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Source: Stuttgarter Beiträge zur Naturkunde A, 10(10) : 19-39

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/sbna.v10.a2

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Update on *Tagalomantis manillensis* (Saussure), with description of the female and comments on its systematic placement and life history (Insecta: Mantodea: Deroplatyinae)

Christian J. Schwarz

Abstract

The female and the ootheca of the Philippine endemic *Tagalomantis manillensis* (Saussure, 1870) are described and illustrated for the first time. The male is re-described in detail. The species was so far only known from the island of Luzon, but also occurs in suitable habitats on Panay. Although locally relatively abundant, it is confined to primary and old secondary rainforests and threatened by habitat loss. The life history of Panay populations is outlined. The name Euchomenellini Giglio-Tos, 1916 is proposed for the oriental members of Angelinae (*Euchomenella*, *Indomenella* and *Tagalomantis*). The tribus is placed among Deroplatyinae due to morphological and genital characters. *Cotigaonopsis* Vyjayandi, 2009 is transferred to Rivetinini. A key to the genera of Deroplatyinae is provided.

K e y w o r d s : Euchomenellini, endemism, stick mantis, crypsis, masquerade, egg guarding.

Zusammenfassung

Das Weibchen und die Oothek der auf den Philippinen endemischen Gottesanbeterin *Tagalomantis manillensis* (Saussure, 1870) werden zum ersten Mal beschrieben und abgebildet. Das Männchen wird ausführlich wiederbeschrieben. Die Art war bisher nur von der Insel Luzon bekannt, kommt aber auch in geeigneten Habitaten auf Panay vor. Obwohl die Art lokal relativ häufig auftreten kann, ist sie auf Primärwälder und alte Sekundärwälder angewiesen und durch Habitatzerstörung bedroht. Die Biologie der Panay-Populationen wird näher beleuchtet. Die orientalischen Gattungen der Angelinae (*Euchomenella*, *Indomenella* und *Tagalomantis*) werden in der Tribus Euchomenellini Giglio-Tos, 1916 zusammengefasst und aufgrund morphologischer und genitalmorphologischer Charakteristika zu den Deroplatyinae gestellt. *Cotigaonopsis* Vyjayandi, 2009 ist mit den Euchomenellini nicht verwandt und wird zu den Rivetinini gestellt. Ein Bestimmungsschlüssel für die Gattungen der Deroplatyinae schließt die Arbeit ab.

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1 Introduction

The genus *Tagalomantis* was created by Hebard (1920) for *Euchomena manillensis* Saussure, 1870, described after a single male from "Manilla" on the Philippine island of Luzon. The same male is re-described in more detail and figured by Saussure in 1871. During subsequent years, the species is just briefly mentioned in Westwood (1889), Kirby (1904) and Giglio-Tos (1916), all records referring to the same specimen mentioned by Saussure. Giglio-Tos (1916) unites all oriental *Euchomena* species into a new genus named *Euchomenella* Giglio-Tos, 1916. It is only in Hebard (1920) that a second *manillensis* specimen is recorded from Los Baños, Laguna Province, likewise on the island of Luzon. Hebard uses the opportunity to give a more detailed description of the species and creates the genus *Tagalomantis* at this occasion. However, both Giglio-Tos (1927) and Beier (1935) continue to treat Saussure's species as a member of *Euchomenella*. While Giglio-Tos was probably not aware of Hebard's (1920) paper, Beier (1935) explicitly considers *Tagalomantis* a synonym of *Euchomenella*, despite a different number of postero-ventral spines on the fore tibiae. No new specimens are mentioned, though.

Some years later, Beier (1952) describes *Euchomenella brevis* after a damaged male specimen from northern Sulawesi. Even though he points out the comparatively high number of 12 postero-ventral spines on the fore tibiae, and the close relationship of his new species with *E. manillensis*, he sees no reason to exclude the two species from

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Euchomenella. No record of *Tagalomantis* or *Euchomenella* is known in the literature for the next decades, except for a drawing of a pinned pair of *Euchomenella molucarum* (Saussure, 1872), published first in Bragg (1997) and reprised unchanged in Prete et al. (1999).

A long overdue revision of the oriental members of Angelinae is finally presented by Roy (2001). He resurrects *Tagalomantis* as a genus, comprising *T. manillensis* and *T. brevis*, and cites the three specimens known so far in the literature. The type of *T. manillensis*, deposited in the MNHN, is figured, but the genitalia could not be depicted, since the tip of the abdomen is missing (this was not yet the case when Saussure described the species in 1870).

The latest record of *T. manillensis* is provided by Shcherbakov (2012), who cites an additional male specimen, collected 1917 in Los Baños and currently housed at the ZMMU. He completes the description of the male sex by describing its basisternum and genitalia, comparing them with *Euchomenella*.

So, as of now, only three males of this species are known, collected over ninety years ago in southern Luzon. No female was ever recorded, and both morphological and distributional boundaries remain to be evaluated.

From 2010 to 2015, during four field trips to the island of Panay, numerous specimens of *Tagalomantis manillensis* in various developmental stages were encountered in their natural habitat. A female from Luzon could also be examined. Here, I give a complete list of synonyms, describe the female, ootheca, and first instar nymph for the first time, revise the systematic placement of the genus, and provide data on life history, phenology and behavior. The new data allow a re-definition of the Oriental angeline genera, which are re-classified among Deroplatyinae.

Acknowledgements

First of all, I would like to thank Evgeny Shcherbakov (ZMMU) for providing data and high-resolution pictures of the Luzon specimen studied by him, for pointing my attention to the status of *Cotigaonopsis*, and for fruitful discussions on the systematics and biogeography of SE Asian mantids. I thank Oliver Zompro (Berlin) for communicating me the data on the Luzon female. Work in the Philippines was facilitated by a Memorandum of Agreement between Ruhr University Bochum through its Philippine operating arm PanayCon (www.panaycon.org) and the Department of Environment and Natural Resources Region VI. Collections were granted by Gratuitous Permits Nos. 195 and 2013-001. I thank Prof. Dr. Eberhard Curio (Ruhr University, Bochum) for facilitating research on Panay, and all employees of PanayCon for valuable help with logistics and field work, particularly Dr. Enrique Sanchez Jr. (Pandan, Antique), Rhea Santillan (Pandan, Antique), Junmar Jamangal (Libertad, Antique), Gersom Operiano (Sebaste, Antique), Alan Absalon (Libertad, Antique), Arcel D. Fernandez (Pandan, Antique), and Jun Tacud (Libertad, Antique). I am grateful to Dr. Maren Gaulke (Munich, Germany) for useful advice and long hours of brainstorming on the Philippine fauna. Dr. Alexander Riedel and Reinhard Ehrmann (SMNK) facilitated the loan of a *Mellierella biroi* pair. Evgeny Shcherbakov, Roger Roy (MNHN), and anonymous reviewers made valuable comments on earlier drafts of the manuscript. This study was supported in part by a grant of the Deutsche Forschungsgemeinschaft (CU 4/41-1). This is publication no. 92 of the Panay Eco-Social Conservation Project (PanayCon).

Acronyms of depositories

MNHN	Muséum National d'Histoire Naturelle, Paris
OZC	Oliver Zompro's collection
PNM	Philippine National Museum, Manila
SMNK	Staatliches Museum für Naturkunde, Karlsruhe
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin
ZMMU	Zoological Museum of Lomonosov State University, Moscow

2 Material and Methods

Region sampled

Most investigated specimens originated from the Northwest Panay Peninsula (NWPP), also known as Buruanga Peninsula (Siler et al. 2012), more precisely from the surroundings of the Sibaliw research station, municipality of Buruanga, Aklan Province, Philippines. The station (11°49.172′N, 121°58.052′E) is located on a mountainous slope at around 460 m a. s. l., and is surrounded by secondary and primary dipterocarp forest. The highlands of the peninsula harbor one of the last lowland rainforests of the Western Visayas biological sub-realm, which basically comprises the islands of the Greater Negros-Panay Pleistocene Aggregate Island Complex (PAIC, see Inger 1954, Heaney 1985, Voris 2000). Twelve thousand hectares were declared Natural Park in 2005 (Gaulke 2011), at least 5,000 ha of which are forested. A few additional specimens were recorded in the Central Panay Mountain Range (CPMR), extending north-south along the west coast of the island. The CPMR holds ~40,000 ha of mostly high elevation (above 900 m) forest (Klop et al. 2000, Curio 2006), with some remote valleys preserving lowland forest at about 200–500 m a. s. l. (Schwarz unpubl.).

The climate of the sampled areas is tropically wet, with a rainy season from June to February, and a short dry season from March to May (Gaulke 2011). The first half of the rain season from June to October is influenced by the southwest monsoon, while cooler northeasterly monsoon prevails from November to February. The dry season is caused by easterly trade winds, which create a short but distinct seasonality in coastal and lowland areas. In contrast, seasonality is weakly expressed in the hilly and mountainous areas of the NWPP and the CPMR, where climate is almost perhumid. Temperatures at Sibaliw range from 17.8 to 37.5 °C, with a minimum temperature mean of 19.4 to 21.0 °C and a maximum temperature mean of 29.7 to 31.9 °C. Annual rainfall spans 4,651 to 9,277 mm (Gaulke 2011). Local precipitation patterns are strongly influenced by passing low pressure zones of varying intensity, and, on a broader scale, by ENSO oscillations. Long-term climate data for the CPMR are not available, but several field trips to the range experienced a climate comparable to the NWPP, except lower temperatures at higher altitudes.

Timeframe

Data on this species were gained during four long-term field trips to Panay, each lasting nine to eleven months: July 2010 to April 2011; July 2011 to June 2012; September 2012 to June 2013;

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and July 2014 to June 2015. In 2011 to 2013, Sibaliw station was visited for periods of 10 to 15 days at intervals of about three to four weeks. Sibaliw stays were sparser and of shorter duration in 2010–2011, and 2014–2015. Trips to the CPMR were conducted in August 2010 (Valderrama area, one day), November 2010 (Mt. Madja-as, 7 days), January–February 2013 (Maria Cristina, Madalag, 8 days), and March 2013 (Mt. Baloy, 6 days). The first and the third expedition yielded *Tagalomantis* specimens.

Collection and preparation

Mantids were collected by hand, killed with ethanol and temporarily stored in silica gel before being softened in a box with damp air and pinned. Some of the preserved males were specimens attracted to the station light after sunset. Young nymphs were preserved in ethanol. For genitalia preparations the tip of the abdomen was removed, macerated in 10 % KOH overnight, and neutralized with acetic acid. The genitalia were then dissected, washed in water, in 70 % ethanol, in 96 % ethanol, and in acetone, respectively, and permanently fixed in Euparal on a slide labeled with the data of the specimen. One pair of *Tagalomantis manillensis* will be deposited in the PNM, MNHN, SMNK, and ZMB, respectively. The remaining Panay specimens are at the author's collection at Bochum University.

Life history observations

Individuals of this species were regularly looked after both day and night, usually during short photographing trips to the immediate environs of the Sibaliw station. Only a fraction of the encountered specimens were actually preserved. Some individuals, particularly females, were observed repeatedly over the course of several weeks, allowing a first qualitative assessment of defensive behavior and brood care in the genus *Tagalomantis*.

3 Results

Systematic part

Tagalomantis manillensis (Saussure, 1870)

Euchomena manillensis Saussure, 1870: 236 (♂).

Euchomena manillensis Saussure, 1870. – In: Saussure 1871: 47–48, pl. 6, fig. 44; Westwood 1889: 9; Kirby 1904: 237; Bruner 1915: 32.

Euchomenella manillensis (Saussure, 1870). – In: Giglio-Tos 1916: 36; Giglio-Tos 1927: 235–236; Beier 1935: 66.

Tagalomantis manillensis (Saussure, 1870). – In: Hebard 1920: 38, pl. 1, fig. 10; Werner 1922: 150; Werner 1926: 231; Roy 2001: 82, fig. 1; Ehrmann 2002: 337; Otte & Spearman 2005: 167; Shcherbakov 2012: 277–278, figs. 3–5, 10.

Examined material: ♂, Northwest Panay Peninsula, Sibaliw Research Station, Buruanga, Aklan, Panay Island, Philippines, secondary forest, 11°49.172′N, 121°58.052′E, ~450 m, 18.IX.2011, C. Schwarz leg. – ♂, same as before, secondary forest, 11°49.172′N, 121°58.052′E, ~450 m, 22.VIII.2011, C. Schwitzke leg. – ♂, same as before, secondary forest, at light, 11°49.172′N, 121°58.052′E, ~460 m, 23.XII.2011, C. Schwarz leg. – ♂, same as before, 3.IV.2011, C. Schwarz leg. – ♂, same as before, 23.XI.2012, C. Schwarz leg. – ♂, same as before, 6.–10.IX.2011, A. Fernandez leg. – ♂, same as before, 3.II.2012, A. Fernandez leg. – ♀, same as before, secondary forest, 11°49.180′N, 121°58.011′E, ~441 m, 7.–12.V.2012, C. Schwarz leg. – ♀, same as before, secondary forest, 11°49′N, 121°58′E, ~460 m, 15.VIII.2010, C. Schwarz leg. – ♀, same as before, secondary forest, 11°49′N, 121°58′E, ~460 m, 20.X.2011, C. Schwarz leg. – ♀, same as before, young secondary growth, 11°49.178′N, 121°58.033′E, ~475 m, 9.X.2012, A. Absalon leg. – 2 ♀♀, Central Panay Mountain Range, Villa Valderrama Resort, Valderrama, Antique, Panay Island, Philippines, mahogany plantation, 22.VIII.2010, C. Schwarz leg. – ♀, Mt. Makiling, Central Forest Experiment Station, Luzon, Philippines, 300 m, 10.–12.X.1995, O. Zompro leg. (OZC). – Ootheca, Northwest Panay Peninsula, Sibaliw Research Station, Buruanga, Aklan, Panay Island, Philippines, secondary forest, 11°49′N, 121°58′E, ~460 m, 12.X.2012, C. Schwarz leg. – Ootheca, same as before, VI.2013, C. Schwarz leg. – Juvenile, same as before, 24.IX.2012, A. Absalon leg. – Juvenile, Central Panay Mountain Range, Brgy. Maria Cristina, Madalag, Aklan, Panay Island, Philippines, mixed primary and secondary forest along creek, 11°30.827′N, 122°11.089′E, ~195 m, 30.I.–1.II.2013, G. Operiano leg.

Description of Panay specimens

Male: Body length 52.5–54.0 mm. Coloration brownish, varying from tan to dark brown, femora of walking legs mostly greenish in life (Figs. 1, 10–12). Chromatic elements usually more expressed in dark-colored specimens, while they can become almost obsolete in tan individuals.

Head (Fig. 2) 3.0–3.3 mm long and 5.0–5.1 mm wide. Eyes slightly kidney-shaped, exophthalmic. Vertex slightly convex, juxta-ocular bulges flat, not protruding, separated from vertex by a deep sulcus. Two very shallow sulci between midline of vertex and juxta-ocular sulcus. A transverse, semicircular sulcus between anterior part of vertex and ocellar region. Ocelli large, forming an isosceles triangle with an angle of about 90°. Frontal shield wider than high, pentagonal, with a marginal ridge and two faintly indicated dorso-ventral ridges; depressed parts slightly darker. Clypeus and labrum keeled, dorsal part of the keel widens into a triangular elevation at dorsal margin of clypeus. A dark band is running from postero-lateral to antero-medial margin of the eyes, continuing along antero-lateral parts of gena and mandible until the tip of the labrum, where it forms a right angle with the opposite band. Maxillary palp segments darkened ventrally, labial palp segments dark with light brown apex, except of last segment, which is fully blackish. Antennae filiform, 29–31 mm long, longer than half of body length. Scapus light brown (matching body coloration), pedicellus and first 13–15 segments light brown with a dark stripe, which becomes successively wider until it encompasses the whole segment. Remaining segments blackish.

Pronotum slightly sinuate dorso-ventrally (Fig. 3), brownish, with numerous small dark spots, 19.8–21.4 mm long and 2.75–2.85 mm wide at supracoxal dilatation, minimum width of metazona 1.70–1.85 mm. Margins denticulate along entire length, teeth suffused with black, slightly longer along prozonal margin than on metazona. Length of prozona 3.5–3.8 mm, of metazona 16.3–17.8 mm, ratio

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metazona/prozona 4.4–4.9. Prozona with a deep longitudinal sulcus just before supracoxal dilatation, with several tubercles on both sides of the midline. Metazona keeled, more or less semi-circular in cross-section anteriorly, becoming progressively more triangular towards posterior end. Supracoxal dilatation with two well-developed tubercles just behind coxal insertion, sometimes with a very minute tubercle just posterior of main tubercle. Posterior margin of metazona with two rounded tubercles. Basisternum tuberculate (see also SHCHERBAKOV 2012), latero-posteriorly produced into a pyramidal projection. Prosternum orange-brown, with small dark spots towards posterior end, two pale, more or less seed-shaped callous spots at its distal fourth (very conspicuous in dark specimens), and two pale tubercles just before its distal margin.

Fore legs slender. Fore coxae much shorter than metazona, triangular in cross-section, 9.6–10.2 mm long, with numerous dark spots and two weakly expressed pale bands posteriorly, orange-brown anteriorly. Dorsal margin darker proximally, with 7–9 very small teeth interspersed with a few even smaller teeth. Teeth and surrounding area whitish. Apical lobes adjacent, but not overlapping. Anterior femora 11.1–11.7 mm long and 1.3–1.5 mm wide, dorsal margin very indistinctly serrulate, slightly sinuate, posterior side mottled with brown, except of two very indistinct pale bands (barely discernible in some specimens), and numerous dark spots. Anterior side pale, very indistinctly banded. Claw-groove at middle of femur. Ventral side of femur with a row of small tubercles between base and second discoidal spine. Four discoidal spines, with third the longest and first about the same length as fourth. Four postero-ventral spines, and an additional small spine on genicular lobe. Fifteen to seventeen antero-ventral spines plus an additional one on the genicular lobe, 16 being the regular number. Regular spination formula iIiIiIiIiIiIiiiI (see also HEBARD 1920). The three distal discoidal spines as well as the long antero-ventral spines (except the apical one) bendable, all spines darkened in their apical half. Anterior tibiae 6.1–6.3 mm long, with 10–11 postero-ventral and 16–17 antero-ventral spines increasing in length distally.

Meso- and metathorax pale brown with dark spots, metathorax with a DK ear (see YAGER & SVENSON 2008). Mid and hind coxae with a dark stripe anteriorly, darkened latero-posteriorly. Mid and hind femora slightly inflated at base, greenish in life, with dark spots and two weakly developed annulations, one at middle and a second, wider and more pronounced one at the apex. Apical lobes well-developed, genicular spines present, but small. Mid tibiae slightly shorter, hind tibiae slightly longer than corresponding femora, with two barely discernible pale annulations. Metatarsus distinctly longer than remaining segments combined.

Wings reaching apex of abdomen (Fig. 1), usually as long as, but in some specimens slightly longer or shorter than apex of subgenital plate. Tegmina 30.4–32.9 mm long and 5.7–6.6 mm wide, 1.5–1.6 times as long as pronotum, with rounded apex. Costal field and the very tip of the wing opaque, remaining parts subhyaline, mottled with smoky. Proximal part of costal field 1.5–1.8 mm wide, then quickly tapering towards radial vein, becoming very narrow. Stigma very small and indistinct, oblique, ivory anteriorly, black posteriorly. Alae subhyaline, mottled with smoky, costal field and apex opaque.

Abdomen parallel-sided, with numerous dark spots and a pair of paramedian dark depressions on each sternite. Supra-anal plate rounded. Cerci surpassing subgenital plate, moniliform, with 15–16 segments, last segment subacute. Subgenital plate trapezoid, with short, spaced apart styli.

Genitalia (Fig. 6, see also SHCHERBAKOV 2012) strongly pigmented, right dorsal phallomere without peculiarities, distal part roughly triangular. Ventral phallomere with a proximal lobe on its right side, left distal side strongly sclerotized, continuing into a hook-like distal process, strongly curved to the right and with acute apex. Left dorsal phallomere with moderately slender apical process and a strongly sclerotized, claw-like phalloid apophysis curved to the left and covered by strong spines along its entire right side.

F e m a l e : Longer and more robust than males, with strongly brachypterous wings (Figs. 1, 11). Body length 63.4–71.0 mm. Coloration much more variable than in males, from grayish white or tan with almost no pattern, to dark brown with contrasting tan bandings (Figs. 8–9). Two paramedian pairs of dark oblique markings are present on the metazona, one just behind the supracoxal dilatation, the second in the posterior fourth of the pronotum. Some specimens also feature a dark median stripe along the pronotum. The markings are more obvious in dark-colored specimens (Fig. 9). The greenish walking leg femora observed in males are not seen in females.

Head (Fig. 2) 4.15–4.60 mm long and 6.00–6.25 mm wide. Vertex higher and more rounded than in males, parietal sulcus less deep. Ocelli very small, forming a broad angle, lateral ocelli connected with frontal ocellus by a small ridge. Marginal ridge of frontal shield more strongly expressed, frontal shield deeper. Palps pale, only indistinctly banded. Antennae 15–17 mm long, filiform, pale.

Pronotum more robust and more sinuate than in males (Figs. 1, 3), dark-spotted, 28.0–29.8 mm long and 4.00–4.55 mm wide at supracoxal dilatation, minimum width of metazona 2.30–2.85 mm. Pronotal margins distinctly serrate, the longer teeth interspersed with 1–3 slightly smaller teeth. Larger teeth black ventrally. Prozona 5.2–5.6 mm long, strongly tuberculate. Metazona 22.7–24.2 mm long, 4.3–4.6 times as long as prozona, keeled, triangular in cross-section, tuberculate laterally and particularly

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along the keel. Tubercles at supracoxal dilatation heavily developed, with a smaller anterior and a longer posterior process, the latter 0.7–0.9 mm long, with black apex. Prosternum as in male, basisternal process more strongly developed, callous spots comparatively more distal.

Fore legs (Fig. 5) more robust than in male. Coxae about half as long as prothorax, 13.5–14.5 mm long, more distinctly banded, more strongly tuberculate along the ventral margin, dorsal margin whitish, with 7–8 blunt teeth interspersed with smaller teeth. Apical lobes slightly overlapping. Anterior femur 15.6–16.9 mm long and 2.20–2.35 mm wide, with some tubercles. Dorsal margin serrulate, sinuous. Posterior side with a more distinct banding. Spination formula as in males. One female shows a supernumerary postero-ventral spine of small size, a very uncommon aberration in cernomantodeans. Anterior tibia 8.0–8.8 mm long, with 10–12 postero-ventral and 16–18 antero-ventral spines.

Meso- and metathorax patterned like in the male, with a DNK ear. Mid and hind legs somewhat inflated at base, brownish, dark-spotted and with two annulations. Mid and hind tibiae as in the male.

Wings very short, barely reaching second abdominal tergite. Tegmina 9.8–10.4 mm long and 4.6–5.1 mm wide, 0.35–0.37 times as long as pronotum, opaque. While the costal field is always of a light tan, the color of the discoidal field may vary and usually corresponds to the coloration of adjacent abdominal tergites (Figs. 1, 8–9, 11). Costal field 1.7–2.0 mm wide, evenly rounded. Jugal veins black. Alae (Fig. 4) very short, costal and discoidal field wine-red, except the very tip, which is light brown, anal field black.

Abdomen slightly widening towards apex (Figs. 1, 8–9). Tergites with a small keel and a dark median mark at posterior end of segment, with a paramedian pair of blackish depressions (barely discernible in some specimens), and a second, more rounded pair of depressions laterocaudad from the first. Sternites dark-spotted, and with a paramedian blackish pair of depressions. Supra-anal plate with sinuous margins and rounded apex.

O o t h e c a (Figs. 7, 15, 17, 19–20): Elongate, trapezoid in cross-section, and of a pinkish-tan color. There is only one layer of eggs arranged into four rows (less towards the ends), so width and height of the egg-bearing part are fairly constant, while its length depends on the amount of eggs deposited by the female. The anterior and posterior ends are devoid of eggs and narrow into a slightly undulating tip of varying length. The measurements of two typical egg-cases are: total length 39 and 70 mm, length of egg-bearing part 23 and 48 mm, width 5.4 and 6.7 mm, height 5.2 and 5.8 mm, respectively. Nymphs emerge on the dorsal side by pushing apart the thin, alternating, slab-like lamellae of the exit zone. However, oothecae are usually deposited on the underside of leaves, so nymphs hang downwards when emerging.

F i r s t i n s t a r (Fig. 20): Relatively large compared to both the size of the egg and of the adult. The measurements of a typical first instar specimen are: length of body 19.5 mm, length of head 1.5 mm, width of head 2.55 mm, length of antennae 10.5 mm, length of pronotum 7.9 mm, of prozona 1.5 mm, of metazona 6.4 mm, width of pronotum at supracoxal dilatation 1.3 mm, fore coxae 3.3 mm, fore femora 4.1 mm, fore tibiae 2.1 mm, mid femora 5.05 mm, mid tibiae 4.5 mm, hind femora 6.3 mm, hind tibiae 6.2 mm.

Coloration patterns, particularly leg bandings, more distinct than in adults. Frontal shield more transverse, about twice as wide as high. Head with trapezoid blackish pattern on both sides of the coronal suture, and a blackish spot on juxtaocular bulges. Additional blackish spots on posterior side of head. Pronotal margins smooth, prozona blackish anteriorly, additional black spots on metazona where tubercles would appear in later instars. Prosternum with an interrupted submarginal blackish stripe. Mesosternum with a median stripe, two shorter paramedian stripes, and a lateral stripe on each side. Dorsal margin of fore coxa with a multiply interrupted black line. Anterior side with four dark spots: a very distinct subbasal one, a very weakly expressed one at proximal fourth, a weakly pronounced one at middle, and a very conspicuous ellipsoid one subapically. Fore femur with five spots along antero-ventral margin: near base, just proximal of claw groove, just distal of claw groove, at 12th antero-ventral spine, and distal of femoral brush. All spines of the tibiofemoral armature emerge from distinct, more or less conical sockets. The first discoidal spine is morphologically different from the remaining three: it is a thin and elongate seta almost as long as the third discoidal spine. Antero-ventral and postero-ventral spines of same number as in adults, arranged in a similar fashion. Fore tibiae with 10 postero-ventral and 14 regular antero-ventral spines plus a very small seta proximally. Hind metatarsus twice as long as remaining segments combined.

Diagnosis

The discovery of females 140 years after the male was described further corroborates the validity of the genus *Tagalomantis*, resurrected from synonymy by Roy (2001), and confirmed by Shcherbakov (2012) after the study of the male genitals. Aside from a different number of postero-ventral spines on the fore tibiae, females of *Tagalomantis* are easily distinguished from those of *Euchomenella*, among other characters, by the possession of two prominent tubercles on the pronotum, by a less elongate prothorax (less than half of body length), and by the color of the hind wings. *Tagalomantis* is distinguished

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from *Indomenella* Roy, 2008 by a more elongate prothorax (ratio metazona/prozona 4.3–4.9 vs. 3.2–3.8 in *Indomenella*), a different number of postero-ventral spines on the fore tibiae, the pair of pronotal tubercles, and by differently shaped and colored wings in both males and females.

The males of the Panay population exhibit slight morphological differences when compared to specimens from the type locality. Thus, body size is greater than on Luzon: pronotum length 19.8–21.4 vs. 18.7–19.5 mm, tegmen length 30.4–32.9 vs. 27.0–28.5 mm. The only available published body length of Luzon males is the 50 mm given by HEBARD for his specimen. The 30 mm in SHCHERBAKOV (2012) are a typographic error; the true length of the specimen is 46 mm (Shcherbakov pers. comm.). Also, the 58 mm published by SAUSSURE (1870) for the type seem to have been inaccurate considering its pronotum length and proportions in this species; an estimate comparable to HEBARD's specimen can be considered more likely. Additionally, in Panay specimens the discoidal and anal fields of both wings are more infumate and more mottled distally than in Luzon specimens. The pronotal tubercles are very small and indistinct in Luzon males, while they are rather prominent in Panay specimens (Fig. 3). Also, the number of the postero-ventral spines of the fore tibiae is slightly below the values observed in Luzon specimens (10–11 vs. 11–12).

However, the values of the only known Luzon female fall into the range of Panay specimens: body length 65 mm, head width 6.1 mm, pronotum length 27.4 mm, pronotum width 3.8 mm, tegmen length 9.5 mm. The ratio pronotum length/body length (0.42) compares to Panay females (0.42–0.46). The specimen has 10–11 postero-ventral spines on the fore tibiae. Its pronotal tubercles are more weakly developed than in Panay specimens. Whether these differences in tuberculation, male body size, and male wing color justify a subspecific separation of the Panay population must await the study of more Luzon specimens, in order to evaluate the morphometric ranges of the species. Also, neighboring islands like Mindoro and Negros should be screened for the occurrence of additional populations. Anyhow, the genitalia of Luzon and Panay specimens are virtually indistinguishable.

Life history

Habitat

Tagalomantis manillensis is a forest species. Despite several cumulative months of sampling activity in all types of available habitats, this species has never been encountered in heavily degraded woodland and open areas. However, it is not confined to primary forests, but also found in old secondary and plantation forests, as long as they provide closed canopy conditions. Yet, *T. manillensis* avoids deep shade but is found at locations where sunflecks penetrate the canopy and provide a slightly warmer and drier microclimate. For this reason, abundances in secondary forest understorey may be higher than in primary forest, due to a lower and less structured canopy. Most specimens at Sibaliw were actually found in the secondary forest surrounding the station, while only very few were encountered in the adjacent primary forest. Whether this is due to overall lower abundances, a diluting effect of the structurally richer understorey, or to activity shifts of the mantids to higher strata (and out of the range of the observer) in primary forests remains unknown at the time. In this context it is to be noted that the secondary forests concerned were all adjacent to or enclosed by primary forest, and thus may experience a constant influx of specimens from the primary forest source. Isolated secondary forests did not produce specimens so far.

Preferred perches are more or less filigree plant assemblages like climbing screw and rattan palms, or fern thickets. Living plants are a prerequisite, while dead plant material, although contributing to their camouflage (Fig. 14), is not. A mixture of both provides the best perch opportunities: while living plant tissue attracts potential insect prey, decaying plant matter nearby provides concealment from predators during daytime. For example, one extensive bracken field building up the ground cover in a part of the secondary forest around Sibaliw harbored a substantial *Tagalomantis* population over the whole course of the study. Bracken thickets provide a good mixture of living and dead plant tissue and are not too shady, while allowing the mantids to conceal themselves underneath the fronds. However, the species is also found in trees, tree ferns, and among vines and epiphytes.

T. manillensis has generalistic diet requirements. Captive individuals will catch any prey item of appropriate size, and can be maintained on standard prey taxa well-tried in praying mantid culturing techniques (YAGER 1999, HESSLER et al. 2008, MCMONIGLE 2013), that is Diptera, Zygentoma, Orthoptera, Blattodea, and Lepidoptera. In nature, an important part of their diet is made up of orthopterans (Fig. 12).

Daily activity rhythms

During daytime the mantids choose a highly cluttered perch, usually closer to the ground or inside vegetation, which conceals them from optically oriented predators. By night activity is higher, and the mantids tend to sit more exposed in the vegetation, or, in the case of adult males, actively search for potential mates. Thus, searching for the species by night is more promising. Individual specimens could be encountered at the same or a nearby place on consecutive nights, while a search by day at the same spot often failed to produce the specimen. Main activity time for males when engaged in long-distance searching for females seems to be just after sunset, as most individuals arrived at the station lights between 18.30 and 19.00 h. This is considerably earlier than other species from the

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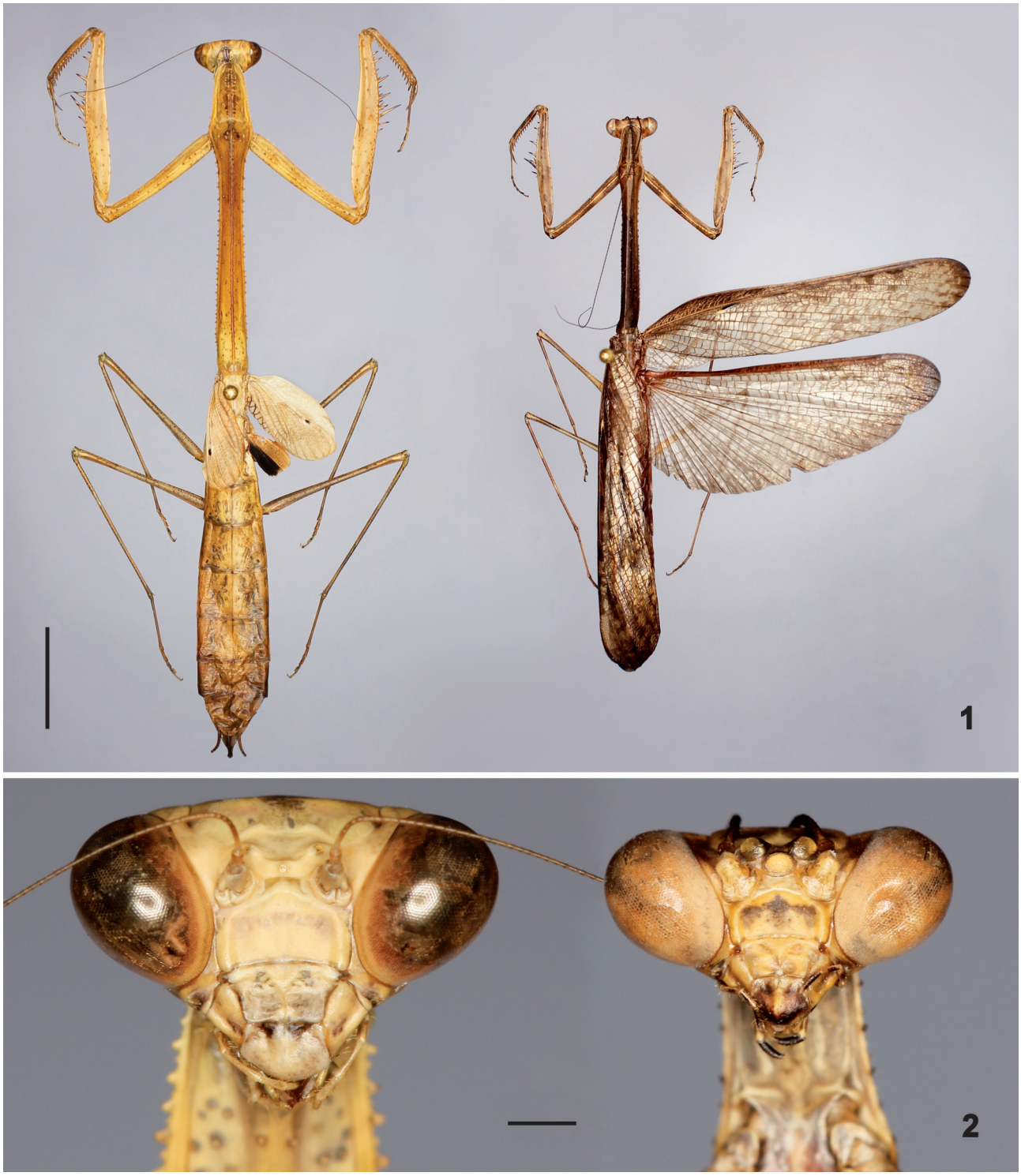

Figs. 1–2. *Tagalomantis manillensis*. – **1**. Dorsal habitus, ♀ (left) and ♂ (right). **2**. Head, anterior view, ♀ (left) and ♂ (right). – Scale bars: 10 mm (1), 1 mm (2)

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Figs. 3–5. *Tagalomantis manillensis*. – **3**. Prothoraces of two ♀♀ (top and center) and ♂ (bottom) in lateral view. **4**. Hind wing of ♀. **5**. Fore leg of ♀ in posterior (left) and anterior view (right). – Scale bars: 5 mm.

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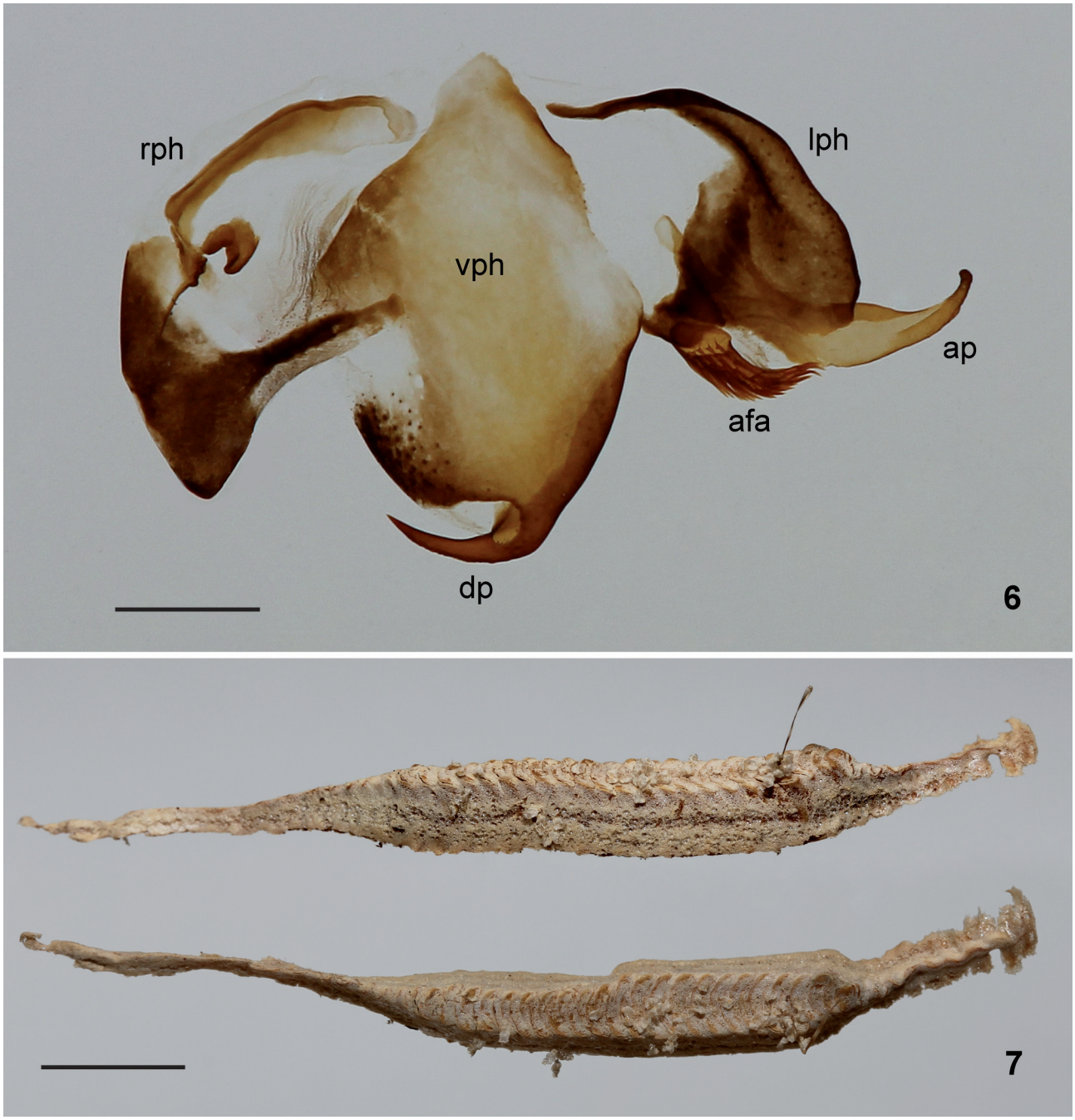

Figs. 6–7. *Tagalomantis manillensis*. – **6**. Male genitalia, ventral view. **7**. Ootheca in dorso-lateral and dorsal view. – Abbreviations: afa = phalloid apophysis; ap = apical process (titillator); dp = distal process; lph = left phallomere; rph = right phallomere; vph = ventral phallomere. – Scale bars: 1 mm (6), 10 mm (7).

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Figs. 8–13. *Tagalomantis manillensis*, life appearance. – **8**. Light-colored ♀ without patterning. **9**. Disruptively mottled ♀ (note oblique markings on pronotum). **10**. Adult ♂ (note greenish walking legs). **11**. Pair in copula. **12**. Subadult ♂ eating tetrigid orthopteran. **13**. Second instar nymph.

same habitat, which used to arrive between 20.30 and 21.30 h (e. g. *Amantis aeta* Hebard, 1920, *Haania* sp., *Leptomantella lactea* [Saussure, 1870], *Hierodula* sp.).

Defense mechanisms

Switching between night and day perches is only one of the species' defensive repertoires. Its morphology plays an important part as well. Despite being less elongate than its relative *Euchomenella*, *Tagalomantis* also belongs to the 'long-bodied stick-mantis' ecotype (sensu Edmunds 1976; see also Robinson 1969b, 1990, Edmunds & Brunner 1999). This holds particularly true for nymphs (Figs. 12–13) and adult females (Figs. 8–9, 11, 14–17), while adult males (Figs. 10–11) are less stick-like due to

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their fully developed wings. Nevertheless, they are also camouflaged by their cryptic color pattern. The species is polyphenic and able to adopt the color and pattern of its background during ontogeny. While fully green individuals have not been encountered (and probably do not exist), the observed colors range from light tan to dark brown, with a disruptive pattern being non-existent to highly developed (Figs. 8–11).

The specialized morphology is enhanced by behavioral components. ROBINSON (1969a, 1969b) and EDMUNDS (1972) point out that mantids do not use special cryptic resting positions by day like many katydids and phasmids, because such a position does not allow for a quick predatory strike with the fore legs in case of an approaching prey item. Due to their good eye-sight (MALDONADO et al. 1970, ROSSEL 1979, KRAL 1999, 2012) mantids can afford to assume the cryptic position only when a predator approaches and spend the rest of the time ready to strike at prey. In the case of *Tagalomantis*, there are several 'concealing postures' that may be used interchangeably, even by the same individual, upon signs indicating the approach of a potential predator (object movements, substrate vibrations).

Pressing against the perch: when approached by a potential threat the mantid brings its body in close proximity to the substrate it hangs on. This reduces betraying shadows and, in case of leaves as perch, visibility from above. Fore legs are closed under the body, while the position of other legs may vary. In its most expressed form, the walking legs are protracted and kept in line with the body

Figs. 14–18. *Tagalomantis manillensis*, life history aspects. – **14**. ♀ (at center) camouflaged among dry bracken fronds. **15**. ♀ in stick attitude (type I) (note protracted fore and mid legs and flattened abdomen). **16**. ♀ in stick attitude (type II) (note bent body and angled fore femur). **17**. ♀ in stick attitude (type I) hiding behind ootheca. **18**. Enlarged pronotum of ♀ showing mossy overgrowth.

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Figs. 19–20. *Tagalomantis manillensis*, brood care. – **19**. Egg-guarding posture (note position of antennae and mossy overgrowth on cuticle). **20**. Same ♀ after emerging of nymphs.

axis. While the mid legs are bent forward, the hind legs are outstretched backwards. This represents one of two types of full stick attitudes.

Hiding behind perch (Fig. 17): like above, but with the difference that the mantid moves on the opposite side of the perch (as viewed from the predator's perspective) and conceals itself behind it. When the predator changes position with respect to the mantid's resting place, the mantid follows, keeping the perch between itself and the disturbance.

Turning to the side (Fig. 15): if the resting place does not allow the mantid to employ one of the two strategies described above, that is, if it is not concealed from view, it flattens the abdomen dorso-ventrally and turns the slim side towards the predator. As in case of hiding behind the perch, when the disturbance changes position, the mantid turns in such a way that it always presents the slim side. This behavior is intended to decrease the betraying outline of an insect body by enhancing stick resemblance and as such is a component of true masquerade.

Fore leg stretching (Fig. 16): like in the previous case, this behavior comes into play when the mantid cannot conceal itself from view. The body is kept in place, but sometimes bent to a certain degree, and the fore legs are stretched forward. While the coxae are adjacent, the femora can adopt two different configurations. They are either both kept in line with the coxae and the fore body, or one of the femora is bent at an angle away from the body ('side branch effect'). The head is concealed by turning it to the side, so that its width is kept in line with the body axis. This represents the second type of complete stick attitude.

In all these cases, the mantid keeps the head turned towards the disturbance. As can be seen from the examples, the range of primary defenses in this species spans the whole range from crypsis to true masquerade (for definitions see Edmunds 1990, Endler 2006, Skelhorn et al. 2010, Diamond & Bond 2013). In spite of the occasionally exhibited stick attitude, the first two strategies are better classified as cryptic, since the background-matching color

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Tab. 1. Brood care in Mantodea. – AT = Afrotropical; MD = Madagascan; OR = Oriental; NT = Neotropical.

Taxon	Region	Available details	Reference
Cardioptera brachyptera Burmeister, 1838	NT	Female guards ootheca until 2 days after hatching	Terra 1992
Photina amplipennis Stål, 1877	NT	Female guards ootheca until a few days after hatching	Terra 1996
Chromatophotina awajun Rivera, 2010	NT	Female guards ootheca	Rivera 2010
Leptomantella lactea (Saussure, 1870)	OR	Female always in proximity of oothecae; female discriminates between nymphs and prey	Schwarz unpubl.
Aetaella bakeri Hebard, 1920	OR	Female always in proximity of oothecae; female discriminates between nymphs and prey	Schwarz unpubl.
Aetaella sp.	OR	Female always in proximity of oothecae; several oothecae are deposited in one location; female discriminates between nymphs and prey; individuals of various developmental stages may be found in close proximity	Schwarz unpubl.
Astape denticollis Stål, 1877	OR	Several oothecae are deposited in one location; female always in proximity of oothecae	Lieftinck 1953
Tarachodes afzelii (Stål, 1871)	AT	Female guards ootheca until hatching	Ene 1964, Gillon & Roy 1968, Edmunds 1976
Tarachodes maurus (Stål, 1856)	AT	Female guards ootheca until hatching	Faure 1940
Tarachodes bicornis Giglio-Tos, 1911	AT	Female guards ootheca until her death	Faure 1940
Tarachodula pantherina (Gerstaecker, 1869)	AT	Female guards ootheca	Preston-Mafham 1990
Galepsus cliquennoisi Roy, 2005	AT	Female guards ootheca	Roy 2005
Paragalepsus toganus (Giglio-Tos, 1911)	AT	Female guards ootheca until hatching	Gillon & Roy 1968
Pseudogalepsus modestus (Gerstaecker, 1869)	AT	Female guards ootheca	Hevers & Liske 1991
Pseudogalepsus nigricoxa (Sjöstedt, 1909)	AT	Female guards ootheca until hatching	Schwarz unpubl.
Pyrgomantis pallida Giglio-Tos, 1917	AT	Female guards ootheca until hatching	Gillon & Roy 1968
Oxyophthalmellus somalicus (Rehn, 1911)	AT	Female guards ootheca until a few days after hatching	Preston-Mafham & Preston-Mafham 2005
Brancsikia aeroplana Lamberton, 1911	MD	Female guards ootheca until hatching	Schulze pers. comm.
Brancsikia freyi (Brancsik, 1893)	MD	Female guards ootheca	Peyrieras & Vadon 1963
Theopropus elegans (Westwood, 1832)	OR	Female guards ootheca	Leong & Teo 2008
Theopropus borneensis Beier, 1942	OR	Female guards ootheca	Shelford 1903
Hymenopus coronatus (Olivier, 1792)	OR	Female found in proximity of ootheca	Shelford 1903
Tagalomantis manillensis (Saussure, 1870)	OR	Female guards ootheca until 1–2 days after hatching	present paper
Deroplatys truncata (Guérin-Méneville, 1843)	OR	Female guards ootheca until 1–2 days after hatching	Grabowitz 1999, Kunz 2008, Delfosse 2009
Deroplatys lobata (Guérin-Méneville, 1838)	OR	Female guards ootheca until 1–2 days after hatching	Grabowitz 1999, Kunz 2008, Delfosse 2009
Deroplatys trigonodera Westwood, 1889	OR	Female guards ootheca until 1–2 days after hatching	Schwarz unpubl.
Hierodula unimaculata (Olivier, 1792)	OR	Female guards ootheca until her death	Polak 1933
Antemna rapax Stål, 1877	NT	Female guards ootheca	Schwarz unpubl.
Stagmomantis theophila Rehn, 1904	NT	Occasional observations of females guarding ootheca	Salazar 1999

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pattern together with the evasive behavior decrease visibility (and hence discovery). The last two strategies come into play when the first two cannot be employed and are not intended to conceal the mantid's presence, but to signal inedibility through stick resemblance (Robinson 1969a, 1969b, Edmunds 1972, 1976, Edmunds & Brunner 1999). The same effect also disguises specimens resting against a non-matching background (e. g. plain green vegetation).

In case of increasing threat, the mantid may jump off the substrate, run, or (in case of males) fly away. A partial deimatic display was observed only once. In this species it seems to be rare, and perhaps employed mainly against similar-sized conspecifics and small predators, interactions which were both not witnessed during the study.

Reproduction and brood care

Despite several dozen individuals encountered over the course of the three years, only one copulation could be witnessed in nature (Fig. 11). Captive individuals refused to mate. The copulation is typical for mantids and shows no peculiarities. On the other hand, this species exhibits brood care in the form of ootheca guarding (Figs. 15, 17–20). This behavior is more common in mantids than recognized previously, and since Polak's (1933) and Faure's (1940) first mention of the phenomenon, a substantial amount of species has added to the list, although most records are scattered in the literature or not published at all. A compilation is given in Tab. 1.

Tagalomantis females deposit their oothecae on the underside of elongate leaves or fern fronds. Then they position themselves with the prothorax above the newly-formed egg-case, and spend most of the incubation time of around five weeks in that position. The antennae are bent towards the ootheca, each antenna passing at some distance from the lateral margin of the egg-case without touching it (Fig. 19). The female does not need to feed during this time, but if a prey item happens to pass by at close distance, it will leave the ootheca to capture it. Upon finishing its meal, the female returns to its egg-case reassuming the guarding position. Despite guarding efforts, oothecae are sometimes raided and destroyed by ants.

Because of the stationary habits during egg-guarding, some parts of the body, particularly pronotum and walking legs, might be overgrown by algae and mosses to a certain degree (Figs. 18–19).

Epizoic growth has so far only been reported in the neotropical leaf mantid genus *Choeradodis* by Lücking et al. (2010). *T. manillensis* females in the wild can lay and guard two or more oothecae during their lifetime, so epizoic growth, once established, may accumulate over the months. In general, however, it is not very common, and most encountered *Tagalomantis* females were devoid of it.

Nymphs hatch during early morning hours (N = 5) and will aggregate on and around the mother for the next two to three days (Fig. 20). When the first nymphs start to disperse, the mother leaves egg-case and remaining nymphs behind and looks for another perch. Whether lack of aggression against the nymphs persists beyond this stage could not be evaluated in the wild. However, on more than one occasion nymphs of different developmental stages were encountered at a small distance from an adult female, presumably the mother, in the same bracken thicket. These casual observations in the wild clearly deserve further study.

Phenology

Both nymphs and adults are basically found year-round. Field data obtained so far suggest about five weeks incubation time and four months postembryonic development. This seems to indicate a bivoltine generation cycle, but yet lacking development data gained from laboratory cultures are needed to validate this assumption. Average longevity in the wild is not known, but individual females attained a life span of at least four to five months, during which 2–3 oothecae were laid. The lack of a severe dry season in combination with long adult life span (of females at least) are probably the reason why distinct phenological patterns are not seen in Panay populations of this species.

4 Discussion

Systematic placement

Beier (1935) not only synonymized *Tagalomantis* with *Euchomenella*, he also united all genera with an elongate body without lobes and more or less brachypterous females into one tribus. It was named Angelini after the neotropical genus *Angela* Audinet-Serville, 1839, the oldest of the genera included, and raised to subfamily level in Beier (1964). Besides *Angela*, Angelini originally comprised the likewise neotropical *Thespoides* Chopard, 1916, palearctic *Sinaiella* Uvarov, 1924, the afrotropical genera *Stenopyga* Karsch, 1892 (including three subgenera), *Leptocola* Gerstaecker, 1883 and *Agrionopsis* Werner, 1908, and oriental *Euchomenella* and *Mythomantis* Giglio-Tos, 1916. *Sinaiella* was later moved from Angelinae to Oxyothespinae by Kaltenbach (1982). Aside from this, no systematic action has been undertaken over the decades, so the composition of the subfamily was reprised unchanged in Ehrmann's (2002) catalogue. Otte & Spearman (2005) listed the same genera, but added without comment *Biolleya* Saussure, 1897, which is actually a blattodean genus (Roth 1971, Beccaloni 2014).

The first new genus to be added to the subfamily for more than 70 years was *Indomenella* Roy, 2008 created for a species that had been described some years before as *Euchomenella indica* Ghate & Mukherjee, 2004. One year later, Vyjayandi et al. (2009) described *Cotigaonopsis*, likewise from India, and placed it in Angelinae. On the

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other hand, the systematic position of *Mythomantis* as a member of Angelinae was doubted by Roy (2001), while that of *Tagalomantis* was questioned by Shcherbakov (2012) due to differences in the male genitalia between this genus and its supposed closest relative *Euchomenella*.

Indeed, recent mantodean phylogenies gained from molecular and morphological data did not support the monophyly of most classic families and subfamilies, including Angelinae (Yager & Svenson 2008, Svenson & Whiting 2009, Agudelo Rondón 2015). This subfamily was shown to be polyphyletic, with neotropical *Angela* widely separated from the paleotropical genera (Yager & Svenson 2008, Agudelo Rondón 2015). The latter, though members of the same clade, did not resolve as sister taxa either. While afrotropical *Stenopyga* and *Leptocola* were found to be sister to likewise afrotropical Danuriini, *Indomenella* and *Euchomenella* clustered with *Deroplatys* Westwood, 1839 (Svenson & Whiting 2009), an oriental genus of leaf-like-looking mantids with foliaceous expansions on pronotum, walking legs and abdomen. The other genera were not included in the analysis. Nevertheless, it became clear that Angelinae should be restricted to the neotropical members and systematic changes would become necessary to accommodate the paleotropical genera.

A first step towards an improved systematic arrangement was taken by Schwarz & Helmkampf (2014), who moved *Mythomantis* to Deroplatyinae alongside *Pseudempusa* Brunner de Wattenwyl, 1893 due to apomorphies in both genital and external morphology. At the same time they transferred *Brancsikia* Saussure & Zehntner, 1895 to Hymenopodidae. Deroplatyinae is now restricted to the three genera *Deroplatys*, *Pseudempusa* and *Mythomantis*. Genital similarities of Deroplatyinae and some oriental members of former Angelinae were noted but further systematic action was not undertaken due to ambiguous data. In the same year, *Thespoides* was shown to be based on a chimerical individual (Rivera 2014), rendering Angelinae monogeneric. Further, *Afrothespis* Roy, 2006, created after females and left incertae sedis so far, could be placed alongside *Stenopyga* after the discovery of males (Roy & Schwarz 2014).

Among the oriental 'angeline' genera, *Cotigaonopsis* exhibits the most unusual morphology, most notably being the micropterous wings with an extended anal field in the tegmina, and the triangular supra-anal plate. Unfortunately, the figured genitalia were obviously damaged during preparation and both insufficiently described and figured. Nevertheless, the aberrant morphology of this genus required the re-examination of its systematic position, and after a thorough consultation of the original description it became evident that this genus is not related to *Indomenella*, *Euchomenella*, or *Agrionopsis* (the genera the authors compared their new genus with), but is a member of Rivetinini (sensu Ehrmann 2002). More precisely, it is most closely related to Indian *Deiphobe* Stål, 1877, *Deiphobella* Giglio-Tos, 1916, and *Indothespis* Werner, 1935. This systematic position is supported by the triangular and keeled supra-anal plate, the claw-groove in the proximal half of the femur, and the enlarged and blackened anal field of the tegmina. More importantly, the figured genitalia show a spine on the posterior lobe of the phalloid apophysis, as well as a well-developed anterior lobe. These features are not seen in oriental 'angeline' genera, but are typical for Rivetinini (see, for instance La Greca 1977, Kaltenbach 1982, La Greca & Lombardo 1983, Lombardo 1993). The eye-spot on the alae in Rivetinini, which already caused some systematic confusion in the past (Schwarz & Helmkampf 2014), is missing in *Cotigaonopsis*, but this may be due to the strongly reduced alae in the latter. The elongate body, which prompted Vyjayandi et al. (2009) to assign *Cotigaonopsis* to Angelinae, is actually also seen in some Rivetinini, like *Deiphobella* (see Wood-Mason 1878, pl. 35), or *Ischnomantis* Stål, 1871. On the other hand, features like the blackened and enlarged anal field, the elongate and keeled supra-anal plate, and a rounded apophysis with a spine, are not seen in *Indomenella*, *Euchomenella*, or *Tagalomantis*, neither alone nor in combination. Therefore, I transfer here *Cotigaonopsis* from Angelinae to Rivetinini.

The three remaining genera are morphologically homogenous, featuring elongate bodies, exophthalmic eyes, femora with the claw-grove in the distal half, supra-anal plates with rounded apices and sinuate margins, macropterous males, and strongly brachypterous females. Further, their sistergroup relationship to Deroplatyinae, first indicated by molecular data (Yager & Svenson 2008, Svenson & Whiting 2009) is supported by genital traits. The two groups are united by a strongly sclerotized, slightly curved and acute phalloid apophysis, and by a short and strongly curved distal process (Roy 2007, 2008, Shcherbakov 2012, Schwarz & Helmkampf 2014). *Tagalomantis*, *Indomenella* and *Euchomenella* are distinguished from Deroplatyinae by their strongly brachypterous (vs. meso- to macropterous) females, the lack of the pale subapical band on the alae (Schwarz & Helmkampf 2014), and by the lack of the sclerotized ridge on the left side of the ventral phallomere produced into a rounded lobe on the distal side of the process (ridge secondarily reduced in *Mythomantis*).

The present data support the current systematic placement of *Tagalomantis* alongside *Indomenella* and *Euchomenella*, but also a close relationship of these three genera with Deroplatyinae. The shape of the phalloid apophysis is shared with *Pseudempusa* (Schwarz & Helmkampf 2014), and, to a lesser degree, *Deroplatys indica* Roy, 2007. *Tagalomantis* also shares with Deroplatyinae a distinct dorso-ventral sinuation of the prothorax, and the two par-

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amedian dark markings on the metazona (Schwarz & Helmkampf 2014). *Indomenella* and *Euchomenella* have a similar number of postero-ventral spines on the fore tibiae. The shape of the phalloid apophysis of *Indomenella* can hypothetically be derived from the shapes exhibited by *Tagalomantis* and deroplatyines. It is secondarily strongly curved to the right. In addition, a spine is found proximal of the basal lobe of the ventral phallomere (Roy 2008). *Euchomenella* features secondarily simplified genitalia (Roy 2001) and the most extreme elongation of the body seen in any of the genera concerned.

Although some of the characters mentioned above are also seen in other mantodean taxa, the combination of all aforementioned traits is only seen in the oriental stick mantids and qualifies them as monophyletic, and as not being the sistergroup of other stick mantids. An elongate body is also found in Hoplocoryphinae, some Rivetinini, Heterochaetinae, Danuriini, Archimantini, and *Rhodomantis*, but these groups exhibit overall different external and genital morphology (e. g. Beier 1954, La Greca 1954, Roy 1975, La Greca & Lombardo 1987, Milledge 1997, 2014, Ehrmann 2002). Metazonal tubercles are also seen in *Scolodera* Milledge, 1989, *Mellierella* Giglio-Tos, 1915, and Mellierinae. However, their external morphology, particularly pronotal shape, differs considerably from the genera treated here. Molecular phylogeny resolved the latter two (see comments in Milledge 2014) as very early 'Mantidae' lineages (the name is used here in a restricted sense for X_1X_2Y mantids only, corresponding to node 267 in Svenson & Whiting 2009).

It is worth mentioning that the males of most long-bodied stick-like genera, even those capable of flight, are brachypterous to mesopterous, while the oriental 'angeline' genera, Deroplatyinae, and the enigmatic Madagascan genus *Euchomena* feature macropterous males. The afrotropical 'angelines', which in other respects are morphologically most similar to the oriental genera, also have brachypterous or mesopterous males. Their genitalia differ from those of their oriental analogues: they exhibit a short, more or less straight distal process, and an anterior lobe on the phalloid apophysis (Beier 1954, Roy 1963, 1973, Roy & Schwarz 2014). The relationships of these African 'angelines' still remain to be elucidated. Molecular data suggest a sistergroup relationship to Danuriini (Svenson & Whiting 2009).

The oriental members of former Angelinae, however, can be united into one tribus. I propose therefore the name Euchomenellini Giglio-Tos, 1916, since *Euchomenella* was the first of the three genera to be named, and because Giglio-Tos already used the family-group name in 1916 (as Euchomenellae). The name Euchomenellini has also been proposed by Agudelo Rondón (2015, p. 96) in his phylogenetic analysis of neotropical Photininae (= Photinainae sensu Svenson & Branham 2007). No new morphological or molecular evidence is presented, though. Instead, the author justifies this step because of the results presented by Svenson & Whiting (2009) and Wieland (2013). However, contrary to the phylogenetic tree published by Svenson & Whiting (2009), Agudelo Rondón (l. c.) unites Euchomenellini with (some of) the afrotropical 'angeline' genera (named Leptocolini Giglio-Tos, 1916) into a subfamily Euchomenellinae at the exclusion of Deroplatyinae and Danuriini. Other recent papers on the systematics of this group are ignored (Vyjayandi et al. 2009, Schwarz & Helmkampf 2014, Roy & Schwarz 2014). As a consequence, his Leptocolini lacks *Afrothespis*, and his Euchomenellini lacks *Cotigaonopsis* but includes *Mythomantis*. Therefore, Agudelo Rondón's (2015) higher-level systematic arrangement is not followed here.

Based on the morphological evidence discussed above, Euchomenellini as defined in this study is placed among Deroplatyinae Westwood, 1889, alongside *Deroplatys*, *Pseudempusa*, and *Mythomantis*. The latter now deserve an own tribus, Deroplatyini Westwood, 1889. Whether afrotropical Leptocolini and Danuriini can be united with Deroplatyinae into one family must await further studies.

Life history and conservation

Daily activity patterns of this species fit what is known from other mantids. Locomotor and sexual activity is highest during dusk and early night-time (e. g. Edmunds 1986, Cumming 1996, Hurd et al. 2004, Gemeno et al. 2005, Perez 2005, Helmkampf et al. 2007, Maxwell et al. 2010, Berg et al. 2011, Schwarz & Konopik 2014), while the days are spent relatively motionless to avoid predation by optically oriented predators. On the other hand, feeding is not dependent on daytime. Praying mantids show several physiological adaptations to these different circadian demands. Thus, pigment migration and lower threshold values of electroretinograms enhance compound eye sensitivity at dusk (Friza 1928, Beier & Jaus 1933, Horridge et al. 1981, Popkiewicz & Prete 2013, Schirmer et al. 2014). This is accompanied by a concurrent increase in locomotor activity of the walking legs and in the sizes of the stimuli that elicit tracking and striking (Schirmer et al. 2014).

Translated into behavior, the relative motionlessness and higher stimulus thresholds during daytime result from the need to hide from optically oriented predators. Smaller prey items are captured, but larger prey elicits comparatively fewer attacks. A likely explanation is that the handling time required to capture and consume such prey increases the likelihood of being discovered by predators. From the viewpoint of nutritional intake, the disadvantage is negligible, since large prey items are scarce during the day at the mantid's resting place, because other arthropod groups face a similar predation risk. After sunset, *Tagalomantis* leaves the day perch and assumes a more exposed position, profiting from decreased predation pressure and

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an increased activity of potential prey species. Stalking larger prey like Orthoptera is advantageous now, since the nutritional intake outweighs predation risk.

Morphologically and ecologically, *Tagalomantis* represents an interesting transitional stage between cryptic mantids, characterized by an unspecialized morphology and background-matching color patterns (including disruptive markings and polyphenism), and masqueraders, which exhibit a highly specialized morphology and associated behaviors signaling non-edibility. More importantly, it provides a good example of how the latter might evolve from the former. The wide range of protective attitudes used by this species in combination with their unpredictability is part of the defensive strategy (Robinson 1969b).

Of the three euchomenellinine stick mantid genera, *Tagalomantis* is the most robust (or least elongate) one. Even though the ratio metazona/prozona is higher than in *Indomenella*, pronotum and abdomen are much more slender in the latter. Unfortunately, not a single width measurement is given in its original description, but the figures are informative in this regard.

The behavioral components exhibited by stick mantids, like fore leg stretching and flattening, also occur in several lineages of mantids with less specialized morphology (Edmunds 1976, Edmunds & Brunner 1999, Schwarz unpubl.), and are thus more ancient than the morphological adaptations. It may be argued that it were these behavioral pre-adaptations which triggered the evolution into a stick-resembling ecotype in many arboricolous taxa. This explains its frequent occurrence in several unrelated mantodean lineages when compared, for example, with cases of leaf resemblance. The latter relies much more on morphology than on special postures, and may evolve from quite different 'starting points'. That is why unrelated leaf mantid lineages are quite different from one another and caused less systematic confusion in the past than stick-like mantids (but see Beier 1935). Among the leaf-like *Deroplatys*, several species also practice flattening and fore leg stretching (Schwarz unpubl.). This underscores their systematic position alongside a group of predominantly stick-resembling genera.

The shape of the *Tagalomantis* ootheca differs from that of related genera (*Euchomenella*, *Pseudempusa*, *Deroplatys*), which have ovoid or largely cylindrical oothecae. Its elongate shape may be related to egg-guarding. As can be seen from Tab. 1, egg guarding behavior is widely scattered among the mantodean phylogenetic tree (see Yager & Svenson 2008, Svenson & Whiting 2009, and Wieland 2013 for recent, conflicting phylogenetic hypotheses). It evolved independently from non-guarding ancestors. However, of the taxa given in Tab. 1, *Tagalomantis* is the only stick mantid. An elongate ootheca deposited on the underside of a leaf is less visible and allows the female to exhibit its full defensive repertoire in case of an approaching threat. That is, it does not betray the stick resemblance of the female that guards it. Among related genera, egg-guarding is practiced by some *Deroplatys* species (Grabowitz 1999, Delfosse 2009; incidentally, these are the same species which exhibit flattening and fore leg stretching upon an approaching threat). Their egg-guarding position does not differ much from normal resting position. Both mantid and ootheca are not concealed from view but protected by means of the female's leaf resemblance. *Euchomenella*, on the other hand, does not guard its small and inconspicuous egg-case (Schwarz unpubl.).

The distribution of *T. manillensis* is insufficiently known. The disjunct occurrence on Luzon and Panay, i. e. on not directly neighboring islands and across PAICs, implies that additional Philippine islands may hold populations of this species. However, of the major islands only Luzon, Palawan, Samar and Mindanao still hold substantial amount of forest. The latter two belong together with Leyte and Bohol to the Greater Mindanao PAIC. Despite previous sampling efforts (Hebard 1920, Werner 1922, 1926), no records of this species exist from this faunal sub-realm. Palawan has a very distinct mantodean fauna, showing affinities with the Sunda Shelf islands and differing from that of the oceanic Philippines. Of the genera concerned, only *Euchomenella* is reported from there so far (Beier 1966). In the Western Visayas sub-realm, Masbate, Ticao, Cebu and Guimaras are virtually denuded and already lost forest-dependent endemics (Sammler et al. 2012), so the chances are rather low that *Tagalomantis* populations, if previously existent, may have survived on those islands. Negros holds less than 4 % of montane forest (Heaney & Regalado 1998, Turner et al. 2001). Of the 8 % forest cover on Panay, only 4 % are truly primary, including the last 1 % of lowland forests in the Western Visayas. The remaining are secondary forests and reforestation areas made up of allochthonous trees such as mahogany (*Swietenia macrophylla*) and gmelina (*Gmelina arborea*) (Gaulke 2011).

As explained above, in certain habitat types on Panay the species may be locally abundant; however, in most parts of the NWPP and the CPMR it is only rarely found. On a global scale, the Panay population, the only reported so far from the Western Visayas, suffered 92–99 % habitat reduction, depending on whether montane forests are also inhabited or not. This raises serious conservation concerns. The situation on Luzon is unknown.

The phylogeny and taxonomy of Mantodea as a whole and of most subclades in particular is still not satisfactorily worked out, although the last years saw some milestone contributions (Yager & Svenson 2008, Svenson & Whiting 2009, Wieland 2013, Svenson et al. 2015). Further research on SE Asian and Philippine mantodeans will yield valuable insights into the biodiversity and complex biogeography of the world's most diverse archipelago.

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5 Key to the genera of Deroplatyinae

1 Head without process; frontal shield not keeled; fore legs without lobes; claw-groove in distal half of femur; males macropterous; alae smoky; supra-anal plate without median lobe; cerci not flattened; membranous lobe of male left phallomere not pilose; pronotum either with foliaceous expansion along entire margin or very elongate (at least 5.5 times as long as wide); if with foliaceous expansion, then female tegmina with conspicuous eye-spot-like pattern on ventral side, and distal process of males acute and curved to the right; if pronotum slender, then hind wings of female either mesopterous with eye spot or macropterous with a pale subapical band or strongly brachypterous, and phalloid apophysis of males without anterior lobe. .....(Deroplatyinae) **2**

– Different combination of characters.....other Mantodea

2 Pronotum with foliaceous expansion along entire margin in males and females; ventral side of female tegmina with conspicuous, eye-spot-like pattern. ..... ***Deroplatys***

– Pronotum slender, at most with an expansion along supracoxal dilatation; female tegmina without eye spot..... **3**

3 Hind wings with an eye spot..... ***Pseudempusa***

– Hind wings at most with a pale subapical banding, but without eye spot..... **4**

4 Apical lobes of walking legs strongly elongate; hind wings with a pale subapical band; females macropterous or slightly mesopterous; distal process bifid, boat-shaped..... ..... ***Mythomantis***

– Apical lobes of walking legs not elongate; hind wings without pale subapical band; females strongly brachypterous; distal process differently shaped. **5**

5 Female pronotum longer than half of body length; distal process of ventral phallomere reduced, knob-like; phalloid apophysis very short, with rounded apex. ..... ***Euchomenella***

– Female pronotum less than half of body length; distal process acute, curved to the right; phalloid apophysis well developed, with acute apex. **6**

6 Fore tibiae with at least 10 postero-ventral spines; phalloid apophysis robust, slightly curved to the left, with numerous thick setae; right side of ventral phallomere with a rounded lobe but without a spine; distal process of ventral phallomere slender..... ***Tagalomantis***

– Fore tibiae with 7–8 postero-ventral spines; phalloid apophysis slender, strongly curved to the right; right side of ventral phallomere with a lobe and a robust spine; distal process robust. ..... ***Indomenella***

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Manuscript received: 2.II.2016, accepted: 30.III.2016.

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