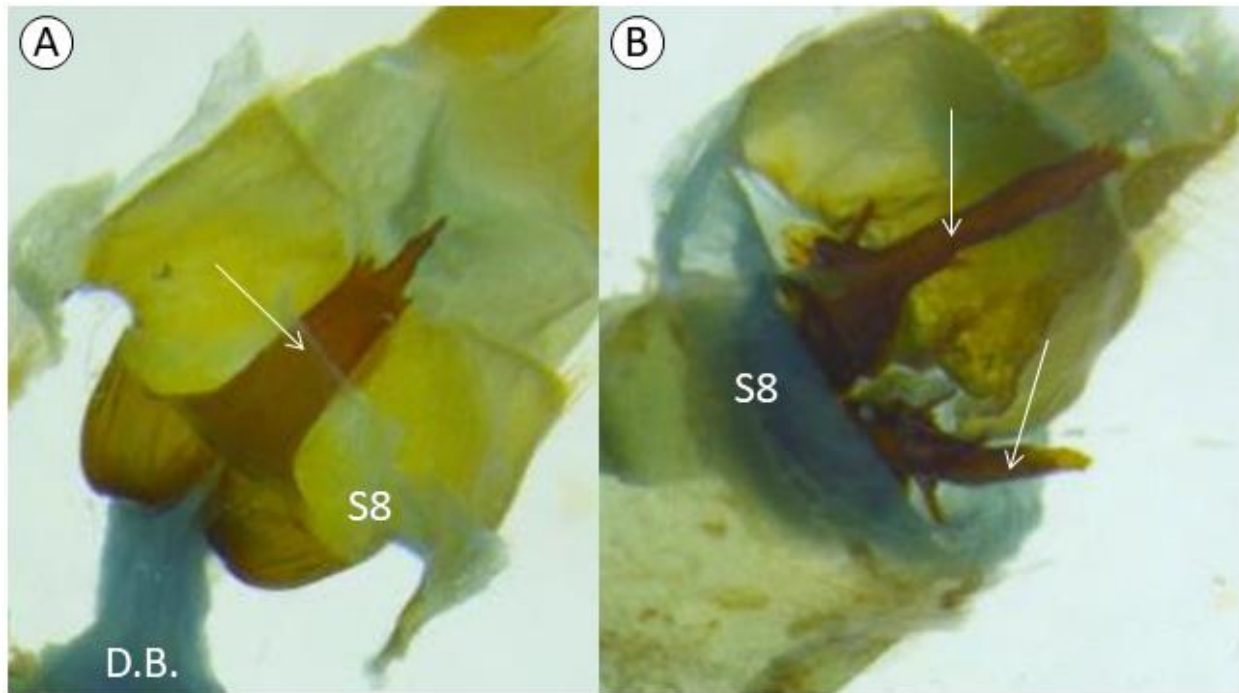
Figure 71. Bifurcate antevaginal spine, Character 65 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. tyrannus* (1, present). Point(s) of antevaginal spine indicated by arrows. Segment 8 (S8) and ductus bursae (D.B.) labelled for reference.

In *Eudocima* possessing an antevaginal spine, the spine may be entire with a singular point (Fig. 71A), as in *E. phalonia*, *E. euryzona*, *E. steppingstonia*, and *E. lequeuxi*; or, the spine may be forked or branched with two terminal points (Fig. 71B), as in *E. cajeta*, *E. jordani*, and *E. tyrannus*.

3.4.4.3   Character 66. *Antevaginal spine texture, Fig. 72*: (0) smooth, Fig. 72A; (1) with pair of lateral tooth-like processi, Fig. 72B; (2) with two pairs lateral tooth-like processi, Fig. 72C; (3) with many lateral tooth-like processi, Fig. 72D.
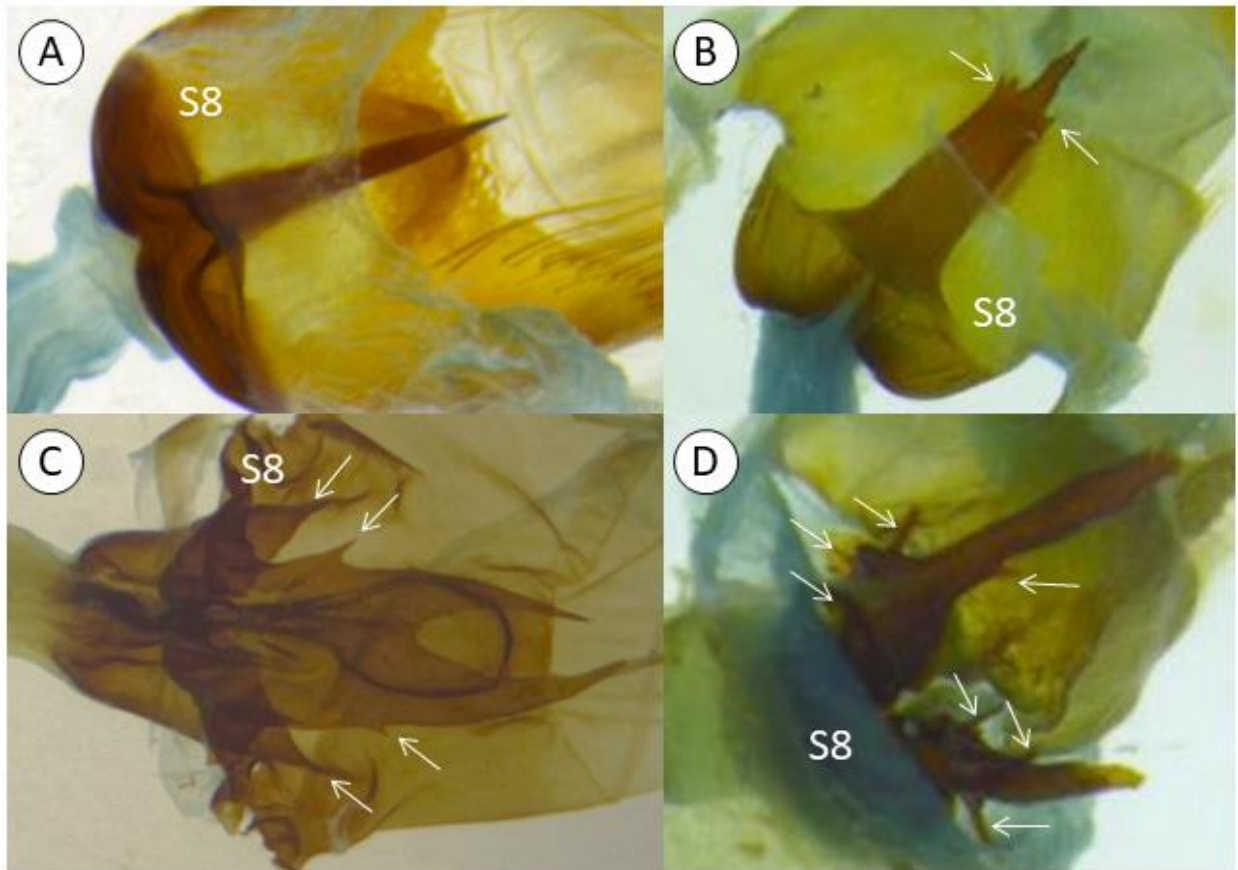
Figure 72. Antevaginal spine texture, Character 66 (state, condition): **A)** *E. steppingstonia* (0, smooth); **B)** *E. phalonia* (1, with pair of lateral tooth-like processi); **C)** *E. cajeta* (2, with two pairs lateral tooth-like processi); **D)** *E. tyrannus* (3, with many lateral tooth-like processi). Processi from antevaginal spine indicated by arrows. Segment 8 (S8) labelled for reference.

In nearly all *E. phalonia* specimens, *E. steppingstonia*, *E. lequexi*, and *E. jordani*, the body of the antevaginal spine is uniform and smooth, without lateral projections (Fig. 72A). In one *E. phalonia* specimen from Australia, a single pair of lateral projections was seen on either side of the spine's apex (Fig. 72B). One lateral pair of projections was also observed in one of the *E. cajeta* specimens. In the remaining *E. cajeta* specimen from Ceylon and in *E. euryzona*, two pairs of tooth-like projections are present (Fig. 72C). *Eudocima tyrannus* possesses many toothlike projections on the antevaginal spine, particularly near the base, giving the spine an overall thorny appearance (Fig. 72D).

3.4.4.4   Character 67. *Antevaginal spine shape, Fig. 73*: (0) straight spike, Fig. 73A; (1) widely bifurcated, broad space between points, Fig. 73B; (2) bifurcated midway with shared trunk, Fig. 73C; (3) less broadly bifurcated than (1), space between points smaller, Fig. 73D.
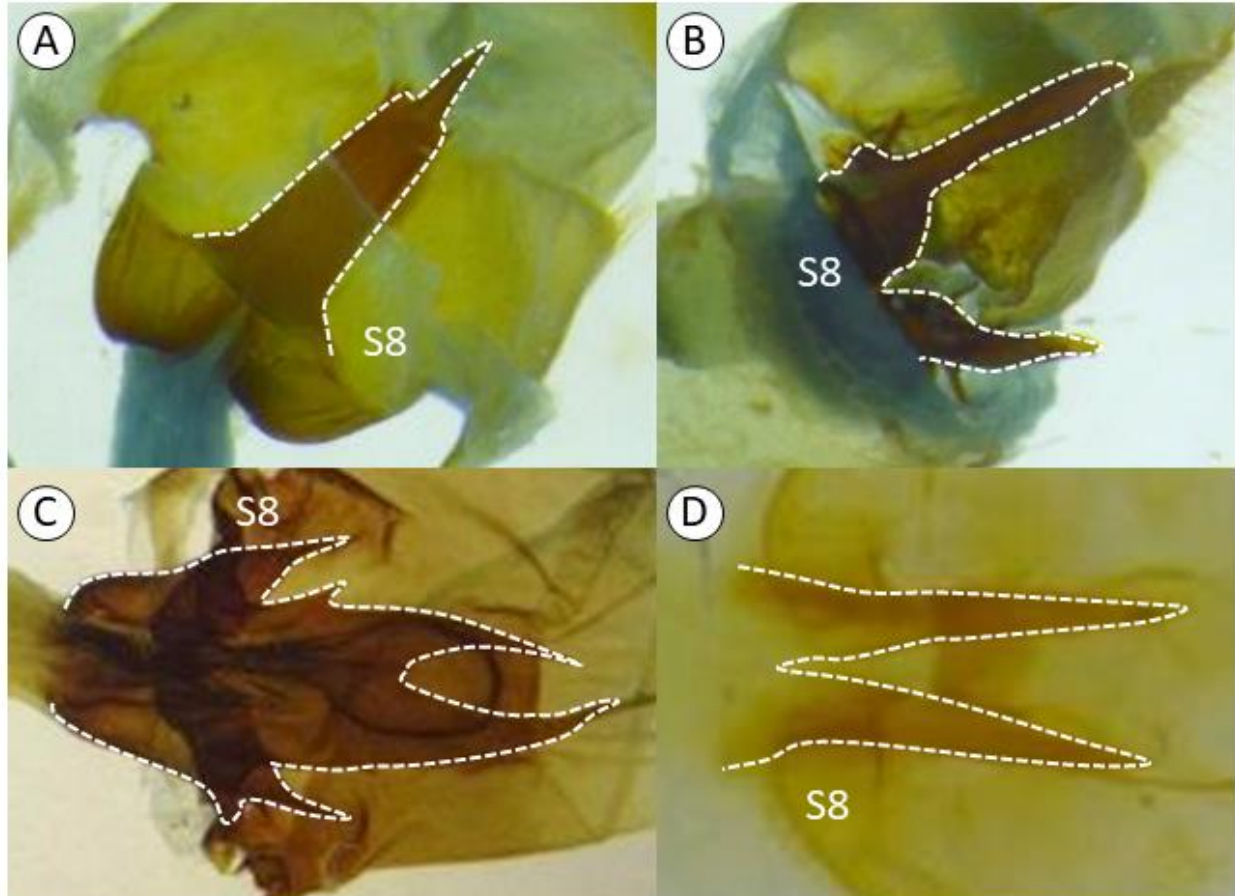
Figure 73. Antevaginal spine shape, Character 67 (state, condition): **A)** *E. phalonia* (0, straight spike); **B)** *E. tyrannus* (1, widely bifurcated, broad space between points); **C)** *E. cajeta* (2, bifurcated midway with shared trunk), **D)** *E. jordani* (3, less broadly bifurcated than 1, space between points smaller). Overall shape of antevaginal spine indicated by dashed line. Segment 8 (S8) labelled for reference.

The overall shape of the antevaginal spine is here discussed. In *E. phalonia*, *E. steppingstonia*, *E. lequeuxi*, and *E. oliveri*, the length of the antevaginal spine can be described as a straight spike (Fig. 73A). In *E. tyrannus*, the antevaginal spine is in the form of two nearly independent spines that are broadly separated from one another, with a wide space between them (Fig. 73B). In the *E. cajeta* specimen from Ceylon and *E. euryzona*, the antevaginal spine has a shared base and continues halfway up its length before forking into two points (Fig. 73C). In *E. jordani* and the

other *E. cajeta* specimen, the antevaginal spine is in two parts, as in *E. tyrannus*; however, the two spines are not as widely separated as those in tyrannus, and the gap between the two is smaller (Fig. 73D).

3.4.4.5   Character 68. *Anterior sclerotization of segment 8, Fig. 74*: (0) absent, Fig. 74A; (1) present, Fig. 74B.
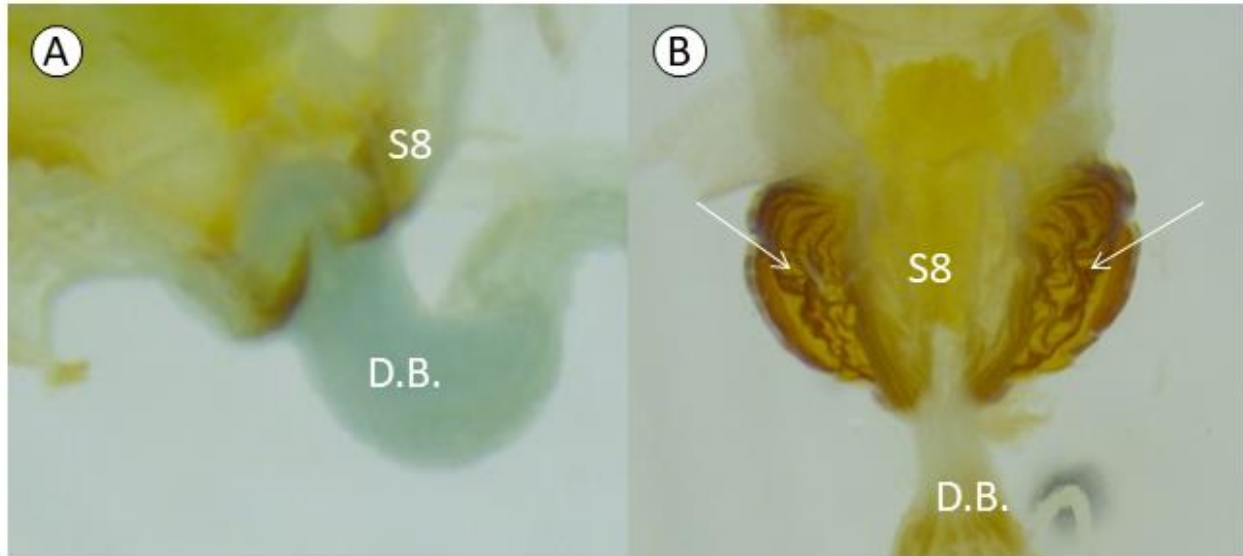
Figure 74. Posterior sclerotization of segment 8, Character 68 (state, condition): **A)** *E. aurantia* (0, absent); **B)** *E. materna* (1, present). Sclerotization of segment 8 indicated by arrows. Segment 8 (S8) and ductus bursae (D.B.) labelled for reference.

The modification of the eighth segment in female *Eudocima* is highly varied and of probable diagnostic value. About 32% of *Eudocima* species have patches of sclerotization or sclerotized plates arising from the eighth abdominal segment (Fig. 74B); this is a similar proportion to *Eudocima* species in which the eighth segment bears a sclerotized antevaginal spine. Species with anterior sclerotization of segment 8 include *E. apta*, *E. materna*, *E. cocalus*, *E. srivijayana*, *E. materna*, *E. dividens*, *E. procus*, *E. talboti*, *E. cajeta*, *E. behouneki*, and *E. treadawayi*. The remaining taxa examined did not show sclerotizations on the eighth segment (Fig. 74A), and the presence of these sclerotizations can be considered derived.

3.4.4.6 Character 69. *Shape of anterior sclerotization of segment 8, Fig. 75*: (0) pair of semi-ovate plates, Fig. 75A; (1) thin band, Fig. 75B; (2) broad rectangular plates with curved margins, smaller pointed elliptical plate between them, Fig. 75C; (3) heavy sclerotization in a "W" shape, Fig. 75D; (4) curved, hook-like plates, Fig. 75E; (5) toothed ridge (not shown, Plate 480 Holloway 2005); (6) trapezoidal plates, Fig. 75F.
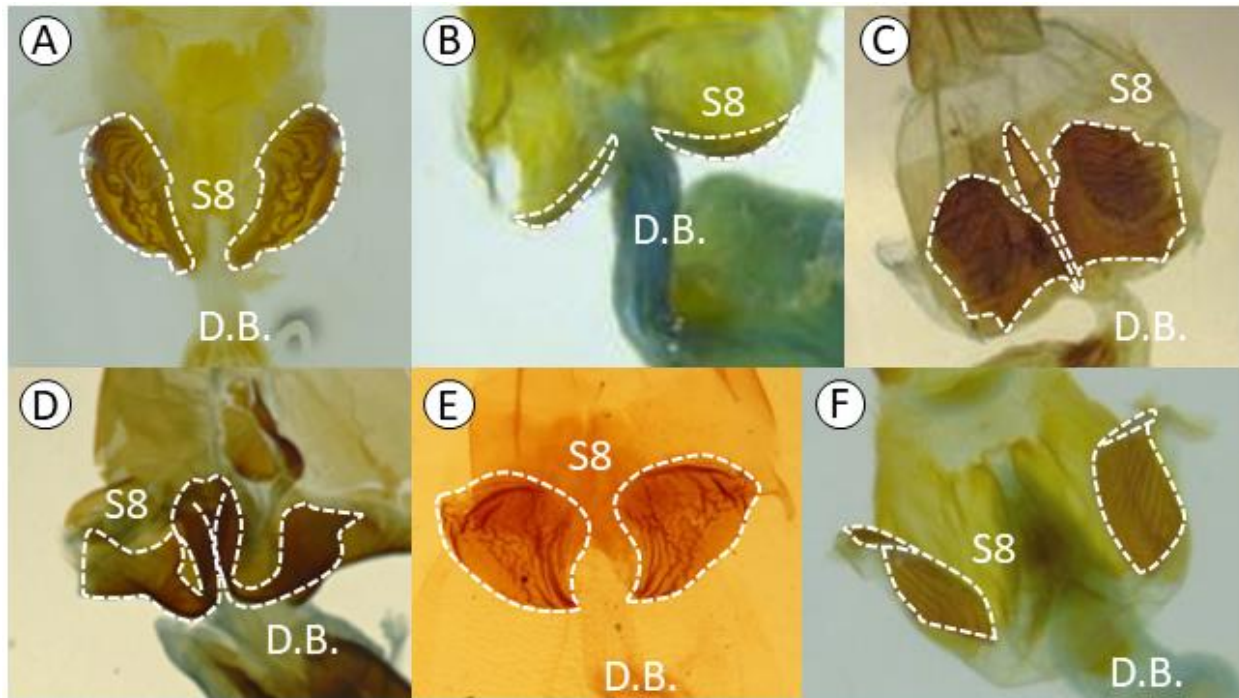
Figure 75. Shape of anterior sclerotization of segment 8, Character 69 (state, condition): **A)** *E. materna* (0, pair of semi-ovate plates); **B)** *E. dividens* (1, thin band); **C)** *E. srivijayana* (2, broad rectangular plates with curved margins, smaller pointed elliptical plate between them); **D)** *E. talboti* (3, heavy sclerotization in a "W" shape); **E)** *E. apta* (4, curved, hook-like plates); **F)**. *E. procus* (6, trapezoidal plates). Shape of anterior sclerotization of segment 8 indicated by dashed line. Segment 8 (S8) and ductus bursae (D.B.) labelled for reference.

Among species exhibiting sclerotization of the eighth segment, *E. materna* has a pair of unmistakable semi-ovate plates on the anterior margin of segment 8 (Fig. 75A). The condition in *E. apta* is similar, although the shape of the plates is broader posteriorly and curves inward anteriorly to points (Fig. 75E); this seemed sufficient for considering the state to be independent. In the majority of *Eudocima* in which sclerotization is present (~46%), there is a thin band of sclerotization on the anterior margin of segment 8, and heavy plates are not present (Fig. 75B). In *E. srivijayana*, two broadly rectangular plates are present with curved margins, and a smaller plate is between them shaped like a diamond or pointed ellipsoid (Fig. 75C). In *E. talboti*, the anterior margin is heavily sclerotized and curled posteriorly in the middle and sides to resemble a

"W" (Fig. 75D). A toothed ridge is formed by the sclerotization on the anterior margin in *E. salaminia* (Holloway 2005). The condition in *E. procus* is likewise distinctive; two plates are present which are widely separated and trapezoidal in shape (Fig. 75F).

3.4.4.7   Character 70. *Lobes of segment 8 prolonging into pouch, Fig. 76*: (0) absent, Fig. 76A; (1) present, Fig. 76B.
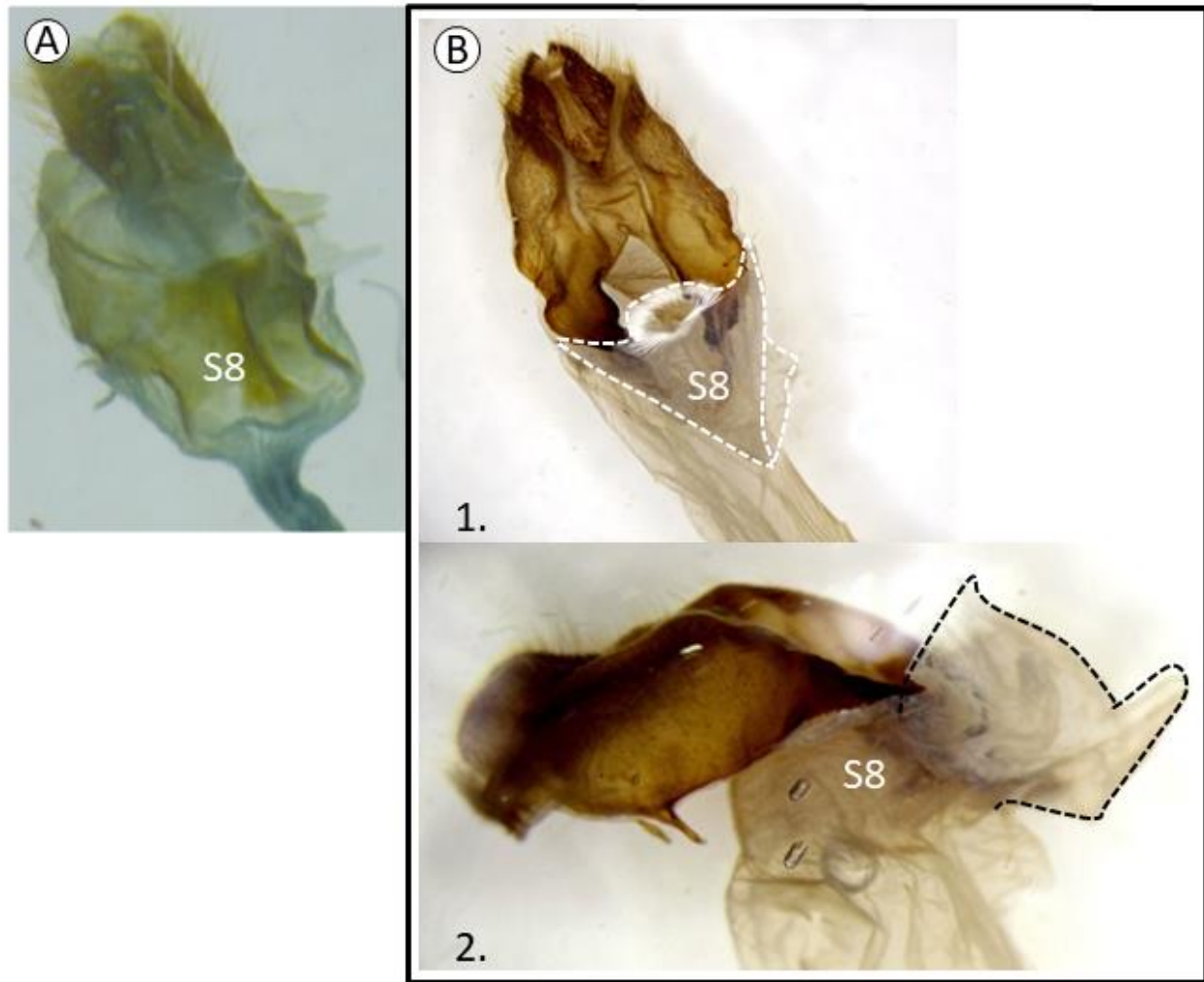
Figure 76. Lobes of segment 8 prolonging into pouch, Character 70 (state, condition): **A)** *E. nigricilia* (0, absent); **B)** *E. kuehni* ventral view (B1), lateral view (B2) (1, present). Pouch from segment 8 (S8) indicated by dashed lines.

This character is descriptive of *E. kuehni*, a *Eudocima* species with several exceptional features including reversed male and female sexual dimorphism (Zilli & Hogenes 2002, Zilli et al. 2017) and characters of the male genitalia which do not agree with typical members of the group. In *E. kuehni*, lobes from segment 8 are fused together and prolong into a pouch near the ostium (Fig. 75B), a condition absent from the other observed taxa (Fig. 75A).

3.4.4.8   Character 71. *Apophyses posteriores, Fig. 77*: (0) long and threadlike, Fig. 77; (1) other (not shown).

Figure 77. Apophyses posteriores, Character 71 (state, condition): *E. talboti* (0, long and threadlike). Apophyses posteriores indicated by dashed white lines.

All observed female taxa displayed apophyses posteriores which were long and threadlike (Fig. 77).

3.4.4.9   Character 72. *Apophyses anteriores, Fig. 78*: (0) reduced, Fig. 78A; (1) long, threadlike, Fig. 78B.
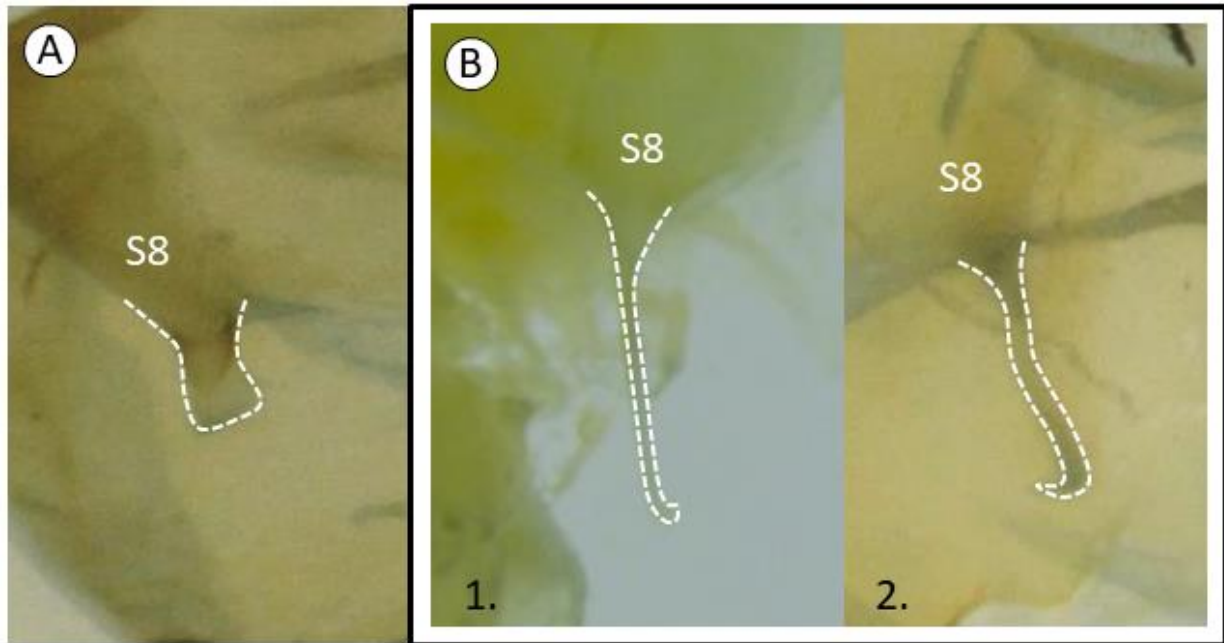
Figure 78. Apophyses anteriores, Character 72(state, condition): **A)** *E. divitiosa* (0, reduced); **B)** *Gonodonta indentata* (B1) and *E. smaragdipicta* (B2) (1, threadlike). Apophyse anterior indicated by dashed line. Segment 8 (S8) labelled for reference.

In *Plusiodonta incitans*, *Phyllodes consobrina*, *Phyllodes verhuelli*, *Gondonta indentata*, and *Oraesia argyrosigna*, the apophyses anteriores agree in form with the apophyses posteriores and are long and threadlike (Fig. 77B). However, the majority of *Eudocima* species (~71%) have apophyses anteriores which are much reduced, and can commonly appear to be pointed (like a triangle), or a rounded nub (Fig. 77A). Although variation was observed in the shape of the apophyses anteriores, scoring the variation was found to have no effect on the phylogenetic analysis and the character was discarded. Exceptions to the reduced condition among *Eudocima* species do occur, and a longer, threadlike condition prevails in *E. kuehni*, *E. euryzona*, *E. smaragdipicta*, *E. dividens*, *E. nigricilia*, and *E. salaminia*. The forms of the apophyses anteriores and apophyses posteriores do not exactly agree in these species as they do in the outgroups, and the threadlike apophyses anteriores are sometimes shorter in *Eudocima*; however, taking the long and threadlike condition to be ancestral, these species could still be easily distinguished from other *Eudocima* females with the typical much-reduced condition.

3.4.4.10 Character 73. *Ductus bursae length, Fig. 79*: (0) intermediate, Fig. 79A; (1) long, Fig.79B; (2) short, Fig. 79C.
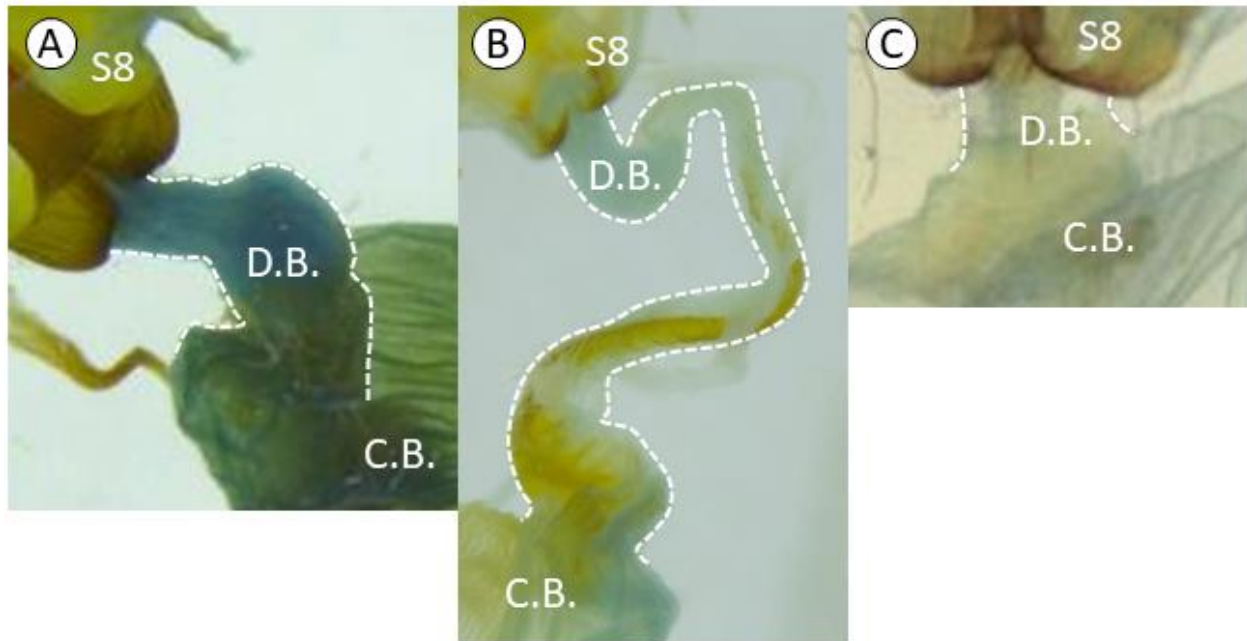
Figure 79. Ductus bursae length, Character 73 (state, condition): **A)** *E. phalonia* (0, intermediate); **B)** *E. aurantia* (1, long); **C)** *E. euryzona* (2, short). Ductus bursae (D.B.) indicated by dashed white lines. Segment 8 (S8) and corpus bursae (C.B.) labelled for reference.

In *E. tyrannus*, *E. aurantia*, *E. martini*, *Phyllodes consobrina*, and *Oraesia argyrosigna*, the ductus bursae is quite long, and is nearly the length of the corpus bursae (Fig. 79B). In contrast, only a small ductus, shorter than the papilla analis (Fig. 79C), connects the ostium to the corpus bursae in *E. treadawayi*, *E. talboti*, *E. mazzeii*, and *E. smaragdipicta*. A ductus bursae of an intermediate length between these extremes (Fig. 79A) is most common in females of *Eudocima* (~72%), and was also observed in *Plusiodonta incitans*, *Phyllodes verhuelli*, and *Gonodonta indentata*.

3.4.4.11 Character 74. *Ductus bursae shape, Fig. 80*: (0) cylindrical, wide diameter, Fig. 80A; (1) cylindrical, small diameter, Fig. 80B; (2) narrow at the top and increasing to larger diameter at bursae, inverted funnel, Fig. 80C; (3) funnel-like anterior and tube-like posterior, Fig. 80D.
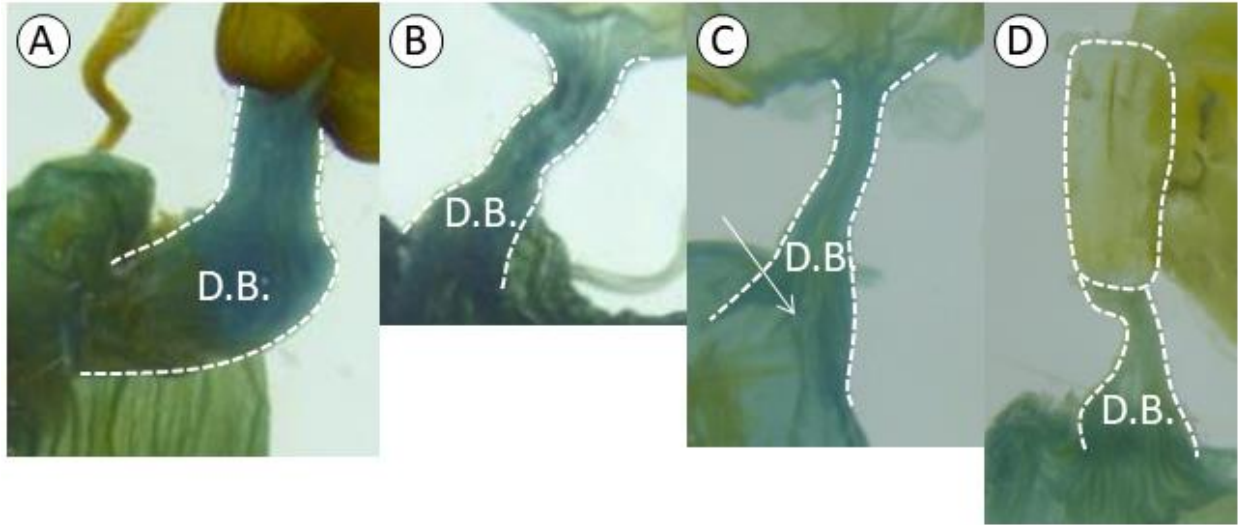
Figure 80. Ductus bursae shape, Character 74 (state, condition): **A)** *E. phalonia* (0, cylindrical, wide diameter); **B)** *E. nigricilia* (1, cylindrical, small diameter); **C)** *E. homaena* (2, narrow at the top and increasing to larger diameter at bursae, inverted funnel); **D)** *Gonodonta indentata* (3, funnel-like anterior and tube-like posterior). Shape of ductus bursae (D.B.) indicated by dashed lines, widening diameter in Fig. 79C indicated by arrow.

The ductus bursae is cylindrical with a wide diameter (Fig. 79A) in the majority of taxa observed, around 55%. In *E. martini*, *E. smaragdipicta*, *E. homaena* from Indonesia and the Philippines, *E. aurantia*, *E. nigricilia*, *E. salaminia*, *Plusiodonta incitans*, and *Oraesia argyrosigna*, the ductus bursae is cylindrical with a noticeably smaller diameter (Fig. 79B). In *E. srivijayana*, *E. materna* from Malawi, *E. homaena* from Taiwan, *E. boseae*, *E. divitiosa*, *E. bathyglypta*, *E. prolai*, the top of the ductus is narrower than where the ductus meets the bursae, forming an inverse funnel-shape (Fig. 79C). Although the top of the ductus can also be somewhat narrower in *E. phalonia*, *E. oliveri*, *E. steppingstonia*, and *E. lequeuxi*, the length of the bursae more closely corresponded with a cylinder than a funnel, and was scored accordingly. In *Gonodonta indentata*, *Phyllodes verhuelli*, and *Phyllodes consobrina*, the ductus appeared to be split, with a tube-like upper portion and a funnel-like lower portion (Fig. 79D). Consequently, these taxa received a unique character state.

3.4.4.12 Character 75. *Ductus bursae sclerotization, Fig. 81*: (0) absent, Fig. 81A; (1) complete, Fig. 81B; (2) half, Fig. 81C.
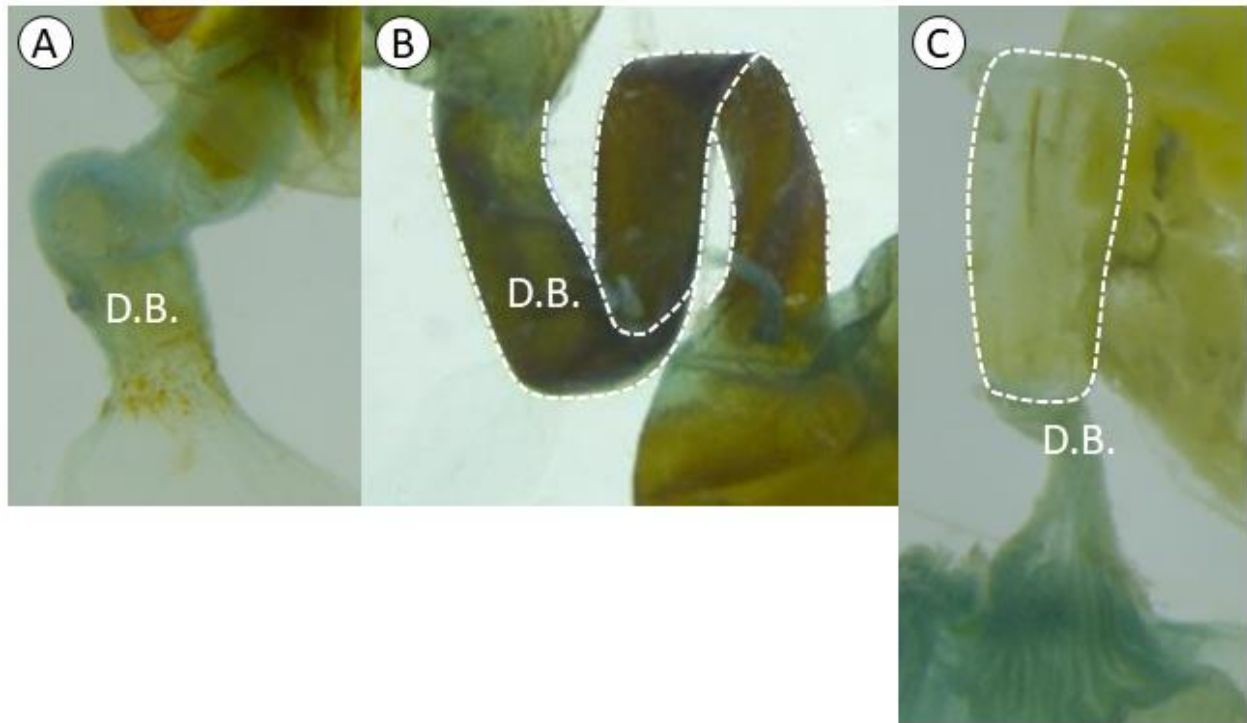
Figure 81. Ductus bursae sclerotization, Character 75 (state, condition): **A)** *E. procus* (0, absent); **B)** *E. tyrannus* (1, complete); **C)** *Gonodonta indentata* (2, half). Scerotization of ductus bursae (D.B.) indicated by dashed line.

In ~67% of observed taxa, no sclerotization of the ductus bursae was present (Fig. 81A). However, the ductus is entirely sclerotized (Fig. 81B) in *E. paulii*, *E. treadawayi*, *E. cocalus*, *E. sikhimensis*, *E. tyrannus*, and *Oraesia argyrosigna*. In *E. behouneki*, *E. martini*, *E. cajeta*, *E. talboti*, *Phyllodes verhuelli*, *Phyllodes consobrina*, and *Gonodonta indentata*, half the ductus is sclerotized (whether anteriorly or posteriorly) while the other half is membranous (Fig. 81C). The intensity of the staining used with some specimens made this character hard at times to determine.

3.4.4.13 Character 76. *Corpus bursae connected directly to ostium, Fig. 82*: (0) absent, Fig. 82A; (1) present, Fig. 82B.

Figure 82. Corpus bursae connected directly to ostium, Character 76 (state, condition): **A)** *E. phalonia* (0, absent); **B)** *E. kuehni* (1, present). Segment 8 (S8), ductus bursae (D.B.) and corpus bursae (C.B.) labelled for reference. Ductus bursae (D.B.) further indicated by arrow.

This character describes *E. kuehni*, in which no ductus bursae is present and the ostium opens directly to the bursae (Fig. 82B). This condition is easily distinguishable from taxa having only a very short ductus bursae, because no constriction of any sort is present in *E. kuehni* between the corpus bursae and the ostium. All other examined taxa presented a ductus bursae (Fig. 82A).

3.4.4.14 Character 77. *Corpus bursae shape, Fig. 83*: (0) pepper or banana shape, Fig. 83A; (1) heart shape, Fig. 83B; (2) rounded oblong rectang1e, Fig. 83C; (3) rectangular, wider posteriorly, Fig. 83D; (4) rounded posterior, extended and pointed anterior, Fig. 83E; (5) posterior bulge, larger anterior sac-like, Fig. 83F; (6) long and narrow, with slight constriction in the middle, Fig. 83G; (7) small, twisted box shape, Fig. 83H; (8) spiral shape, Fig. 83I; (9) wide angled posterior, constricting abruptly to fingerlike anterior (not shown, Plate 480 Holloway 2005); (A) sigmoidal, Fig. 83J.
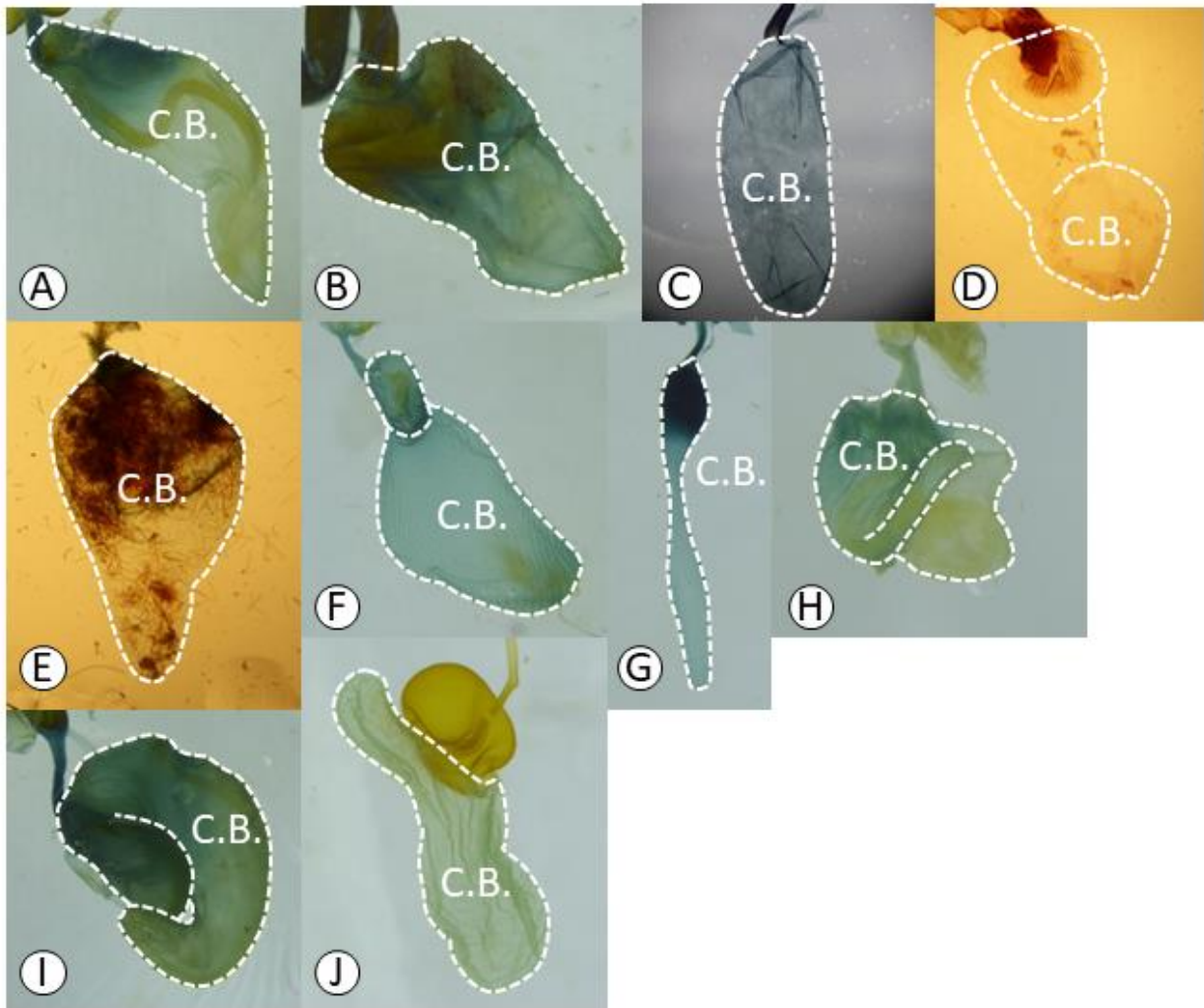
Figure 83. Corpus bursae shape, Character 77 (state, condition): **A)** *E. dividens* (0, pepper or banana shape); **B)** *E. tyrannus* (1, heart shape); **C)** *E. paulii* (2, rounded oblong rectang1e); **D)** *E. sikhimensis* (3, rectangular, wider posteriorly); **E)** *E. boseae* (4, rounded posterior, extended and pointed anterior); **F)** *E. homaena* (5, posterior bulge, larger anterior sac-like); **G)** *Plusiodonta incitans* (6, long and narrow, with slight constriction in the middle); **H)** *Gonodonta indentata* (7, twisted box shape); **I)** *Phyllodes consobrina* (8, spiral shape); **J)** *Oraesia argyrosigna* (A, sigmoidal). Shape of corpus bursae (C.B.) indicated by dashed lines.

The corpus bursae is widely variable across the examined taxa. A banana-like or jalapeño pepper-like bursae (Fig. 83A) was present in the majority of the taxa (~46%). In *E. tyrannus*, *E. apta*, and *E. materna*, the corpus bursae is pointed anteriorly and is roughly heart-shaped (Fig. 83B). *Eudocima paulii* and *E. homaena* from Indonesia and the Philippines possess a bursae which is oblong and uniformly shaped, similar to a rectangle without corners (Fig. 83C). The corpus bursae in *E. sikhimensis* is also vaguely rectangular, although the posterior portion of the rectangle is wider (Fig. 83D). *Eudocima boseae*, *E. materna*, *E. euryzona*, *E. smaragdipicta*, and *E. treadawayi* have a corpus bursae which is broad and rounded posteriorly and extends anteriorly into a point (Fig. 83E). In *E. homaena* from Taiwan, the ductus bursae opens into a smaller posterior chamber or bulge of the corpus bursae, which constricts and then widens anteriorly into a larger anterior chamber (Fig. 83F). This specimen was the only one observed to exhibit this condition. *Plusiodonta incitans* has a long and narrow corpus bursae with a slight constriction or "waist" in the middle (Fig. 83G), while *Phyllodes consobrina* has a distinctive spiral-shaped bursae (Fig. 82I). The corpus bursae in *Gonodonta indentata* is in the form of a twisted box-like shape with raised ridges (Fig. 83H); although this character state also applies to *E. martini* and *Phyllodes verhuelli*, in *E. martini* no ridges are present, and in *Phyllodes verhuelli* deep clefts cause the box to be almost 8-shaped. However, in both cases the corpus bursae is relatively small, and conforms more closely to this character than to the others; creating new states did not seem justifiable. In *E. salaminia*, the posterior portion of the corpus bursae is quite broad, and the ductus bursae does not attach to the corpus bursae in the center, giving the posterior part of the bursae an asymmetric appearance (Holloway 2005). The broad posterior then constricts abruptly to form a fingerlike anterior portion, which makes up about half the length of the corpus bursae. In *Oraesia argyrosigna*, the corpus bursae can be described as sigmoidal, with the main membranous body curved around the sclerotized appendix bursae (Fig. 83J) (the appendix bursae is not included in characterization of the shape of the corpus bursae).

3.4.4.15 Character 78. *Corpus bursae texture, Fig. 84*: (0) smooth, Fig. 84A; (1) wrinkled, Fig. 84B; (2) wrinkled posterior portion and smooth anterior portion, Fig. 84C.
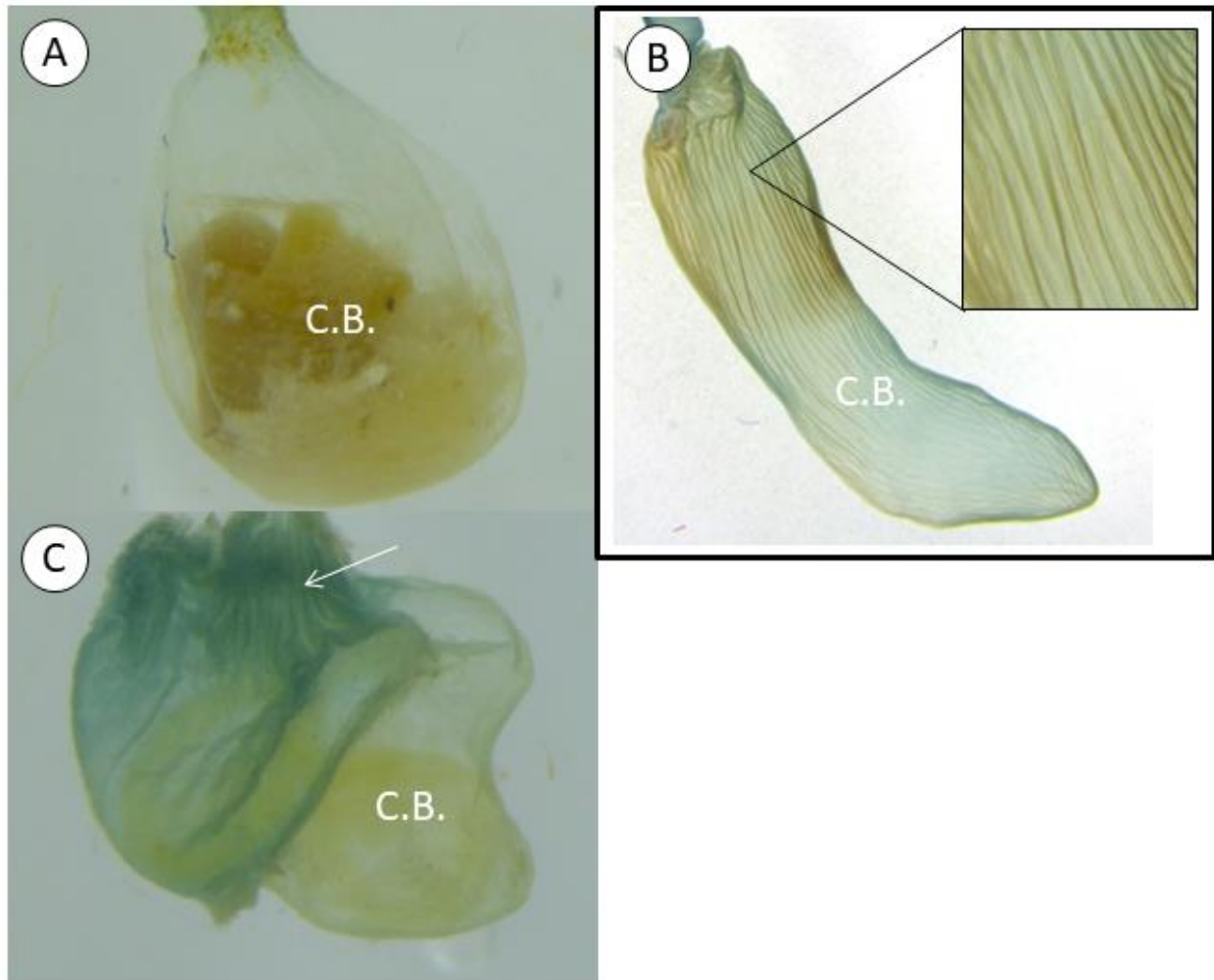
Figure 84. Corpus bursae texture, Character 78 (state, condition): **A)** *E. procus* (0, smooth); **B)** *E. steppingstonia* (1, wrinkled); **C)** *Gonodonta indentata* (2, wrinkled posterior portion and smooth anterior portion). Wrinkled portion enlarged in Fig. 83B, and wrinkled area indicated in Fig. 83C by arrow. Corpus bursae (C.B.) labelled for reference.

The wrinkled condition (Fig. 83B) is most prevalent among the examined taxa (~56%), although this condition was sometimes difficult to assess because of incomplete inflation of the corpus bursae. A smooth corpus bursae (Fig. 83A) is present in *E. martini*, *E. prolai*, *E. behouneki*, *E. mazzeii*, *E. euryzona*, *E. kuehni*, *E. procus*, *E. boseae*, *E. homaena* from the Philippines, *E. jordani*, *E. bathyglypta*, *E. sikhimensis*, *E. phalonia* from Ghana, *Plusiodonta incitans*, and

Oraesia argyrosigna. In *E. nigricilia*, *E. dividens*, and *Gonodonta indentata*, the corpus bursae appears to be divided into a wrinkled posterior and a smooth anterior (Fig. 83C).

3.4.4.16 Character 79. *Cervical sclerites, Fig. 85*: (0) absent, Fig. 85A; (1) present, Fig. 85B.
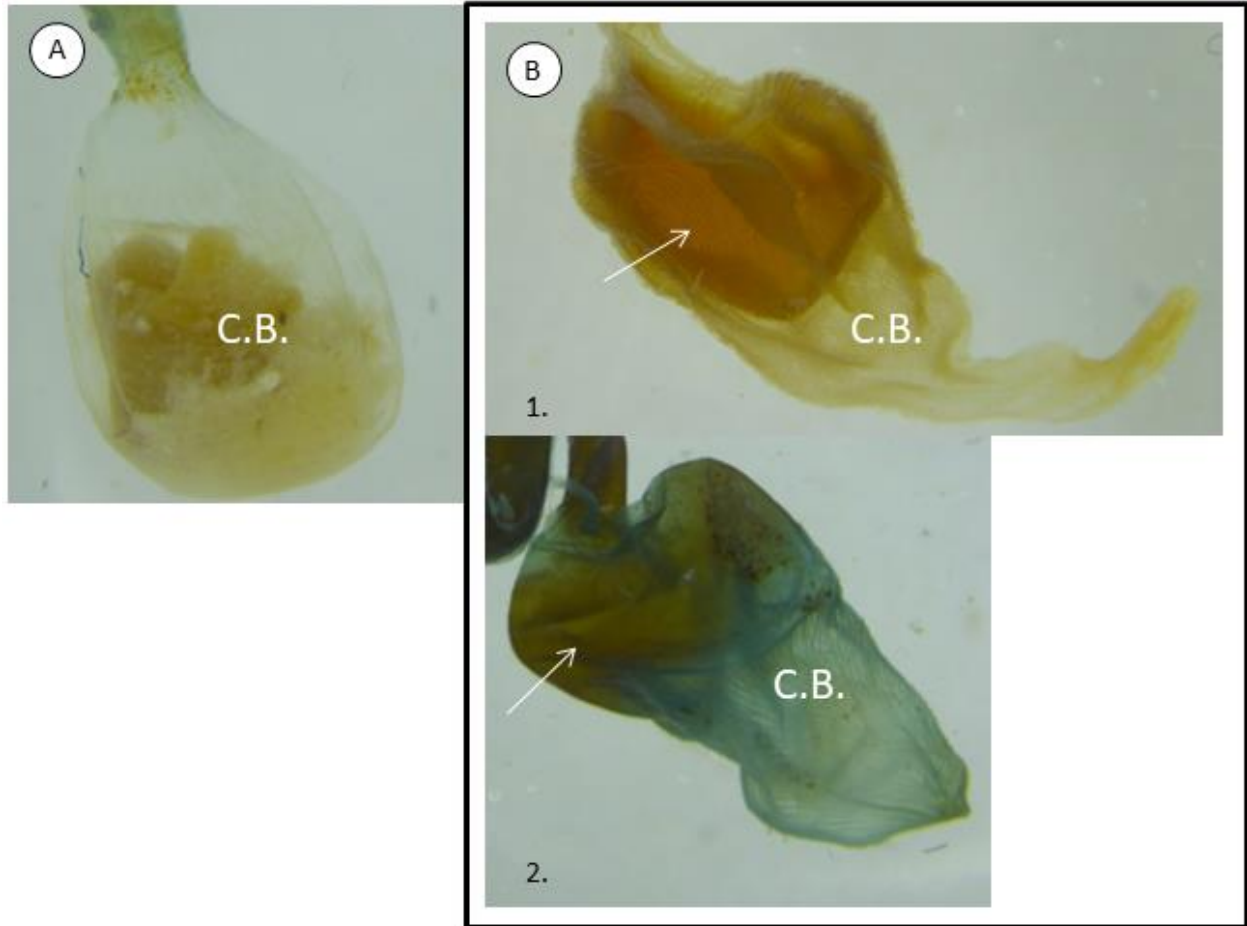
Figure 85. Cervical sclerites, Character 79 (state, condition): **A)** *E. procus* (0, absent); **B)** *E. materna* (B1) and *E. tyrannus* (B2) (1, present). Cervical sclerites indicated by arrows. Corpus bursae (C.B.) labelled for reference.

In *E. materna* and *E. apta*, broad sclerotized plates are present on the corpus bursae (Fig. 84B, 1). In *E. tyrannus*, the upper half of the corpus bursae is sclerotized proximal to the ductus bursae (Fig. 84B, 2). Although variation in the shape of the cervical sclerites is noted, inclusion as a character did not affect the phylogenetic analysis. Cervical sclerites were not observed (Fig. 84A) in other *Eudocima* species. This character was at times difficult to determine due to intense staining, or darkening of the bursae due to the presence of detachable cornuti or spermatophores.

3.4.4.17 Character 80. *Appendix bursae, Fig. 86*: (0) absent, Fig. 86A; (1) present, Fig. 86B.
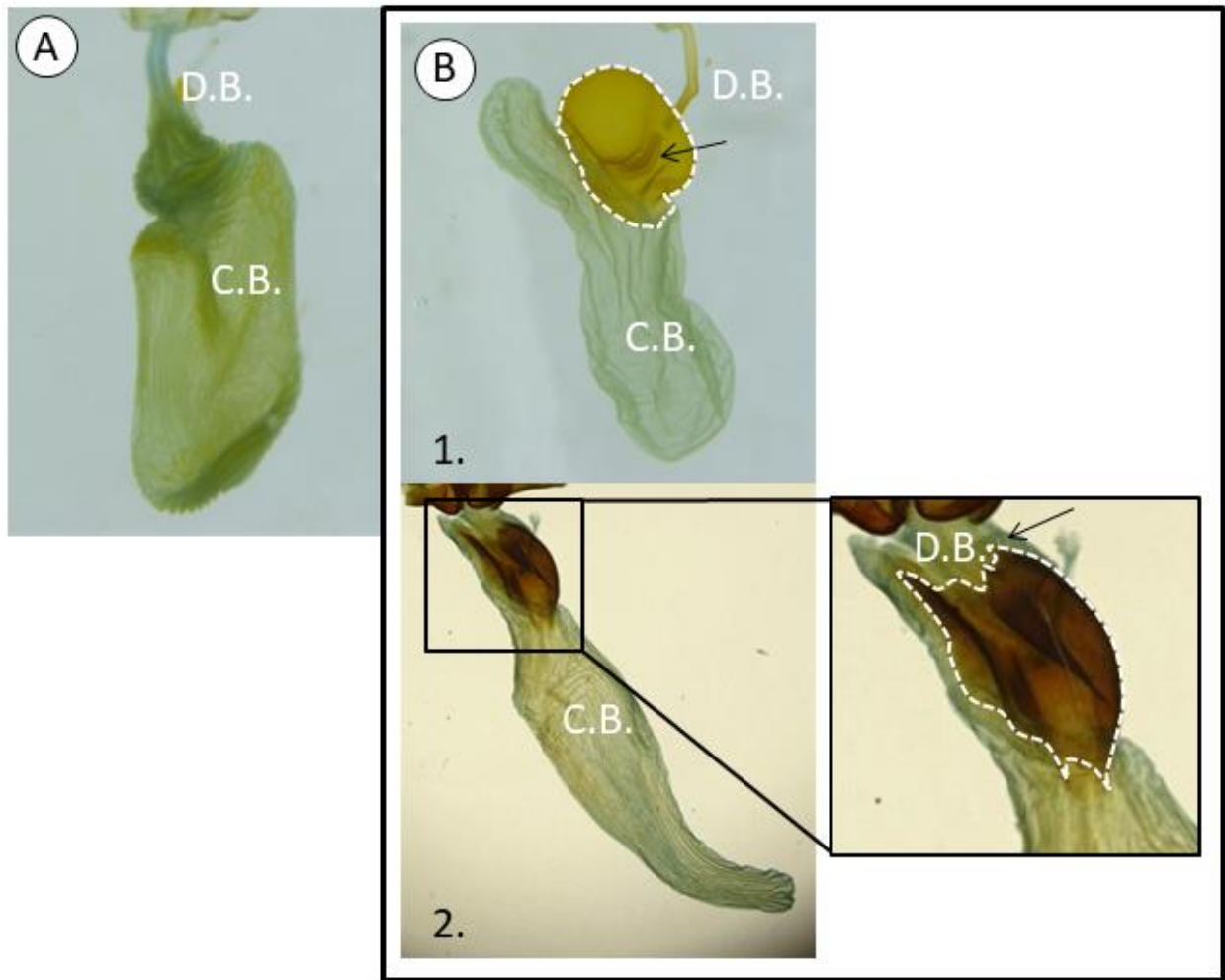
Figure 86. Appendix bursae, Character 80 (state, condition): **A)** *E. homaena* (0, absent); **B)** *Oraesia argyrosigna* (B1) and *E. talboti* (B2) (1, present). Appendix bursae indicated by dashed line. Arrows indicate where ductus bursae (D.B.) joins with appendix bursae. Area with appendix bursae enlarged in Fig. 85B2. Corpus bursae (C.B.) labelled for reference.

The appendix bursae is here defined as a separate, sclerotized bulge or diverticulum of the corpus bursae into which the ductus bursae connects (Fig. 85B). The taxon examined in this study with a clearly apparent appendix bursae is *Oraesia argyrosigna* (Fig. 85B, 1). In *E. talboti*, the conditions determining presence of an appendix bursae were also met, despite its small size (Fig. 85B, 2). The presence of an appendix bursae can be distinguished as a separate condition from the corpus bursae configuration in the Philippines specimen of *E. homaena*; although the ductus

bursae enters the neatly divided bulge on the posterior portion of the bursae, the bulge itself is membranous in *E. homaena* and not sclerotized.

3.4.4.18 Character 81. *Ductus seminalis position, Fig. 86*: (0) at the top of the corpus bursae, near the junction of the corpus bursae and the ductus bursae, Fig. 86A; (1) on the ductus bursae, Fig. 86B.
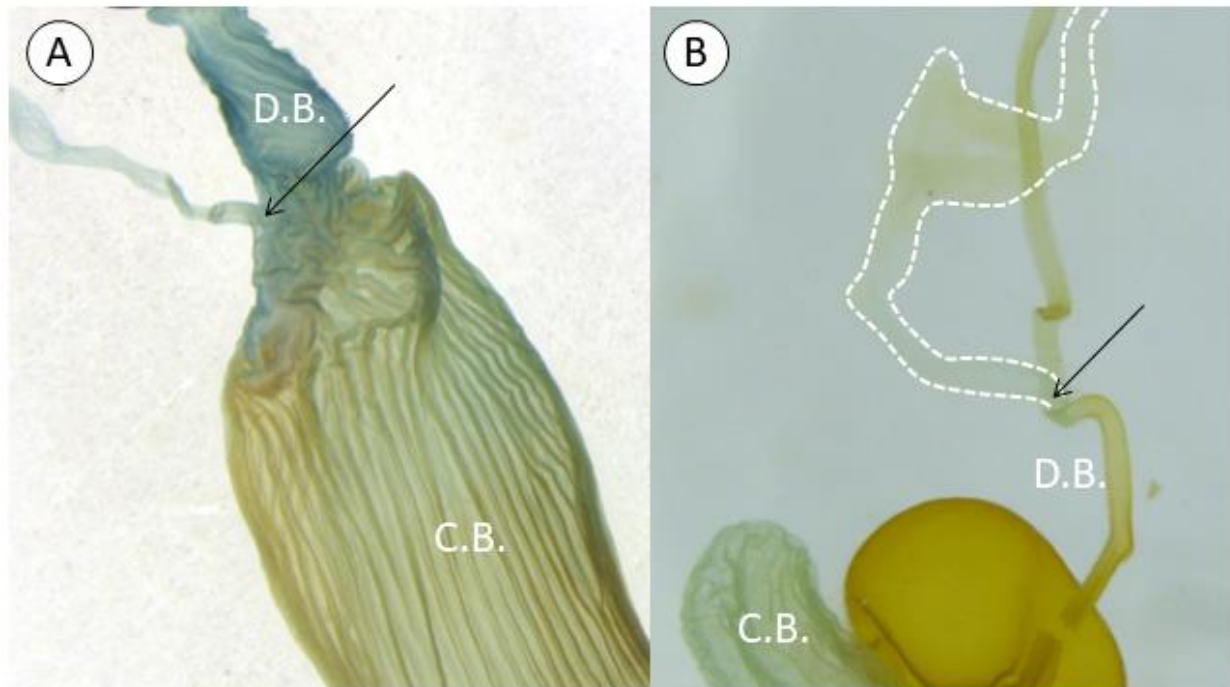
Figure 87. Ductus seminalis position, Character 81 (state, condition): **A)** *E. steppingstonia* (0, at the top of the corpus bursae, near the junction of the corpus bursae and the ductus bursae); **B)** *Oraesia argyrosigna* (1, on the ductus bursae). Arrow indicates junction of the ductus seminalis with the rest of female reproductive tract. Ductus seminalis in Fig. 87B further indicated by dashed line. Ductus bursae (D.B.) and corpus bursae (C.B.) labelled for reference.

The position of the ductus seminalis where it joins with the rest of the female copulatory tract is a feature of biological significance which could influence systematic placement. In nearly all taxa examined (~95%), the ductus seminalis connects at the top of the corpus bursae, near where the ductus bursae joins (Fig. 87A). However, in *Oraesia argyrosigna* and *E. procus*, the ductus seminalis connects directly to the ductus bursae (Fig. 87B).

3.4.4.19 Character 82. *Ductus seminalis shape, Fig. 88*: (0) narrow at junction, widening in diameter for the rest of the length, Fig. 88A; (1) narrow at junction, widening, then narrowing again, Fig. 88B; (2) narrow along its length, Fig. 88C; (3) expanding from junction to a large sac, then becoming narrow, Fig. 88D.
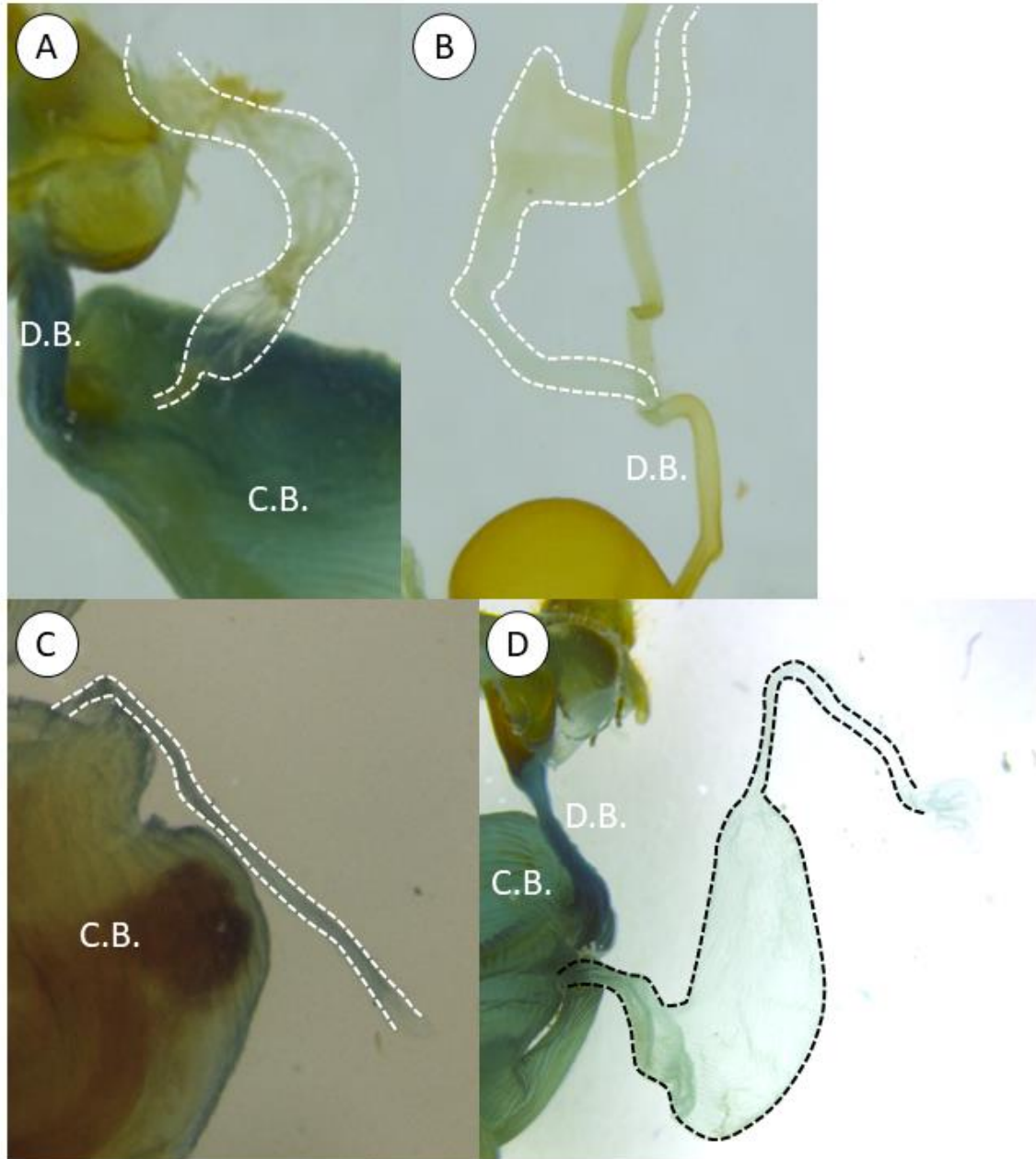
Figure 88. Ductus seminalis shape, Character 82 (state, condition): **A)** *E. dividens* (0, narrow at junction, widening in diameter for the rest of the length); **B)** *Oraesia argyrosigna* (1, narrow at junction, widening, then narrowing again); **C)** *E. smaragdipicta* (2, narrow along its length); **D)** *Phyllodes consobrina* (3, expanding from junction to a large sac, then becoming narrow). Shape of ductus seminalis indicated by dashed lines. Ductus bursae (D.B.) and corpus bursae (C.B.) labelled for reference.

This character describes changes in the diameter of the ductus seminalis along its observed length. Because the length of the ductus seminalis can be influenced by dissection preparation, this character may have been affected. In general, the examined taxa had a uniformly narrow ductus seminalis (~70%) (Fig. 88C). In one of the Australian *E. phalonia* specimens, the Australian *E. cocalus* specimen, the *E. materna* specimen from Malawi, and *E. dividens*, the ductus seminalis has a narrow diameter where it connects to the corpus bursae, but then widens as it continues (Fig. 88A). In *Oraesia argyrosigna*, *E. procus*, and one of the Chinese *E. tyrannus* specimens, the ductus seminalis is narrow where it meets the bursae, then widens into a pouch or pocket before becoming narrow once more (Fig. 88B). In *Phyllodes consobrina* and *Phyllodes verhuelli*, the ductus seminalis is a wide diameter where it meets the corpus bursae and further dilates into a large sac before becoming narrow again (Fig. 88D).

3.5   Results and discussion

3.5.1   Maximum parsimony consensus tree

The heuristic search yielded ten maximum parsimony trees with a tree length of 556; the strict consensus of these had a calculated C.I. of 0.33 and R.I. of 0.59. Jackknife supports were calculated for the strict consensus tree using TNT. The strict consensus tree (Fig. 89, Fig. 90, Fig. 91, Fig. 92) shows the following phylogenetic sequence: (*Gonodonta indentata* (*Plusiodonta incitans* (*E. procus* (*Oraesia triobliqua* + *Oraesia argyrosigna*) ((*E. splendida* (*E. kinabaluensis* + *E. smaragdipicta*)) (*E. martini*, *E. kuehni* (*Phyllodes verhuelli* + *Phyllodes consobrina*)) (remaining *Eudocima*)))))). Thus, the monophyly of *Eudocima* was not supported. In this analysis, *E. procus* forms a clade with both species of *Oraesia*, while *E. splendida*, *E. kinabaluensis*, *E. smaragdipicta*, *E. kuehni*, and *E. martini* form a clade with the two *Phyllodes* species. The remaining *Eudocima* species are recovered together in a large, well-resolved clade from *E. nigricilia* to *E. cajeta* Ceylon, with a jackknife support value of 5. This clade is indicated in Fig. 89 by the name "E s.l.", since it encompasses the older generic designations. Within clade E s.l., two major clades were recovered: *E. collusoria* to *E. tyrannus* (clade I), and *E. muscigera* to *E. cajeta* Ceylon (clade II) (Fig. 89). The clade (*E. nigricilia* (*E. dividens* + *E. salaminia*)) was recovered outside of these two clades, and is therefore sister to clade I + clade II. Clade I is divided into two subclades: subclade IA, comprising *E. collusoria* to *E. homaena* Indonesia + Philippines; and subclade IB, comprising *E. behouneki* to *E. tyrannus*. Within clade II, *E. boseae*, *E. muscigera*, and *E. discrepans* are sister to two other large subclades: subclade IIA (*E. imperator* to *E. apta*) and subclade IIB (*E. jordani* to *E. cajeta* Ceylon). Subclade IIB is further split into two major clades: the *E. phalonia* clade (from *E. jordani* to *E. steppingstonia*), and the clade from *E. treadawayi* to *E. cajeta* Ceylon (Fig. 89). Although significant backbone structure is present throughout the phylogeny, jackknife supports are generally low except for shallow nodes, which often represent replicates of a single species (Fig. 89, Fig. 90). The same strict consensus tree was used to test the historical generic concepts *Adris*, *Othreis*, *Trissophaes*, *Rhytia*, and *Eudocima* s.str. (Fig. 90), reconstruct the most parsimonious area of origin (Fig. 91, Fig. 92), and examine dispersal across the Indo-Australian Archipelago.
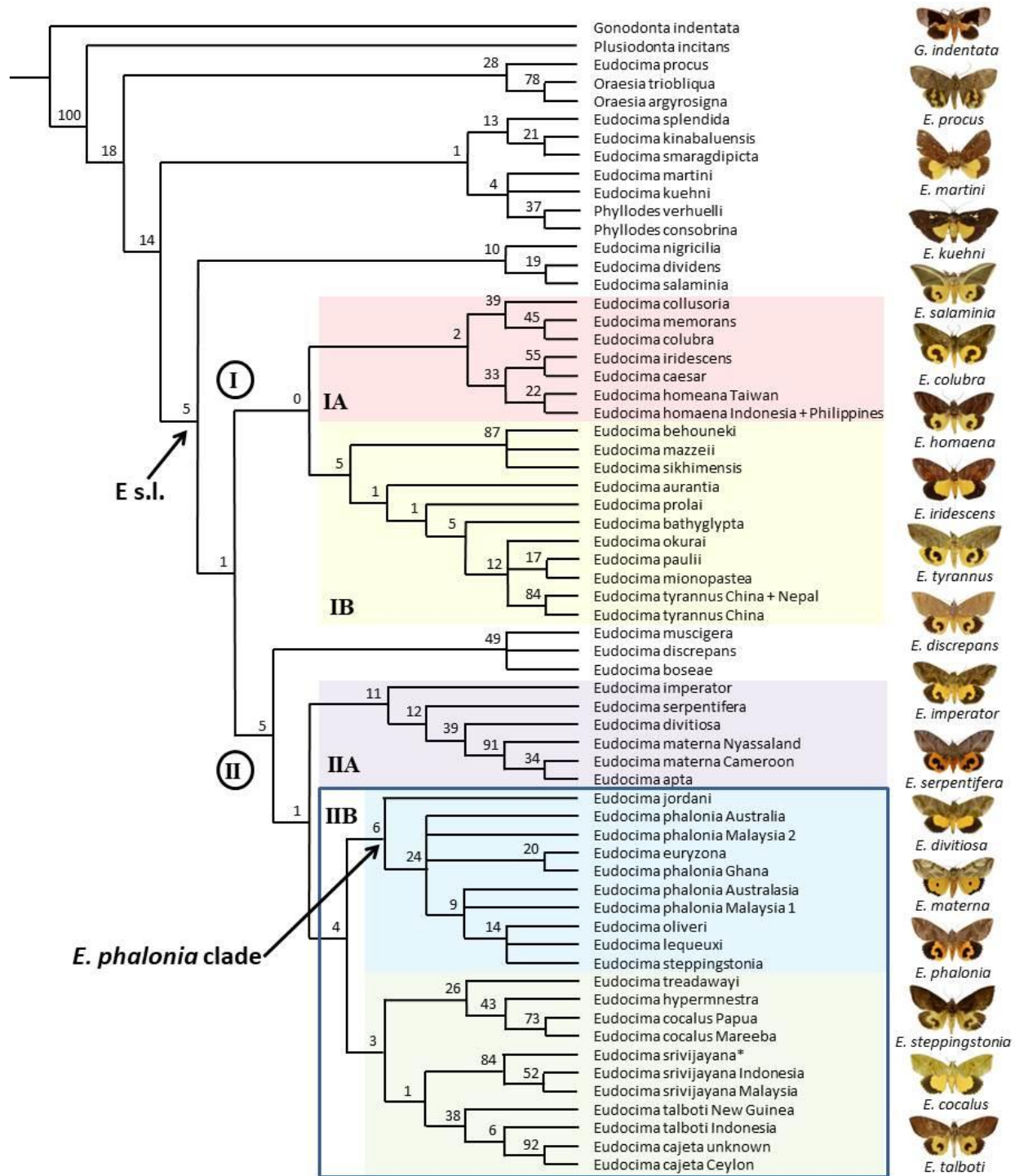
Figure 89. Strict consensus tree (tree branch length = 565, C.I. = 0.33, R.I. = 0.58) with jackknife branch supports and clade designations of ingroup taxa. *E. srivijayana* = *E. srivijayana* Philippines + Celebes + Timor. Images from BOLD Systems (Ratnasingham & Hebert 2007): *E. procus* adapted from record ANIAF903-11 (Axel Hausmann), *E. serpentifera* adapted from record 97-SRNP-11055 (Dan Janzen).
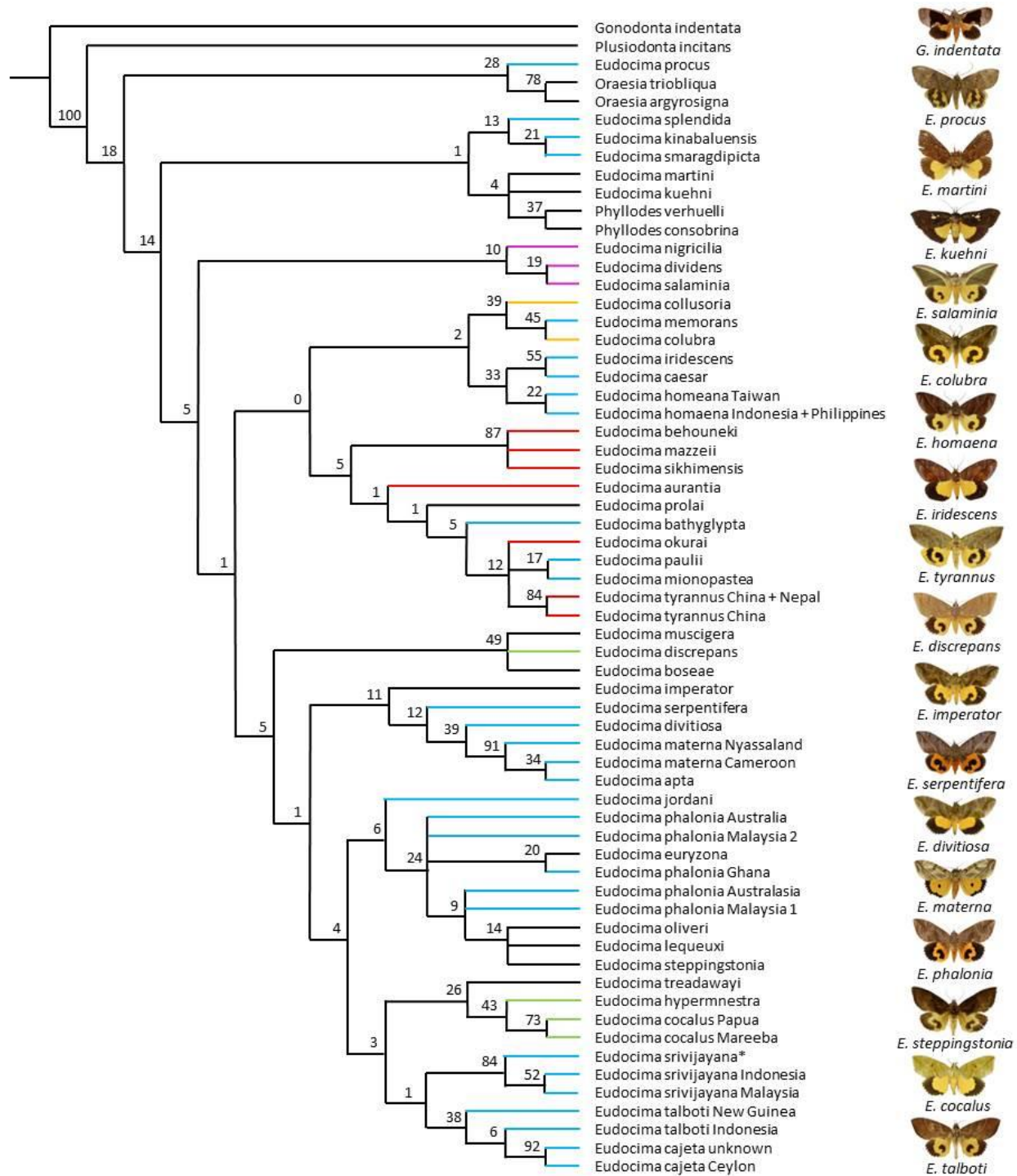
Figure 90. Strict consensus tree (tree branch length = 565, C.I. = 0.33, R.I. = 0.58) with jackknife branch supports and historical generic designations of ingroup taxa. Blue = *Othreis*, red = *Adris*, green = *Rhytia*, orange = *Trissophaes*, pink = *Eudocima* s.str. *E. srivijayana** = *E. srivijayana* Philippines + Celebes + Timor. Images from BOLD Systems (Ratnasingham & Hebert 2007): *E. procus* adapted from record ANIAF903-11 (Axel Hausmann), *E. serpentifera* adapted from record 97-SRNP-11055 (Dan Janzen).

3.5.2   Character trends

Although many clades are recovered for *Eudocima*, support is low for the majority of them because characters with fully-consistent transformations (objectively unique synapomorphies) occur rarely. Homoplasy in the postulated phylogeny is also common. Despite this, some character trends may be observed for the main divisions within *Eudocima*, and these are discussed as putative synapomorphies for these clades. Exceptions to character trends are elaborated when the exceptions are meaningful to determining the most parsimonious (MP) ancestral state of the character, except where noted. MP character states for the common ancestors of clades are discussed when just one most parsimonious state is calculated for the given character; however, multiple MP ancestral states are listed when they occur for the majority of *Eudocima* (recovered in clade E s.l.) in Table 5. Characters states are discussed as "character number - state".

Two clades containing ingroup taxa are recovered outside clade E s.l., which is inclusive of nearly all *Eudocima* species. These clades are united with clade E s.l. by sclerotization of the apical region of the proboscis (which is either entirely sclerotized (5-1, Fig. 6B); or half-sclerotized (5-2, Fig. 6C), as in the two *Oraesia* species), the attachment of the sacculus with the cucullus (17-0, Fig. 22A), and a sacculus that does not extend past the cucullus (18-0, Fig. 23A). These are the MP ancestral states. Exceptions to these character states do not cause the MP ancestral state to be calculated differently, but are here worth mentioning because exceptions are so rare. One species is *E. kuehni*, which has an unattached sacculus (17-1, Fig. 22B) which extends past the tip of the cucullus (18-1, Fig. 23B). Likewise, *E. procus* has a sacculus which, though attached (17-0), exceeds the length of the cucullus (18-1). Another feature which is only seen in *E. procus* and *E. serpentifera* (recovered in the main body of *Eudocima* in Fig. 89) is the presence of a saccular process, which is differently shaped in both cases; in the rest of *Eudocima*, a saccular process is absent (19-0, Fig. 24A).

The most basal clade in which *Eudocima* species are recovered includes *E. procus*, which is sister to *Oraesia triobliqua* and *Oraesia argyrosigna*. Distinguishing character states for this small group which are also found for *E. procus* include the following: 19-1 (one uniformly-wide saccular process, Fig. 24B); 32-2 (slender, attenuate uncus, Fig. 37D); 37-1 (one cornuti patch,

Fig. 42B); 43-1 (medium, non-deciduous cornuti present, Fig. 48B); 51-0 (juxta less than half as long as valvae, Fig. 56A); 54-6 (juxta shaped like upright triangle with a single spike instead of paired processi, Fig. 59G); 72-1 (long apophyses anteriores, Fig. 78B); 74-1 (thin, cylindrical ductus bursae, Fig. 80B); 81-1 (ductus seminalis arising from the ductus bursae rather than the corpus bursae, Fig. 87B); and 82-1 (ductus widening at the middle, Fig. 88B). In addition to these are the proboscis and labial palp characters of the *Oraesia* species which are recovered as ancestral: 2-1 (proximal region of proboscis with circular ribs, Fig. 3B); 4-1 (smooth proboscis apex, Fig. 5B); 5-2 (apical region of proboscis partly sclerotized, Fig. 6C); 6-0 (no erectile barbs at junction of ribbed and smooth areas of proboscis apex); 7-1 (more than four and less than nine tearing hooks, Fig. 8B); 8-1 (no serrated ridges on proboscis apical region, Fig. 9B); 11-0 (short labial palp third segment, Fig. 13A); and 12-1 (ovate labial palp second segment, Fig. 14B). MP ancestral states for this clade include 2-1, 4-1, 7-1, 8-1, 11-0, 19-1, 32-2, 37-1, 43-1, 51-0, 54-6, 72-1, 74-1, 81-1, and 82-1.

In the clade from *E. splendida* to *Phyllodes consobrina*, the other clade in which *Eudocima* species fall outside the rest of the genus in clade E s.l., seven species are represented. Five of these are ingroup taxa. Character trends distinguishing taxa in this clade are: 15-1 (dentate female termen, Fig. 18B); 30-2 (stirrup-shaped saccus arms that widen toward the base, Fig. 35C); 31-2 (long uncus, Fig. 36C); 32-3 (slender, attenuate uncus, Fig. 37D); 37-0 (cornuti absent from the body of the vesica, Fig. 42A); 43-0 (medium-sized cornuti absent, Fig. 48A); 49-0 (ovate vesica, Fig. 54A); 53-1 (lateral processi present on juxta, Fig. 58B); 54-3 (tweezer-like juxta, Fig. 59D); 60-1 (narrow, notch-shaped space between juxta processi with parallel sides, Fig. 65B); 72-1 (long apophyses anteriores, Fig. 78B); 74-1 (cylindrical ductus bursae with small diameter, Fig. 80B); and 77-7 (small, box-like corpus bursae, Fig. 83H). Proboscis and labial palp characters come from *Phyllodes consobrina*, and are also recovered as ancestral: 2-1 (proximal region of proboscis with circular ribs, Fig. 3B); 6-0 (no erectile barbs at junction of ribbed and smooth areas of proboscis apex); 7-2 (more than nine tearing hooks, Fig. 8C); 8-1 (no serrated ridges on proboscis apical region, Fig. 9B); and 11-0 (short labial palp third segment, Fig. 13A). MP ancestral states for these characters are 2-1, 6-0, 8-1, 11-0, 15-1, 30-2, 31-2, 32-3, 37-0, 43-0, 49-0, 53-1, 54-3, 60-1, 72-1, 74-1, and 77-7. Characters that separate this clade from nearly all the rest of *Eudocima* are a long, slender and attenuate uncus (31-2, 32-3), long

apophyses anteriores (72-1), and a box-like corpus bursae (77-7). The *E. splendida* to *E. smaragdipicta* group are aggregated within this clade by a broadly-notched sacculus with an intermediate point (20-1, Fig. 25A, and 21-6, Fig. 26G, respectively), a clavate uncus with fingerlike projections (32-4, Fig. 37E), a thick, thumb-like aedeagus (34-0, Fig. 39A), no carina spines (35-0, Fig. 40A), an apical vesica spike (41-1, Fig. 46B), a vesica roughly the same length as the aedeagus (50-1, Fig. 55B), and an unsclerotized ductus bursae (75-0, Fig. 81A). Character trends which unite *E. kuehni*, *E. martini*, and the two species of *Phyllodes*, in addition to the character states ancestral to the whole clade, include a relatively straight anal forewing margin (13-0, Fig. 16A), an un-notched sacculus (20-0, Fig. 25A), a fingerlike aedeagus (34-1, Fig. 39B), no apical vesica spike (41-0, Fig. 46A), a vesica shorter than the aedeagus (50-0, Fig. 55A), and a half-sclerotized ductus bursae (75-2, Fig. 81C).

The E s.l. clade, which includes taxa from *E. nigricilia* to *E. cajeta* Ceylon, comprises most of the *Eudocima* species included in the analysis. Primary character support for this clade is provided by 2-0 (simple and smooth surface microstructure of proboscis proximal region, Fig. 2), 4-0 (serrate proboscis apex, Fig. 5A), 6-1 (row of erectile barbs present below junction of ribbed and smooth areas of proboscis, Fig. 7), 7-0 (four tearing hooks occurring on proboscis apical region, Fig. 8A), 8-0 (two serrated ridges present on apical proboscis region, Fig. 9A), 11-1 (medium length of second labial palp segment, Fig. 13B), 31-0 (medium-length uncus, Fig. 36A), 32-0 (clavate uncus with a hooded tip, Fig. 37A), and 72-0 (reduced apophyses anteriores, Fig. 78A). The most notable exception to these character trends concerns state 11-1, which is uniformly not present within clade I. Instead, the state recovered within clade I is 11-2 (long labial palp second segment), and is also ancestral. The MP ancestral states for clade E s.l. for each character are given in Table 3, as ancestral states for *Eudocima*.

Within clade E s.l., the clade consisting of *E. nigricilia* (*E. dividens* + *E. salaminia*) is sister to both of the other major subclades, clade I and clade II, together. Distinguishing features of this group include 11-1 (medium-length labial palp third segment, Fig. 13B), 13-0 (a relatively straight anal margin of the forewing, Fig. 16A), 21-3 (a triangular saccular notch, Fig. 26D), 22-4 (wedge-shaped valvae, Fig. 27E), 43-1 (medium, non-deciduous cornuti present, Fig. 48B), 45-1 (dense spiculi present along creases of the vesica instead of in patches, Fig. 50B), 50-1 (vesica

about the same length as aedeagus, Fig. 55B), 53-1 (lateral processi present on juxta, Fig. 58B), 54-9 (plate-like juxta, Fig. 59J), 57-2 (notch-shaped space in juxta processi, Fig. 62C), 60-5 (juxta space as a shallow indentation or depression, Fig. 65F), 62-0 (straight juxta peak tips, Fig. 67A), 68-1 (anterior sclerotization of segment 8, Fig. 74B), 69-1 (anterior sclerotization of segment 8 in the form of a thin band, Fig. 75B), 72-1 (long apophyses anteriores, Fig. 78B), 74-1 (thin, cylindrical ductus bursae, Fig. 80B), and 78-2 (corpus bursae with wrinkled posterior portion and smooth anterior portion, Fig. 84C). For *E. nigricilia*, the anterior portion of segment 8 is unsclerotized (68-0, Fig. 74A). No data for male genitalia of *E. nigricilia* was available, so trends for those characters are entirely due to *E. salaminia* and *E. dividens*. Characters that are more unique to this group (not found in many other taxa) are 13-0, 45-1, 54-9, 60-5, 72-1, and 78-2. The following characters are not the single most parsimonious state for the common ancestor of this group, but are worth noting. Stout spikes on the vesica were observed in both *E. dividens* and *E. salaminia*; multiple were present for *E. dividens* (40-2, Fig. 45C), while only one was present for *E. salaminia* (40-1, Fig. 45B). Two vesica lobes are present in *E. dividens* (48-1, Fig. 53B) and four vesica lobes are present in *E. salaminia* (48-3, Fig. 53D). For both these taxa, the shape of the vesica is tripodal or bifurcate, and the lobe size is balanced (49-4, Fig. 54E). MP ancestral states for *E. nigricilia* (*E. salaminia* + *E. dividens*) for this tree (Fig. 89) are 11-1, 13-0, 21-3, 22-4, 43-1, 45-1, 50-1, 53-1, 54-9, 60-5, 62-0, 68-0, 69-1, 72-1, and 78-2.

Clade I contains 16 species (18 terminals) and is mainly supported by the following characters: 11-2 (long labial palp third segment, Fig. 11C); 15-0 (smooth female termen, Fig. 18A); 21-2 (narrow, deep, rectangular saccular notch, Fig. 26C); 50-0 (vesica shorter than aedeagus, Fig. 55A); and 51-1 (juxta about half the length of the valvae, Fig. 56B). For this tree, the most recent common ancestor of this group has MP states which include the above characters (11-2, 15-0, 21-2, 50-0, 51-1), as well as 57-2 (notch-shaped space between juxta processi, Fig. 62C).

Within clade I, subclade IA (the smaller of the two subclades) is supported by: 16-0 (the lack of a forewing apex process, Fig. 19A); 26-1 (distal cucullus process present, Fig. 31B); 49-5 (main lobe of vesica with smaller buds, Fig. 54F); and 53-0 (juxta without lateral processi, Fig. 58A). MP ancestral states for this subclade include the above characters (16-0, 26-1, 49-5, 53-0), as well as 54-9 (plate-like juxta with bump-like processi, Fig. 59J). Distinguishing features of the

clade (*E. collusoria* (*E. memorans* + *E. colubra*)) include broad, ovoid valvae (22-3, Fig. 27D); cornuti that are evenly dispersed over the surface of the vesica (37-4, Fig. 42E); and the presence of jaculiferous cornuti (46-1, Fig. 51B). Features of interest for ((*E. iridescens* + *E. caesar*) (*E. homena* Taiwan + *E. homaena* Indonesia + Philippines)) include a character that is otherwise diagnostic of subclade IIB, deciduous cornuti (39-1, Fig. 44B), as well as rounded or faintly-apparent tips of juxta processi (55-1, *E. iridescens* to *E. homaena* Taiwan, Fig. 60B; and 55-2, *E. homaena* Indonesia + Philippines, Fig. 60C, respectively). The *E. iridescens* to *E. homaena* clade is also notable for a single patch of cornuti on the vesica (37-1).

Subclade IB includes 10 species (11 terminals). Members can be commonly recognized (with exceptions) by a combination of nine characters that include: (**i**) 13-2 (anal margin of forewing with sharply curved and pronounced tornal hook and rounded or pointed subbasal extension, Fig. 16C); (**ii**) 16-1 (presence of an apex process on the forewing, Fig. 19B); (**iii**) 25-2 (blunt, rectangular valve tip, Fig. 30B); (**iv**) 35-1 (carina spines extending completely around the phallobase, Fig. 40B); (**v**) 37-0 (cornuti absent from the body of the vesica, Fig. 42A); (**vi**) 41-1 (apical spike present on vesica, Fig. 46B); (**vii**) 49-2 (slender, tube-like vesica, Fig. 54C); (**viii**) 57-1 ("V"-shaped space between juxta processi, Fig. 62B) (**ix**) 63-1 (bulge present on juxta inner margin) (Fig. 68B). Exceptions to these character trends are discussed if the calculated ancestral state does not fit the trend. These characters are not synapomorphic from a phylogenetic standpoint, but most are shared by only a few taxa outside this subclade (13-2, 16-1, 25-2, 35-1, 37-0, 41-1, 49-2, and 63-1). For example, 16-1 is present for all taxa and only occurs outside subclade IB in both *Phyllodes* species, and 63-1 (although not present in all taxa in this subclade, see below) is only shared by 3 other *Eudocima* species: *E. jordani*, *E. euryzona*, and the Malaysian and Indonesian replicates of *E. srivijayana*. A curved valve tip shape (25-0, Fig. 30A) is observed in *E. prolai*, *E. aurantia*, and *E. paulii*. The presence of carina spines in general is mostly confined to subclade IB (except in 6 species), with *E. mazzeii*, *E. aurantia*, and *E. mionopastea* showing carina spines that only extend partway around the phallobase (35-2, Fig. 40C) as opposed to completely around (35-1), which is the more common state. Carina spines are absent from *E. prolai* and *E. bathyglypta*. Although the most commonly-observed character state for this subclade is a long and slender vesica (49-2), the vesica in *E. sikhimensis* is ovate (49-0, Fig. 54A), *E. behouneki* has a bifurcate vesica with evenly-sized lobes (49-4, Fig. 54E),

and *E. mazzeii* has a vesica with one main lobe that has smaller buds (49-5, Fig. 54F). A notch-shaped space between the juxta processi (57-2, Fig. 62C) is observed in the clade of *E. sikhimensis*, *E. behouneki*, and *E. mazzeii*, as well as in *E. okurai*. Nearly all taxa were observed to have a bulge on the lower inner margins of the juxta processi (63-1), but from *E. prolai* and *E. mionopastea* the bulge was absent (63-0, Fig. 68A). According to this tree (Fig. 89), the MP states for the most recent common ancestor of subclade IB include: 16-1, 25-0, 35-1, 37-0, 41-1, 49-5, 57-2, and 63-1.

Clade II is the larger of the two main divisions within *Eudocima*, and contains 20 species (30 terminals). More species replicates are also contained in this clade, particularly for *E. phalonia*. For this tree (Fig. 89), clade II is primarily supported by: 11-1 (medium-length labial palp third segment, Fig. 13B); 13-1 (indented anal margin of forewing with tornal and subbasal projections, Fig. 16B); 15-1 (dentate female termen, Fig. 18B); 43-1 (medium, non-deciduous cornuti present, Fig. 48B); 50-1 (vesica about the same length as aedeagus, Fig. 55B); 51-2 (juxta same length as valvae or longer, Fig. 56C); 54-0 (flame-shaped juxta, Fig. 59A); 57-0 (vase-shaped space between juxta processi, Fig. 62A); and 78-1 (wrinkled or striated corpus bursae, Fig. 84B). The clade comprising *E. muscigera*, *E. discrepans*, and *E. boseae*, which is sister to both subclade IIA and IIB, has several character traits which are discordant with these trends. *Eudocima boseae* has an anal forewing margin characterized by a pronounced curved tornal hook and a rounded subbasal extension (13-2, Fig. 16C), while *E. muscigera* and *E. discrepans* share an anal forewing margin with a sharply curved tornal hook and diminished subbasal extension (13-4, Fig, 16E). The *E. muscigera* to *E. boseae* clade also is characterized by a smooth female termen (15-0, Fig. 18A); dense spiculi (44-1, Fig. 49B); four vesica lobes (48-3, Fig. 53D), although *E. boseae* has 3 (48-2, Fig. 53C); the absence of deciduous cornuti (39-0, Fig. 44A); and a smooth corpus bursae (78-0, Fig. 84A). MP ancestral states for clade II include: 11-1, 13-1, 15-0, 39-0 (Fig. 44A), 43-1, 50-1, 51-2, 54-0, 57-0, and 78-0.

Subclade IIA is comprised of 5 species, represented by 6 terminals. Members of this subclade can usually be distinguished by the combination of 14 characters (exceptions are noted when the state is not ancestral). These include: (**i**) 14-1 (dentate male termen, Fig. 17B); (**ii**) 22-2 (broad valvae with two rounded prominences at the apex, Fig. 27C); (**iii**) 23-1 (split cucullus, Fig. 28B);

(**iv**) 26-1 (distal cucullus process present, Fig. 31B); (**v**) 36-1 (rugose vesica texture, Fig. 41B); (**vi**) 37-3 (three or more patches of cornuti on vesica, Fig. 42D); (**vii**) 38-1 (multiple types of cornuti present, Fig. 43B); (**viii**) 39-0 (no deciduous cornuti, Fig. 44B,); (**ix**) 40-1 (one stout spike present on the body of the vesica, Fig. 45B); (**x**) 44-1 (dense spiculi, Fig. 49B); (**xi**) 48-3 (four vesica lobes, Fig. 53D); (**xii**) 49-3 (thick, box-like vesica with radially-arranged lobes, Fig. 54D); (**xiii**) 51-1 (juxta roughly half the length of the valvae, Fig. 56B); and (**xiv**) 52-2 (a deep-clefted juxta base, Fig. 57C). Besides in *E. tyrannus*, this is the only subclade containing taxa with observed cervical sclerites (*E. materna* and *E. apta*) (79-1, Fig. 85B). As in subclade IB, these traits are not synapomorphic from a phylogenetic standpoint, but some of them (23-1, 37-3, and 49-3) are entirely exclusive to this subclade, while others (14-1, 22-2, 36-1, 44-1, 48-3, and 79-1) are shared with scant other taxa in the phylogeny. *Eudocima imperator*, which is the most basal member of this clade, represents the exception to many of these trends: for this species, the male termen is smooth (14-0, Fig. 17A), the valvae are half-crescent shaped with a triangular apex (22-7, Fig. 27H), the cucullus is not split (23-0, Fig. 28A), no distal process of the cucullus is present (26-0, Fig. 31A), the vesica is smooth rather than rugose (36-0, Fig. 41A), three lobes are present on the vesica (48-2, Fig. 53C), the vesica shape is tripodal with a balanced lobe size (49-4, Fig. 54E), and the juxta is about as long as the valvae (51-2, Fig. 56C). Another exception is *E. serpentifera*, for which the male termen is smooth (14-0 Fig. 17A), the vesica is smooth (36-0, Fig. 41A), and one vesica lobe is present (48-0, Fig. 53A) which is in the shape of a main lobe with buds (49-5, Fig. 54F). The valvae in *E. divitiosa* are wedge-shaped with a rounded tip (22-0, Fig. 27A), and the cucullus is not split (23-0, Fig. 28A). For *E. apta*, the vesica shape is rhizome-like (49-1, Fig. 54B). MP ancestral states for subclade IIA are as follows: 14-0, 22-7, 23-0, 26-0, 36-0, 37-3, 38-1, 39-0, 40-1, 44-1, 48-0, 49-5, 51-2, and 52-2.

Subclade IIB is a large clade (21 terminals representing 12 species), and is the most replete with species replicates of any of the other subclades. It can be further divided into two clades, one comprising *E. jordani* to *E. steppingstonia*, and the other including from *E. treadawayi* to *E. cajeta* Ceylon. Characters that help define subclade IIB include: 39-1 (deciduous cornuti present, Fig. 44B), 44-0 (absence of dense spiculi, Fig. 49A), 51-2 (juxta the same length as the valvae or longer, Fig. 56C), and 74-0 (ductus bursae cylindrical with a wide diameter, Fig. 80A). MP ancestral states for this tree (Fig. 89) include the above (39-1, 44-0, 51-2, and 74-0), as well as

37-2 (two cornuti patches on the vesica, Fig. 42C). Of these, the most notable character that sets this subclade apart is the presence of deciduous cornuti (39-1), which is only observed elsewhere in the tree in the clade ((*E. iridescens* + *E. caesar*) (*E. homaena* Taiwan + *E. homaena* Indonesia + Philippines)) within subclade IA. Additional informative character divisions can be observed in the two major clades within subclade IIB.

The *E. phalonia* clade encompassing *E. jordani* to *E. steppingstonia* corresponds most closely with the concept of the "*phalonia*-group" discussed by Zilli & Hogenes (2002) and Zilli et al. (2017), at minimum due to the number of *E. phalonia* replicates. Six species are represented by ten terminals, comprising *E. phalonia* and close relatives. The most prominent feature of this clade is the polytomy which includes the five *E. phalonia* replicates and four of the other species, from which the clades (*E. euryzona* + *E. phalonia* Ghana) and (*E. phalonia* Australasia, *E. phalonia* Malaysia 1 (*E. oliveri*, *E. lequeuxi*, *E. steppingstonia*)) precipitate out. *Eudocima jordani* is recovered basally and is sister to the rest of the species in the clade. Members of this clade can best be described within subclade IIB by the combination of eleven characters: (**i**) 22-7 (half-crescent-shaped valvae with a distinct triangular prominence at each apex, Fig. 27H); (**ii**) 24-2 (valve inner margin with protruding proximal corner at apex and projecting distal apical corner, Fig. 29C); (**iii**) 30-0 (shallow, "U"-shaped saccus with slim arms, Fig. 35A); (**iv**) 34-0 (thick, thumb-like aedeagus, Fig. 39A); (**v**) 37-1 (one cornuti patch, Fig. 42B); (**vi**) 38-0 (only one kind of cornuti present, Fig. 43A); (**vii**) 43-0 (absence of medium-sized, non-deciduous cornuti, Fig. 48A); (**viii**) 48-0 (one vesica lobe, Fig. 53A); (**ix**) 49-0 (ovate vesica shape, Fig. 54A); (**x**) 62-2 (inward-curving tips of juxta processi, Fig. 67C); and (**xi**) 64-1 (antevaginal spine present, Fig. 70B). Of these characters, 30-0, 62-2, and 64-1 are very nearly exclusive to this clade, although they are not synapomorphic. Exceptions to these character trends which cause the MP ancestral states to be calculated differently come solely from *E. jordani*. For *E. jordani*, two patches (37-2, Fig. 42C) of medium-sized cornuti (43-1, Fig. 48B) are present on the vesica, and deciduous cornuti are absent (39-0, Fig. 44A). *Eudocima jordani* also has a vesica organized as a main lobe with smaller buds (49-5, Fig. 54F) rather than an ovate vesica (49-0). Additionally, the juxta of *E. jordani* has points that curve outward toward the valvae (62-1, Fig. 67B) rather than inward (62-2). MP ancestral states for the *E. phalonia* clade are calculated as 22-7, 24-2, 30-0, 34-0, 37-2, 38-0, 43-1, 48-0, 49-5, 62-1, and 64-1 for this tree (Fig. 89).

The remaining clade within subclade IIB, *E. treadawayi* to *E. cajeta* Ceylon, consists of 6 species and is represented by 11 terminals. Within subclade IIB, character trends of this clade include: 21-5 (sacculus notch with projecting proximal portion and diminished distal portion, Fig. 26F); 34-1 (thinner, finger-like aedeagus, Fig. 39B); 37-2 (two cornuti patches, Fig. 42C); 38-1 (multiple types of cornuti present, Fig. 43B); 43-1 (medium, non-deciduous cornuti present, Fig. 48B); 48-1 (two vesica lobes, Fig. 53B); 64-0 (absence of an antevaginal spine, Fig. 70A); and 68-1 (anterior sclerotization of segment 8, Fig. 74B). Within this clade, features of note for the smaller clade (*E. treadawayi* (*E. hypermnestra* (*E. cocalus* Mareeba + *E. cocalus* Papua))) are 24-3 (straight inner margin of valvae, Fig. 29D), 25-2 (blunt, rectangular valve tip, Fig. 30B), 30-3 (shallow "V" or cup-shaped saccus with small dip in the center, Fig. 35D, 2), 49-5 (vesica in the form of main lobe with smaller buds, Fig. 54F), and 75-1 (completely sclerotized ductus bursae, Fig. 76B). The other smaller clade within *E. treadawayi* to *E. cajeta* Ceylon, which is comprised of *E. srivijayana* unknown to *E. cajeta* Ceylon, includes character trends such as the presence of a cucullus process (26-1, Fig. 31B), a stirrup-shaped saccus (30-2, Fig. 35C), one cornuti patch (37-1, Fig. 42B), an apical vesica spike (41-1, Fig. 46B), a tripodal or bifurcate vesica with a balanced lobe size (49-4, Fig. 54E), and a partly-sclerotized ductus bursae (75-2, Fig. 81C). MP ancestral states for the entire clade from *E. treadawayi* to *E. cajeta* Ceylon according to this tree (Fig. 89) are as follows: 21-5, 37-2, 38-1, 43-1, 48-1, 64-0, and 68-1. Of these states, those that are nearly exclusive to this clade are 21-5, 48-1, and 68-1.

3.5.3   Support for historical genera

The *Eudocima* s.str. clade comprising *E. salaminia*, *E. dividens*, and *E. nigricilia* was recovered as monophyletic (jackknife support = 10, Fig. 90), based mainly on a level anal forewing margin, placement of dense spiculi along creases in the vesica, a plate-like juxta with a dip or depression in the center, long apophyses anteriores, and a partially-wrinkled corpus bursae. This clade is recovered outside clade I and clade II, as sister (Fig. 89). The name *Eudocima* is recorded in Billberg's Enumerato Insectorum (1820) associated with *salaminia*, and *E. salaminia* is the type species of *Eudocima* Billberg (=*Eudocima* s.l.) in Poole's catalogue (1989). Holloway (in Barlow 1982) assigned *E. salaminia, E. dividens,* and *E. nigricilia* to *Eudocima* s.str. based on their similar appearance and forewing markings. This name is also used in Bänziger (1987) and

Fay (1996), so *Eudocima* s.str. is here considered the genus in which *E. salaminia*, *E. nigricilia*, and *E. dividens* were placed. Moore's (1881) description of *Maenas* (=*E. salaminia*), in which the generic concept from Hübner [1823] is reestablished, includes mention of a straight exterior margin, which concurs with our observation of a smooth male and female termen (14-0 and 15-0, respectively), and short labial palpi, with a "small, very short, and conical" third segment (Moore 1881). Labial palp data is missing for *E. salaminia* and *E. nigricilia* in this study, so this trait could not be confirmed. Interestingly, Moore (1881) considered *E. dividens* as a genus unto itself, *Vandana*, due to a less angular forewing profile and a "very long and slender" third labial palp segment. According to Zilli & Hogenes (2002), the length of the labial palp third segment in *E. dividens* is similar to other species in *Eudocima* s.l., and is an exception to the condition present in *E. salaminia* and *E. nigricilia* (Zilli & Hogenes 2002). In this study, labial palp data was only available for *E. dividens* in this clade, and the third segment was scored as medium-length (11-1), which is the same condition recovered for members of clade II (Fig. 89). Notwithstanding, the third labial palp segment in *E. dividens* is not as long as the condition (11-2) present in species recovered in clade I (Fig. 89), among which are members of the *Adris* group.

Members of *Trissophaes* were recovered together in the monophyletic clade *E. collusoria* (*E. memorans* + *E. colubra*) (jackknife support = 39, Fig. 90) within subclade IA (Fig. 89). This small clade can be distinguished by the presence of broad, ovoid valvae, and evenly-distributed, jaculiferous cornuti. *Trissophaes* was first described by Hübner [1823] (type species *E. collusoria*), and followed by Schaus (1911) (n. sp. *E. colubra* and *E. anguina*). Descriptions in these accounts do not include characters used in this study, so no historical counterparts of the characters used here are available for discussion. *Eudocima memorans*, described under the appellation *Ophideres* (Walker [1858]), is also recovered in this clade. This species is referred to by Draudt & Gaede (1944) under the name *Othreis*, which is here used as the historical generic designation. All species in this clade are Neotropical.

The *Adris* group of *Eudocima*, including *E. aurantia*, *E. tyrannus*, *E. okurai*, *E. behouneki*, *E. mazzeii*, and *E. sikhimensis*, was recovered together in subclade IB (Fig. 89) with a jackknife support value of 5 (Fig. 90). These taxa (except *E. aurantia*) correspond to the "tyrannus-group" of Zilli & Hogenes (2002), which is discussed as synonymous with *Adris*. Along with *E.*

aurantia (which also belongs to *Adris*, see section 2.2 on assignment of historical genera), other taxa in this subclade are *E. prolai*, for which no historical generic designation is available, and *E. bathyglypta*, *E. paulii*, and *E. mionopastea*, which have historically belonged to the genus *Othreis* (Zilli & Hogenes 2002). Character support for this group arises from the anal margin and apical process of the forewing; a blunt rectangular valve apex; a bulge on the inner margins of the juxta processi, the space between which is "V"-shaped; the presence of carina spines on the aedeagus; and an apical spike on the slender vesica, which is otherwise free of cornuti. The genus *Adris* was erected by Moore (1881), on the basis of wing shape and labial palp characters; of these, his details of "Fore wing… apex being produced into a lengthened point" and "posterior margin [of forewing]... lobe much produced, excavation beyond short" (Moore 1881) agree with our analysis. Moore (1881) also discusses "larger and stouter" labial palpi as a characteristic of this group, with a "large, flattened, dense tuft above" the third joint. Although hairs were removed to better view the shape of the labial palp segments, available evidence does suggest a longer labial palp third segment for the *Adris* group in our analysis (subclade IB, Fig. 89), which is also shared with its sister clade, subclade IA (Fig. 89).

Members of *Rhytia* were recovered together as a clade (jackknife support = 26, Fig. 90) from *E. treadawayi* to *E. cocalus* Papua within clade IIB (Fig. 89), with the exception of *E. discrepans*. This clade corresponds to the "*cocalus*-group" of Zilli & Hogenes (2002), and is primarily supported within clade IIB by valvae with a straight inner margin and a blunt rectangular tip; a shallow, cup-shaped saccus with a small dip in the center; a vesica organized as a main lobe with smaller buds; and a completely sclerotized ductus bursae. Like *Eudocima* s.str., the concept of *Rhytia* originates in Hübner [1823] and is reinstated by Moore (1881). In Moore's (1881) description of *Rhytia*, the palpi are "very long", which corresponds to his characterization of the palpi in *E. dividens* (=*Vandana*). As in *E. dividens*, the length of the third labial palp segment for *E. cocalus* (the only species in this group with relevant data) is here scored as medium (11-1). Moore (1881) also characterizes *Rhytia* members as having an even exterior margin of the forewing, both in males and females. In our analysis, a smooth male termen is observed, but females in this group exhibited a dentate termen condition. *Eudocima discrepans* is recognized by Moore (1881) as a genus unto itself in *Purbia*; however, it is referenced in Barlow (1982) as *Rhytia discrepans*, and Leong (2009) makes mention of other authors using this name. *Eudocima*

muscigera, a very similar species, was first described by Butler (1882) in the genus *Purbia* also, and is not referenced in the literature by any other names. On this basis (as well as external appearance), it is likely that the name *Rhytia* is assigned to *E. discrepans* in error, in which case the *Rhytia* group recovered in this analysis (*E. treadawayi* to *E. cocalus* Papua) is indeed monophyletic.

The most poorly-recovered historical genus is *Othreis* Hübner [1823], which was circumscribed by Moore (1881) combining the original concepts of *Othreis* (=*E. phalonia* and *E. homaena*) and *Corycia* (=*E. cajeta*) from Hübner's Verzeichniss bekannter Schmetterlinge [1823]. *Eudocima procus*, which is recovered as sister to both *Oraesia* species, was assigned by Hübner [1823] to a genus unto itself, *Acacallis*, after its description by Cramer (1779). Draudt & Gaede (1944) reference this species by its synonymous name *scabellum* (Zilli & Hogenes 2002), under the generic name *Othreis*. Therefore, *E. procus* is assigned here to *Othreis*. Similarly, *E. serpentifera* and *E. apta*, which were originally described under *Ophideres*, are also referenced in Draudt & Gaede (1944) under *Othreis*. *Eudocima divitiosa* is referenced under the name *Othreis* as well (Beccari & Gerini [1975], cited in Zilli & Hogenes 2002). Characters from Moore's (1881) description include "exterior margin… even in the male, scalloped in the female", "posterior margin short, with a fringed lobe near base, and slight excavation beyond", "palpi large, long, ascending… third joint slender, long", and "antennae filiform". On the whole, these characters concur in large part with our observations, although many times they are more universally present in *Eudocima* s.l. In *E. smaragdipicta*, which is recovered outside clade E s.l., and in *E. jordani*, recovered in subclade IIB (Fig. 89), the male termen is dentate (14-1) as well as the female termen (15-1). The termen in males of *E. steppingstonia* and *E. lequeuxi* is also scored as dentate (14-1); these species are recently described, but are closely related to *E. phalonia*. In subclade IIA (Fig. 89), *E. divitiosa*, *E. materna*, and *E. apta* are also characterized by a dentate male termen (14-1). The condition of the anal margin of the forewing described by Moore (1881) corresponds most closely with 13-1. This condition is present in nearly all *Othreis* members in this analysis (excepting *E. smaragdipicta* (13-0), *E. iridescens* (13-0), *E. caesar* (13-0), and *E. bathyglypta* (13-2)), but is by no means constrained to *Othreis*, being also present in members of the *Trissophaes* group, the *Adris* group, and in all of the *Rhytia* group. The labial palp third segment in members of *Othreis* is characterized as medium-length (11-1) for *E. phalonia* and *E.*

materna; in *E. homaena* the third labial palp segment displays the long condition (11-2) similar to members of the *Adris* group (subclade IB, Fig. 89). Filiform male and female antennae (9-0 and 10-0, respectively) are present in all *Eudocima*.
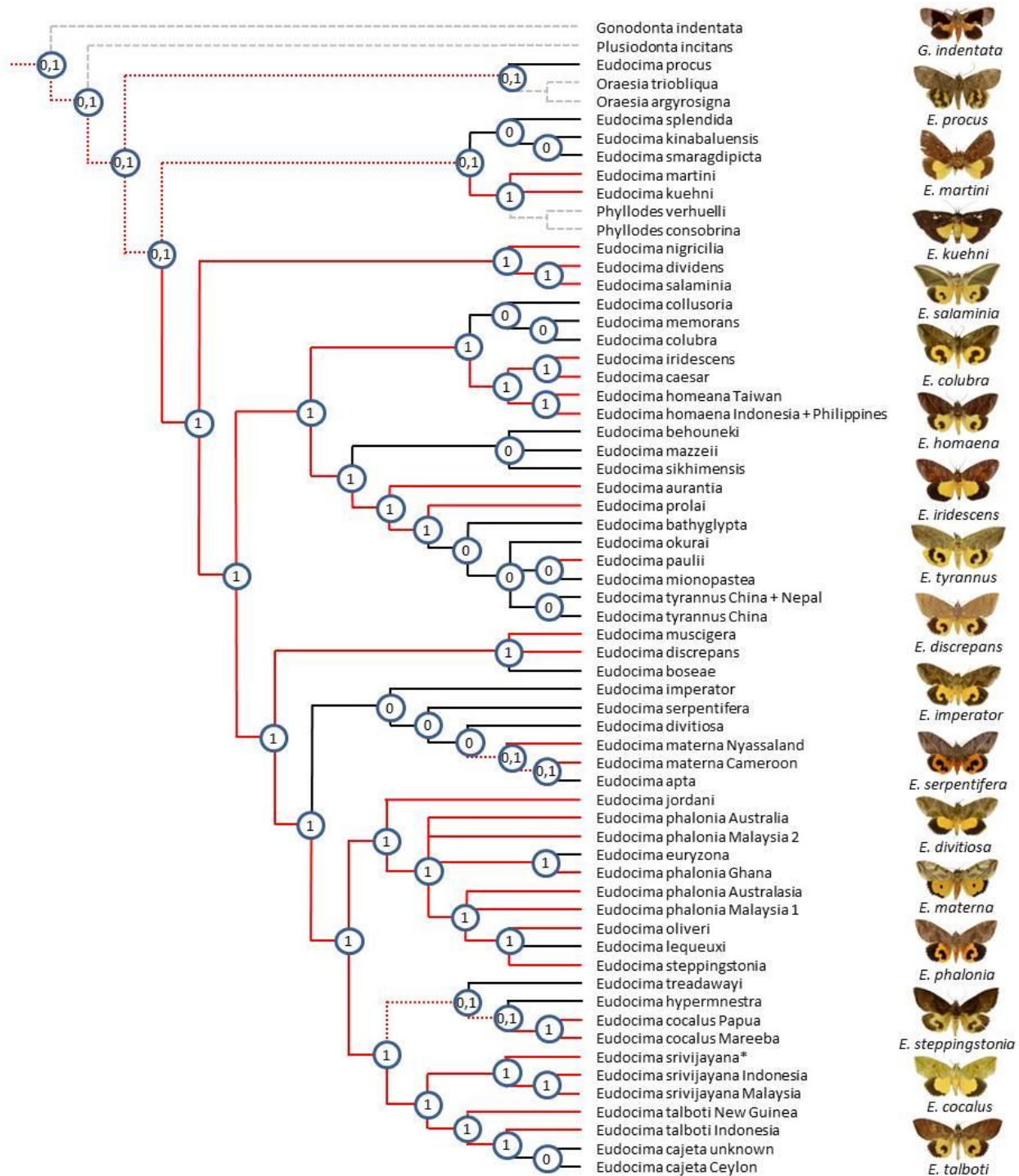
Figure 91. Strict consensus tree with parsimony ancestral reconstruction of biogeographic regions. Present in the Australian region = state 1 (solid red), not present = state 0 (solid black), equivocal = state 0.1 (broken red). Dashed gray indicates outgroup terminals, which were not included in the analysis. State numbers for nodes labeled. Images from BOLD Systems (Ratnasingham & Hebert 2007): *E. procus* adapted from record ANIAF903-11 (Axel Hausmann), *E. serpentifera* adapted from record 97-SRNP-11055 (Dan Janzen).
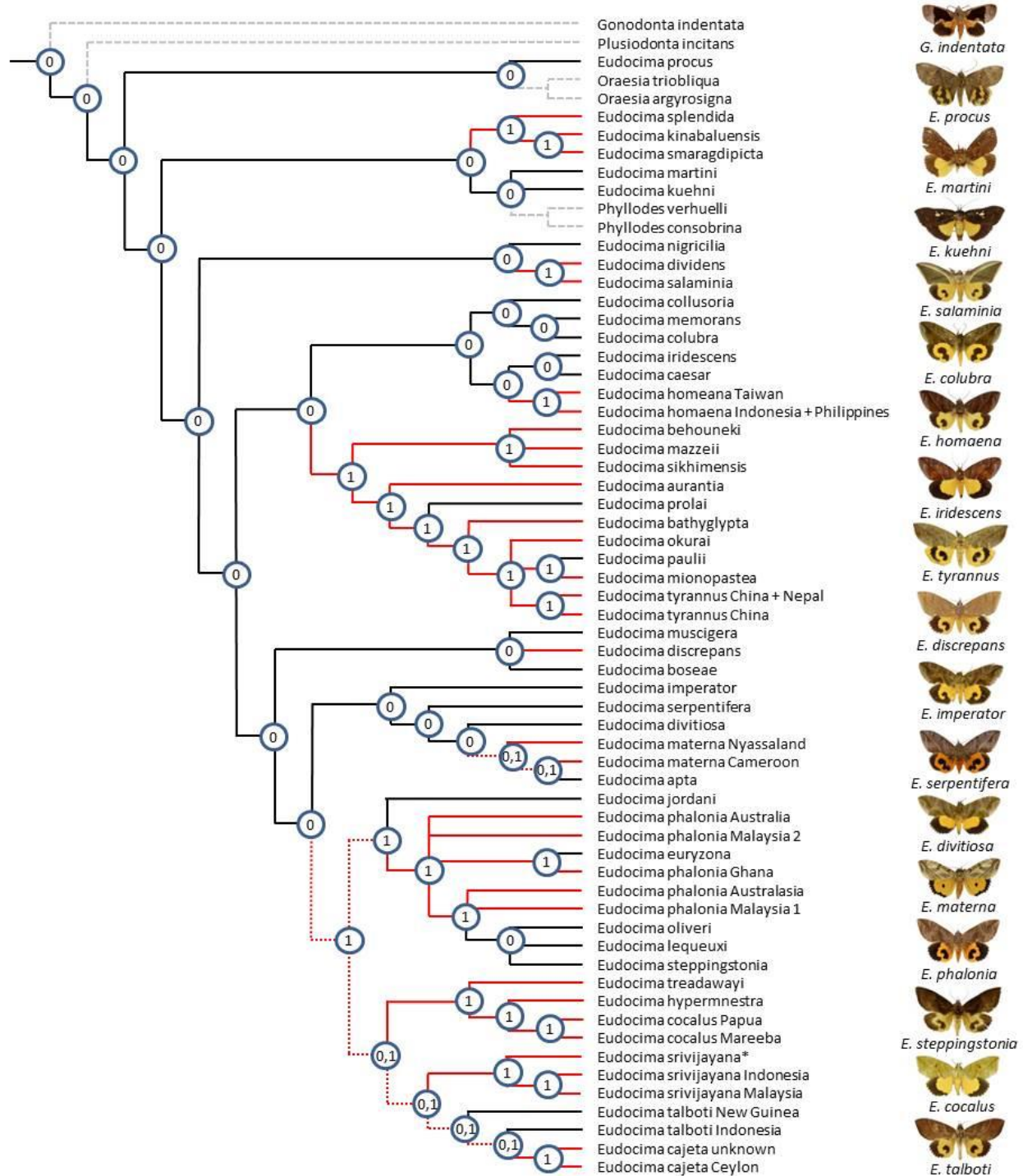
Figure 92. Strict consensus tree with parsimony ancestral reconstruction of biogeographic regions. Present in the Oriental region = state 1 (solid red), not present = state 0 (solid black), equivocal = state 0.1 (broken red). Dashed gray indicates outgroup terminals, which were not included in the analysis. State numbers for nodes labeled. Images from BOLD Systems (Ratnasingham & Hebert 2007): *E. procus* adapted from record ANIAF903-11 (Axel Hausmann), *E. serpentifera* adapted from record 97-SRNP-11055 (Dan Janzen).

3.5.4 Biogeographic region of origin and inter-regional dispersal hypotheses

The Australian region is recovered as the most parsimonious ancestral biogeographic region for the genus *Eudocima* (Fig. 91, 15 steps). Eight radiations out of this region can be discerned, including the following clades and taxa: (1) *E. splendida* to *E. smaragdipicta*, (2) *E. collusoria* to *E. memorans*, (3) *E. behouneki* to *E. sikhimensis*, (4) *E. bathyglypta* to *E. tyrannus* China, with a reversal occurring in *E. paulii*, (5) *E. boseae*, (6) *E. imperator* to *E. apta*, with *E. materna* expanding its range back into the Australian region, (7) *E. treadawayi* to *E. cocalus*, with a return into the Australian region due to range expansion occurring in *E. cocalus*, and (8) *E. cajeta* unknown + *E. cajeta* Ceylon. Based on the close relationship of *Eudocima* with the genus *Phyllodes* (Zahiri et al. 2011, Zahiri et al. 2012, Zaspel et al. 2012), the common ancestor of *Eudocima* is estimated to have diverged approximately 35 mya using the dating analysis in Toussaint et al. (2014), near the end of the Eocene. Because species of *Eudocima* are known to be strong fliers (e.g., Davis et al. 2005, Bhumannavar & Viraktamath 2012) and diverged within Ereibidae relatively recently, dispersal is the most likely mechanism for the current extent of the genus (Müller 1986, Zilli et al. 2017).

Outside clade E s.l. (Fig. 89), *E. procus* is a Neotropical species. *Eudocima splendida*, *E. kinabaluensis*, and *E. smaragdipicta* are all restricted to the Oriental region; as such, this region was reconstructed as ancestral for the most common ancestor of the clade containing these species (Fig. 92, 15 steps). Within subclade IA (Fig. 89), *E. collusoria*, *E. memorans*, and *E. colubra* are exclusively Neotropical species. The clade from *E. collusoria* to *E. colubra* within subclade IA (Fig. 89) may have split from the other taxa in subclade IA by means of a trans-Pacific immigration event into the Neotropical region by the clade's common ancestor, while the common ancestor of the clade from *E. iridescens* to *E. homaena* Indonesia + Philippines remained in the Australian region. *Eudocima homaena* is also found in the Oriental region as far north as the Palearctic, and likely represents a range expansion for this species from the Australian region, where it occurs.

Two main dispersal events from the Australian region (Fig. 91) can be inferred within subclade IB (Fig. 89). The common ancestor of the clade from *E. behouneki* to *E. sikhimensis* is Oriental (Fig. 92, 15 steps), which is expected because both *E. behouneki* and *E. mazzeii* are Philippine

endemics. Divergence of this clade within subclade IB likely occurred by an early dispersal event from the Australian region into the Oriental region by the clade's common ancestor. Another dispersal event into the Oriental region occurred for the common ancestor of the clade from *E. bathyglypta* to *E. tyrannus* China; *E. prolai* is sister to this clade, and *E. aurantia* is sister to *E. prolai*. The radiation of the clade from *E. aurantia* to *E. tyrannus* China is similar to the pectinate phylogenetic hypothesis of Reilly (2016) indicating direction of dispersal; because of the recovery of *E. aurantia* (a widespread Australian species) and *E. prolai* (a Papuan endemic) as ancestral, colonization in this lineage may have progressed from the Australian region (east) into the Oriental region (west) (Reilly 2016). *Eudocima bathyglypta* is recorded from the Korintji Valley and Mount Korintji (Prout 1928) in Borneo. *Eudocima tyrannus* and *E. okurai*, two Palearctic species, could have differentiated due to northern range expansion of the lineage. *Eudocima mionopastea*, an uncommon species, is known to occur on the Malay Penninsula, Sumatra, and Borneo, and is grouped in our analysis with the Fijian endemic *E. paulii* in the Australian region. This could be a case of homoplasy due to the disparity between the ranges of these two species.

In the clade sister to subclade II (Fig. 89) encompassing *E. muscigera* to *E. boseae*, *E. boseae* represents a radiation from the Australian region into Madagascar, where this species is restricted. Within subclade II, subclade IIA (Fig. 89) represents an early migration event of the clade's common ancestor from the Australian region into the African region (*E. imperator*, *E. divitiosa*, and *E. materna*, 7 steps), and two later migration events into the Neotropical region (*E. serpentifera*, *E. apta*, 4 steps). In the case of *E. serpentifera*, differentiation is likely to have occurred because of dispersal from the African region into the Neotropical region, while the route of dispersal for *E. apta* is less clear due to the extensive range of *E. materna*. Within the *E. phalonia* clade in subclade IIB (Fig. 89), two separate differentiations occur in the African region in the cases of *E. euryzona* and *E. lequeuxi*, perhaps due to sympatric differentiation within the wide-ranging species *E. phalonia* (see Zilli et al. 2017). *Eudocima lequeuxi* is recovered in the same clade as the insular Pacific endemics *E. oliveri* and *E. steppinstonia*; this is likely to be due to homoplasy. In the clade from *E. treadwayi* to *E. cajeta* Ceylon, two radiations from the Australian region occurred. In the *E. treadawayi* to *E. cocalus* clade, the common ancestor likely diverged in the Oriental region (Fig. 92, 15 steps, and equivocal in Fig. 91, 15 steps), followed

by *E. treadawayi* in the Philippines and *E. hypermnestra* on the Oriental continent, and *E. cocalus* extended its range back into the Australian region. In the clade containing *E. talboti* and *E. cajeta*, *E. cajeta* diverged into the Oriental region (Fig. 92, 15 steps) from the Australian region.

3.5.5 Island biogeography in the Indo-Australian Archipelago

3.5.5.1   Geologic context

In order to form a basis for understanding the pattern of dispersal for *Eudocima*, a brief explanation of the geologic history of the islands in the Indo-Australian Archipelago and the Pacific islands is in order. This summary takes as its beginning 30-40 mya, which is the approximate age of the common ancestor of *Eudocima* (Toussaint et al. 2014, see section 3.5.4 on regional biogeography).

(1) *Borneo and the Greater Sunda Islands*. Cenozoic reconstructions of Hall (1966) and Lohman et al. (2011) support Borneo as one of the earliest landmasses to form in the Indo-Australian Archipelago which was not later submerged by ocean. Between 30 and 40 mya, Borneo was connected to the continental mainland, along with modern-day Sumatra, while all but the northern tip of Java was covered by shallow sea (Hall 1996, Lohman et al. 2011). By 20 mya (early Miocene), nearly all of the western Greater Sunda Islands was covered by shallow seas, and remained submerged until about 5 mya (early Pliocene). This submersion is likely to have caused extinction of all terrestrial and freshwater life (Lohman et al. 2011). During this time, between 20 mya and 5 mya, the elevation of Borneo continued to increase (Lohman et al. 2011).

(2) *Lesser Sunda Islands*. Reilly (2016) dates the formation of the Lesser Sunda Islands (mostly due to volcanism) between 10 mya (when the oldest islands, Lombok, Sumbawa, and Flores emerged) and 2 mya, when the youngest islands of Sumba, Sabu, Timor, and Tanimbar appeared. The remaining islands in the Lesser Sundas are thought to have been in place by 5 mya (Lohman et al. 2011, Reilly 2016).

(3) *Philippines*. The islands of the Philippines reached their current configuration about 5 mya, with the central and southern Philippines moving northward from their position 20 mya in the present-day Molucca Sea to join the northern islands (Hall 1996, Lohman et al. 2011).

(4) *Sulawesi and the Mollucas*. Sulawesi is estimated to have become a composite landmass shortly before 15 mya (Hall 1996, Lohman et al. 2011). The Moluccas have separate geologic histories for North Maluku (Halmahera, Buru, Seram), and the southern islands (Hall 1996, Heads 2008). The northern Moluccas are thought to have affinities with Papua New Guinea, possibly moving westward 4 mya at the earliest from the Bird's Head peninsula (Hall 1996). The origin of these terranes may be even further east, with New Britain, New Ireland, or the Bismarck Archipelago, as shown by current disjunct faunal distributions (Heads 2008).

(5) *Papua New Guinea*. The emergence of New Guinea is thought to have begun approximately 20 mya as small islands on the northern edge, becoming complete approximately 2 mya (de Boer & Duffels 1996, Lohman et al. 2011).

(6) *Pacific islands*. The Solomon island group became emergent during two distinct phases of volcanic activity, the second of which began 7 mya and is ongoing (Neall & Trewick 2008). In Vanuatu, the entire archipelago went through periods of submergence and emergence after the initial formation of the islands 14 mya, with the last period of emergence occurring only 2 mya (Hamilton et al. 2009). Uplift of the first land mass in Fiji, likely Viti Levu, occurred in the middle to late Miocene (Neall & Trewick 2008). Until 9-12 mya, the Solomons, Vanuatu, and Fiji formed a continuous island arc; at this time, the arc was fragmented due to collisions in the area of New Guinea, which caused Vanuatu and Fiji to rotate in opposite directions and which brought about a complete isolation of Fiji 3 mya (Ewart 1988, de Boer & Duffels 1996), while Vanuatu became less isolated (Hamilton et al. 2009). The Marquesas Islands were formed between 5.5 and 0.4 mya, and comprise a linear island chain formed over a hot spot (Neall & Trewick 2008).

3.5.5.2   Pattern of dispersal for *Eudocima*

Within the Indo-Australian Archipelago, dispersal for *Eudocima* species occurred in roughly five stages: (1) Borneo, (2) the Philippines, (3) Sulawesi and the Moluccas, (4) Papua New Guinea (which could be concurrent with dispersal to Sulawesi and the Moluccas), and (5) the Pacific (Solomons, Vanuatu, Fiji, Marquesas) (Fig. 93). Although the geophysical timing of the western Greater Sunda Islands and the Lesser Sunda Islands is known, equivocal reconstructions for these areas prohibit inferences about when dispersal may have occurred there for *Eudocima* (Fig. 93).

In the Indo-Australian Archipelago, Borneo is the most parsimonious area of origin for *Eudocima* s.l. (12 steps). The next radiation event for *Eudocima* likely occurred from Borneo to the Philippines, a pattern also seen in many avian taxa (see Lohman et al. 2011). Dispersal may have occurred in *Eudocima* from Borneo to the Philippines 10 mya at the earliest, when the northern and southern Philippine island groups were in relatively close proximity, and when Borneo was separated from the Philippines by shallow seas (Hall 1996, Lohman et al. 2011). Radiation of *Eudocima* species may have proceeded from the Philippines to Sulawesi and the Moluccas around 4 or 5 mya. Ancestral reconstruction of these areas supports colonization around the same time. Shallow seas connected the northern arm of Sulawesi to the Philippine islands beginning 10 mya (Lohman et al. 2011), allowing easier dispersal. *Eudocima* is estimated to have dispersed to Papua New Guinea between 2 and 5 mya, either concurrently with dispersal to Sulawesi and the Moluccas or just after. In ancestral reconstruction of this area, the presence of *Eudocima* in New Guinea becomes less clear at deeper nodes in the phylogeny; although the ancestor of clades IIA and IIB (Fig. 89) is present in Papua New Guinea (10 steps), the presence of *Eudocima* is equivocal for all deeper ancestral nodes with the exception of clade I, for which *Eudocima* is ancestrally absent (10 steps). Another, more recent wave of dispersal (after 5 mya) for *Eudocima* occurred east of Papua New Guinea, to the Solomon Islands, Vanuatu, Fiji, and the Marquesas Islands in the remote Pacific. Reconstruction of these areas supports a later dispersal to all of them around the same time.
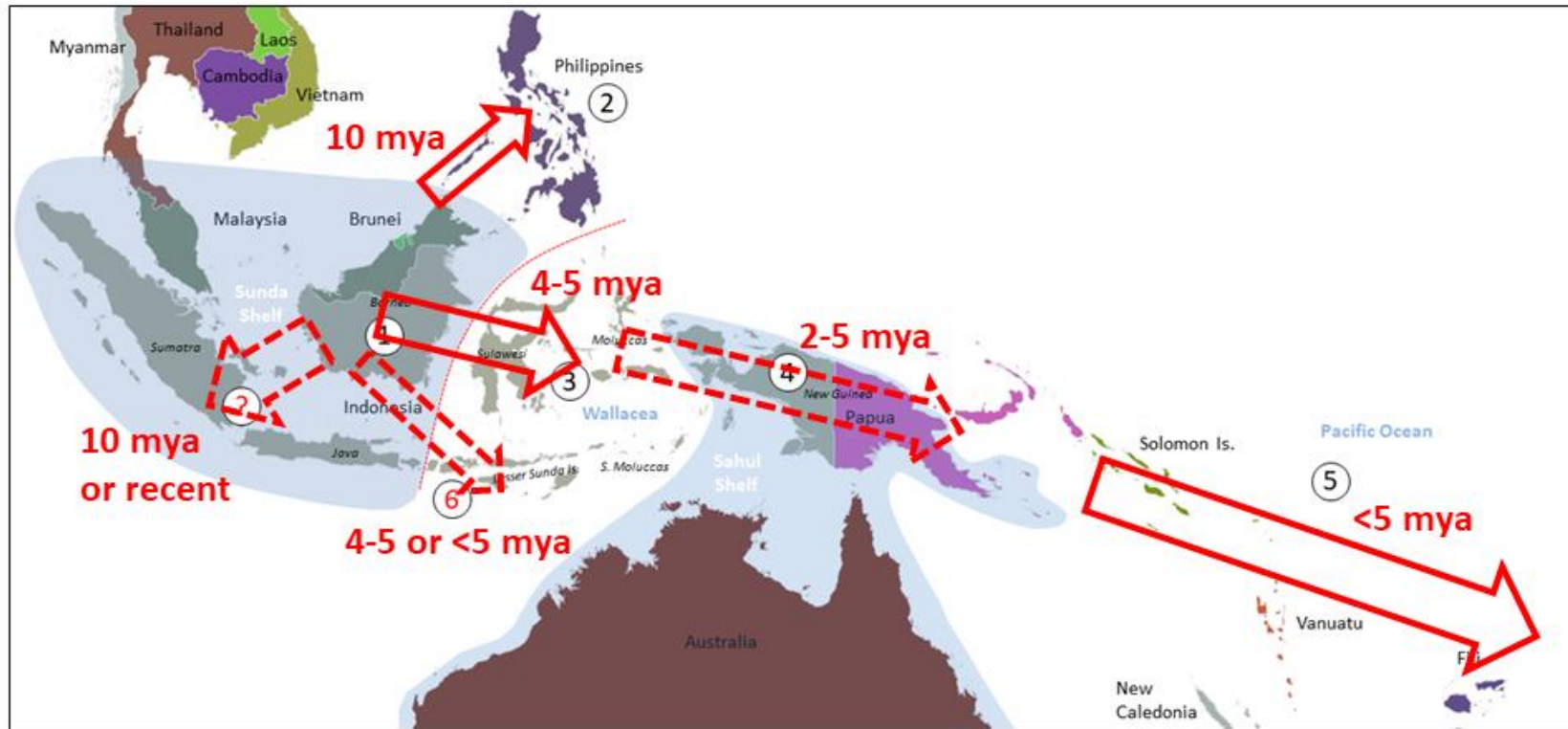
Figure 93. Map of the Indo-Australian Archipelago. Map layers for administrative boundaries from GADM (Hijmans 2018), developed in ArcGIS Pro v.2.2.4 (ESRI, Redlands, USA). Extent of Sunda and Sahul shelves from O'Connell & Allen (2004), Voris (2000), and Mayr (1944). Thin dashed line = Wallace's line. Hypothesized order of colonization indicated by numbers and arrows, with approximate dates in red. Uncertain dispersal events indicated by arrows with dashed lines.

The ancestral presence of *Eudocima* in the western Greater Sunda Islands is equivocal at nearly all nodes of the phylogeny (except for *E. dividens* + *E. salaminia*, the clade from *E. phalonia* Australia to *E. steppingstonia*, *E. cocalus* + *E. cocalus*, and the clade containing replicates of *E. srivijayana*), and therefore its placement in the order of colonization by *Eudocima* is uncertain. Dispersal to the other Greater Sundas from Borneo around the same time as the Philippines, or just after (assuming dispersal to the Philippines 10 mya), would coincide with the gradual development of Sumatra and Java as major land areas during the Pliocene, beginning about 5 mya (Lohman et al. 2011). However, an even later dispersal to the western Greater Sundas is possible. During the last glacial maximum in the Pleistocene, savannah or seasonal forest extended from the Malay Peninsula to Java due to low rainfall, causing a dispersal barrier between Borneo and Sumatra for rainforest taxa (Lohman et al. 2011); thus, the western Greater Sunda Islands may have only become habitable to tropical species relatively recently. In the Lesser Sunda Islands, the common ancestor of clade II (Fig. 89) is reconstructed as equivocally present in this area (10 steps); therefore, it is possible that dispersal to the Lesser Sundas occurred around the same time as dispersal to Sulawesi and the Moluccas. Alternately, these islands could have been colonized much later, perhaps concurrently with the Pacific islands.

3.5.5.3   Biogeographical notes on *Eudocima* species

(1) *Borneo*. In Borneo, the mountain ranges which formed between 20 mya and 5 mya may have served as refugia for tropical taxa during the Plio-Pleistocene, preserving old lineages and causing speciation of new taxa with restricted ranges in this area (Lohman et al. 2011). This may be a compelling explanation for speciation of the Bornean endemic *E. kinabaluensis*, and for *E. smaragdipicta* and *E. mionopastea*, other species in Borneo with a limited range. *Eudocima kinabaluensis* is recovered together with *E. smaragdipicta* in the clade from *E. splendida* to *Phyllodes consobrina* (Fig. 89), and *E. mionopastea* is recovered within clade IB (Fig. 89).

(2) *Philippines*. The Philippine endemics, *E. mazzeii* (in the northern Philippines) and *E. behouneki* (in the central and southern Philippines), are recovered in a clade with *E. sikhimensis* in subclade IB (Fig. 89). This two species replace *E. sikhimensis* in the Philippine archipelago (Zilli & Hogenes 2002). The other species found only in the

Philippines, *E. treadawayi*, is recovered as sister to *E. hypermnestra* (*E. cocalus* Papua + *E. cocalus* Mareeba) (Fig. 89).

(3) *Moluccas*. Many avian species show disjunct distributions involving the Moluccas, eastern Papuan islands, and the Solomon Islands without involving mainland New Guinea (see Heads 2008). In *Eudocima*, a less extreme example of a disjunct distribution in the Moluccas is seen in *E. jordani*, which can be found from Sulawesi eastwards into New Guinea as far as New Caledonia, and south into Australia, but which is absent from the southern Moluccas and is only known from Halmahera, Buru, and Seram (Zilli et al. 2017). *Eudocima jordani* is recovered as the most ancestral member of the *E. phalonia* clade (Fig. 89). The Moluccan species *E. caesar* is recovered along with *E. iridescens*, a close relative extending into the Moluccan islands from Papua New Guinea, in clade IA (Fig.88). *Eudocima talboti* is recovered as sister to *E. cajeta* (*E. talboti* New Guinea to *E. cajeta* Ceylon) in clade IIB (Fig. 89).

(4) *Papua New Guinea*. The Papuan endemic *E. nigricillia* forms a clade with *E. dividens* and *E. salaminia* (which is also present in New Guinea) (Fig. 89), and *E. prolai* is recovered in clade IB (Fig. 89). Other taxa centered on Papua New Guinea (*E. kuehni*, *E. iridescens*, and *E. muscigera*) are recovered separately throughout the phylogeny; *E. kuehni* is recovered outside clade E s.l. in the clade from *E. splendida* to *Phyllodes consobrina* (Fig. 89), *E. iridescens* is recovered as part of clade IA (Fig. 89), and *E. muscigera* forms a clade with *E. discrepans* and *E. boseae* in clade II, as sister to clades IIA and IIB (Fig. 89).

(5) *Pacific*. In each of the island groups, the common ancestor of the clade from *E. phalonia* Australia to *E. steppingstonia* was reconstructed as present, as well as the common ancestor of the clade comprising the replicates of *E. materna* and *E. apta* (Soloman Islands, 6 steps; Vanuatu, 4 steps; Fiji, 5 steps; and Marquesas Islands, 4 steps). In the Solomon Islands, *E. cocalus* Papua + *E. cocalus* Mareeba was also recovered as present (6 steps). In all island groups, the presence of the common ancestor of the members of clade IIA (Fig. 89) was equivocal (Soloman Islands, 6 steps; Vanuatu, 4 steps; Fiji, 5

steps; and Marquesas Islands, 4 steps). The majority of *Eudocima* species present on these islands are wide-ranging, such as *E. salaminia*, *E. materna*, and *E. phalonia*. Endemics to Vanuatu (*E.oliveri*) and the Marquesas Islands (*E. steppingstonia*) are recovered in the *E. phalonia* clade as close relatives, providing evidence for a "stepping stone" hypothesis of dispersal for *E. phalonia* to these islands, where speciation occurred. *Eudocima martini*, which is endemic to the Solomons, is recovered outside clade E s.l. in the clade from *E. kuehni* to *Phyllodes consobrina* (Fig. 89), and the Fijian endemic *E. paulii* is recovered in clade IB (Fig. 89).

(6) *Lesser Sunda Islands*. Ancestral reconstruction of *Eudocima* species in the Lesser Sunda Islands shows the same pattern of unequivocal presence as that in the Pacific islands, involving the wide-ranging species *E. materna*, *E. phalonia*, and *E. salaminia*, with the additional presence of *E. homaena*, *E. dividens*, *E. sikhimensis*, *E. aurantia*, *E. discrepans*, *E. cocalus*, and *E. srivijayana* (10 steps).

3.6   Conclusions

Although some character trends can be deciphered, no new nomenclatural changes are proposed to the taxonomy of *Eudocima*. While the historical generic groups *Eudocima* s.str. and *Trissophaes* were each recovered as monophyletic, character and phylogenetic support for these groups is not robust enough for them to be raised to generic status at this time. The historically-recognized group *Rhytia* was also recovered as monophyletic (contingent upon the possibly incorrect assignment of *E. discrepans* to *Rhytia* by some authors), and all members of the former genus *Adris* were recovered together in the same clade along with other taxa. The recovery of few unambiguous synapomorphies for historical groups could be due to previous systematists using combinations of external characters to set apart groups, which may be homoplastic or plesiomorphic. Furthermore, it seems clear that the name *Othreis* has been applied liberally over time to a wide variety of taxa within the current genus *Eudocima*, perhaps by workers confined to different areas and possibly not in communication with each other, such that the group's criteria was not uniformly applied. The wide range of *Eudocima* across the tropics of the world would also be an exacerbating factor in this scenario.

Despite low jackknife supports, stable clades and well-resolved relationships were recovered for *Eudocima* using morphological data. Of the 57 recovered clades from the strict consensus phylogeny, 87% were completely resolved and without polytomies. It is noted by Giribet (2003) that low nodal support does not necessarily correspond to an unlikely phylogenic hypothesis:

> *"It is also important to note that the opposite situation may also occur in real data sets; low nodal support values may be related to highly stable clades… This behavior is logically expected when a clade has just a few unambiguous characters supporting it and no characters that contradict it".*

This scenario corresponds with the situation presented in this study. Despite the strongly-resolved relationships recovered for the genus *Eudocima*, limited phylogenetic support is available for previously-used names, and for any new groupings supported by synapomorphies. Although significant backbone structure is apparent in the consensus tree obtained from the analysis, there is a paucity of synapomorphies which can uniformly be applied to any of the clades. Despite this, the recovery of only ten most parsimonious trees in the phylogenetic analysis, coupled with the resolution of so many clades in the strict consensus of these trees, lead us to the conclusion that the phylogeny presented here is a reasonable hypothesis for *Eudocima* until further evidence (such as molecular data) can be gathered for the genus.

Additionally, available phylogenetic evidence does not indicate a single, monophyletic *Eudocima*. While most *Eudocima* were grouped together in clade E s.l. from *E. nigricilia* to *E. cajeta* Ceylon (Figs. 88, 89), support for this clade is substantiated mainly by characters of the proboscis, which were not observed for many taxa, and by the reduced condition of the apophyses anteriores. This last character would be strengthened (and other informative traits might be discovered) by the inclusion of more data from female genitalia, which was incompletely available across *Eudocima* at the time of this study. The length and shape of the uncus were also found to be unifying characteristics of clade E s.l., and these characters are important among those that isolate some *Eudocima* species from the rest of the current genus. In particular, the extraordinary character conditions present in *E. procus*, *E. martini*, and *E. keuhni* leave little doubt that their exclusion from the rest of *Eudocima* in this analysis is not an artefact, and systematic placement outside *Eudocima* for these taxa ought to be considered. The

placement of the clade *E. splendida* (*E. kinabaluensis* + *E. smaragdipicta*) outside the rest of *Eudocima* leads to similar questions about its current position within the genus, although many of the character states present within this group are less incongruous with the greater part of *Eudocima*.

The utility of a more thorough morphological understanding of *Eudocima* will manifest itself as investigation into this group of moths continues. The character systems and descriptions presented here will hopefully form the basis for further inquiries on form and function, evolution and adaptation within *Eudocima*. Though the number of sampled characters is greater than the number of included taxa, some of the characters do not lend themselves well to the exemplar approach to character coding which is typically used (Yeates 1995). Gradual variation that is present across a large and diverse genus such as *Eudocima* (and which is present in many of the morphological characters) is challenging to score discretely, and some of these characters can also be affected by specimen preparation, such incomplete inflation of the bursae, intensity of staining, or artefacts created by slide mounting. Despite these obstacles, anatomical information useful to *Eudocima* classification and species delimitation, particularly with regard to internal morphological characters, is now more readily available.

A foundation is also provided by this study for understanding the biogeography of *Eudocima*. The Australian region is recovered as the most parsimonious area of origin, in contrast with the Oriental region as proposed by Waterhouse & Norris (1987). The hypothesized area of origin in the Oriental region is not unreasonable; using Wallace's line as the traditionally-accepted boundary between the Oriental and Australian regions in our biogeographic analysis, the greatest *Eudocima* species richness is present in these two regions. Patterns of dispersal, particularly between the Oriental and Australian regions along the Indo-Australian Archipelago, are now better understood. In this study, the Pacific islands extending to the east of Papua New Guinea across the Pacific basin are also considered part of the Australian region; this may be problematic considering the species richness and the antiquity of *Eudocima* in the Pacific alone (Zilli et al. 2017). Our results estimate an arrival of *Eudocima* in the Pacific islands subsequent to presence of the genus in the Indo-Australian Archipelago. An order of dispersal for *Eudocima* out of the Australian region is also postulated to other biogeographic regions of the world where

members of the genus are currently present. These dispersal hypotheses are the first of their kind for this economically-important genus, and can provide a basis for future investigation.

Although this study provides a foundation for further hypothesis testing within this enigmatic genus, more work is needed to elucidate strongly-supported relationships, and *Eudocima* would be an excellent candidate for future molecular studies.

CHAPTER 4.   MOLECULAR PHYLOGENY, SPECIATION, AND BIOGEOGRAPHY OF *EUDOCIMA PHALONIA* (LINNAEUS), WITH A NOVEL RISK ASSESSMENT OF PROBABILITY OF PRESENCE AND ESTABLISHMENT

4.1   Abstract

The *Eudocima phalonia*-complex is distributed throughout the Old World and has been the subject of increasing interest and research due to its economic impact in the tropics and status as a potential invasive species. The recent description of closely-related sister species, as well as morphological variation documented within *E. phalonia* itself, suggests possible speciation occurring within *E. phalonia* populations across its wide geographic range. To test species boundaries for this taxon, a molecular phylogeny is constructed using anchored hybrid enrichment and a next-generation sequencing approach. Sampling for this phylogeny was informed using a global range map for *E. phalonia*, which was developed using georeferenced specimen data from natural history collections. Biogeographic analyses are also conducted in BioGeoBEARS, using the molecular phylogenetic hypothesis to investigate the area of origin and dispersal patterns of *E. phalonia* with a view to elucidating possible speciation modes and gene flow. Georeferenced range information is also utilized along with environmental variables in constructing a correlative environmental niche model using MaxEnt. This model is used to evaluate a previous mini risk assessment for environmental suitability in the continental United States for *E. phalonia* establishment. Results suggest that *E. phalonia* is monophyletic, with gene flow still occurring between populations. The area of origin for *E. phalonia* is postulated to be the Oriental region, although further investigation is needed. In general, range predictions for *E. phalonia* from environmental modelling in the Old World concurred well with expectations based on current distribution information, and new areas of high environmental suitability were projected in the New World. Assessment of environmental suitability for *E. phalonia* in the continental United States based on environmental niche modelling suggests areas of greatest potential suitability occurring in Florida and along the Gulf Coast.

4.2 Introduction

4.2.1   The *E. phalonia*-complex and species boundaries

Eudocima phalonia (Linnaeus, 1763) is a well-known pest of orchards which is distributed throughout the Old World tropics and across the Pacific and southeast Palearctic, occasionally extending into northeast areas of the Palearctic region as a stray (Zilli et al. 2017). Within this large geographic range (one of the largest within the genus *Eudocima*), regional differences in morphology are evident in some populations (Zilli & Hogenes 2002, Brou & Zilli 2016, Zilli et al. 2017). Characterization of morphological differences in specimen genitalia within some areas has led to the description of three closely-related species: *E. lequeuxi*, an Afrotropical species (Brou & Zilli 2016), and two Pacific insular species, *E. oliveri* from New Hebrides and *E. steppingstonia* from the Marquesas Islands (Zilli et al. 2017). Together with *E. phalonia*, these species make up the *E. phalonia*-complex. Besides solid morphological differences used to delineate *E. lequeuxi* in Africa, additional differences were also observed in juxta thickness between confirmed African *E. phalonia* specimens and *E. phalonia* from the Indo-Australian Archipelago, though these differences were not pronounced enough to merit description as a separate species (Zilli & Hogenes 2002, Zilli et al. 2017). Morphological evaluation of *E. phalonia* in other areas has also revealed patches of local differentiation in forewing shape and coloration (such as in the Solomon and Samoan Islands), although no meaningful differences have been discovered in genitalia comparisons (Zilli et al. 2017). These local differences in phenotype, as well as the recent description of close relatives within the *E. phalonia*-complex, could indicate speciation or incipient speciation occurring in other *E. phalonia* populations. This explanation would also account for regional differences in hostplant preference by *E. phalonia* larvae, which develop in some areas usng trees of the genus *Erythrina* (Fabaceae) rather than menisperm vines (Tams 1935, Cochereau 1977, Bänziger 1982, Hammes & Putoa 1986, Muniappan et al. 1994, Fay 1996, Sands & Chan 1996, Reddy et al. 2005). Regional preferences are even in evidence in some areas between different Menispermaceae (Bänziger 1982; Fay & Halfpapp 1993b; Fay 1994, 1996). Species-specific control methods for *E. phalonia*, such as pheromone traps, have also been ineffective (e.g., Fay 2002), possibly due to cryptic species within this taxon (see Zilli et al. 2017). Despite this, species boundaries within *E. phalonia* have not yet been tested using a molecular phylogenetic framework.

4.2.2 *Eudocima phalonia* biogeography and speciation

Eudocima phalonia is an ideal taxon for addressing questions of biogeography and dispersal due to its diversity and extensive range, especially considering its economic impact in the tropics and status as a potential invasive species (Bhummannavar & Viraktamath 2012). Biogeographic analysis of this taxon can also provide clarification on the center of origin for this species (thought by Waterhouse and Norris (1982) to be the Indo-Malaysian (=Oriental) region). Dispersal of *E. phalonia* is thought to have occurred from the Oriental region to Africa (Waterhouse & Norris 1982), and more recently to the Pacific (Waterhouse 1997). Although significant advances have been made recently towards determining the global extent of *Eudocima* species (i.e., Zilli et al. 2017), the precise range extent is unknown for some fauna (e.g., Fay & Halfpapp 2006), and detailed range information has not yet been made available for *E. phalonia* despite its agricultural significance. Mechanisms of dispersal and divergence can be investigated based on a robust phylogeographic hypothesis.

Three modes of speciation are generally agreed upon by authors: allopatry, sympatry, and parapatry. The primary division can be drawn between speciation due to allopatry, which involves the subdivision of an ancestral gene pool by physical changes in range or geography (Wiley and Lieberman 2011), and speciation due to sympatry, which does not involve changes in the physical range or distribution of the original species when a sister species emerges (Wiley and Lieberman 2011). Allopatric speciation can further be split into two competing hypotheses: vicariance, a splitting of the original genetic population by a geographic event which creates a barrier to gene flow; and dispersal, by which a subpopulation of the species extends the current range over a geographic barrier and begins to diverge independently from the parent population (Wiley and Lieberman 2011, Ronquist 1997). Parapatric speciation can be considered an intermediate between these allopatric speciation and sympatric speciation, and involves speciation via partially-separated geographic populations that undergo isolation and differentiation, but are close enough to facilitate limited gene flow over a hybrid zone (Wiley and Lieberman 2011, Futuyuma 2013). Allopatric, parapatric and sympatric speciation can be understood to form a continuum regarding the amount of gene flow each population experiences initially; gene flow during the onset of speciation is predicted to be minimal during allopatric

speciation, and maximal during sympatric speciation (Futuyuma 2013). Biogeographic analysis of *E. phalonia* will help elucidate speciation mode if speciation is occurring within this group.

4.2.3 Environmental niche modelling

4.2.3.1 Rationale

While all members of *Eudocima* could potentially be damaging pest species if introduced to the continental United States, *E. phalonia* is considered the species of greatest agricultural significance. *E. phalonia* is cited by Bänziger (1982) to be the sole species responsible for an estimated 70-90% and 50-70% of total damage on longan and citrus crops respectively by primary fruit-piercing moths in Thailand. In Queensland, *E. phalonia* was the most damaging pest of seven *Eudocima* species with overlapping ranges attacking lychees and carambolas (Fay & Halfpapp 1999a), and caused up to a 50% crop loss in citrus, lychees, and carambolas in northeast Australia (Fay 1994). *Eudocima phalonia* is also cited to be the dominant fruit pest in many parts of India (Bhumannavar & Viraktamath 2012), Nigeria (Golding 1945), and Sierra Leone (Hargreaves 1936). International trade of fruits, seeds, plant parts, and packing materials can lead to the inadvertent introduction of pest species to uncolonized areas (Kumar et al. 2015). To prevent this, the World Trade Organization has established Sanitary and Phytosanitary Measures which must be observed by its members (WTO 2014); pests and pathogens regulated by these measures cost an estimated 80 billion dollars in damage to the United States economy (Pimentel et al. 2000, Kumar et al. 2015). Biologically and ecologically-relevant pest risk analyses are valuable tools which can be used to preempt introduction of invasive pests via implementation of surveillance and quarantine measures (Kumar et al. 2015). Correlative ENMs using species occurrences and environmental variables are a common means of assessing establishment potential for invasive species (Li et al. 2009, De Meyer et al. 2010, Evangelista et al. 2011, Lozier and Mills 2011, Kumar et al. 2015) and can be useful for informing pest management descisions and negotiating trade.

In the United States, the citrus industry in California alone is worth an estimated 1.6 billion dollars, second only to California's grape industry, which is worth between 1.8 and 1.9 billon (Andy Cline pers. comm.). Florida is the world's foremost producing region of grapefruit, the second largest producer of oranges worldwide after Brazil, and produces over 80 percent of

citrus in the United States (Hodges et al. 2001). Significant economic damage could therefore result from establishment of *E. phalonia* in these areas. Two *Eudocima* species, *E. apta* and *E. serpentifera*, have occasionally been recorded as strays in the continental United States; *E. apta* has been recorded from Arizona, Florida, Missouri, New Mexico, North Carolina, Louisiana, Oklahoma, Texas, Vermont, and Wisconsin, and *E. serpentifera* has been recorded from Louisiana and Colorado (Brou & Águila 2013, Gilligan & Passoa 2016). A previous predictive analysis (Davis et al. 2005) compared biomes in countries where *E. phalonia* is reported in the literature with biomes in the contiguous United States to assess environmental suitability. This mini assessment projected large areas of the eastern Unites States as environmentally suitable, and classified the ecological suitability of the United States for *E. phalonia* as medium (Davis et al. 2005); however, further in-depth analyses of environmental suitability have not yet been performed.

4.2.3.2   Possible bias

One disadvantage of using presence-only data for environmental modeling is the assumption that the range has been randomly and systematically sampled (Phillips 2008, Elith et al. 2011, Kramer-Schadt et al. 2013). The principle of spatial autocorrelation states that localities which are close together will be more similar to one another than localities which are distant. Most biological survey data tend to be sparse or limited in coverage, or are available from natural history collections, which can only provide presence data (Elith et al. 2011, Kramer-Schadt et al. 2013). Museum collections represent large and important repositories of occurrence data throughout time for many species, and as such are a significant source of data for ecological models (Phillips et al. 2006, Phillips 2008, Elith et al. 2011). However, presence-only occurrence records are often biased towards areas of greater accessibility or greater sampling effort (such as cities, roads, or rivers), which may lead to over-representation of environmental features common to these areas (Reddy & Dávalos 2003, Elith et al. 2011, Kramer-Schadt et al. 2013). Furthermore, the definition of presence and absence may not be strictly binary depending on the study system; although a plant might be either present or absent from a survey area, a bird could not be easily categorized as definitively absent from an area in which it is not found (Elith et al. 2011). As strong fliers (e.g.,, Baptist 1944, Sands & Schotz 1991, Davis et al. 2005,

Bhumannavar & Viraktamath 2012, Zilli et al. 2017), *Eudocima* species align closely with the bird example, making definitive absence data potentially difficult to collect during survey efforts.

MaxEnt is a distribution modeling program which uses maximum entropy to infer the potential distribution of a species by relating presence-only data to environmental variables (Phillips et al. 2006). One of the strengths of MaxEnt is its robustness to small sample sizes and sparse distributions, making it very suitable for modeling data derived from collections (Phillips et al. 2006, Phillips 2008, Elith et al. 2011, Kramer-Schadt et al. 2013). To account for sampling bias in MaxEnt during model construction, two methods are used: manipulation of the environmental or climatic data, or manipulation of the input occurrence data (Kramer-Schadt et al. 2013). Manipulation of the environmental data is a common approach which involves the creation of a "bias file" which is included along with the input data and variables during model configuration (Phillips et al. 2009, Kramer-Schadt et al. 2013). In this approach, the environmental variable layers are altered based on the bias file (a kernel density layer of the input point data) such that denser sampling of certain areas will be accounted for (Elith et al. 2011, Kramer-Schadt et al. 2013). The other approach to bias correction in MaxEnt is known as "spatial filtering", and involves direct manipulation of the species occurrence data. This method directly accounts for areas of disproportional sampling effort by thinning occurrence records in areas that are known to be more heavily sampled, such that a more even sampling surface is created for model-building (Kramer-Schadt et al. 2013, Boria et al. 2014). According to a study investigating spatial bias on Malay civets in Borneo, spatial filtering of occurrence data minimized both omission (type II) and commission (type I) errors in comparison with background manipulation (i.e., creating a bias file) (Kramer-Schadt et al. 2013). Although spatial filtering may negatively influence model performance for small datasets, overparameterization is less likely when the number of occurrence records exceeds the number of environmental variables (Warren & Seifert 2011, Kramer-Schadt et al. 2013).

4.2.4   Study objectives

In this study, the monophyly of *E. phalonia* is evaluated using a molecular phylogenentic approach, which is accomplished using next-generation sequencing of anchored hybrid enrichment collected from *E. phalonia* specimens across the documented range (Lemmon et al.

2012). The resulting phylogeny is then subjected to further testing using Possion Tree Processes (PTP) (Zhang et al. 2013), a method which identifies operational taxonomic units (OTUs) which are indicative of separate species. Reconstructed molecular relationships between *E. phalonia* populations are also used for biogeographic analyses weighing dispersal scenarios and modes of speciation. The risk evaluation of the previous mini assessment by Davis et al. (2005) is also tested using more refined methods; a correlative ENM is constructed to this end using bioclimatic variables along with current distribution information to evaluate areas of greatest risk in the United States for *E. phalonia* establishment. In order to increase the independence of the occurrence data, spatial filtering was used in this study as a means of accounting for sampling bias. Two levels of filtering were employed and compared: in one dataset, occurrence records were thinned within 10 km (~6 miles) of one another (Boria et al. 2014, Kumar et al. 2015), and in second dataset, thinning was performed on records within 16 km (~10 miles). This greater distance was tested because *Eudocima* species are known to migrate large distances (Sands & Schotz 1991, Zilli et al. 2017). Response curves were also calculated for each bioclimatic variable to ascertain which variables most influence the range of *E. phalonia*.

4.3   Materials and methods

4.3.1   Range mapping

In order to 1) inform collection of frozen tissues for DNA extraction for *E. phalonia* specimens across the range extent, 2) set up biogeographic analyses, and 3) perform niche modeling, a worldwide distribution map was necessary. A global range map was constructed using 2,239 specimen records from the museum collections, personal collections, and institutions listed in Table 7. The Atlas of Living Australia (ALA) database (2017) was also used to download georeferenced physical specimen records from the AM, NVM, and WINC collections in the amount of 34 records, for a total dataset of 2,273 specimen occurrences. Georeferencing was accomplished using the point-radius method (Wieczorek et al. 2004) in the GEOLocate web application (Rios & Bart 2010, www.geo-locate.org), and a total of 467 unique localities from 51 countries (Table 8) was imported into ArcGIS Pro v.2.2.4 (ESRI, Redlands, USA) for mapping (Fig. 94). Multiple specimen records for a single georeferenced location were incorporated into the point map using symbology (increasing circle size) to convey number of records (Figs. 95,

96), and localities with more than 10 specimen records were focal areas for tissue collection for molecular sampling (Figs. 95, 96).

Table 7. Institutions hosting specimen records used to generate distribution map, and institutions which provided tissues for DNA extraction. Tissues were also obtained by fieldwork performed on behalf of the PERC by Jennifer Zaspel (in Australia and Thailand) and Gareth Powell (in Northern Vietnam).

*NMV, WINC, and AM accessed via Atlas of Living Australia.

†FDACS provided tissue for *E. apta* outgroup sample, and was not used for the distribution map.

Coden	Institution	Tissues for DNA Extraction
FLMNH	Florida Museum of Natural History, Gainesville, Florida, US	X
H.A.C. Fay	Personal Collection of H.A.C. Fay, Mareeba, Queensland, AU	X
HNHM	Hungarian Natural History Museum, Budapest, HU	
M. Fibiger	Personal Collection of M. Fibiger, Sorø, DK	X
NHMUK	Natural History Museum, London, GB	
PERC	Purdue Entomological Research Collection, West Lafayette, Indiana, US	X
USNM	National Museum of Natural History, Washington DC, US	
V.A. Brou Jr.	Personal Collection of V.A. Brou Jr., Abita Springs, Louisiana, US	X
NMV	Museum of Victoria, Melbourne, AU*	
WINC	Waite Insect and Nematode Collection, Adelaide, AU*	
AM	Australian Museum, Sydney, AU*	
DAF	Queensland Department of Agriculture and Fisheries, Mareeba, AU	X
DKI-PBARC	Daniel K. Inouye U.S. Pacific Basin Agricultural Research Center, Hilo, Hawaii, US	X
FDACS	Florida Department of Agriculture and Consumer Services, Gainesville, Florida, US†	X

Figure 94. Range map of *E. phalonia* showing unique localities across global extent.

Table 8. List of 51 countries with *E. phalonia* occurrence records, including number of unique georeferenced localities within each country.

Country	Number of unique records
Angola	3
Australia	46
Bangladesh	1
Benin	2
Bhutan	1
Brunei	4
Cameroon	3
China	19
Comoros	1
Congo, DRC	5
Cote d'Ivoire	4
Ethiopia	1
Fiji	6
French Polynesia	1
Ghana	14
Guinea	1
India	49
Indonesia	95
Japan	2
Kenya	2
Laos	1
Liberia	1
Madagascar	14
Malawi	2
Malaysia	22
Myanmar	14
Namibia	1
Nepal	4
New Caledonia	4
Nigeria	14
North Korea	1
Pakistan	1
Palau	1
Papua New Guinea	46
Philippines	11
Reunion	2
Rwanda	1
Samoa	3
Sierra Leone	6

Table 8 continued

Country	Number of unique records
Singapore	1
Solomon Is.	6
Solomon Islands	2
Sri Lanka	7
Taiwan	1
Tanzania	5
Thailand	12
Timor-Leste	2
Uganda	9
United States	1
Vanuatu	7
Vietnam	5
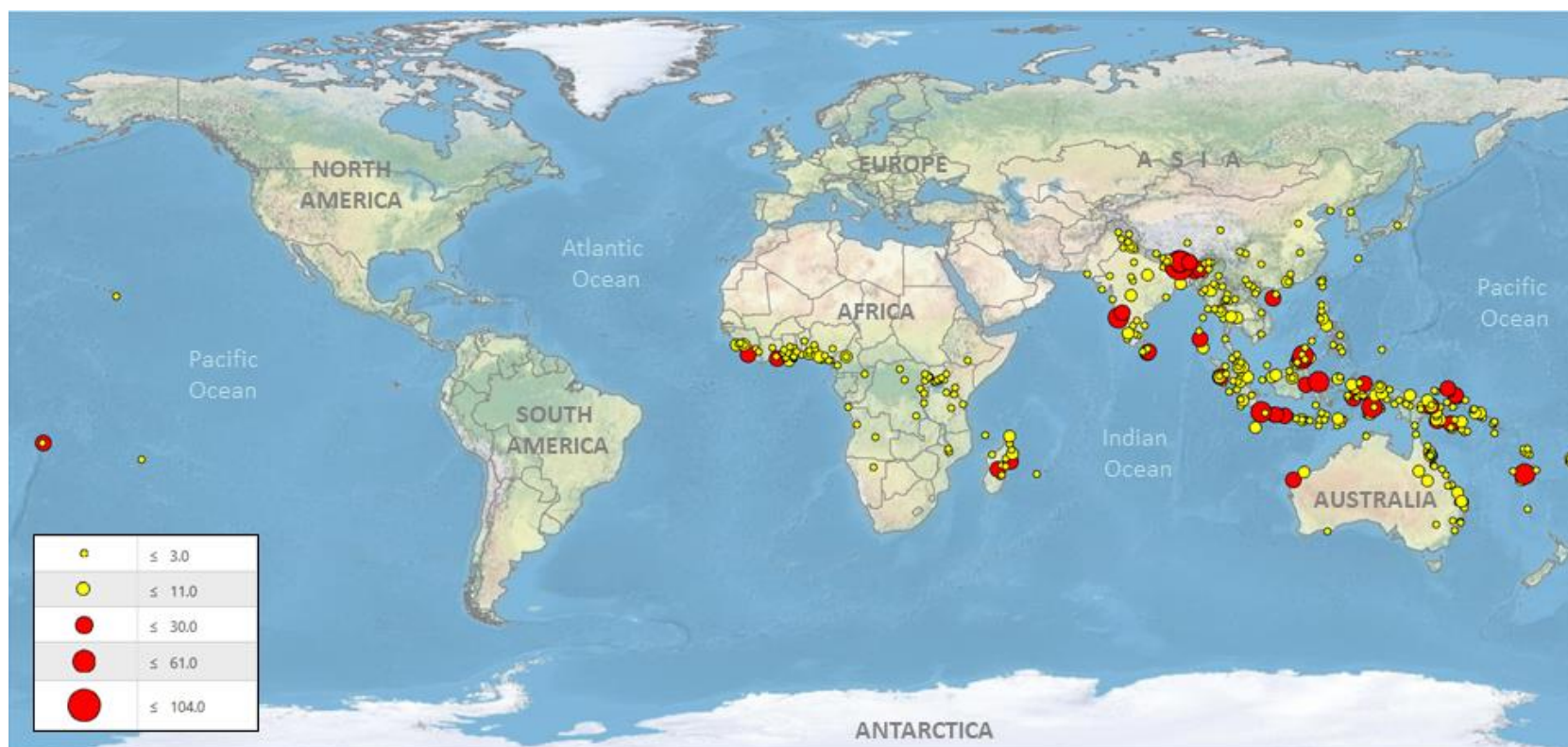
Figure 95. Range map of *E. phalonia* showing worldwide distribution, with unique localities symbolized by number of records. Increasing circle size indicates increasing number of specimen records per locality (refer to legend). Localities with 10 or fewer specimen records symbolized in yellow, and localities with 11 or more specimen records symbolized in red.
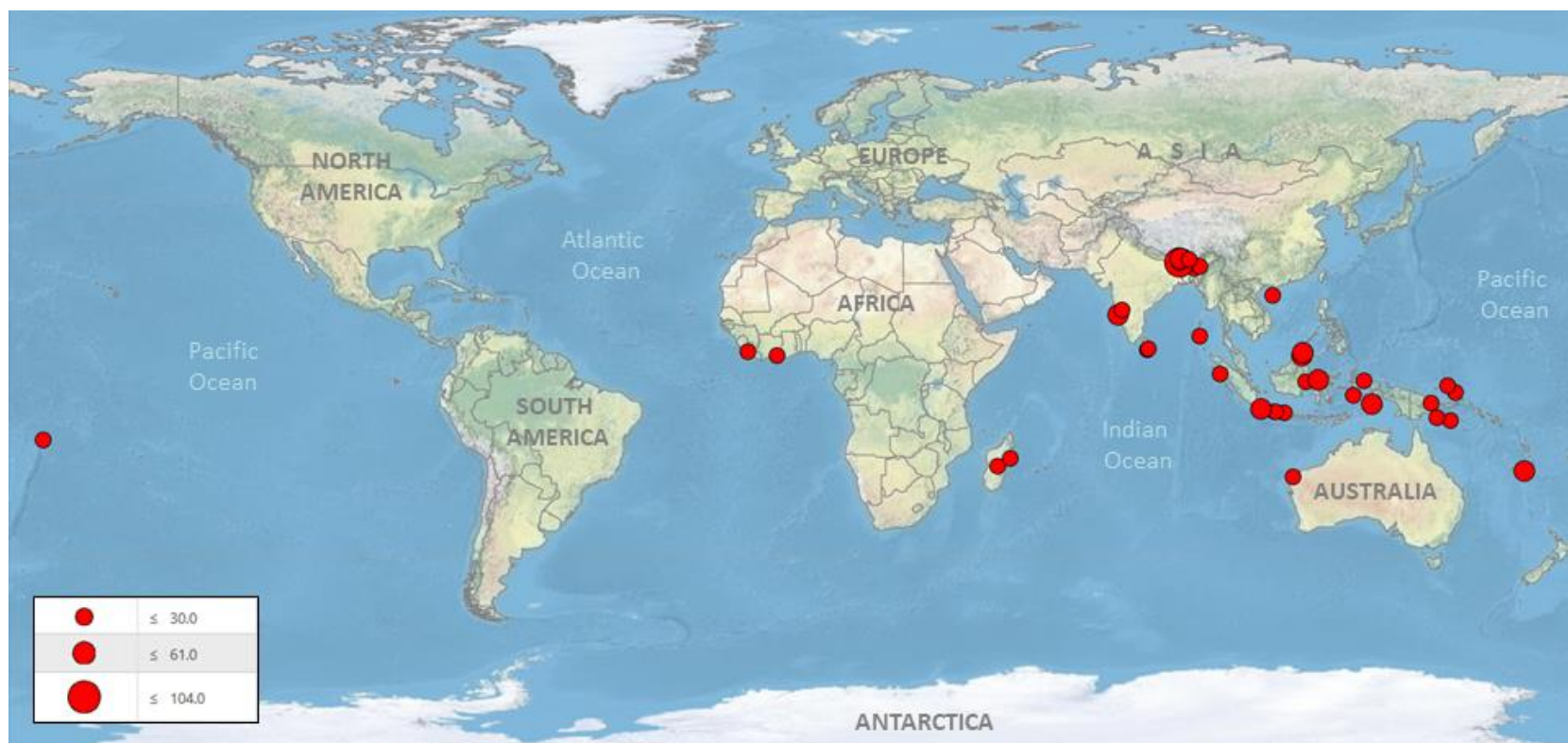
Figure 96. Range map of *E. phalonia* showing worldwide distribution, with unique localities symbolized by number of records. Increasing circle size indicates increasing number of specimen records per locality (refer to legend). Localities with 11 or more specimen records symbolized in red, and localities with 10 or fewer specimen records removed for clarity.

4.3.2   Materials examined and phylogenetic methods

Tissues from 77 specimens from 41 unique localities (Fig. 97) were obtained from the institutions listed in Table 7, and DNA extractions were performed using DNeasy kits (Qiagen, Hilden, Germany). Three other *Eudocima* species were also included as outgroups: *E. materna* from Queensland, Australia; *E. apta* from Florida, United States (Reeves et al. 2017); and *E. okurai* from Nepal. Several specimens of *Calyptra minuticornis* were also included as outgroups outside of *Eudocima*. Eighty-three percent of tissues obtained for molecular sampling were collected from specimens taken within the past 15 years in order to avoid excessive DNA degradation (e.g., Hoy 2013). Successful extractions of purified genomic DNA (37 ingroup taxa representing 26 locations) were then sent to the Center for Anchored Phylogenomics at Florida State University (Lemmon et al. 2012). There, next-generation sequencing using anchored hybrid enrichment (Lemmon et al. 2012) and downstream bioinformatics were accomplished using a nested probe design for Erebid moths (Zaspel et al. in prep). Twenty-two samples from 10 unique localities were successfully processed through the Anchored Phylogenomics pipeline (Lemmon et al. 2012). Trimmed alignments were visualized in SeaView v.4.7 (Galtier et al. 1996, Gouy et al. 2010) and concatenated using Sequence Matrix v.1.8 (Vaidya et al. 2011). A concatenated analysis was conducted in RAxML v.8 (Stamatakis 2014), and species tree analyses were implemented in ASTRAL-II using coalescent units (Mirarab & Warnow 2015) and bootstrapping (Felsenstein 1985). Operational taxonomic units were also analyzed using Poisson tree processes (PTP) (Zhang et al. 2013) on ingroup taxa only using the maximum likelihood topology as the input. Trees were visualized in FigTree v.1.4.3 (Rambaut 2006).
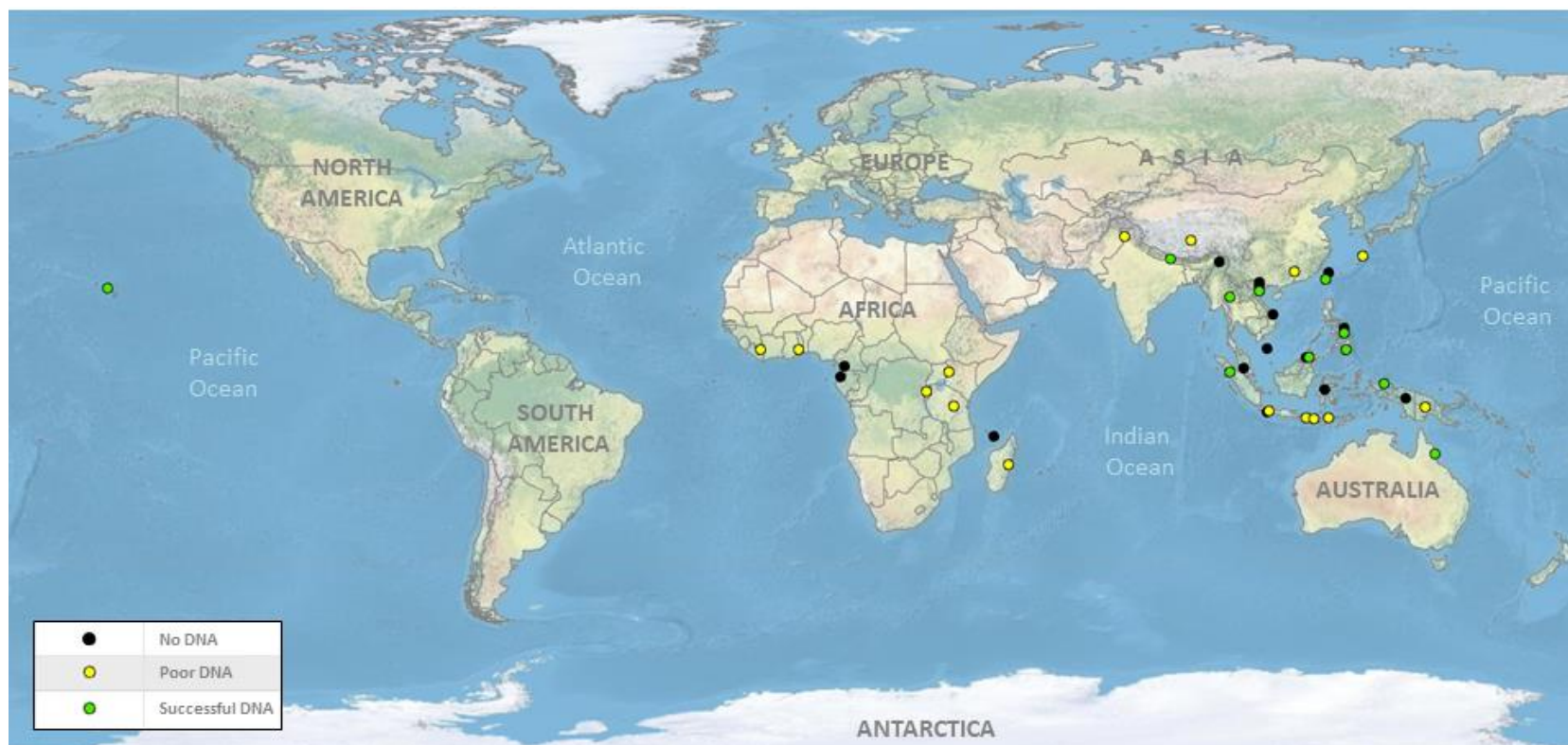
Figure 97. Range map of *E. phalonia* showing molecular sampling across distribution. All points indicate localities of specimens from which tissues were acquired. Black points indicate samples for which DNA extraction failed, yellow points indicate samples for which DNA extraction was successful but which failed during sequencing, and green points indicate samples which were sequenced successfully.

4.3.3 Biogeographic methods

A penalized likelihood (PL) approach (Sanderson 2002) was implemented in R v.3.5.3 (R Development Core Team 2008) to construct an ultrametric tree using the maximum likelihood topology as the base. The root age of the base tree was set to 30 mya to reflect the approximate age of the most recent common ancestor of *Eudocima* based on the analysis by Toussaint et al. (2012). Correlated, discrete, and relaxed evolutionary clock models (Paradis 2013) were tested for the base tree ingroups and evaluated based on the likelihood-ratio test (LRT). The time-calibrated tree was then utilized as the input for biogeographic analyses in the R package BioGeoBEARS (Matzke 2013a), which was used to explore four maximum likelihood (ML) dispersal models: DEC (dispersal-extinction-cladogenesis) (Ree 2005, Ree & Smith 2008), DIVALIKE (dispersal-vicariance-analysis) (Ronquist 1997, Matzke 2013b), DEC+J, and DIVALIKE+J. The last two models, DEC+J and DIVALIKE+J, emphasize founder-event speciation by adding a "jump dispersal" parameter to account for rare long-range colonization events which result in genetically-isolated populations (Matzke 2013b, 2014). Criticism of DEC+J, and to a lesser extent DEC, faults these models for prioritizing cladogenic events over branch lengths and ignoring the time component of dispersal (Ree & Sanmartín 2018). This problem is said to be exacerbated by the inclusion of the free "jump" parameter, such that the DEC+J model cannot be compared equally with the DEC model (Ree & Sanmartín 2018). However, because our analysis constrains the maximum likelihood topology to be ultrametric based on a molecular clock model from a calculated root age, these concerns are less important, as we are more interested in the speciation mode than the speciation rate for the purposes of the present study. The best dispersal model (of DEC, DEC+J, DIVALIKE, or DIVALIKE+J) was chosen using the ML approach in BioGeoBEARS based on LRT and the Akaike information criterion (AIC). Both the normal and corrected AIC were examined for the dataset. The analysis was unconstrained, with a two-area maximum. Specimen locality data was used to assign successful molecular samples to either the Oriental (O) or Australian (A) region. Hawaii was considered for our analysis to be part of the Australian region, in conformity with consideration of the Pacific Islands by Zilli et al. (2017).

4.3.4   Niche modeling

In order to increase the independence of the occurrence data, the original dataset of 467 unique localities was thinned using two different distances, creating two datasets. Locality records within 10 km were thinned to a single point (Boria et al. 2014, Kumar et al. 2015), resulting in a dataset of 423 localities out of the original 467 (un-thinned). To account for the strong dispersal capabilities of *Eudocima* species (Baptist 1944, Sands & Schotz 1991, Bhumannavar & Viraktamath 2012, Zilli et al. 2017), a further input dataset was created which thinned occurrence data within 16 km (~10 miles) in order to see how greater distances between input points affected the projection model. This dataset consisted of 348 localities. In areas where occurrence records were thinned, the most precise locality was retained. Each filtered dataset was input into MaxEnt v.3.4.1 (Phillips et al. 2006) along with 19 bioclimatic variables from WorldCLIM v.1.4 at 2.5 arc-minutes spatial resolution (~4.5 km) (http://www.worldclim.org/; accessed 28 May 2019) (Hijmans et al. 2005). The cloglog transformation was used, and each analysis was performed using default settings to predict the probability of presence for *E. phalonia* (Phillips et al. 2017). Response curves were also calculated and jackknifing accomplished for each dataset in order to determine the importance of each bioclimatic variable to the distribution of *E. phalonia*. A worldwide range was used in both cases to allow validation of the predictive model by existing locality points and projection of suitable areas for future colonization (e.g.,, Kumar et al. 2015). Evaluation of model performance was accomplished by comparing the AUC value for each model, which is an ordinal-based statistic on a scale of 0 to 1 (Phillips 2008). Values equal to or less than 0.5 are considered on par with randomly-generated data or worse, values from 0.5 to 0.7 indicate poor model performance, values between 0.7 and 0.9 indicate moderate performace, and values of 0.9 or above indicate high performance (Peterson et al. 2011, Kumar et al. 2015). Along with AUC scores, lower omission rate is another indicator of model performance; at the lowest predicted threshold and at the ten percent training presence threshold, the omission rates are expected to be 0 and 0.10 respectively, with higher omission rates signifying a poorer model (Boria et al. 2014, Kumar et al. 2015). Spatial results from the best MaxEnt model were mapped using ArcGIS Pro.

4.4   Results

4.4.1   Molecular phylogeny and species delimitation

In both the concatenated (Fig. 98) and coalescent (Figs. 99, 100) analyses, all specimens of *E. phalonia* are recovered together in a monophyletic clade with 100% nodal support. This clade is reconstructed in all analyses as sister to the remaining taxa, which are recovered in this sequence: *E. okurai* ((*E. apta* + *E. materna*) (*Calyptra minuticornis*)). *Eudocima okurai*, a continental Palearctic species, is recovered as sister to the clade containing *E. apta* and *E. materna*. The similarities between *E. apta* and *E. materna* (see Zilli & Hogenes 2002) make their close relationship in this analysis unsurprising, and these taxa are recovered together with 100% support in all analyses. *Eudocima apta* and *E. materna* are recovered as sister to the remaining clade encompassing all the included *Calyptra minuticornis* specimens. In contrast to the consistent recovery of *E. phalonia* specimens in a monophyletic group, few stable relationships were recovered within the *E. phalonia* clade. This is evidenced by the generally low support for internal nodes (Figs. 98, 99, 100), and for the differences in topology when the same ASTRAL-II analysis was implemented using different support measures (coalescent units, Fig. 99, and bootstrapping, Fig. 100). The concatenated topology recovered using RAxML will now be discussed in main.

Ten operational taxonomic units (OTUs) were recovered by the PTP analysis of the ML tree. Of these, the OTU which received highest support was a single specimen, the *E. phalonia* sample from Hawaii, with a support value of 1.0. Of the remaining nine OTUs recovered, FU1415 and FU316 (both Australian) were recovered together with a support value of 0.587; CKV07 (Borneo) and JZTH180 (Thailand) comprised a species group with a support value of 0.578; and CKV14 and CKV18 (both from Leyte I., Philippines) were grouped together with a support value of 0.519. These groups were each recovered as clades in the ML tree: FU1415 + FU316 was recovered with a bootstrap support value of 53, CKV07 + JZTH180 had bootstrap support of 59, and CKV14 + CKV18 was recovered with bootstrap support of 95. These pairs of taxa represent some of the clades within the *E. phalonia* clade which received the highest bootstrap support, although they represent shallow groups; other similar clades, such as FU2215 + JZJM111 (both Australian) and CKV16 + CKV29 (both from Papua New Guinea), were strongly supported (with bootstrap values of 100 and 64 respectively) but were not recovered as OTUs.

Figure 98. RAxML tree. The topology was rooted along the branch at the base of the *E. okurai* ((*E. apta* + *E. materna*) (*Calyptra minuticornis*)) clade. Specimens of *Calyptra minuticornis* are collapsed within their monophyletic clade. Blue indicates Oriental region, red indicates Australian region.
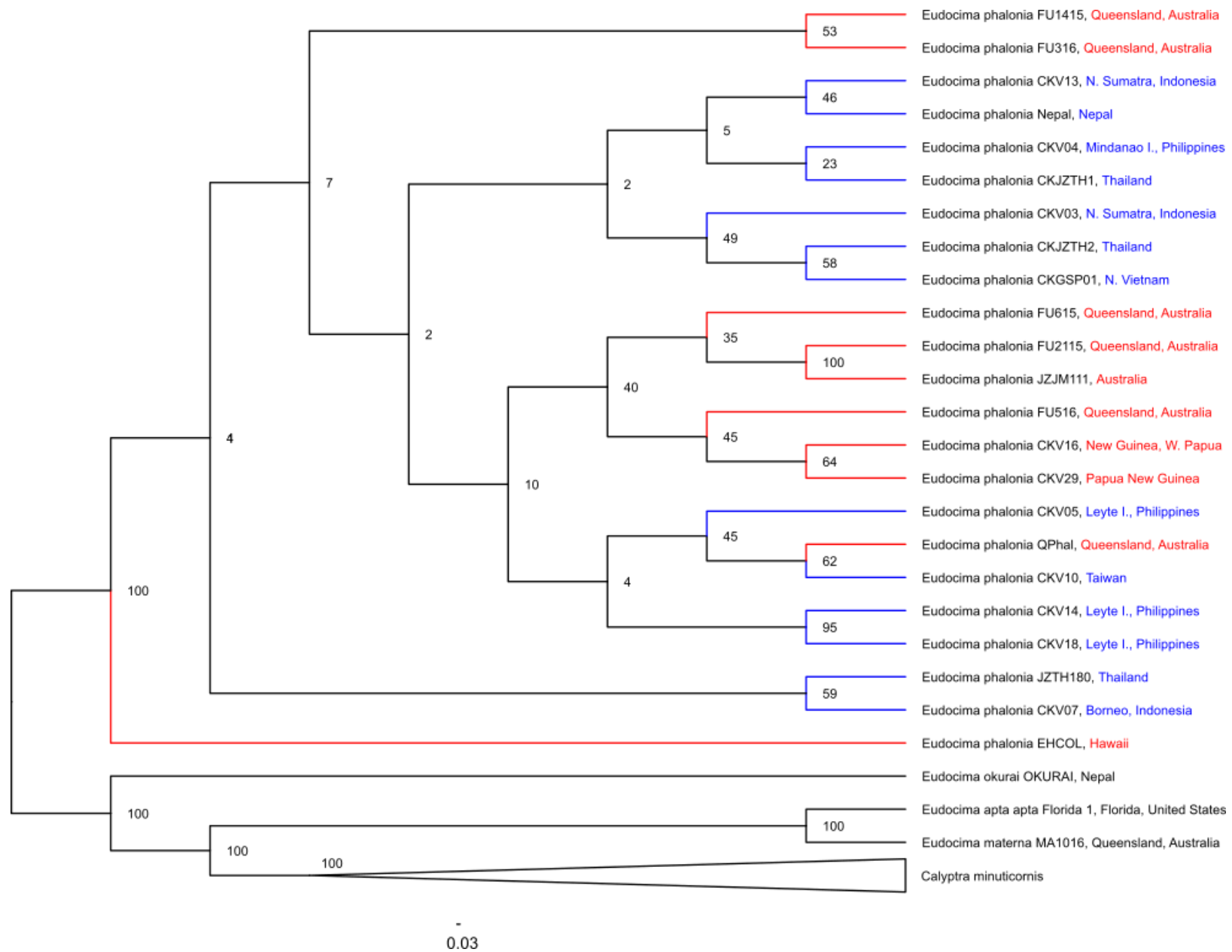
Figure 99. ASTRAL tree with coalescent units. The topology was rooted along the branch at the base of the *E. okurai* ((*E. apta* + *E. materna*) (*Calyptra minuticornis*)) clade. Specimens of *Calyptra minuticornis* are collapsed within their monophyletic clade. Blue indicates Oriental region, red indicates Australian region.
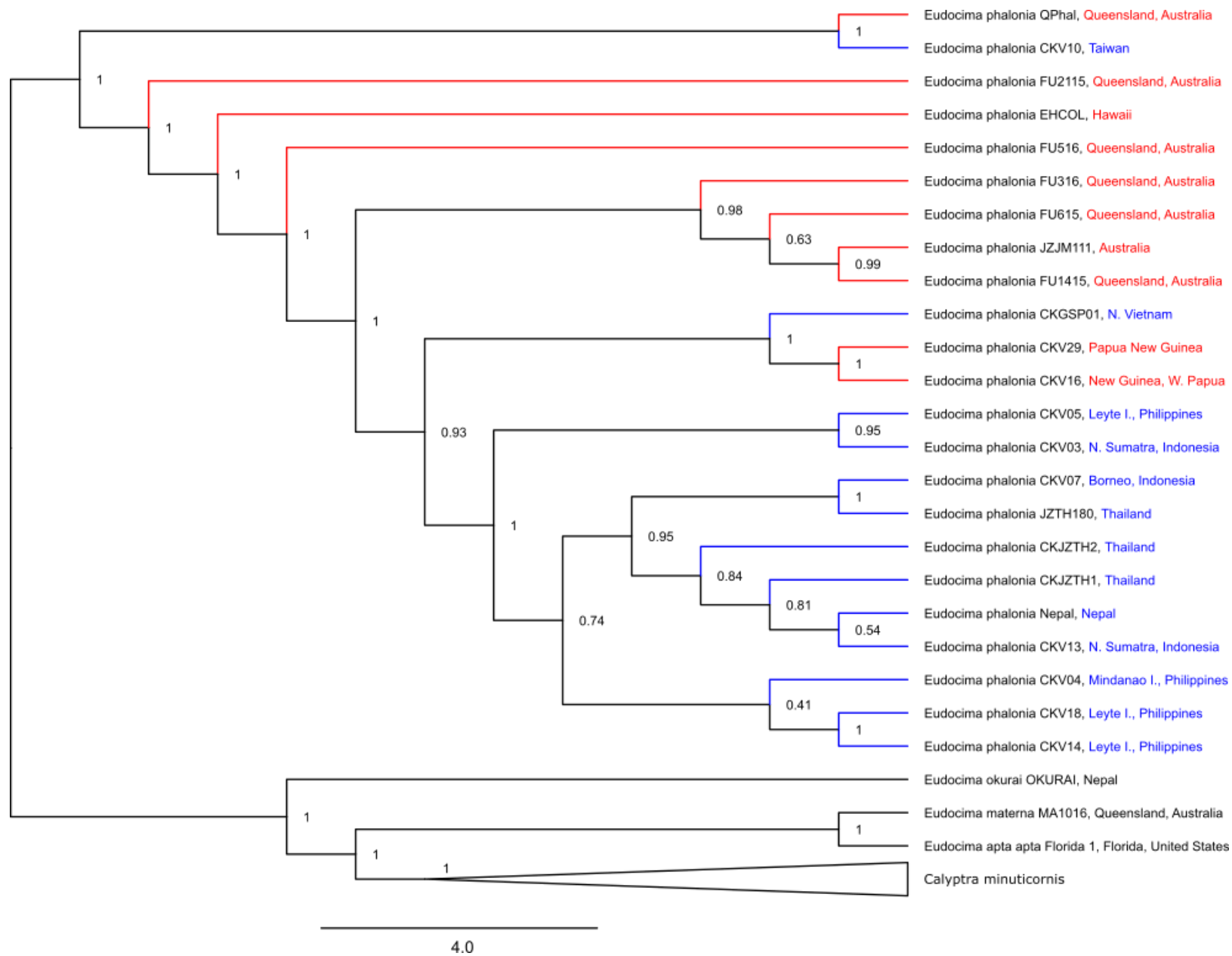
Figure 100. ASTRAL tree with bootstrap units. The topology was rooted along the branch at the base of the *E. okurai* ((*E. apta* + *E. materna*) (*Calyptra minuticornis*)) clade. Specimens of *Calyptra minuticornis* are collapsed within their monophyletic clade. /Blue indicates Oriental region, red indicates Australian region.
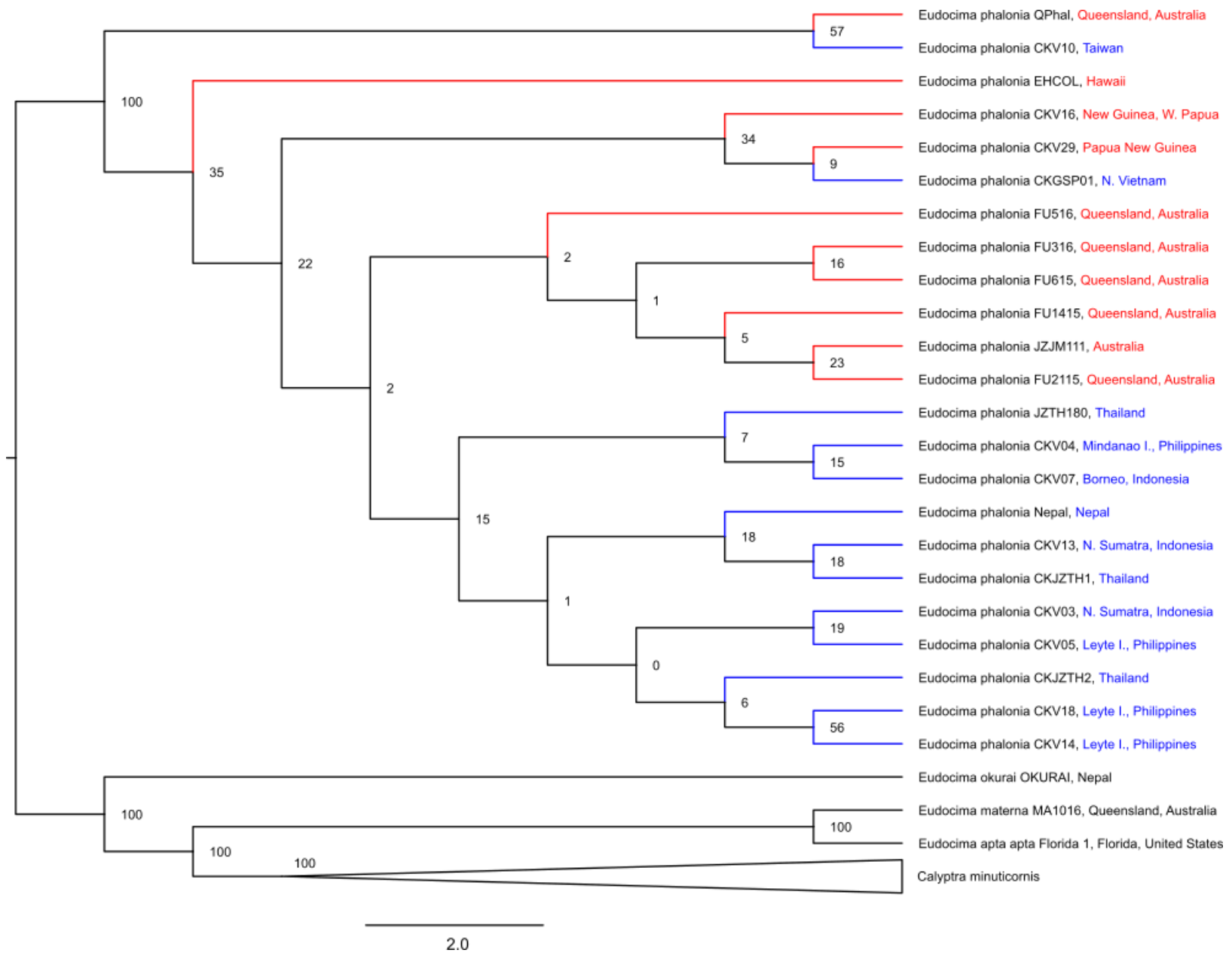
4.4.2 Biogeography

The correlated evolutionary clock model was adopted for time-calibration of the ML tree (Table 9). The DIVALIKE+J dispersal model was adopted based on LRT and AIC, and the DEC+J model was also highly favored (Table 10, 11). Results are reported for both normal AIC (Table 10) and corrected AIC (AICc, Table 11), along with parameters used.

At the deepest node of the ancestral area reconstruction in BioGeoBEARS (Fig. 101), the probability of ancestral occurrence in both areas is proportionally greatest, followed by the Australian region. The recovery of the *E. phalonia* specimen from Hawaii at the base of the tree, which is coded as Australian, likely influenced this outcome. At the node ancestral to the remainder of the *E. phalonia* specimens, greatest probability is given to an ancestral origin in the Oriental region (Fig. 101). An Oriental origin is also calculated as most probable for all internal nodes of the *E. phalonia* group, with the exception of two clades: the clade from CKV29 (Papua New Guinea) to FU615 (Australia), and the clade FU316 (Australia) + FU1415 (Australia). For both of these clades, all nodes were reconstructed as having an ancestral range in Australia, since all of the samples in these clades were coded as Australian (i.e., with localities in Australia and Papua New Guinea). Two dispersal events therefore occurred from the Oriental region into the Australian region after divergence from the Hawaiian population, although gene transfer between populations continues to take place (Fig. 101). Evidence of continued gene flow comes from the recovery of QPhal (Australia) within the clade from CKV10 (Taiwan) to CKV14 (Leyte I., Philippines), a clade reconstructed from the Oriental region (Fig. 101).

Table 9. Evolutionary clock model negative log-likelihood values based on maximum likelihood topology.

Evolutionary clock model	LnL
Discrete	-7.45
Correlated	-1.56
Relaxed	-18.04

Table 10. AIC results from BioGeoBEARS analysis, including negative log-liklihood scores (LnL), number of parameters (numparams), parameter values (d, e, and j), AIC score (AIC), and weighted AIC score (AIC_wt).

Model	LnL	numparams	d	e	j	AIC	AIC_wt
DEC	-19.61	2	0.023	1.00E-12	0	43.22	0.0011
DEC+J	-12.65	3	1.00E-12	1.00E-12	0.15	31.3	0.43
DIVALIKE	-20.32	2	0.046	1.40E-09	0	44.64	0.0005
DIVALIKE+J	-12.37	3	1.00E-12	1.00E-12	0.15	30.74	0.57

Table 11. AIC results from BioGeoBEARS analysis, corrected for small sample size. Includes negative log-liklihood scores (LnL), number of parameters (numparams), parameter values (d, e, and j), corrected AIC score (AICc), and weighted corrected AIC score (AICc_wt).

Model	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-19.61	2	0.023	1.00E-12	0	43.22	43.82
DEC+J	-12.65	3	1.00E-12	1.00E-12	0.15	31.3	32.56
DIVALIKE	-20.32	2	0.046	1.40E-09	0	44.64	45.24
DIVALIKE+J	-12.37	3	1.00E-12	1.00E-12	0.15	30.74	32.01
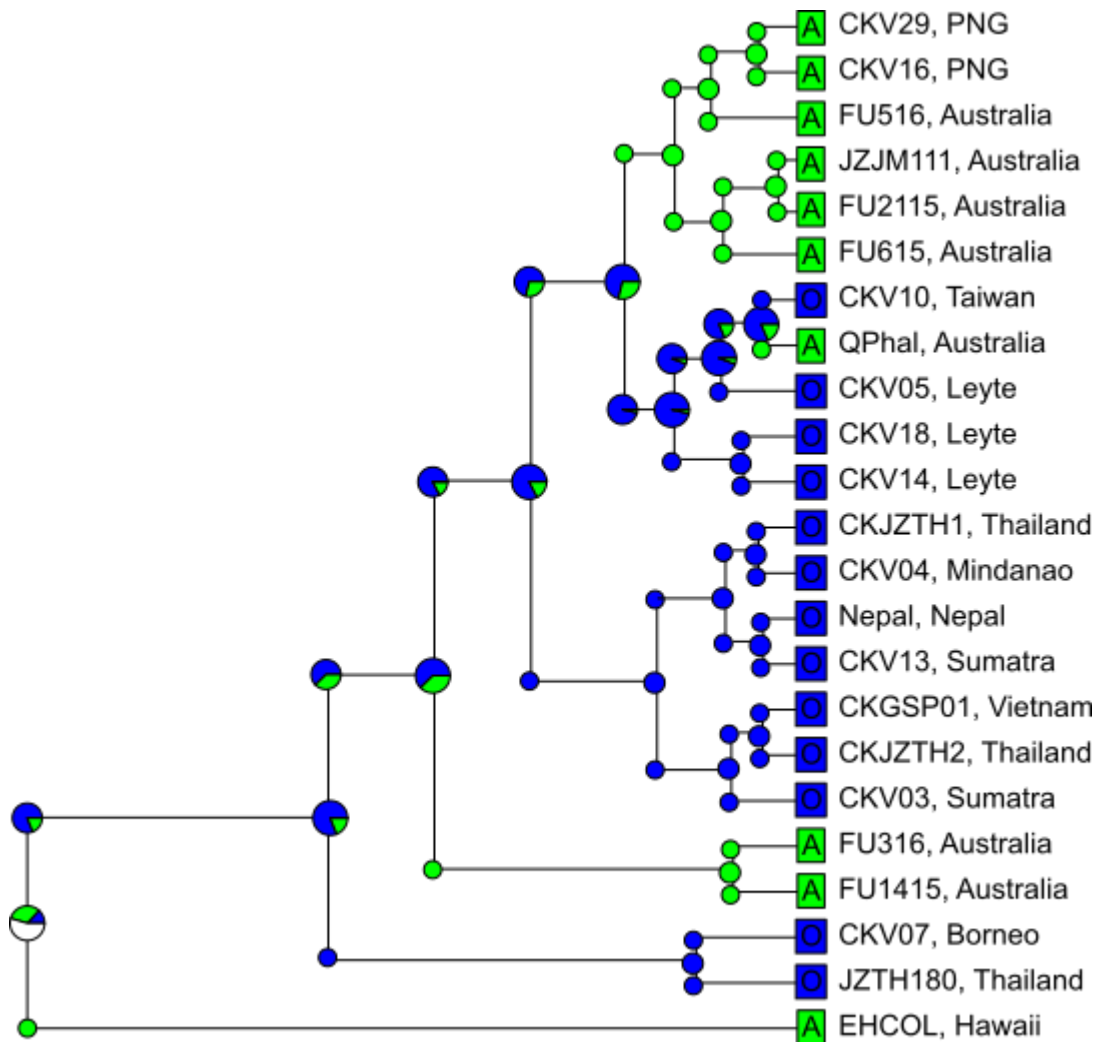
Figure 101. ML topology with results from BioGeoBEARS analysis for ingroup taxa (*E. phalonia*) only. Oriental region (O) is indicated in blue, and Australian region (A) is indicated in green. Pie charts at each node give probability of ancestral occurrence in either of these regions, or in both (white). Terminals are labeled by sample ID and simplified location. PNG = Papua New Guinea.

4.4.3 Probability of presence for *E. phalonia*

4.4.3.1 Model performance

Two MaxEnt models with 2 levels of spatial filtering applied to the occurrence dataset and 18 bioclimatic variables were evaluated for predicting the potential distribution of *E. phalonia*. Both models performed better than random, with AUC values of 0.947 (10 km thinning radius) and 0.953 (16 km thinning radius). Both models also had low omission rates at both the minimum training presence threshold (0 for both models), and the 10th percentile training presence threshold (0.099 and 0.098, respectively). The best model had input occurrence data thinned within a 16 km radius, with a higher AUC score of 0.953 and a lower omission rate of 0.098.

4.4.3.2 Potential distribution of *E. phalonia*

The predicted distribution of the best MaxEnt model (Fig. 102) conforms well with the occurrence records in the established range of *E. phalonia* (Fig. 103). The highest suitability for *E. phalonia* occurrence was predicted in the world's tropics, extending northward to the Himalayan Mountains in the Old World and to the southern points of Florida and Texas in the New World (Figs. 102, 103). This prediction was validated in the Old World by the occurrence dataset (Fig. 103). Despite good overall performance, there appeared to be some overprediction of suitable range by the model. Much of continental Europe was predicted to have low environmental suitability for *E. phalonia*, with areas of moderate suitability in Portugal (Figs. 102, 103). Low-to-medium suitability was also predicted for Iceland, with areas of high suitability near the southeastern coast (Figs. 102, 103). However, as anticipated, the MaxEnt model projected northern Africa and much of the Arabian Penninsula as unsuitable or with areas of low suitability (Figs. 102, 103). In the New World where *E. phalonia* does not yet occur, areas projected to be at highest risk for establishment by *E. phalonia* have their northernmost extent in the Bahamas, Florida Keys, the southern tip of the Florida Penninsula, and the southern tip of Texas; to the south, areas of maximum suitability extend to northern Argentina (Fig. 104). *Eudocima phalonia* occurs already in Hawaii and in French Polynesia, and may be introduced from these locations (Fig. 104).

In the United States, areas of low suitability were predicted for southern Alaska, and low-to-medium suitability was predicted for the Pacific Northwest (Figs. 105A, 105B). Along the

eastern edge of the Central Valley in California low suitability was also predicted, with small pockets of medium-to-high suitability; areas of low suitability also were predicted along the Appalachian Valley (Fig. 105A). All of these areas seem unlikely and may be overpredictions. Nearly all of Hawaii, where *E. phalonia* is already present, is predicted to have high suitability, with areas of medium suitability on Big Island (Fig. 105C). In the continental United States, areas of greatest suitability occurring along the Gulf Coast, from southern Texas to the tip of Florida (Fig. 105A), have the greatest likelihood to support *E. phalonia* establishment.
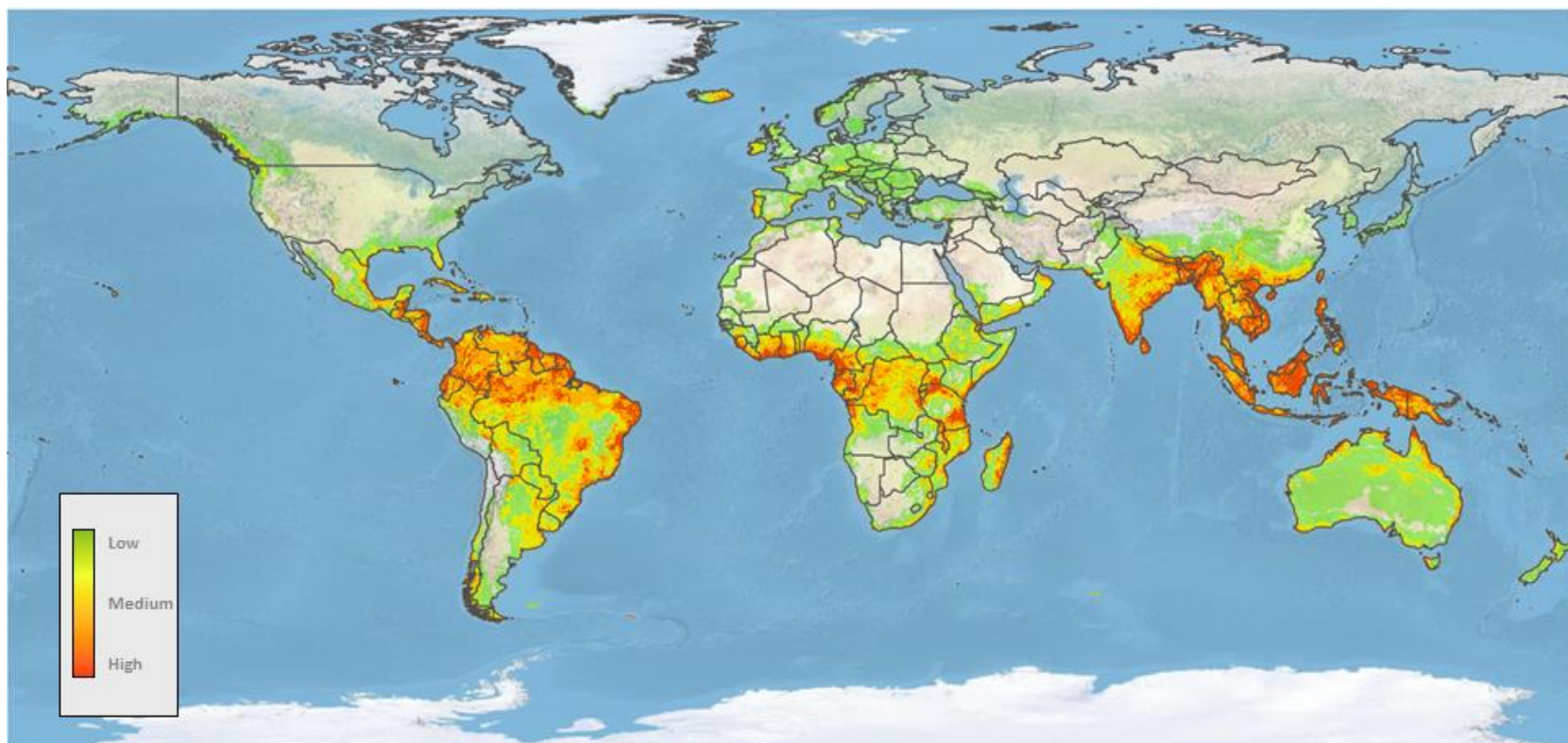
Figure 102. Global risk of establishment of *E. phalonia* using best MaxEnt model, mapped in ArcGIS Pro. Risk level indicated by legend; uncolored areas are climatically unsuitable.
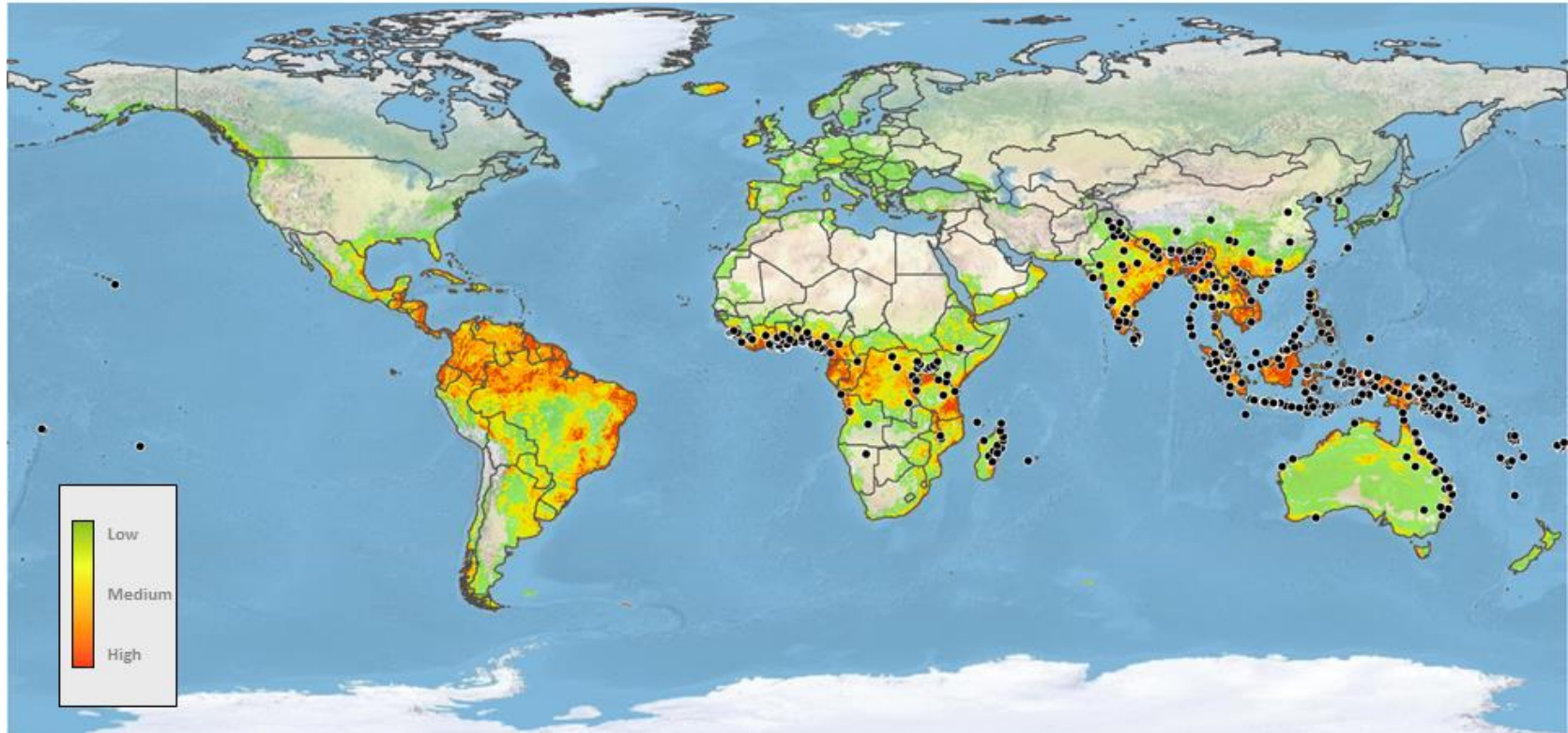
Figure 103. Global risk of establishment of *E. phalonia* using best MaxEnt model, mapped in ArcGIS Pro. Specimen occurrence data used for MaxEnt analysis overlaid on predictive map. Risk level indicated by legend; uncolored areas are climatically unsuitable.
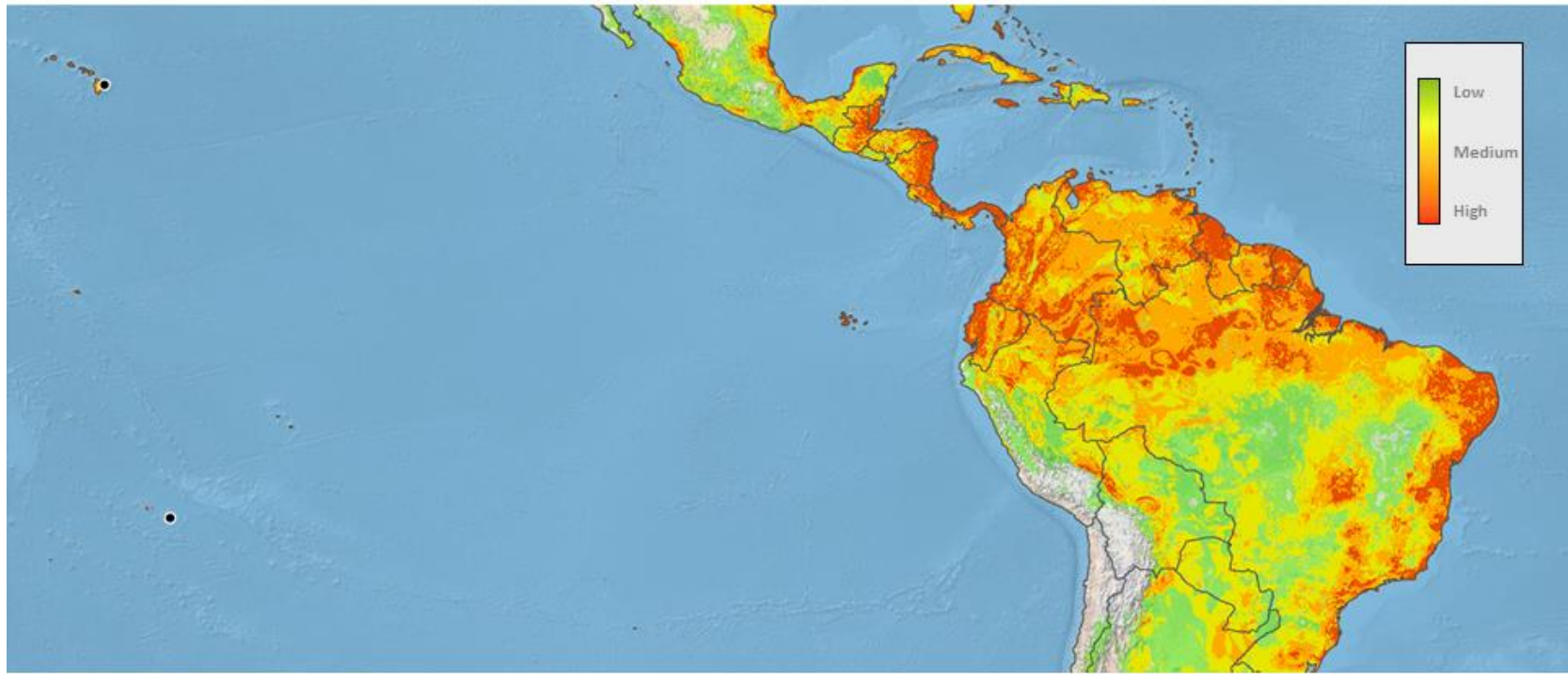
Figure 104. Areas of highest risk of establishment in the New World by *E. phalonia* using best MaxEnt model, mapped in ArcGIS Pro. Points in Hawaii and French Polynesia indicate current presence of *E. phalonia*. Risk level indicated by legend; uncolored areas are climatically unsuitable.

Figure 105. Risk of establishment of *E. phalonia* in the United States using best MaxEnt model, mapped in ArcGIS Pro: **A)** continental United States; **B)** Alaska; and **C)** Hawaii. Same projection extent used for depicting Alaska and the continental United States (Figs. 105A and 105B), while Hawaii is enlarged (Fig. 105C). Point in Hawaii indicates current presence of *E. phalonia*. Risk level indicated by legend in Fig. 105A; uncolored areas are climatically unsuitable.
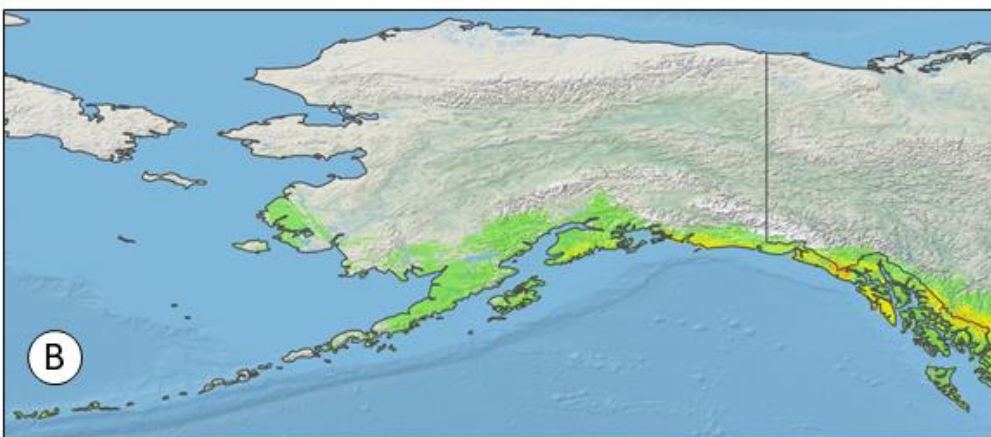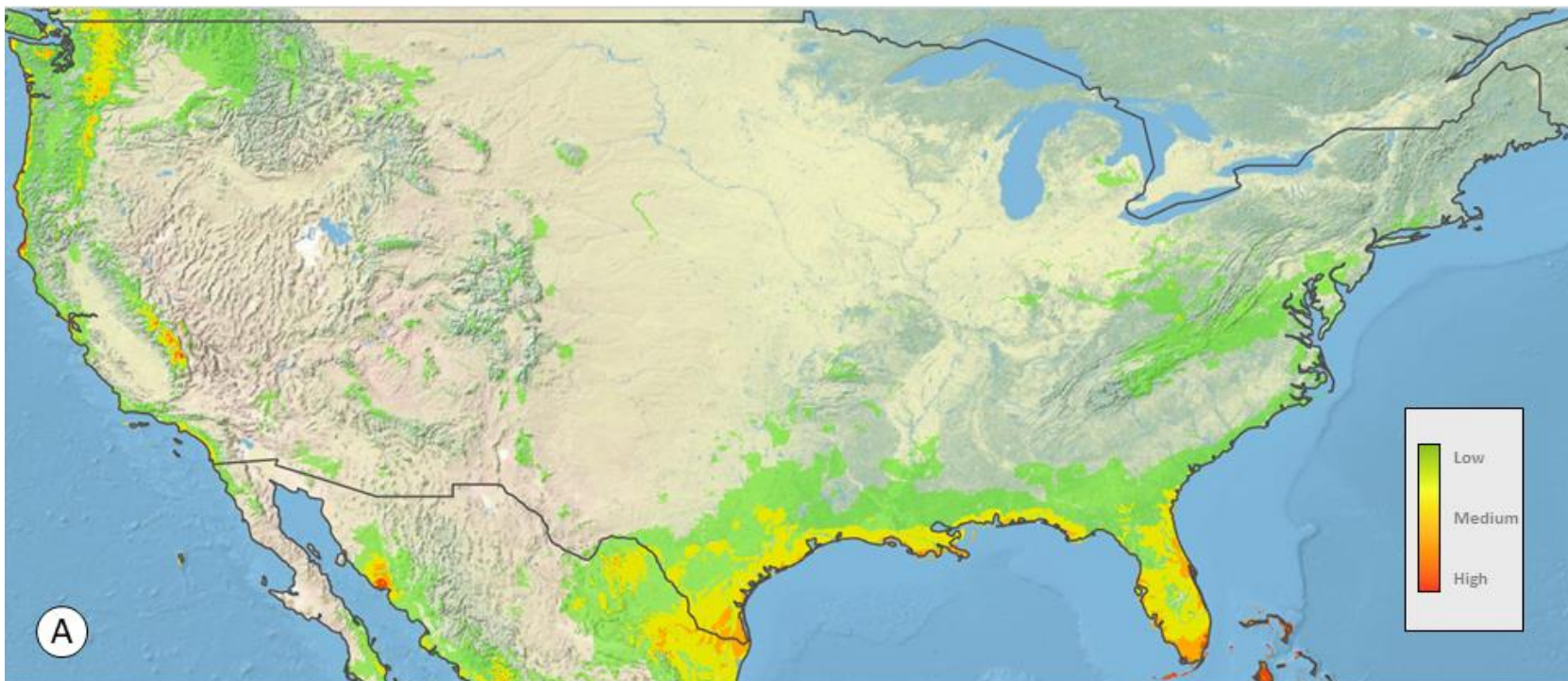
4.4.3.3   Effects of environmental factors

Mean diurnal range in temperature and isothermality were the top environmental factors influencing the distribution of *E. phalonia*, with contributions to the model of 44.9% and 23.1% respectively (Fig. 106). Mean diurnal range is calculated as the average of the changes in monthly temperature (difference between the maximum and minimum temperatures per month); isothermality is calculated as the mean diurnal range in temperature divided by the annual temperature range (the difference between the maximum temperature of the hottest month and the lowest temperature of the coldest month) (www.worldclim.org/bioclim). The importance of these variables to the predictive model was confirmed by the jackknife variable tests (Fig. 106). The probability of *E. phalonia* presence was highest at mean diurnal temperature ranges of approximately 75°C and lower, experiencing a rapid decrease at temperature ranges higher than 75°C (Fig. 107A). For isothermality, the other important environmental factor in the model, the probability of presence increased exponentially between approximately 20°C and 50°C, and plateaued at approximately 80°C (Fig. 107B).

Figure 106. Plot of jackknife variable tests showing relative importance of bioclimatic variables. Environmental variables are listed on the y-axis. Regularized training gain values of the model without the given variable, with only the given variable, and with all variables are shown (see legend).

Regularized Training Gain

Without variable
With only variable
With all variables

337
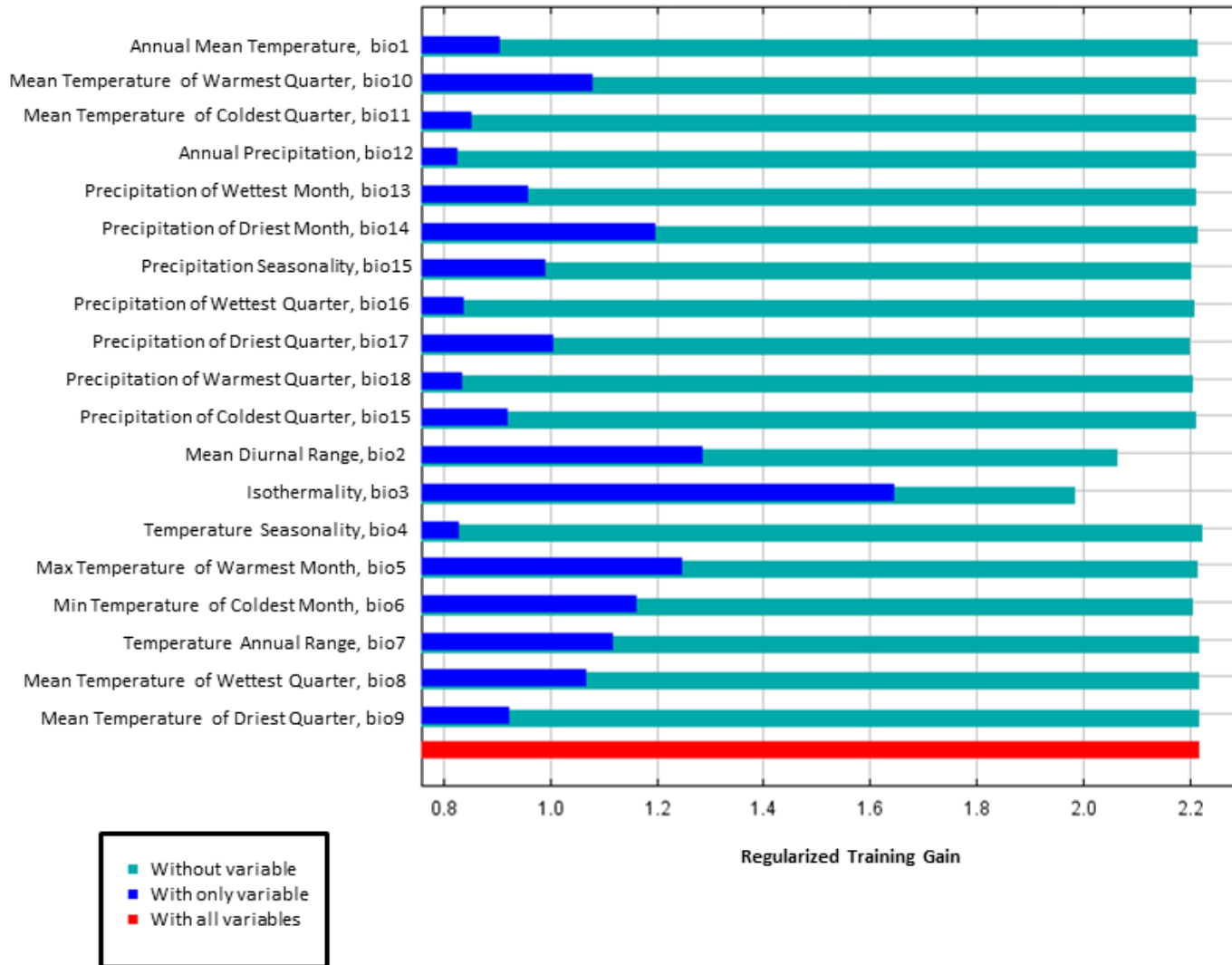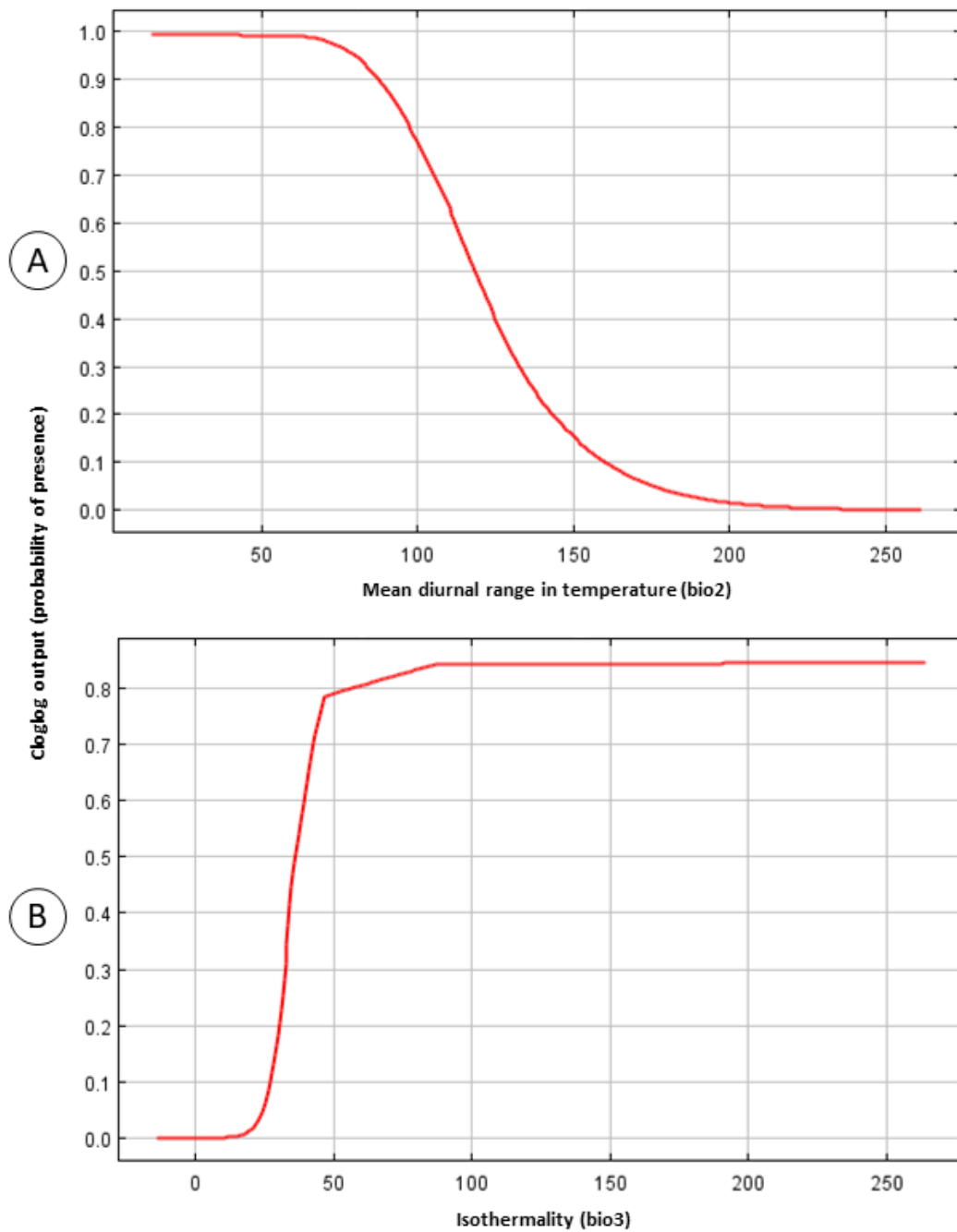
Figure 107. Response curves of the best predictors of *E. phalonia* in the best MaxEnt model: **A)** mean diurnal range in temperature (bio2, °C); **B)** isothermality (bio3, °C).

4.5   Discussion

4.5.1   Molecular phylogeny and species boundaries

Molecular sampling across the Oriental and Australian regions indicates that *E. phalonia* is a monophyletic taxon. The recovered molecular phylogeny of *E. phalonia* suggests continued gene flow between populations in the Oriental and Australian regions, ruling out total allopatric speciation. The exception is the Hawaiian *E. phalonia* specimen, which is recovered as sister to the remaining *E. phalonia* in the concatenated analysis and which received the highest PTP support as an OTU. This result would suggest a higher degree of genetic isolation between the Hawaiian population and populations in the Oriental and Australian regions (i.e., in the Indo-Australian Archipelago, from which the rest of the *E. phalonia* samples were collected). Stronger support for Hawaiian *E. phalonia* populations comprising a novel species would be gained by a more thorough molecular sampling of *E. phalonia* populations across the Pacific range in order to more precisely determine the degree of genetic isolation. Because African *E. phalonia* samples were unable to be sequenced, the relationship of sampled *E. phalonia* to populations in Africa remains unknown.

4.5.2   *Eudocima phalonia* biogeography and speciation mode

The two most highly-supported biogeographic models for *E. phalonia*, DIVALIKE+J and DEC+J, both included the free "jump" parameter. This aligns with accounts in the literature of long-distance migration events by *E. phalonia* (e.g., Sands & Schotz 1991), which is a plausible mechanism for range expansion and colonization of islands across the Pacific (see Zilli et al. 2017). Explanation of the "j" parameter by Matzke (2013b) rationalizes its use for modeling patterns of island dispersal (a pattern which occurs in *E. phalonia*) and differentiation into new lineages. The preference of models including the "jump" parameter suggests differentiation via long-range dispersal events as a possible evolutionary process for speciation in *E. phalonia*. The additional possibility of sympatric speciation due to larval hostplant switching (either within menisperms or between menisperm vines and *Erythrina*) also merits further investigation (see Bänziger 1982, Sands & Chan 1996, Reddy et al. 2005).

Assignment of the Pacific Islands to a biogeographic region has proved problematic for many authors (see Morrone 2015). One reason for this difficulty is that prolonged isolation causes many Pacific Island groups to act as independent evolutionary centers (Müller 1986, Triantis et al. 2016). Although islands in the Pacific are assigned by Morrone's (2015) biogeographic regionalization to the Oriental region to emphasize their affinities with the tropics, Zilli et al. (2017) considers the Pacific Islands as part of the Australian region. In conformity with Zilli et al. (2017), our molecular sample from Hawaii (EHCOL) was assigned to the Australian region. This choice proved highly influential during biogeographic reconstruction of ancestral areas. Although the ancestral distribution for the main part of *E. phalonia* (represented by the node of all included *E. phalonia* specimens except for EHCOL) was recovered as Oriental, inclusion of the Hawaiian specimen resulted in an area reconstruction which involved an origin in both the Oriental and Australian regions (Fig. 101). This would denote an ancestral range of *E. phalonia* including area in both of these regions, possibly in the Indo-Australian Archipelago at their intersection at Wallace's Line. It is also possible for the ancestral range of *E. phalonia* to involve both the Oriental region and the Pacific, a scenario which would contradict hypotheses involving a more recent arrival of *E. phalonia* in the Pacific (i.e., Waterhouse 1997). Additional molecular sampling of Pacific *E. phalonia* populations is needed. Coding of the Hawaiian specimen as belonging to the Oriental region (i.e., according to the biogeographical regionalization proposed by Morrone (2015)) would definitively confirm the hypothesis of Waterhouse and Norris (1982) of an Oriental origin for *E. phalonia*. In any of these scenarios, the antiquity of presence of *E. phalonia* in the Pacific postulated by Zilli et al. (2017) receives further support from this study by the recovery of the Hawaiian *E. phalonia* specimen as basal to the rest of *E. phalonia*, signaling at least one early Pacific dispersal event. The situation suggested by Zilli et al. (2017) of multiple waves of colonization appears likely, not least because two dispersal events are inferred by this analysis from the Oriental region to the Australian region (i.e., to Australia and Papua New Guinea). Unsuccessful sequencing of African molecular samples prohibits inferences about dispersal to this region, and investigation into the genetic relationships between African *E. phalonia* and other populations would be a good subject of future study.

4.5.3 Global projections of *E. phalonia* distribution and importance of environmental variables

The current distribution of *E. phalonia*, as represented by specimen occurrence data, correlates well in the Old World with the distribution predicted by the MaxEnt model (Fig. 103), which improves validation for range predictions in areas where *E. phalonia* does not currently occur. In the New World, *E. phalonia* is not present but is predicted in 18 continental countries (including the United States) and 26 Caribbean island countries (Table 12). Introduction to these areas may occur from *E. phalonia* populations in tropical Africa or at the eastern edge of the current range extent; the easternmost records of this species across the Pacific are from Hawaii (Heu 1986), Kiribati (Davis et al. 2005), Society Islands (Viette 1949) and Rapa I. (Zilli et al. 2017). Introduction of *E. phalonia* to uncolonized areas may also occur via trade with countries where this species is already established (e.g., Kumar et al. 2015). The superior performance of the MaxEnt model with occurrence data thinned within 16 km confirms that *E. phalonia* is a mobile species, with the potential to reach areas which are farther apart than the 10 km thinning distance used in other environmental modelling studies (e.g., Boria et al. 2014, Kumar et al. 2015). The greatest importance to the MaxEnt model of mean diurnal temperature range and isothermality when determining the range of *E. phalonia* is also intriguing, since *E. phalonia* activity is reported to fluctuate in response to the rainy and dry seasons in different range areas (Bänziger 1982; Bhumannavar & Viraktamath 2012; Sands & Schotz 1989; Fay & Halfpapp 1993a, 1999a; Baptist 1944; Kumar & Lal 1983; Hargreaves 1936; Leong & Kueh 2011). Availability of larval hostplants, another important factor (e.g., Bänziger 1982, Leong & Kueh 2011), was not taken into account during model construction, and represents an environmental variable which is likely to be a strong predictor of *E. phalonia* presence. Possible multicollinearity between the included bioclimatic variables (Dormann et al. 2013) was also not explored. Despite these drawbacks, the resulting distribution from this predictive model broadly corresponded to observations in major areas of the world, and is a useful starting point. Although caution should be employed when using these results as a predictive tool due to the limitations inherent to correlative environmental modelling (see Kumar et al. 2015), the maps generated by this study can be used to help identify at-risk areas for *E. phalonia* introduction and establishment.

Table 12. Alphabetized list of New World countries with high probability of presence for *E. phalonia* based on best MaxEnt model.

List of predicted New World countries and islands
Anguilla
Antigua and Barbuda
Argentina
Aruba
Bahamas
Barbados
Belize
Bolivia
Brazil
British Virgin Islands
Cayman Islands
Colombia
Costa Rica
Cuba
Dominica
Dominican Republic
Ecuador
El Salvador
French Guiana
Grenada
Guadeloupe
Guatemala
Guyana
Haiti
Honduras
Jamaica
Martinique
Montserrat
Netherlands Antilles
Nicaragua
Panama
Paraguay
Peru
Puerto Rico
Saint Barthelemy
Saint Kitts & Nevis
Saint Lucia
Saint Martin
Saint Vincent
Trinidad & Tobago
Turks & Caicos Islands
United States
US Virgin Islands
Venezuela

4.5.4   Environmental suitability in the United States

In contrast with the mini risk assessment conducted by Davis et al. (2005), results from the best MaxEnt model indicate that environmental conditions in the continental United States are generally unsuitable or have low suitability for *E. phalonia*. Similarly to the MaxEnt model, the assessment by Davis et al. (2005) assigns higher probability of occurrence to regions in the Pacific Northwest, the Appalachian Valley, and to the southern points of Florida and Texas. However, in these areas of agreement, the size of the area projected by the MaxEnt model exceeded that of the prediction by Davis et al. (2005). The projected distribution by Davis et al. (2005) also includes a large area covering much of the eastern United States. This area extends south to coastal Lousiana and follows the Appalachian Valley north to Maine, stretching westward across the northern border of the United States to Minnesota, and to Missouri and Arkansas (Davis et al. 2005). In the distribution model projected by MaxEnt, this area is largely unsuitable with only small pockets of low suitability (Fig. 104A).

An interesting difference between the projected distributions by Davis et al. (2005) and the MaxEnt model lies in the suitability predicted along coastlines. In the worldwide projection by the MaxEnt model, coastal regions represent areas of increased suitability for *E. phalonia* across the predicted range (Figs. 102, 103). This trend holds when examining the distribution model projected for the United States, which assigns medium suitability to the Gulf Coast from southern Texas throughout most of the state of Florida, and a thin region of low suitability along the southern part of the East Coast to the Appalachian Valley (Fig. 104A). In contrast, the predicted distribution of Davis et al. (2005) does not include any suitable areas along coasts, avoiding the Gulf Coast (except for small areas in southern Texas) and the southern part of the East Coast (Davis et al. 2005). The prediction also entirely omits the Florida Penninsula, aside from very small areas near the tip (Davis et al. 2005). The absence of coasts from the predicted distribution by Davis et al. (2005) might be explained by the comparison of biomes in their analysis, which might emphasize environmental conditions present toward the interior of countries where *E. phalonia* is recorded. The increased suitability of coastlines predicted by the MaxEnt model may also be an effect of sampling bias, as coasts might be more accessible to collecting expeditions.

Despite predictions of low suitability or unsuitable conditions for *E. phalonia* in most of the continental United States by the MaxEnt model, the presence of two other *Eudocima* species, *E. apta* and *E. serpentifera*, has occasionally been recorded. *Eudocima serpentifera* (a Neotropical species) has been observed and an individual collected near Alamosa in Colorado (Pague & Brou 2013), an area predicted by the MaxEnt model to be unsuitable for *E. phalonia*. Spurious *E. apta* specimens have also been collected in North America as far north as Ontario, Canada, but no established populations of *Eudocima* have yet been recorded in Canada or the United States (Brou & Águila 2013, Gilligan & Passoa 2016, Reeves et al. 2017). Most of the United States and northern Mexico is predicted to be climatically unsuitable for *E. phalonia* (Fig. 104A). However, areas of medium suitability occur along the Gulf Coast, with the southernmost tips of Texas, Lousiana, and Florida having the greatest suitability at medium-to-high (Fig. 104A). This is consistent with the observations and collection of *E. apta* specimens in the Everglades National Park, near Miami, and in the Florida Keys (Reeves et al. 2017), as well as collection of *E. serpentifera* near Abita Springs in Lousiana (Brou 2006). These occurrences of *Eudocima* species in the continental United States indicate that the future presence of *E. phalonia* is not impossible, and areas along the Gulf Coast represent the highest risk of *E. phalonia* establishment.

4.6   Conclusions

The monophyly of *E. phalonia* is supported by this study, despite local patterns and variation in morphology. Although morphological diversity and taxonomic richness are often correlated because morphology is used to describe new species, wide morphological variation may also be present when considering a species distributed over a large area, particularly a lineage undergoing intense diversification before peak taxonomic diversity is reached (see Triantis et al. 2016). This scenario of morphological diversity decoupled from taxonomic diversity appears to describe the situation in *E. phalonia*, at least for populations occurring in the Oriental and Australian reigons. Although morphological differences may be accumulating in different populations, current molecular analyses indicate that speciation in *E. phalonia* in these regions remains incomplete. The intriguing recovery of the Hawaiian *E. phalonia* specimen as a separate taxonomic unit underlines the necessity of further sampling of Pacific populations, since island groups and archipelagos may serve as isolated evolutionary centers (e.g., Müller 1986, Triantis et

al. 2016). Despite reconstruction of an ancestral area of origin for *E. phalonia* in both the Oriental and Australian regions resulting from the basal recovery of the *E. phalonia* specimen from Hawaii, we feel that evidence remains wanting from *E. phalonia* populations in the Australian region to support this result, particularly with respect to the Pacific Islands. We therefore tentatively postulate an Oriental origin for *E. phalonia* in agreement with Waterhouse and Norris (1987) based on the reconstruction for the remainder of the included specimens, until further molecular evidence (especially from Africa and from the Pacific) can be taken into account.

Range projections for Old World *E. phalonia* based on environmental modelling generally concurred well with expectations based on current distribution information, and new areas of high environmental suitability were projected in 44 countries in the New World. This information can inform policies and preventative measures in these areas where *E. phalonia* is not yet known to occur. Assessment of environmental suitability for *E. phalonia* establishment in the continental United States reveals most areas to be unsuitable or with low suitability, with the greatest potential suitability occurring in Florida and along the Gulf Coast.

CONCLUSION

Two adverse effects of agricultural intensification include landscape simplification and the increasing prevalence of monoculture. In agricultural systems, the designation of pest species is anthropocentric, and is based on both plant and insect characteristics. One helpful means of examining insect behaviors to inform pest status is the use of pest injury guilds, which distinguish different pest groups based on similar injuring behaviors to comparable plant parts. Lepidoptera represents the largest clade of herbivorous insects, with many agriculturally significant species. Pest injury guilds are examined within this order and examples of Lepidoptera pests within each injury guild are reviewed, with reference to specialized behaviors present within certain guilds. In particular, the fruit-piercing habit, which is a specialized behavior within fruit-feeding Lepidoptera pests, is discussed and contextualized within pest Lepidoptera. Fruit-piercing moths are highly unusual within agriculturally significant Lepidoptera because they are economically relevant as adults rather than as larvae. In consequence, control options for fruit-piercing moths are very different from the preponderance of Lepidoptera pests. The fruit-piercing habit has also influenced systematic placement for moths with this behavior, and until recently all primary fruit-piercers were classified together in the same subfamily until the availability of molecular evidence.

Despite the economic importance of Lepidoptera species, distribution information for many species is lacking. To address this need within North America, we provide the first checklist of pest Lepidoptera of human food crops for the United States and Canada, including eighty agriculturally significant Lepidoptera species and complexes. For each species or complex, information is provided on distribution, geographic origin, establishment in North America, generations per year, larval hostplants, species delimitation, and established economic injury levels. Sixteen Lepidoptera families are represented in the checklist, with the two most prominent families being Noctuidae (35 species/complexes) and Tortricidae (16 species).

Fruit-piercing moths in the genus *Eudocima* Billberg, 1820 have significant pest status as adults rather than as larvae, and directly injure fruits using a specially-adapted proboscis. There are at least 48 *Eudocima* species which are found in the world's tropics, but confusion persists in the

classification of this genus and there are several suspected complexes. Additionally, the area of origin for this group is uncertain, although the Oriental region has been postulated. A comprehensive phylogenetic analysis using 82 morphological characters suggests that *Eudocima* is not monophyletic. Although strongly-resolved relationships were recovered, no recovered clades corresponded with previous generic concepts. The Australian region is recovered as the most parsimonious area of origin for *Eudocima*, and patterns of dispersal, particularly between the Oriental and Australian regions along the Indo-Australian Archipelago, are discussed.

Within *Eudocima*, *E. phalonia* is distributed throughout the Old World and has been the subject of increasing interest and research due to its economic impact in the tropics and status as a potential invasive species. This species, together with its recently described sister species *E. oliveri*, *E. lequeuxi*, and *E. steppingstonia*, constitutes the *E. phalonia*-complex. In addition to these closely-related species, which were delineated using morphology, documented morphological variation within *E. phalonia* itself suggests possible speciation occurring across its wide geographic range. The molecular phylogeny constructed using anchored hybrid enrichment and a next-generation sequencing approach suggests that *E. phalonia* is monophyletic, with gene flow still occurring between populations. The area of origin for *E. phalonia* is postulated to be the Oriental region, although further investigation is needed, especially in Hawaii and the Pacific. Range predictions for *E. phalonia* from environmental niche modelling were performed for both the Old World, which concurred well with occurrence data, and for the New World. Forty-four New World countries including the United States were predicted by the model to have environmental conditions suitable for *E. phalonia* establishment. Within the continental United States, assessment of environmental suitability for *E. phalonia* suggests areas in Florida and along the Gulf Coast are most favorable for establishment.

APPENDIX A. MORPHOLOGICAL AND BIOGEOGRAPHICAL DATA MATRIX (CHAPTER 3)

Replicates of taxa are listed with the specimen locality following the species name. Characters progress in order under each taxon from left to right. Phylogenetic analysis was performed excluding characters for biogeographic data (in red). Coding for biogeographic regions is appended to morphological matrix, and coding for island groups is given in parentheses.

E. phalonia Malaysia 1

????????00??10100001070200??0000100010100?00?0000120000000??02010000?00?0000010002010111
(11111111111)

E. phalonia Ghana

????????00??10000001000200??0000100010100?00?0000121000000??02010000?0000000000002010111
(11111111111)

E. phalonia Malaysia 2

????????00??10?00001070200??0000100010100?00?0000121000000??020?0?????????????????010111
(11111111111)

E. phalonia Australasia

????????00?010?00001070200??0000100010100?00?0000120000000??020?0?????????????????010111
(11111111111)

E. phalonia Australia

0000110000101000001070200??0000100010100?00?0000121000000??02010100?0000000010000010111
(11111111111)

E. tyrannus China

????????00??20?10000?40320??0300111000001000?000221214001?0?111????????????????????010010
(???????????)

E. tyrannus China + Nepal

0000110000202001000?40320??0300111000001100?000221314001?0?11111310?0001010111001010010
(???????????)

E. sikhimensis

????????00??10010000?40120??0400101001001000?010001302012??00010???0?000001030000?000010

(11010000000)

E. apta

????????00??11100001121??14001001021310200110003111211002??00300???14000000011100?101000

(??????????)

E. bathyglypta

????????00??200?0001280220??0201100000001000?000211202101?0?0?10???0?00?0200200002000010

(11000000000)

E. okurai

????????00??00?10001440420??0001111000001000?000221213002??1001??????????????????010010

(??????????)

E. cocalus Mareeba

00001100001010100001440320??0300110021100010?0015021000001??3200???110000010??0000000011

(11111111000)

E. cocalus Papua

????????00??10?00001440320??0300112021100010?0015021000001??310??????????????????000011

(11111111000)

E. srivijayana Malaysia

????????00??101000015504011?0010110021110010?002411104001?1?011??????????????????000011

(11111000000)

E. srivijayana Indonesia

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E. srivijayana Philippines + Celebes + Timor

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E. salaminia

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E. nigricilia

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E. materna Nyassaland

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E. materna Cameroon

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E. aurantia

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E. jordani

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E. homaena Taiwan

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E. homaena Philippines + Indonesia

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E. dividens

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E. kuehni

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E. iridescens

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E. talboti **New Guinea**

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E. talboti **Indonesia**

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E. mionopastea

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E. paulii

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***E. cajeta* Ceylon**

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E. euryzona

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E. behouneki

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E. lequeuxi

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E. martini

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E. kinabaluensis

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E. splendida

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Plusiodonta incitans

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Phyllodes verhuelli

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Phyllodes consobrina

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Gonodonta indentata

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Oraesia argyrosigna

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Oraesia triboliqua

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