

A Newly Established Non-Native Praying Mantis Species, *Liturgusa maya* (Mantodea: Liturgusidae) in Florida, USA, and a Key to Florida Mantis Genera

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A newly established non-native praying mantis species, *Liturgusa maya* (Mantodea: Liturgusidae) in Florida, USA, and a key to Florida mantis genera

Andrew J. Nisip¹, Gavin J. Svenson², Brian Fridie, Jr.³, and Andrea Lucky^{1,*}

Abstract

Exotic insect species pose an increasing threat to Florida's native ecosystems through direct negative effects as predators of native taxa, and indirect effects by competing for food and habitat resources. Although many exotic species established in Florida have no demonstrable negative impact on native insect communities, it is nonetheless important to document the presence of newly established species in order to evaluate their invasive potential. This study documents for the first time an established population of an introduced mantis, *Liturgusa maya* Saussure & Zehntner (Mantodea: Liturgusidae), in the USA. The paper includes a review of the species' natural history in its native range in Central and South America. At present, this mantis is known only from a small, localized area; however, more widespread establishment in and beyond south Florida is possible because of the region's subtropical climate. To facilitate monitoring of the introduced population of *L. maya*, an identification key to the genera of Florida mantises is included to help non-specialists easily differentiate *L. maya* from the native mantis genera that occur in Florida.

Key Words: exotic species; identification guide; introduced species; invasion biology

Resumen

Las especies de insectos exóticos representan una amenaza creciente para los ecosistemas nativos de la Florida a través de efectos negativos directos como depredadores de taxones nativos y efectos indirectos al competir por los recursos de alimentos y hábitat. Aunque muchas especies exóticas establecidas en Florida no tienen un impacto negativo demostrable en las comunidades de insectos nativos, sin embargo es importante documentar la presencia de especies recién establecidas para evaluar su potencial invasivo. Este estudio documenta por primera vez una población establecida de una mantis introducida, *Liturgusa maya* Saussure y Zehntner (Mantodea: Liturgusidae), en los Estados Unidos. El documento incluye una revisión de la historia natural de la especie en su área de distribución nativa en América Central y del Sur. En la actualidad, esta mantis solo se conoce de un área pequeña y localizada; sin embargo, es posible un establecimiento más extenso en y más allá del sur de la Florida debido al clima subtropical de la región. Para facilitar el monitoreo de la población introducida de *L. maya*, se incluye una clave de identificación para los géneros de mantis de la Florida para ayudar a los no especialistas a diferenciar fácilmente a *L. maya* de los géneros de mantis nativas que existen en Florida.

Palabras Clave: especies exóticas; guía de identificación; especies introducidas; biología invasiva

Exotic insect species are a major threat to the biodiversity of native ecosystems (Mack et al. 2000). Nearly 50,000 non-native plants and animals have been documented as introduced into the US since the country's founding (USBC 2001). The state of Florida is home to considerable insect diversity, comprising both native (approximately 11,500) and non-native (at least 949) species (Frank & McCoy 1995). This number of documented introductions to Florida undoubtedly underestimates the true number of exotic insect species because many introductions occur without record, and species can be established for years before their presence is documented, either in publications or through specimens vouchered in collections.

The abundance of exotic species occurring in Florida can be attributed to its warm and humid subtropical climate, the varied habitats with diverse plant communities, and the high volume of transport and trade that provides many opportunities for accidental species' introductions on cargo. Nearly all established exotic insects in Florida were

transported to the state unintentionally in shipments of other materials; only 59 species are listed as intentionally introduced biocontrol agents of weeds and pests (Frank & McCoy 2007). Large and charismatic insects, such as mantises, are relatively rare among insect introductions. In fact, only 4 exotic mantises have been documented in the US to date: *Tenodera sinensis* Saussure (Mantodea: Mantidae), *Tenodera angustipennis* Saussure (Mantodea: Mantidae), *Mantis religiosa* L. (Mantodea: Mantidae), and *Iris oratoria* L. (Mantodea: Tarachodidae).

This article documents a population of the non-native praying mantis species, *Liturgusa maya* Saussure & Zehntner (Mantodea: Liturgusidae) in Florida. As far as we are aware, it is the first record of this species in North America. Although the geographic extent of the introduced population is unknown, the presence of multiple individuals at different life stages at 2 sites indicates an established population and not simply isolated individuals. Because accurate identification of juveniles is difficult, we outline laboratory rearing practices to easily raise mantises to adulthood. To fur-

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ther facilitate exotic species detection, we also present a key to adults of all the praying mantis genera that occur in Florida, with the inclusion of *Liturgusa maya*.

INTRODUCED PRAYING MANTISES IN THE USA

Mantis introductions in the USA are relatively uncommon, a surprising fact considering that predatory insects are well-represented among introduced species worldwide (Maxwell & Eitan 1998; Snyder & Evans 2006). Exotic mantises have the potential to remain undetected long after establishment in introduced ranges because of their cryptic habits, camouflaged appearance, ability to feed on diverse prey, and low population densities.

Although few mantis species have been introduced into the US, the history of these species suggests that once established, exotic mantises can become widespread. For example, the Chinese praying mantis, *Tenodera sinensis*, was first introduced to the Philadelphia, Pennsylvania, USA, area in 1896, and after multiple re-introductions, spread across much of the eastern USA and into the western part of the country (Laurent 1898; Skinner & Calver 1902; Blatchley 1920; Rathet & Hurd 1983). This species has been recorded in all states east of the Mississippi River except for Louisiana, Mississippi, and Florida, as well as in Kansas, Nebraska, Utah, California, and Washington.

Of all the introduced temperate zone praying mantises in the USA, *T. sinensis* is the most common and wide ranging, and also has the best-documented ecological impact. Like most praying mantises, *T. sinensis* is a generalist predator feeding primarily on insects, but also can take vertebrate prey, including hummingbirds (Nyffeler et al. 2017). This mantis is regarded as responsible for displacing the native Carolina mantis, *Stagmomantis carolina* Johansson (Mantodea: Mantidae) (Slingerland 1899; Hurd 1999).

The history of establishment and spread of *T. sinensis* across North America over the past century indicate that other exotic mantises could be equally successful adventive species in the USA, as well as pose threats to other insects, both native and non-native. *Tenodera sinensis* has been found to suppress populations of other non-native species, including another exotic mantis, *Tenodera angustipennis* (Snyder & Hurd 1995), an Asian mantis species first found in Maryland in 1926. From this first discovery site, *T. angustipennis* spread throughout the region and now also occurs in Delaware, New Jersey, New York, North Carolina, and Pennsylvania (Caudell 1927; Gurney 1950; Maxwell & Eitan 1998), where its range overlaps with that of *T. sinensis*. A third exotic mantis in the USA, *Mantis religiosa*, is native to Europe and likely was introduced in the early 20th century on ornamental plants (Scudder 1900; Rathet & Hurd 1983; Kisselburg & Cochran 2001; Snyder & Evans 2006). Little is known about this species' ecological impact, but experimentally, this and other mantises have been shown to alter community composition through predation preferences (Fagan et al. 2002). This species' ability to colonize new territory is evident even on its native continent where its range is expanding northward as a result of the warming climate (Linn & Griebeler 2015), as well as human-assisted dispersal to new areas (Pupinš et al. 2012).

Examples from mantis introductions beyond the US provide additional cause for concern about potential impacts on native insect populations, especially other praying mantises that require similar food and habitat resources (Fagan et al. 2002). In New Zealand, for example, the South African springbok mantis, *Miomantis caffra* Saussure (Mantodea: Mantidae), was first documented in suburban Auckland in 1978. Since then, its range has expanded to cover much of the North Island (Ramsay 1990). This species is thought to be responsible for the dis-

placement of New Zealand's only native mantis, *Orthodera novaezealandiae* Colenso (Mantodea: Mantidae) (Ramsay 1990; Fea et al. 2013).

Given the rarity of exotic mantises becoming established in the US, and the potential for introduced mantises to negatively impact ecological communities, this paper details what is known about a previously undocumented mantis in Florida, *Liturgusa maya* Saussure & Zehntner (Mantodea: Liturgusidae), with the aim of supporting future research and population monitoring. It remains to be seen whether the few individuals sampled in this study represent an isolated, innocuous population, or an invasive species that could pose a threat to Florida's native fauna.

NATURAL HISTORY OF *LITURGUSA*

No mantis species of the genus *Liturgusa* Saussure have been previously documented in the USA or Canada. This genus belongs to an exclusively Neotropical praying mantis family (Liturgusidae) that comprises 5 bark-dwelling genera (Rivera & Svenson 2016). The family is situated within an early-evolving lineage of mantises within the superfamily Acanthopoidea that is characterized by the lack of a hearing organ (Yager & Svenson 2008; Svenson & Whiting 2009; Rivera & Svenson 2016).

The geographic range of *Liturgusa* extends from Central America to southern Bolivia, and east to central Brazil. The vast majority of records for the genus are from moist tropical forests, but some species also have been found in seasonally dry forests in Central and South America. Of the 24 described species of *Liturgusa*, *L. maya* (Fig. 1A) is by far the most widely distributed, with records from central Mexico, central Venezuela, and as far south as southern Peru (Svenson 2014). *Liturgusa maya* is also one of the only species in the genus that occurs in a variety of habitat types, including wet tropical forests, dry seasonal forests, disturbed forest margins, and semi-urban areas. Beyond the ability to thrive in a range of habitats across a large geographic area, this species is adaptable also in terms of its size plasticity, with the largest females being nearly 1.5× the size of the smallest females (Svenson 2014). These qualities support the reasonable possibility that an established population of this species could survive and even spread in subtropical Florida and throughout the southeastern USA.

All species of *Liturgusa* are strictly associated with tree bark habitats (Svenson 2014). *Liturgusa* are long-legged but dorsoventrally flattened, and hold their bodies close to the substrate. Like other praying mantises, they are highly visual predators and fast-moving, an asset for both hunting and predator avoidance. When startled, individuals often run quickly from the perceived danger to the opposite side of the tree trunk. The *Liturgusa* behavioral repertoire includes escape tactics such as jumping and fluttering to the ground, as well as feigning death through immobility, a behavior known as thanatosis (Svenson 2014). Adults of all species of *Liturgusa* retain functional wings, but only a few have been observed flying. There are records of *Liturgusa* flying to light traps at night, and it is possible that flight is used as an escape behavior (Svenson 2014).

Liturgusa species dwell almost exclusively on tree trunks and branches; it is not known if juveniles and adults preferentially choose different parts of trees. Adults and nymphs of *Liturgusa* have been found together on the same tree, suggesting overlap of generations in the same habitat, but parental care has not been documented. Females lay their small oothecae on tree bark. The egg case itself is largely spherical, and narrows to a tube that extends away from the base (Fig. 1B). The eggs are laid within the rounded base, and nymphs upon hatching crawl out through the extended tube. A thorough account of *Liturgusa* natural history can be found in Svenson (2014).

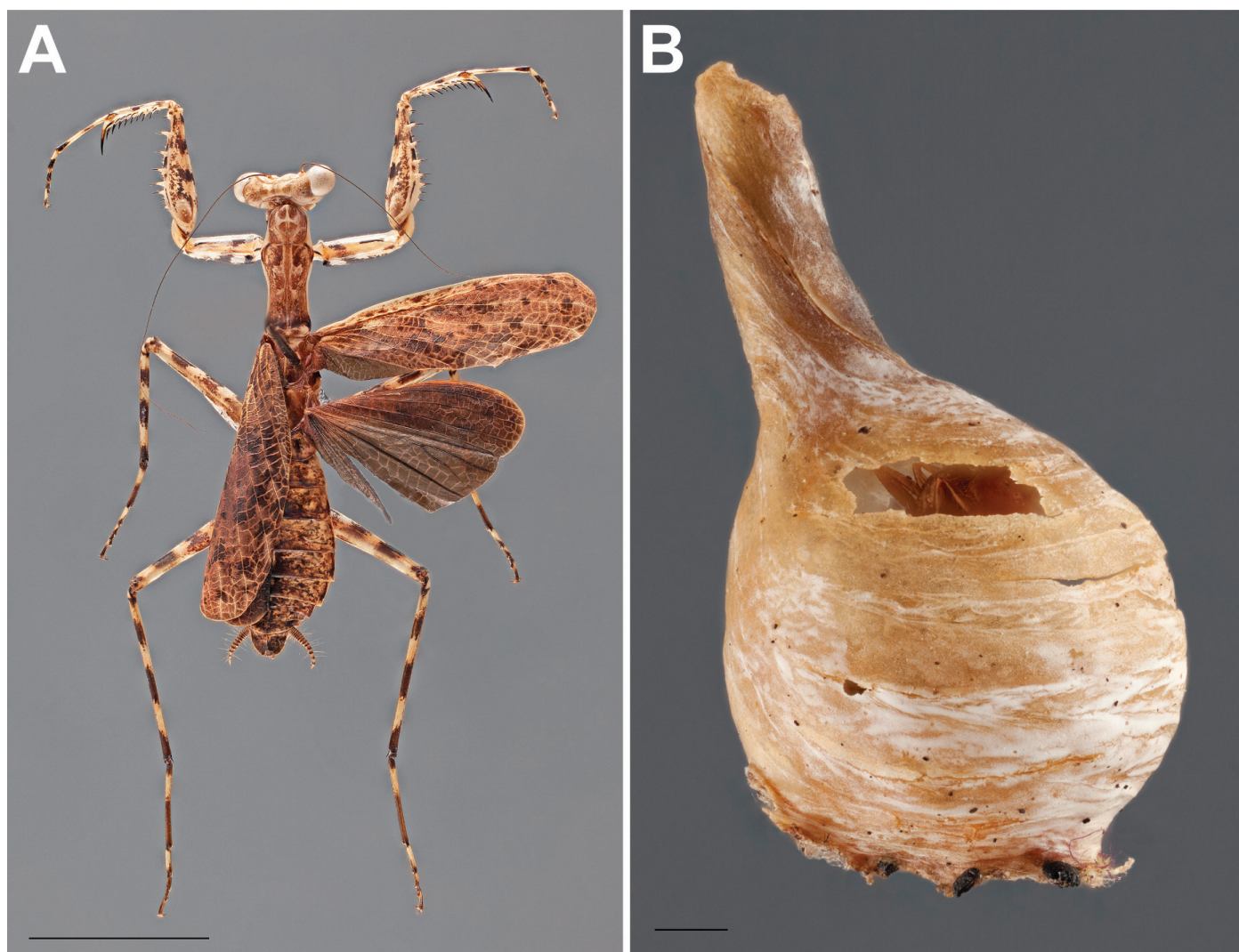


Fig. 1. Habitus images of *Liturgusa maya* collected in Long Key Natural Area and Nature Center, Davie, Florida. (A) Adult female (scale = 1 cm); (B) ootheca produced by captive female (scale = 1 mm) (photographs by Rick Wherley).

Materials and Methods

To document the presence of an established population of *Liturgusa maya* in Florida, we first compiled anecdotal reports (see below) of the species' occurrence in the state and reviewed the Florida State Collection of Arthropods for specimens or records of this species (none were found). We searched for specimens in the region where *L. maya* was reported to have been, and collected all individuals encountered for observation in captivity. All specimens were measured, photographed, and vouchered.

SPECIMEN COLLECTION

The first known collection of this species occurred in 2014, when BF captured 1 nymph at Long Key Natural Area and Nature Center in Davie, Florida (Fig. 2). A comparison with nymphs of the native bark mantis, *Gonatista grisea* F. (Mantodea: Liturgusidae), indicated that this was a different species. Unfortunately, this specimen was not retained.

In Sep 2015, pictures of *Liturgusa maya* (mistakenly identified as *G. grisea*) were posted in an online mantis forum. After a collection trip to Long Key Natural Area and Nature Center that month produced

the first confirmed and captured *L. maya* specimens, the search was expanded to the surrounding area.

On 1 Mar 2016, 11 live specimens and 2 empty (hatched) oothecae were found and collected at Long Key Natural Area and Nature Center. Mantises were found on a faux-wood fence bordering an equestrian trail. One ootheca was found on the fence, whereas the other ootheca was found on oak bark approximately 1.5 m above the ground on another part of the property. Of the 11 live specimens found, 1 was an adult female and the other 10 were nymphs ranging from first instar to sub-adult (sex-determinable nymphs were all female). Specimens were collected either by corralling individuals from the fence into an open vial, or hand capturing them from the ground when several leapt from the tree to the ground and feigned death.

In a search of the same area of Long Key Natural Area and Nature Center on 29 Dec 2016, 4 nymphs were found (3 second instar and 1 fifth instar), 2 of which were collected (1 second and 1 fifth instar).

An additional specimen of *L. maya* was collected in Apr 2016, approximately 6.4 km north-northwest of Long Key Natural Area and Nature Center, at Markham Park and Target Range (J. Hildebrandt, personal communication). Positive identification of the mantis as *L. maya* was confirmed by AJN but the specimen was unfortunately lost before being vouchered.



Fig. 2. *Liturgusa maya* specimens were collected in and near Long Key Natural Area and Nature Center (red star on large map) in Davie, Florida. The inset map indicates the proximity of the 2 collection sites (adjacent red stars) to National Parks and Preserves. (Maps modified from www.freemapsonline.com and www.nps.gov).

OBSERVATIONS IN CAPTIVITY

Eleven mantises were observed in captivity from 1 Mar 2016 to 28 Jun 2016. Mantises were placed individually in 1.0 L (32 oz) plastic cups with cloth or metal mesh lids (4.5 cm diam), with 4.0 cm × 2.0 cm screen windows for air circulation. Each cup contained a thin (2.0–2.5 cm) oak branch (*Quercus* sp.), placed vertically in the center so that all sides were accessible to the mantis.

Diet consisted of lab-reared wingless fruit flies (*Drosophila melanogaster* Meigen) (Diptera: Drosophilidae), lab-reared house crickets (*Acheta domesticus* [L.]) (Orthoptera: Gryllidae), and wild-collected pyramid ants (*Dorymyrmex bureni* [Trager]) (Formicidae: Dolichoderinae). Initially, the only food accepted was *D. bureni* ants. The ants were offered based on field observations of *L. maya* successfully hunting *D. bureni* in the field. Other ant genera were observed nearby (*Crematogaster* spp., *Camponotus* spp.) (both Hymenoptera: Formicidae), but *L. maya* was not seen eating them. In captivity, food was offered 3× per

wk, regardless of type. Any uneaten food was left in the enclosure until subsequent feeding, unless the mantis displayed visible distress, and in that case it was removed.

Water was provided twice per wk in the form of 3 sprays per d from a mist bottle. If a mantis was observed exhibiting pre-molt behavior, such as lethargy, aggressively defensive activity toward prey (raptorial flicking), skittishness in response to prey, or swollen wing-buds in sub-adults, food was withheld for 3 d. Humidity was maintained above 50% by placing rearing cups within a large plastic bin that was partially covered. Moist paper towels lined the bottom of the bin, and the lid was left unsealed with a gap of 2.5 cm for air circulation.

MEASUREMENTS AND IMAGING

Measurement data were captured for the 2 adult females using a Leica M165C stereo-microscope and a Leica IC80 HD coaxial video

camera (Leica Microsystems, Wetzlar, Germany) using the live measurements module of the Leica Application Suite (LAS). High resolution images of type and voucher specimens were captured using a Canon 5D SLR Camera outfitted with macro lenses (50 mm, 100 mm, and MP-E 65 mm) and three Speedlight 580EX II flash units (Canon USA, Melville, New York, USA) attached to , , an associated computer running the Canon EOS utility (Canon USA, Melville, New York) and Adobe Lightroom 3.6 software (Adobe Inc., San Jose, California, USA). Images were taken using a stack-shot z-stepper (Cognisys Inc., Traverse City, Michigan, USA), controlled through Zerene Stacker 1.04 (Zerene Systems LLC, Richland, Washington, USA) with images processed using the P-Max protocol. All images were captured over an 18% grey card background for white balance standards. Images were processed in Adobe Photoshop CS6 Extended (Adobe Inc., San Jose, California) to adjust levels, contrast, exposure, sharpness, and add scale bars (10 mm). Minor adjustments were made using the stamp tool to correct background aberrations and to remove distracting debris. Plates were constructed using Adobe Illustrator CS6 (Adobe Inc., San Jose, California).

IDENTIFICATION KEY

A key to the mantis genera of Florida was developed based on direct examination of mantis specimens in the Florida State Collection of Arthropods in Gainesville, Florida, USA, and at the Cleveland Museum of Natural History, Cleveland, Ohio, USA. Specimens represented all of the documented species of praying mantises established in Florida, as well as *L. maya*. Species determinations were confirmed based on available literature, legacy specimen labels, and consultation with taxonomic experts (Yager & Svenson 2008; Svenson 2014; Rivera & Svenson 2016; Rodrigues & Svenson 2018; Rivera & Svenson in press).

Results

Several specimens of *Liturgusa maya* that were collected in Florida are now vouchered in praying mantis collections at the Department of Entomology at the National Museum of Natural History, Smithsonian Institution in Washington, DC, USA, and in the entomology collection at the Florida State Collection of Arthropods in Gainesville, Florida. Two adult specimens were pinned; nymphs were stored in 70% ethanol.

SPECIMENS EXAMINED

Liturgusa maya was collected 3 times, resulting in a total collection of 2 adult females, 12 nymphs, and 2 oothecae. Because the number of specimens examined are limited, the measurements should not be taken to represent the full morphological range of this species.

Collection data are listed for each date:

23 Sep 2015. USA, Florida, Broward County, Long Key Nature Center and Natural Area, 26.076700°E, 80.325100°N. Collected by

Brian Fridie. One adult female (USNMENT01091960), 1 nymph (USNMENT01091961), both deposited at National Museum of Natural History, Smithsonian Institution.

1 Mar 2016. USA, Florida, Broward County, Long Key Nature Center and Natural Area, 26.076700°E, 80.325100°N. Collected by Andrew Nisip and Gabriel Somarriba. One adult female, 10 nymphs (2 first instar, 1 second instar, 4 fourth instar, 1 fifth instar, 1 pre-subadult, 1 subadult), and 2 oothecae deposited at Florida State Collection of Arthropods.

29 Dec 2016. USA, Florida, Broward County, Long Key Nature Center and Natural Area, 26.076700°E, 80.325100°N. Collected by Andrew Nisip and Gabriel Somarriba. One nymph (second instar) deposited at Florida State Collection of Arthropods.

MEASUREMENTS OF ADULT FEMALES

Adult female (collected 1 Mar 2016; deposited at Florida State Collection of Arthropods): Body length 25.04 mm; forewing length 15.23 mm; hindwing length 11.46 mm; pronotum length 6.81 mm; prozone length 2.79 mm; pronotum width 2.14 mm; pronotum narrow width 2.12 mm; head width 5.74 mm; head vertex to clypeus 2.37 mm; frons width 2.17 mm; frons height 0.76 mm; prothoracic femur length 6.99 mm; mesothoracic femur length 7.99 mm; metathoracic femur length 8.07 mm; anteroventral femoral spine count 15 to 16; posteroventral femoral spine count 4; anteroventral tibial spine count 9 to 10; posteroventral tibial spine count 7.

Adult female (collected 23 Sep 2015; USNMENT01091960): Body length 24.99 mm; forewing length 15.61 mm; hindwing length 11.88 mm; pronotum length 6.78 mm; prozonelength 2.05 mm; pronotum width 2.70 mm; pronotum narrow width 2.06; mm head width 5.69 mm; head vertex to clypeus 2.35 mm; frons width 2.09 mm; frons height 0.82 mm; prothoracic femur length 6.68 mm; mesothoracic femur length 7.85 mm; metathoracic femur length 7.98 mm; anteroventral femoral spine count 15 to 16; posteroventral femoral spine count 4; anteroventral tibial spine count 10; posteroventral tibial spine count 7.

SPECIMEN CARE AND OBSERVATION

All specimens were captured alive and observed in captivity. All individuals fared well in captivity, although the initial adjustment to the enclosures was faster in younger nymphs. Adults and older nymphs took longer to become accustomed to the boundaries of the clear plastic enclosure wall. This was inferred by consistent eye rubbing and regular raptorial flicking against enclosure siding.

Mating was never witnessed in captivity; all adult specimens were female. One of the wild-caught adult females produced 3 oothecae, 2 of which hatched. Nymphs that hatched in captivity failed to feed successfully and died within 4 d of hatching. A wild caught sub-adult female later molted to adult and laid 5 oothecae, but all were deformed and no hatchlings emerged from them.

KEY TO FLORIDA MANTIS GENERA USING ADULT MALES AND FEMALES

- 1.— Body length equal to or smaller than 2.0 cm. Pronotum length nearly equal to width *Mantoida* (Fig. 3A)
- 1.'— Body length longer than 2.0 cm. Pronotum longer than wide 2
- 2.— Body dorsoventrally flattened with long laterally swept legs. Body and wings mottled for camouflage; bark dwelling 3
- 2.'— Body elongated. Can be cylindrical and delicate or broader and more robust 4
- 3.— Discoidal spines arranged in a zigzag pattern. Rounded supra-anal plate covering the ovipositor and tapering cerci. No cuticular outgrowths on abdomen of female *Liturgusa* (Fig. 3F)

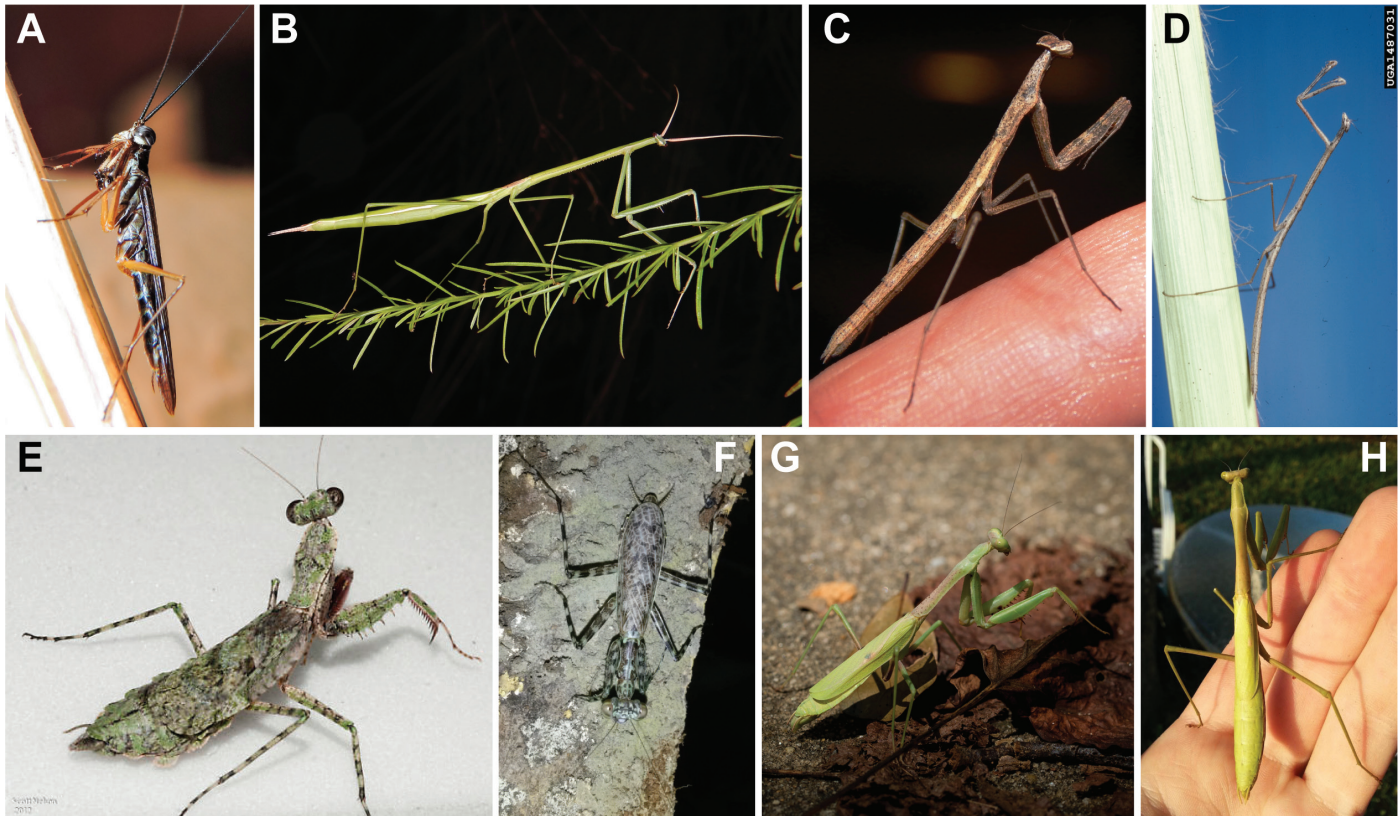


Fig. 3. Praying mantis genera in Florida: (A) *Mantoida maya* female (photograph by Cheryl Harleston (www.inaturalist.org, CC BY-NC-SA)); (B) *Brunneria borealis* female (photograph by Gary L. Dearman); (C) *Oligonicella scudderii* female (photograph by Jennifer Thompson); (D) *Thesprotia graminis* female (photograph by Sturgis McKeever, Georgia Southern University (www.Bugwood.org, CC-BY-NC)); (E) *Gonatista grisea* female (photograph by Scott D. Nelson); (F) *Liturgusa maya* female (photograph by Brian Fridle Jr.); (G) *Stagmomantis carolina* female (photograph by Wendy Garfinkel-Gold); (H) *Stagmomantis floridensis* female (photograph by Andrew Nisip).

- 3.— Discoidal spines arranged in a straight line. Triangular supra-anal plate does not cover the ovipositor and the cerci do not taper to the last segment. Females with lateral cuticular outgrowths on the abdomen *Gonatista* (Fig. 3E)
- 4.— Cyclopean ear present in males, present or partially reduced in females (present between metathoracic coxa on sternum). Robust body. Wings in females reduced, but never absent *Stagmomantis* (Fig. 3H)
- 4'— Cyclopean ear absent in males and females (present between metathoracic coxa on sternum). Wings absent or highly reduced in females 5
- 5.— Foretibiae with dorsally oriented terminal spine. Forefemora with 1 posteroventral spine *Thesprotia* (Fig. 3D)
- 5'— Foretibiae without dorsally oriented terminal spine. Forefemora with 4 or 5 posteroventral spines 6
- 6.— Antenna uniformly threadlike, not narrowing from base to tip. Forefemora with 4 discoidal spines and 4 posteroventral spines *Oligonicella* (Fig. 3C)
- 6'— Proximal antennal flagellomeres swollen, narrowing significantly from base to tip. Forefemora with 3 discoidal spines and 5 posteroventral spines *Brunneria* (Fig. 3B)

Discussion

Exotic praying mantis introductions are relatively uncommon despite the fact that these insects are adaptable generalist predators. Of the species that have become established outside of their native range, only a few have been documented to be invasive and to negatively impact native insect communities. However, there is cause for concern about the potential for exotic predators to alter local ecological processes. Considering how little is known about the introduction history, range limits, feeding preferences, and reproductive potential of

introduced mantises, including *Liturgusa maya*, further study of these species in their introduced range is warranted.

Liturgusa maya may have been introduced accidentally into Florida on imported plant material, or deliberately released into the wild after being kept in captivity as a pet. The population in Florida appears to have been established since at least 2015, and based on the presence of oothecae, nymphs, and adults, the population is functionally reproductive. Although all of the specimens were collected from a single, localized area in or near Long Key Natural Area and Nature Center in Broward County, Florida, we expect that this species has the potential to expand its range throughout the southeastern US, where the

subtropical climate and lush vegetation are especially hospitable for a tropical bark-dwelling mantis.

The most pressing concern about *L. maya* in its introduced range is its potential to impact local populations of the native bark-dwelling mantis, *G. grisea* (F.), which is of comparable size and occupies a similar ecological niche. To date, we have not observed interactions between *L. maya* and *G. grisea*, but expect that the 2 would compete for prey and habitat resources where they co-occur.

The extent of *Liturgusa maya* in the USA is currently unknown, but we hope this paper provides a strong foundation for monitoring or managing the introduced population. One of the challenges in documenting this species and characterizing its ecological effects is the lack of easy-to-interpret and reliable identification materials for local mantis species. Our aim in providing a comprehensive identification guide to the mantis genera of Florida is to make it easy to distinguish *L. maya* from native species, as well as any other mantises that may be introduced into Florida, in an effort to protect our native mantis fauna.

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References Cited

- Blatchley WS. 1920. Orthoptera of northeastern America: with especial reference to the faunas of Indiana and Florida. The Nature Publishing Company, Indianapolis, Indiana, USA.
- Caudell AN. 1927. Report on the orthopteroid insects collected by the Fiji-New Zealand Expedition from the University of Iowa. University of Iowa Studies in Natural History 12: 3–22.
- Fagan WF, Moran MD, Rango JJ, Hurd LE. 2002. Community effects of praying mantids: a meta-analysis of the influences of species identity and experimental design. Ecological Entomology 27: 385–395.
- Fea MP, Stanley MC, Holwell GI. 2013. Fatal attraction: sexually cannibalistic invaders attract naive native mantids. Biology Letters 9: 20130746. doi: 10.1098/rsbl.2013.0746
- Frank JH, McCoy ED. 1995. Introduction to insect behavioral ecology: the good, the bad, and the beautiful: non-indigenous species in Florida. Invasive adventive insects and other organisms in Florida. Florida Entomologist 78: 1–15.
- Frank JH, McCoy ED. 2007. The risk of classical biological control in Florida. Biological Control 41: 151–174.
- Gurney AB. 1950. Praying mantids of the United States, native and introduced. Annual Report of the Board of Regents of the Smithsonian Institution 1950: 339–362.
- Hurd LE. 1999. Ecology of praying mantids, pp. 43–60 In Prete FR, Wells H, Wells PH, Hurd LE [eds.], The Praying Mantids. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Kisselburg MA, Cochran PA. 2001. *Mantis religiosa* (Mantodea: Mantidae) in Door County, Wisconsin. Great Lakes Entomologist 34: 27–28.
- Laurent P. 1896. A species of Orthoptera. Entomological News 9: 144–145.
- Linn CA, Griebeler EM. 2015. Reconstruction of two colonisation pathways of *Mantis religiosa* (Mantodea) in Germany using four mitochondrial markers. Genetica 143: 11–20.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz F. 2000. Biotic invasions: causes, epidemiology, global consequences and control. Ecological Applications 10: 689–710.
- Maxwell M, Eitan O. 1998. Range expansion of an introduced mantid, *Iris oratoria*, and niche overlap with a native mantid, *Stagmomantis limbata* (Mantodea: Mantidae). Annals of the Entomological Society of America 91: 422–429.
- Nyffeler M, Maxwell MR, Remsen Jr JV. 2017. Bird predation by praying mantises: a global perspective. The Wilson Journal of Ornithology 129: 331–344.
- Pupinš M, Kalniņš M, Pupina A, Jaundalere I. 2012. First records of European mantid *Mantis religiosa* (Linnaeus, 1758) (Insecta: Dictyoptera, Mantidae) in Latvia. Acta Biologica Universitatis Daugavpiliensis 12: 175–184.
- Ramsay G. 1990. Mantodea (Insecta) with a review of aspects of functional morphology and biology. Fauna of New Zealand 19: 1–96.
- Rathet I, Hurd L. 1983. Ecological relationships of three co-occurring mantids, *Tenodera sinensis* (Saussure), *T. angustipennis* (Saussure), and *Mantis religiosa* (Linnaeus). The American Midland Naturalist 110: 240–248.
- Rivera J, Svenson GJ. 2016. The Neotropical 'polymorphic earless praying mantises' – Part I: molecular phylogeny and revised higher-level systematics (Insecta: Mantodea, Acanthopoidea). Systematic Entomology 41: 607–649.
- Rivera J, Svenson GJ. In Press. A Review of the Genera of the Acanthopoidea, the "Polymorphic Earless Praying Mantises" (Insecta: Mantodea). Thomas Say Publications in Entomology. Entomological Society of America, Annapolis, Maryland, USA.
- Rodrigues HM, Svenson GJ. 2018. Epaphroditidae sensu novo, an endemic Caribbean family of morphologically divergent praying mantises (Insecta, Mantodea). Neotropical Entomology 4: 502–507.
- Scudder SH. 1900. *Mantis religiosa* in America. Psyche 9: 119–120.
- Skinner H, Calvert PP [eds.]. 1902. Entomological news and Proceedings of the Entomological Section of the Academy of Natural Sciences of Philadelphia 13: 24–26.
- Slingerland MV. 1899. Occurrence of *Stagmomantis carolina* in New York. Entomological News 10: 288–289.
- Snyder W, Evans E. 2006. Ecological effects of invasive arthropod generalist predators. Annual Review of Ecology, Evolution, and Systematics 37: 95–122.
- Svenson GJ. 2014. Revision of the neotropical bark mantis genus *Liturgusa* Saussure, 1869 (Insecta, Mantodea, Liturgusini). ZooKeys 390: 1–214.
- Svenson GJ, Whiting MF. 2009. Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. Cladistics 25: 468–514.
- USBC (United States Bureau of the Census). 2001. Statistical abstract of the United States 2001. U.S. Bureau of the Census, U.S. Government Printing Office. Washington, DC, USA.
- Yager DD, Svenson GJ. 2008. Patterns of praying mantis auditory system evolution based on morphological, molecular, neurophysiological, and behavioral data. Biological Journal of the Linnean Society 94: 541–568.