

Three new praying mantises from Panay Island, Philippines (Insecta: Mantodea)

Author: Schwarz, Christian J.

Source: Integrative Systematics: Stuttgart Contributions to Natural History, 3(1) : 35-56

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/insy.v03.a2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Three new praying mantises from Panay Island, Philippines (Insecta: Mantodea)

CHRISTIAN J. SCHWARZ

Abstract

Three new species of praying mantids from the forest remnants of Panay Island, Philippines are described and illustrated. *Pliacanthopus (Malayamantis) visayanus* **n. sp.** extends the distribution of the genus, so far only known from Sundaland, to the Philippine archipelago. *Compsogusa rheae* **n. gen. n. sp.** and *Theopompa schulzeorum* **n. sp.** are bark mantids endemic to Panay. The ecological adaptations and the systematic and biogeographic affinities of the new taxa are discussed.

Keywords: bark mantis, insular endemism, new genus, new species, PAIC.

Zusammenfassung

Es werden drei neue Arten von Gottesanbeterinnen aus den noch verbliebenen Wäldern der Insel Panay, Philippinen, beschrieben und abgebildet. *Pliacanthopus (Malayamantis) visayanus* **n. sp.** erweitert das Verbreitungsgebiet der Gattung, die bisher nur von Sundaland bekannt war, um den philippinischen Archipel. *Compsogusa rheae* **n. gen. n. sp.** and *Theopompa schulzeorum* **n. sp.** sind auf Panay endemische Baumrindenbewohner. Die ökologischen Anpassungen sowie die systematischen und biogeographischen Beziehungen der neuen Taxa werden diskutiert.

Contents

1	Introduction	35
2	Material and Methods	36
	Results	
4	Discussion	52
	References	
e		

1 Introduction

The diversity of terrestrial invertebrates in the Philippines is both highly diverse and largely understudied, exemplified by the fact that virtually every recent sampling effort resulted in the description of new taxa (e.g. PARK & BYUN 2008, KREHENWINKEL et al. 2009, JAVIER & COLEMAN 2010, KALKMAN & VILLANUEVA 2011, LOURENS 2011, GIUPPONI & MIRANDA 2012, LOWRY & COLEMAN 2012. FREUDENSCHUSS et al. 2016). This holds also true for smaller insect orders like praying mantids (Mantodea). All data on this group available to date are decades-old expedition collections from Luzon, Mindanao, and Palawan, or without any specific locality. The most important historical contributions are those of STÅL (1877), HEBARD (1920), WERNER (1922, 1926) and BEIER (1966). Preliminary catalogues of the Philippine mantodean fauna were compiled by Bruner (1915) and Werner (1926). The Western Visayas are an endemic-rich faunal sub-province of the archipelago, comprising the islands of the Greater Negros-Panay Pleistocene Aggregate Island Complex (PAIC, see INGER 1954, HEANEY 1985, VORIS 2000). They are notoriously undersampled, with only two Mantodea specimens from Negros referenced in the literature (HEBARD 1920, Roy 2011).

The specimens collected in the years 2010 to 2017 on the island of Panay produced so far three mantodean taxa new to science, the description of which is given below. The new taxa include an undescribed genus and a new generic record for the archipelago. In addition, information on life history is given where available.

Acknowledgements

Work in the Philippines was facilitated by a MOA between Ruhr University Bochum and its Philippine operating arm PhilinCon (www.philincon.org) and the Department of Environment and Natural Resources Region VI. Collections were granted by Gratuitous Permits No. 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 (Kiel, Germany) for useful advice. I thank KRIS ANDERSON (Las Vegas, NV, USA) for communicating the data on the Luzon *Compsogusa* specimen. This study was supported in part by a grant of the Deutsche Forschungsgemeinschaft (CU 4/41-1). This is publication no. 98 of the Philippine Initiative for Conservation of Environment and the People, Inc. (PhilinCon).

2 Material and methods

Region sampled and timeframe

The taxa treated here were collected in the course of five long-term field trips to Panay: July 2010 to April 2011, July 2011 to June 2012, September 2012 to June 2013, July 2014 to June 2015, and August to October 2017. The specimens originated from the Northwest Panay Peninsula Natural Park (NPPNP), and the Central Panay Mountain Range (CPMR), a mountainous ridge stretching north-south along the west coast of the island (Fig. 1). The specimens from the peninsula were collected in the environs of Sibaliw Research Station (11° 49' N, 121° 58' E, ~460 m, Fig. 2). Previously considered to be a part of Buruanga, Aklan (e.g. Javier & Coleman 2010, Schmidt-Rhaesa & SCHWARZ 2016, SCHWARZ 2017), new provincial boundary delineations have revealed it to be located in the neighboring municipality of Libertad, Antique. A characterization of the areas has been given elsewhere (SCHWARZ 2017).

Collection and preparation

The Pliacanthopus male has been lured at night to the light source of Sibaliw Station. All bark mantids were collected by hand. Specimens were killed upon collection by ethyl acetate or ethanol, or were kept alive for some time in order to obtain photographs and life history information. Preserved specimens were immediately dried in silica gel and pinned after several months. Male genitalia were separated from the specimens together with the terminalia and treated for 12-24 hours with 10% water solution of KOH to clear important structures from soft tissues. After maceration, genital structures were neutralized with acetic acid, washed in water and dehydrated in 70% ethanol, 95% ethanol and acetone, respectively, and fixed permanently in Euparal on a slide. Material used in this study is deposited in the PNM, SMNK, CeNak, and the personal collection of the author at Bochum University.

Specimens were studied using a Müller stereomicroscope. Photographs taken directly from the specimens via a Canon EOS 60D camera. Measurements, if not stated otherwise, always refer to the two most distant points of the respective structure (e.g. maximum length, maximum width etc.).

Terminology of the external morphology follows WIELAND (2013), with some exceptions. Male genital structures and systematic arrangement are based on SCHWARZ & ROY (2019).

Abbreviations and acronyms

CeNak	Centrum für Naturkunde (Zoologische Sammlung),
	Hamburg
CSC	author's personal collection
NRM	Naturhistoriska Riksmuseet, Stockholm
PAIC	Pleistocene Aggregate Island Complex
PNM	Philippine National Museum, Manila
SMNK	Staatliches Museum für Naturkunde Karlsruhe
TSC	TOBIAS SCHULZE'S personal collection
afa	phalloid apophysis
paa	apical process of left phallomere
pda	primary distal process
sdpl	lateral secondary distal process of Cernomantodea

lateral secondary distal process of Cernomantodea

3 Results

Fam. Nanomantidae Brunner de Wattenwyl, 1893 Subfam, Tropidomantinae Giglio-Tos, 1915 Tribus Tropidomantini Giglio-Tos, 1915

Pliacanthopus (Malayamantis) visayanus n. sp. (Figs 3-8, S1)

Material examined

Type material: Holotype: \Im , Northwest Panay Peninsula, Sibaliw Research Station, Libertad, Antique, Panay Island, Philippines; secondary forest, at light, 11°49.172' N, 121°58.052' E, ~460 m; 05.V.2012, C. Schwarz leg. (genitalia preparation Schwarz No. 122) (PNM).

Description

Male (Figs 3-4, S1): Body length 22.1 mm. Life coloration pale green with irregular grass-green bandings. Median part of pronotum and costal field of wings bright vellow. Bandings faded in preserved specimen.

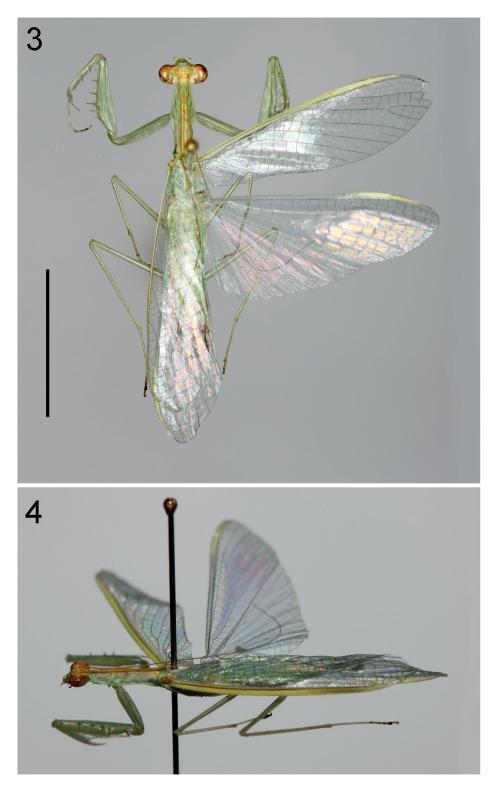
Head (Fig. 5) 1.9 mm long and 3.3 mm wide. Eyes kidney-shaped, exophthalmic. Vertex slightly concave but with a blunt tubercle above the ocelli, juxta-ocular bulges slightly protruding, juxta-ocular sulcus with a reddish color pattern. Two rather deep sulci between midline of vertex and juxta-ocular sulcus. Ocelli large, forming an angle of about 70°. Frontal shield transverse, ventral margin evenly curved, lateral part of dorsal margin concave semicircular (surrounding the base of antenna), median part more or less straight. Lateral corners of frontal shield with a ruby spot, this spot continuing as a transversal dark band across the eyes until merging with the pattern on the juxta-ocular sulcus. Palps pale green. Antennae pale green (becoming darker towards apex), moniliform, 19.5 mm long.

Pronotum slender, 5.0 mm long and 1.7 mm wide at supracoxal dilatation, with a strong median keel along entire length and finely denticulated margin. Length of prozona 1.6 mm, of metazona 3.4 mm. Ratios: length/ width 2.9, metazona/prozona 2.1. Prozona subconical, with slightly sinuous margins. Supracoxal sulcus interrupting the median keel, dilatation well-marked. Metazona with subparallel margins, a strong median keel, and two rounded tubercles at posterior margin.

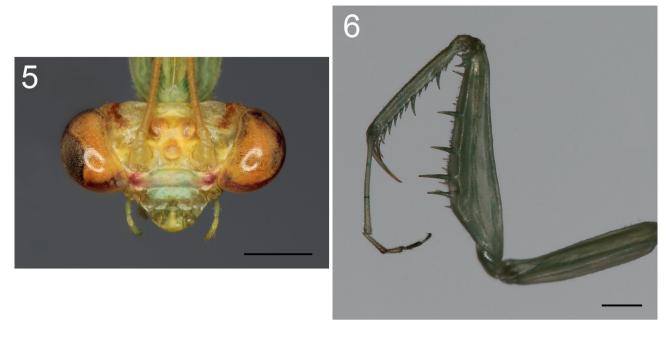
Forelegs (Fig. 6) relatively slender. Fore-coxae pale green, exceeding posterior margin of metazona, slightly shorter than pronotum, 4.2 mm long. Three irregular greenish bands have been present on the posterior side of the coxae in the living individual, but are totally faded away in preserved specimen. Anterior side pale, with numerous minute denticulations on dorsal margin. Apical lobes divergent. Anterior femora pale green, 5.4 mm long and 1.1 mm wide. Dorsal margin slightly sinuate. Posterior side pale green, in life with five irregular green bands.



Figures 1–2. Sampled habitats. – **1**. Primary forest, Mt. Madja-as, CPMR, November 2010. **2**. Secondary forest at "fern field", in the vicinity of Sibaliw Research Station, NPPNP, February 2012.



Figures 3–4. *Pliacanthopus (Malayamantis) visayanus* n. sp. 3. Holotype in dorsal view. 4. Same, dorsolateral view. – Scale bar: 10 mm.



Figures 5–6. *Pliacanthopus (Malayamantis) visayanus* **n. sp. 5**. Head in anterior view. **6**. Foreleg in posterior view. – Scale bars: 1 mm.

Anterior side pale green. Claw-groove at first quarter of femur. Ventral side of femur with a row of small tubercles stretching from base along discoidal spines and just mediad of postero-ventral spines to its apex. Area between rows of spines setose. Three discoidal spines, with second the longest and first the shortest. Four postero-ventral spines, and an additional spine at base of genicular lobe. Right femur with 15, left femur with 17 antero-ventral spines, plus an additional spine on the genicular lobe. Spination patterns: iIiIi(i)IiIIiIi(i)iiI. Anterior tibiae 4.0 mm long, with 12 postero-ventral and 17 antero-ventral spines. The postero-ventral spines are of different lengths, so it is useful to give their spination pattern: left tibia iIiiiIiiiiiI, right tibia iIiIiIiiiiI. Metatarsus longer than remaining segments combined.

Meso- and metathorax pale green, metathorax with a DK ear (see Yager & Svenson 2008). Mid and hind femora pale green, 5.6 and 6.1 mm long, respectively. Mid tibiae 4.1 mm, hind tibiae 6.7 mm long, slightly setose. Hind metatarsus much longer than remaining segments combined.

Wings (Figs 3–4) hyaline with greenish veins, iridescent. Tegmina 16.8 mm long and 4.6 mm wide, 3.4 times longer than pronotum, with rounded apex. Costal field gradually tapering towards apex, 0.6 mm wide, yellow opaque, distally with a reddish stripe along radial vein. Stigma strongly reduced, almost missing. Alae surpassing tegmina at rest by about 2 mm, hyaline, except the distal part of the costal field, which is yellow opaque as in the tegmina. Abdomen parallel-sided, pale green. Supra-anal plate (Fig. 7a) triangular with acute apex. Cerci with 13 segments, last segment elongate, only slightly shorter than remaining segments combined, with subacute apex. Subgenital plate (Fig. 7b) with differently shaped styli, right stylus short and wide, left stylus slender and somewhat longer.

Genitalia (Fig. 8) very weakly sclerotized, **sdpl** short and robust, with acute apex and curved to the right. **Afa** short, truncate, **loa** digitiform.

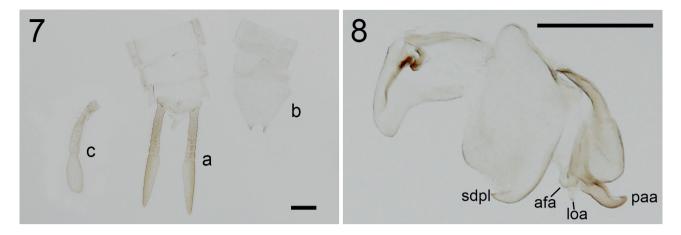
Female: unknown.

Distribution: Panay Island, Philippines.

Etymology: named after the Visayas, the central Philippine islands.

Differential diagnosis

The new species is most closely allied to *Pliacanthopus (Malayamantis) flavus* (Giglio-Tos, 1915) from Borneo. A specimen from the SMNK with the following data was used for comparison: 3° , Poring Lodge, Poring Hot Springs, District Ranau, Sabah, Borneo, MY; 06.02° N, 116.42° E, ca. 650 m, lux; 14.–16.V.2002, T. Kothe leg. Its measurements (in mm; see also BEIER 1931) are: body length 19.7; head length 1.6; head width 3.0; antennae 16.0; pronotum length 4.2; pronotum width 1.4; prozona 1.4; metazona 2.8; fore coxa length 3.7; fore femur length 4.5; fore femur width 0.8; fore tibia length 3.0; mid femur length 5.1; mid tibia length 3.7; hind femur length 5.5; hind tibia length 6.1; tegmen length 14.7; fore wing width 3.5.



Figures 7–8. *Pliacanthopus (Malayamantis) visayanus* n. sp. 7. Terminalia. a. Supraanal plate and cerci. b. Subgenital plate. c. Cercus of *Pliacanthopus (Malayamantis) flavus* (Giglio-Tos, 1915). 8. Genitalia. – Scale bars: 1 mm.

The two species share the iridescent, hyaline wings and the opaque costal field which are typical for the genus, a similar number of postero-ventral spines on the foretibiae, the keeled pronotum, the elongate last segment of the cerci, and similar male genitalia. However, *P. visayanus* is distinguished from *P. flavus* by a differently shaped last segment of the cerci (4.4 vs. 2.5 times longer than wide, and with subacute vs. rounded apex, Fig. 7c), and a slightly different distal process (SCHWARZ & ROY 2019, fig. 8c). Also, the morphology of the fore-tibial spines differs in the two species: the antepenultimate postero-ventral spine (corresponding to the ninth spine out of twelve or tenth out of thirteen) is short in *P. visayanus*, while it is longer than the neighboring spines in *P. flavus*.

P. (M.) visayanus and P. (M.) flavus are distinguished from P. (M.) malayanus (Beier, 1931) from the Malay Peninsula by the yellowish (vs. greenish) costal field, and a different number of postero-ventral spines on the foretibiae (12-13 vs. 10). Subgenus Malayamantis Koçak & Kemal, 2008 is distinguished from the Bornean monotypic Pliacanthopus Giglio-Tos, 1927 by a different number of tibial spines: Malayamantis has 10-13 postero-ventral and 17-18 antero-ventral spines, while in *Pliacanthopus* these numbers are 25-26 and 25, respectively (Hebard 1920). The two subgenera share the opaque costal field of the tegmina and the elongate last segment of the cerci, and may be well united into one genus. Oligocanthopus Beier, 1935, on the other hand, lacks these features, and also exhibits differently shaped wings and somewhat different genitalia (SCHWARZ & ROY 2019, fig. 8d), and is therefore better treated as a valid genus. Its fore-tibiae are armed with 6 postero-ventral and 10-11 antero-ventral spines. This genus currently only comprises the Bornean O. ornatus (Beier, 1931). For a review of past nomenclatural changes in this genus, ignored by BRANNOCH & SVENSON (2016), see SCHWARZ & KONOPIK (2014).

Pliacanthopus (Malayamantis) visayanus extends the distribution of this genus to the Philippine archipelago.

Fam. Gonypetidae Westwood, 1889 Subfam. Gonypetinae Westwood, 1889 Tribus Gonypetini Westwood, 1889 Subtribus Compsomantina Giglio-Tos, 1915

Compsogusa n. gen.

Type species: Compsogusa rheae n. sp., by monotypy.

Diagnosis

Medium-sized, slightly depressed, relatively slender, brachypterous mantids with a disruptive color pattern related to the bark-living lifestyle.

The new genus is most closely related to the Oriental genus *Compsomantis* Saussure, 1872. The two genera share a largely similar body shape, the smooth pronotum with its distinct pattern of paramedian markings, and the shape and color pattern of the wings. *Compsogusa* is, however, more elongate than *Compsomantis* (ratio pronotum length/width >1.9 in *Compsogusa*, <1.9 in *Compsomantis*), has a more transverse frontal shield (about two times as wide as high in *Compsomantis*), and a less convex vertex with more protruding juxta-ocular bulges. In *Compsomantis*, the widest part of the pronotum is the prozona, while it is the supracoxal dilatation in *Compsogusa*. The number of postero-ventral spines on the fore-tibiae overlaps: 7–9 in *Compsomantis*, 9–10 in *Compsogusa*.

Description

Head wider than long, vertex without process, juxtaocular bulges protruding in the female, less so in the male. Frontal shield transverse, narrow, antennae filiform.

Pronotum slightly longer than fore-coxae, about two times as long as wide, with moderately expressed supracoxal dilatation and denticulate margins, metazona slightly less than twice as long as prozona.

Forelegs rather robust, without lobes, fore-coxae extending well beyond posterior margin of pronotum, with divergent apical lobes. Femora robust, with 4 discoidal, 4 postero-ventral, and 14–16 antero-ventral spines, postero-ventral margin denticulate, the two proximal postero-ventral spines close together. Claw-groove near base. Anterior tibiae robust, with 9–10 postero-ventral and 11–12 antero-ventral spines. Fore metatarsus longer than remaining segments combined. Mid and hind legs rather long, simple, hind metatarsus about as long as remaining segments combined.

Wings of both sexes brachypterous, reaching the sixth abdominal segment in the male, fifth to sixth in the female, tegmina opaque, alae colored, anterior part subopaque, posterior part smoky. Abdomen simple, parallel-sided in males, slightly ovoid in females. Supra-anal plate triangular with rounded apex, cerci slightly surpassing subgenital plate. Male subgenital plate slightly asymmetrical. Female ovipositor protruding.

Male genitalia simplified, ventral phallomere with primary but without secondary distal process, phalloid apophysis short, with rounded apex.

Distribution: Panay and Luzon.

Etymology: Named for the striking resemblance to both its Oriental relative *Compsomantis* and the unrelated Neotropical bark-living genus *Liturgusa*, all of which share a similar lifestyle on the stems and branches of trees and bushes (WERNER 1924, SCHWARZ 2003, SVENSON 2014).

Compsogusa rheae n. sp. (Figs 9–23, S2–3)

Material examined

Type material: Holotype: ♂, Northwest Panay Peninsula, Sibaliw Research Station, Libertad, Antique, Panay Island, Philippines; secondary forest at "fern field", 11°49.2′ N, 121°58.1′ E, ~480 m; 21.IV.2015, C. SCHWARZ leg. (genitalia preparation SCHWARZ No. 192) (PNM). Allotype: ♀, same as



Figure 9. Compsogusa rheae n. gen. n. sp., dorsal view. a. ♀ allotype. b. ♂ holotype. – Scale bar: 10 mm.

before, secondary forest, 11°49.172′ N, 121°58.052′ E, ~460 m; 24.X.2011, C. SCHWARZ leg. (PNM). Paratypes: 3° , same as before, secondary forest at "fern field", 11°49.2′ N, 121°58.1′ E, ~480 m; 23.IX.2017, leg. C. SCHWARZ (SMNK). – 2° , same as before, secondary forest at "fern field", 11°49.2′ N, 121°58.1′ E, ~480 m; 18.I.2013, leg. C. SCHWARZ (SMNK). – 2° , same as before, 02.III.2012, C. SCHWARZ leg. (CSC). – 2° , same as before, secondary forest, 11°49′ N, 121°58′ E, ~450 m; 19.I.2013, C. SCHWARZ leg. (SMNK).

Additional material: \bigcirc , Central Panay Mountain Range, Maria Cristina, Madalag, Aklan, Panay Island, Philippines; mixed primary and secondary forest along creek, 11°30.827' N, 122°11.089' E, ~195 m; 31.I.2013, leg. G. OPERI-ANO & J. JAMANGAL; with two emerging specimens of *Chordodes caledoniensis* Villot, 1874 (Nematomorpha) (SCHMIDT-RHAESA & SCHWARZ 2016; CeNak).

Description

Male (Fig. 9b): Body length 21–22 mm. Life coloration greenish to greenish-red, intensively mottled with reddish-brown and dark (Figs 16, 18, S2). Greenish parts faded to tan in preserved specimens.

Head (Fig. 10b) 2.7–2.8 mm long and 4.6–4.65 mm wide. Eyes kidney-shaped, moderately exophthalmic. Vertex straight, juxta-ocular bulges slightly protruding, separated from vertex by a deep sulcus. Two very shallow sulci between midline of vertex and juxta-ocular sulcus. Ocelli small, forming an obtuse angle of about 115°. Frontal shield transverse, pentagonal, ventral margin evenly curved, dorsal margin sinuous, elevated into a ridge. A transversal dark band is crossing the eyes via the frontal shield. Palps pale, reddish in the holotype due to its reddish ground color. Antennae filiform, 17 mm long. Scapus pale, pedicellus annulated, flagellum brownish.

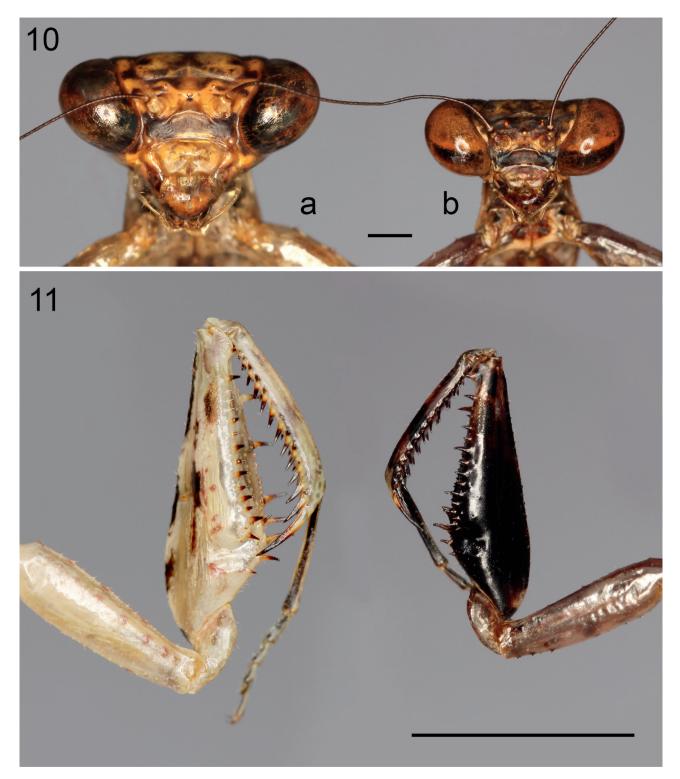
Pronotum robust, 5.5–5.6 mm long and 2.5 mm wide at supracoxal dilatation, slightly tapering towards anterior and posterior margin. Margins denticulate along entire length. Length of prozona 1.95–2.0 mm, of metazona 3.55– 3.6 mm. Ratios: length/width 2.2, metazona/prozona 1.8. Prozona rounded anteriorly, with sinuous margins. Supracoxal sulcus rather deep, dilatation with rounded margins. Metazona with a faint keel, and two pairs of paramedian depressions at first and just behind second quarter, respectively, these depressions with a dark spot. Posterior part of metazona with two rounded tubercles at posterior margin and two paramedian black spots (as in *Compsomantis*), which may be obscured by the mottling pattern. Prosternum with two comma-shaped spots behind supracoxal dilatation, and a dark median stripe in its posterior half.

Forelegs (Fig. 11b) robust. Fore-coxae exceeding posterior margin of metazona, slightly shorter than pronotum, ovoid in cross-section, 4.4–4.5 mm long, with three interrupted dark bands posteriorly. Anterior side pale with two (holotype) to 6–7 (paratype) submarginal small tubercles with a reddish-brown corona. Dorsal margin with 4 very small teeth, surrounded by a reddish-brown corona, and interspersed with even smaller teeth. Apical lobes divergent. Anterior femora very dark, 5.8-6.0 mm long and 1.7 mm wide, dorsal margin serrulate, slightly sinuate. Posterior side green to reddish-brown, with four interrupted dark bands merging with a median row of dark spots. Anterior side shiny black except the apex. Claw-groove at first quarter of femur. Ventral side of femur mostly black in the holotype, black in most of the proximal part in the paratype. with a row of small tubercles stretching from base along discoidal spines and just mediad of postero-ventral spines to its apex; additional tubercles on ventral side between postero-ventral and antero-ventral row of spines. Four discoidal spines, with third the longest and first slightly shorter than the fourth. Four postero-ventral spines, and an additional spine on genicular lobe, the first two spines very close together. Fourteen to sixteen antero-ventral spines, plus an additional spine on the genicular lobe. Observed spination configurations: IiIiIiIiIiIiI, iIiIiIiIiIiIii(i)I. Anteroventral spines dark, remaining femoral spines darkened in their apical half. Anterior tibiae 4.2 mm long, with three dark bands dorsally, armed with 9 postero-ventral and 12 antero-ventral spines. The tibial spines are darkened and increase in length toward apex, except of the fourth postero-ventral spine, which is slightly longer than neighboring spines. Fore-tarsi darkened ventrally, metatarsus longer than remaining segments combined.

Meso- and metathorax pale with some dark marks, metathorax with a DNK ear. Mid and hind femora 6.8– 6.9 and 7.2–7.3 mm long, respectively, slightly inflated at base, posterior side green to reddish in life, pale in preserved specimen, with four disrupted bands, anterior side pale. Mid tibiae 5.7–5.8 mm, hind tibiae 8.2–8.3 mm long, slightly setose, with four dark bands. Mid and hind tarsi slightly darkened ventrally, hind metatarsus as long as remaining segments combined.

Wings reaching the sixth abdominal segment, tegmina 11.5–11.9 mm long and 2.9–3.1 mm wide, 2.0–2.2 times longer than pronotum, with rounded apex. Costal field 0.75–0.8 mm wide, gradually tapering towards apex, Subcosta posterior displaced from Radius anterior (sensu Béthoux & Wieland 2009). Tegmina opaque, mottled with dark. Stigma oblique and narrow, very indistinct. Costal, most of discoidal, and anterior part of anal field of alae subopaque, reddish brown, posterior part of anal field and apex of discoidal field smoky.

Abdomen parallel-sided, anterior part (covered by wings) brownish and shiny, posterior part strongly mottled with dark. Sternites brownish, with small dark spots becoming more numerous towards posterior margin, and with a pair of paramedian comma-shaped dark spots. Supra-anal plate (Figs 12a, 13a) triangular with rounded apex. Cerci moniliform, with 12 segments, last segment subacute. Subgenital plate (Figs 12b, 13b) asymmetrical, with dark margins and long styli.



Figures 10–11. *Compsogusa rheae* **n. gen. n. sp. 10**. Head in anterior view. **a**. \bigcirc paratype. **b**. \bigcirc holotype. **11**. Forelegs in anterior view. **a**. \bigcirc paratype. **b**. \bigcirc holotype. **-** Scale bars: 1 mm (10), 5 mm (11).

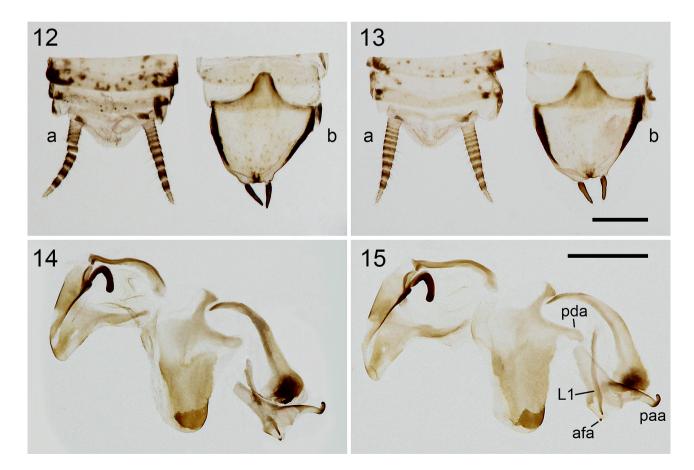
INTEGRATIVE SYSTEMATICS

Genitalia (Figs 14–15) strongly simplified, ventral phallomere with rounded apex, without **sdp** but with prominent **pda**, **afa** small, with a rounded and slightly serrulate apex, separated from L1 by a membranous area.

Female (Fig. 9a): Like male, but larger and more robust. Body length 28.6–31.3 mm. Life coloration tan to greenish, intensively mottled with brown and dark (Figs 17, 19, 22–23, S3). Greenish parts usually fade to tan in preserved specimens. Polyphenic color adaptation to the bark of the inhabited tree is possible to a certain degree; thus, the lighter parts may become more or less reddish, while the intensity of the mottling pattern varies from brown to black.

Head (Fig. 10a) as in male, but with convex vertex and more pronounced juxta-ocular bulges, 3.8–4.0 mm long and 5.7–5.9 mm wide. Ocelli very small. Frontal shield as in male. Labrum keeled, clypeus less so, the latter with two dark spots. Palps pale. Antennae filiform, 17–20 mm long. Scapus pale, annulation of pedicellus more pronounced anteriorly, flagellum brownish. Pronotum as in male, robust, 6.7–7.0 mm long and 3.1–3.2 mm wide. Denticulation along margin somewhat heavier than in male. Length of prozona 2.3–2.4 mm, of metazona 4.3–4.5 mm. Ratios length/width 2.1–2.2, metazona/prozona 1.8–1.9. Paramedian spots more distinct than in male.

Forelegs (Fig. 11a) robust. Fore-coxae 5.4–5.5 mm long, with three interrupted dark bands posteriorly. Anterior side pale with a submarginal row of small tubercles, 6–7 of which have a ruby corona. Dorsal margin with 4 very small teeth, surrounded by a ruby corona, and interspersed with even smaller teeth. Apical lobes divergent. Anterior femora 7.2–7.4 mm long and 2.2–2.3 mm wide, dorsal margin serrulate, slightly sinuate, posterior side with four interrupted dark bands merging with a median row of dark spots. Anterior side pale, with three to four dark marks along dorsal margin, an interrupted median line, and two submarginal black marks, one at femoral brush, the other just distad of it. Claw-groove at first quarter of femur. Ventral side of femur with a row



Figures 12–15. *Compsogusa rheae* n. gen. n. sp. 12–13. ♂ terminalia. 12. Holotype. a. Supraanal plate and cerci. b. Subgenital plate. 13. Paratype. a. Supraanal plate and cerci. b. Subgenital plate. 14–15. ♂ genitalia. 14. Holotype. 15. Paratype – Scale bars: 1 mm.



Figures 16–19. *Compsogusa rheae* **n. gen. n. sp.**, life appearance. **16**. \Diamond , dorsolateral view. **17**. \wp , dorsolateral view. **18**. \Diamond , anterolateral view. **19**. \wp , anterolateral view.

tral and 11–12 antero-ventral spines. The spines are darkened in their apical half and increase in length toward apex, except of the fourth postero-ventral spine (fifth in case of 10 spines), which is slightly longer than neighboring spines. Fore-tarsi darkened ventrally, metatarsus longer than remaining segments combined.

Meso- and metathorax pale ventrally, with some dark marks laterally, metathorax with a DNK ear. Mid and hind femora 7.5–7.7 and 7.8–8.3 mm long, respectively, slightly inflated at base, greenish in life, posterior side with four disrupted bands, anterior side pale. Mid and hind tibiae

46

and tarsi as in male, mid tibiae 6.5-7.0 mm, hind tibiae 9.4-9.9 mm long.

Wings reaching fifth abdominal segment. Tegmina as in male, 13.6–14.1 mm long and 3.7–4.0 mm wide, 2.0– 2.1 times longer than pronotum, with rounded apex. Costal field 0.8–0.9 mm wide. Alae as in male, anterior part yellowish to reddish brown, posterior part of anal field and apex of discoidal field smoky.

Abdomen slightly ovoid, anterior part (covered by wings) brownish and shiny, posterior part strongly mottled with dark. Sternites pale, with small reddish spots becoming more numerous towards posterior margin, and with a pair of paramedian comma-shaped dark spots. Supraanal plate triangular with rounded apex. Cerci slightly surpassing subgenital plate, moniliform, with 15–16 segments, last segment subacute. Subgenital plate with reddish spots, setose, genital valves strongly protruding, setose, with rounded apices.

Distribution: Panay Island, Philippines.

Etymology: named after RHEA SANTILLAN (PhilinCon), multitasking secretary, bookkeeper, and facilitator of everything, without whose generous assistance I would not have accomplished anything in the Philippines.

Remarks

The dark forelegs of the male are also present in young nymphs (Fig. 21), and are further seen in some species of the related genus *Amantis* Giglio-Tos, 1915.

A second species of this genus has been collected in November 2018 in the Bicol region of Luzon (K. ANDERSON, pers. com.). The single female known is distinguished from females of *Compsogusa rheae* **n**. **sp**. by longer wings (reaching the sixth abdominal tergite) and a wider pronotum (pronotum length/width about 1.9 as compared to 2.1 in *C. rheae* **n**. **sp**.).

Life history

Compsogusa rheae **n. sp.** occurs sympatrically, but not syntopically, with *Compsomantis mindoroensis* Beier, 1942 on Panay. The latter species is reported here outside Mindoro for the first time. Both species can be characterized as bark mantids, but respresent different ecotypes. *C. mindoroensis* prefers slim stems of scrubs in open habitats, filling a niche that is represented in Africa and southern Asia by tarachodids like *Galepsus* Stål, 1877, *Pseudogalepsus* Beier, 1954, and *Oxyophthalma* Saussure, 1861.

In contrast, *Compsogusa rheae* **n. sp.** is confined to rainforests, but prefers sunlit forest edges and secondary growth with many young trees (Fig. 2). It is never found in the understorey of primary forests. During rest, it prefers the geotropic orientation (see LADAU 2003). Upon an approaching threat, the mantids switch to the opposite side of the trunk, run several centimeters up and flatten them-

selves against the bark. If the threat persists, they quickly run up the tree. The observed specimens frequently engaged in "foreleg waving" (LOXTON 1979, SCHWARZ 2003, SCHWARZ & KONOPIK 2014). For unknown reasons, females seem to be much more abundant than males. During the five field trips, around a dozen adult and juvenile females but only three males have been encountered in the wild.

Oothecae (Fig. 20) are ochre and about 9–13 mm long. They are laid into crevices or dried, shriveled leaves, so their shape is variable.

On Panay, *Compsogusa* represents the "slender bark mantis" ecomorph (SVENSON & WHITING 2009) which convergently evolved around the tropics in several unrelated lineages: *Liturgusa* Saussure, 1869 and allies in the Neotropics, *Dactylopteryx* Karsch, 1892 in Africa, *Liturgusella* Giglio-Tos, 1915 in Madagascar, *Tricondylomimus* Chopard, 1930 in continental SE Asia, and *Ciulfina* Giglio-Tos, 1915 and *Stenomantis* Saussure, 1871 in Australasia (SCHWARZ 2003, HILL et al. 2004, HOLWELL et al. 2007, SVENSON & WHITING 2009, HOLWELL 2014, SVENSON 2014, SCHWARZ & EHRMANN 2017, SCHWARZ 2018).

In both the NPPNP and the CPMR, *Compsogusa* occurs syntopically with a larger and more robust taxon. This "broad bark mantis" ecomorph is represented by the following new species.

Subtribus Humbertiellina Brunner de Wattenwyl, 1893

Theopompa schulzeorum **n. sp.** (Figs 24, 25, 29)

Type material: Holotype: \bigcirc , Northwest Panay Peninsula, Sibaliw Research Station, Libertad, Antique, Panay Island, Philippines; secondary forest at "fern field", 11°49.194′ N, 121°58.157′ E, ~490 m; 29.XI.2010, leg. juv. C. SCHWARZ (PNM). Paratype: \bigcirc , Mt. Madja-as, Camp at Toog Bakong, Culasi, Antique, Panay Island, Philippines; primary forest along river, ~500 m; 17.XI.2010, leg. C. SCHWARZ et al. (SMNK); parasitized by four *Chordodes* cf. *moutoni* Camerano, 1895 (SCHMIDT-RHAESA & SCHWARZ 2016; CeNak).

Description

Female (Figs 24, 29): Medium-sized for the genus, with well-developed sculpture on pronotum. Body depressed, robust, tuberculate, 43.6–51.4 mm long. Coloration grayish-brown, intensively mottled with white and dark.

Head (Fig. 25) 6.4–7.1 mm long and 9.7–10.1 mm wide. Eyes kidney-shaped, exophthalmic. Upper portion of vertex slightly convex with median depression, juxta-ocular bulges strongly protruding, separated from vertex by a deep sulcus. Lower portion of vertex with two deep sulci between convex median part and juxta-ocular sulci, part between paramedian sulcus and juxta-ocular sulcus pro-



Figures 20–23. *Compsogusa rheae* **n. gen. n. sp.**, life history aspects. **20**. Ootheca. **21**. Second instar nymph. **22–23**. Subadult $\bigcirc \bigcirc$ showing polyphenic adaptation to tree bark.

truding. Ocelli small, forming an obtuse angle of about 110°. Frontal shield transverse, hexagonal, with two paramedian tubercles, its ventral margin evenly curved, lateral and dorsal margins elevated into a ridge, dorsal margin trapezoidal, projected forward. Central part of clypeus elevated into a conical projection, medio-ventral part incised. Palps pale, maxillar palp with a blackish spot on penultimate segment and blackish tips. Antennae filiform, scapus and pedicellus pale, flagellum brownish.

Pronotum robust, 10.8–12.2 mm long and 7.7–8.3 mm wide, with a narrow foliaceous expansion obscuring both supracoxal dilatation and a second pair of lateral bulges on the metazona just posteriad of it. Greatest width of pronotum at prozona, margins of metazona tapering towards posterior margin. Margins denticulate along entire length, antero-lateral corners with one to three stronger spines. Length of prozona 4.1–4.3 mm, of metazona 6.7–7.9 mm.

Ratios: length/width 1.4-1.5, metazona/prozona 1.6-1.8. Prozona rounded anteriorly, with two tuberculate keels projecting antero-laterad from supracoxal sulcus towards anterior margin, and with additional tubercles on the disc. Supracoxal sulcus rather deep, dilatation with rounded margins. Metazona sculptured, with a median sulcus and numerous tubercles along lateral margin (not on foliaceous part), antero-lateral corners of metazona with one or two strong teeth. Median part of metazona just posteriad of supracoxal sulcus depressed, a second transverse depression is located at posterior third of metazona. Posterior margin of metazona with two conical tubercles. Prosternum with a large black marking surrounding the supracoxal dilatation and the base of the coxae, and with a smaller vellowish patch between the base of the coxae. Remaining parts of prosternum brownish, ventral side of foliaceous expansion pale yellowish-white.



Figures 24. Theopompa schulzeorum n. sp., holotype in dorsal view. – Scale bar: 10 mm.



Figures 25. Theopompa schulzeorum n. sp., head and forelegs of holotype in anterior view. - Scale bar: 10 mm.

Forelegs (Fig. 25) slightly dilated, robust, tuberculate. Fore-coxae exceeding posterior margin of metazona, slightly shorter than pronotum, triangular in cross-section, 9.2-10.7 mm long. Posterior side with a broad black stripe along dorsal margin. Ridges separating posterior from ventral, and ventral from anterior side denticulate. Anterior side black with numerous creamy-white tubercles. Apical lobes divergent, margin of posterior lobe testaceous. Dorsal margin with 4-5 conical, creamy-white teeth, interspersed with smaller teeth. Anterior side of trochanter black. Anterior femora 13.7-16.0 mm long and 4.4-5.1 mm wide, slightly sinuate, dorsal margin denticulate, 5-6 of the denticules black. Posterior side pale, tuberculate, some of the tubercles black. Anterior side with a pattern typical for the genus, proximal half of non-dilated part shiny black, distal part pale with a black spot and a black stripe at base of genicular lobus. Dilated part pale with a black marking just proximad of middle, and two additional black markings in its distal half. Claw-groove near base. Ventral side of femur with a black groove accommodating the last postero-ventral spine of the tibia, and with a row of small tubercles stretching from base along discoidal spines and above-mentioned groove, then medio-ventrad of postero-ventral spines to apex of femur. Ventral side of femur between antero-ventral and postero-ventral spines with a black stripe in the holotype; in the paratype, there is just an irregular row of blackened tubercles. Four discoidal spines, with first the shortest, third the longest, and second and fourth of about the same length. Four postero-ventral spines, and an additional spine on base of genicular lobe, the first two spines closer together than the remaining. Antero-ventral side with 13-14 spines of very similar length, plus an additional spine on base of genicular lobe. Spination configuration: iIiIiIiIii(i)I. Anteroventral spines dark with black corona, discoidal spines darkened in their apical half, postero-ventral spines with dark tips. Anterior tibiae slightly convex, 10.8-12.8 mm long, with three dark interrupted bands dorsally, armed with 9 postero-ventral and 10-11 antero-ventral spines increasing in length toward apex. Postero-ventral spines with dark tips, antero-ventral spines in addition with a black base. Ventral side of tibia with a black stripe (holotype) or two black markings (paratype). Ventral side of fore-tarsomeres darkened at apex. Metatarsus with a black annulation at middle, slightly longer than remaining segments combined.

Meso- and metathorax and coxae pale ventrally, with some dark marks laterally. Metathorax with a DNK ear. Mid and hind femora 13.0–14.8 and 14.1–15.6 mm long, respectively, depressed, widened at base, posterior side strongly mottled with dark and in addition with four disrupted dark bands, anterior side pale except of some dark apical markings and a dark annulation at the apical fourth. Mid and hind tibiae with black base and with three dark annulations. Mid tibiae 11.8–13.5 mm, markedly sinuate, hind tibiae less so, 16.5–18.7 mm long. Mid and hind tarsi black, metatarsus dorsally with a pale marking at proximal third, second tarsomere pale in its proximal half, and third metatarsus with a small pale spot. Hind metatarsus slightly shorter than remaining segments combined. Wings surpassing tip of abdomen. Tegmina opaque, mottled with dark, 35.4–38.6 mm long and 14.3–17.1 mm wide, 3.2–3.3 times longer than pronotum, slightly truncate at apex. Ratio tegmen length/width 2.3–2.5. Subcosta posterior displaced from Radius anterior. Costal field very wide, with maximal width at first third of tegmen, then tapering sinuously towards apex. Distance from costal to subcostal vein 5.4–7.2 mm, from costal to radial vein 6.1–8.3 mm. Stigma oblique and narrow. Alae subhyaline, smoky, apex of costal and discoidal field subopaque, mottled with white.

Abdomen ovoid, tergites extended into small subacute, sternites into rounded lateral lobes. Tergites with extensive mottling pattern, sternites with numerous black spots. Supra-anal plate triangular, with sinuate margins and rounded apex. Cerci setose, surpassing ovipositor.

Male: unknown.

Distribution: Panay Island, Philippines.

Etymology: named after HELGA SCHULZE, Oldenburg, for her invaluable contributions to nature conservation in the Philippines and elsewhere, and after TOBIAS SCHULZE, Obermichelbach, for his numerous loans of Mantodea specimens to the scientific community over the years.

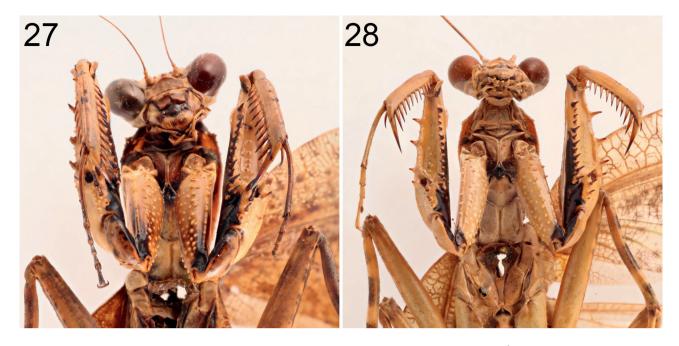
Differential diagnosis

Theopompa schulzeorum **n. sp.** is most closely related to *T. tosta* Stål, 1877 and *T. servillei* (De Haan, 1842). It resembles the former in the shape and sculpture of the pronotum, and in the color pattern of the antero-ventral foreleg spines (black on femur, with black bases and tips on tibia, BRAGG 2010). It resembles *T. servillei* in the color of the fore-coxae and of the antero-ventral spines on the fore-femur. *T. schulzeorum* is distinguished from *T. servillei* by the narrower and less heavily sculptured pronotum (length/width 1.4–1.5 vs. 1.2–1.3 in females of servillei), and the color of the antero-ventral spines on the fore-tibiae (black in *T. servillei*). *T. schulzeorum* is distinguished from females of *T. tosta* by the entirely black fore-coxae.

Of the other species of the genus, *T. ophthalmica* (Olivier, 1792) has a similarly shaped pronotum in the female sex (length/width 1.4), but lacks the dark fore-coxae and has antero-ventral spines with black tips on both femur and tibia. *T. burmeisteri* (De Haan, 1842) is much larger, has a very weakly sculptured pronotum, differently shaped tegmina, testaceous fore-coxae, and black spines on both femur and tibia. Finally, *T. borneana* Giglio-Tos, 1917 has differently colored forecoxae, and a less extensive black pattern on its fore-femur (see BRAGG 2010).



Figures 26. Theopompa tosta Stål, 1877, ♀ and ♂ syntypes (NRM) in dorsal view. – Scale bar: 10 mm. Photos: G. LINDBERG, © NRM.



Figures 27–28. Theopompa tosta Stål, 1877, forebody of syntypes in anteroventral view. 27. Q. 28. J. Photos: G. LINDBERG, © NRM.

Theopompa tosta as currently conceived may consist of more than one species. The taxon has been described by Stål (1877) from an unknown location in the Philippines. However, a male specimen from Homonhon Island near Samar housed in the SMNK agrees with the types (Fig. 26) in most respects. Samar belongs to a different faunal subprovince than Panay (see GAULKE 2011 for an overview). It was GIGLIO-Tos (1921) who first recorded T. tosta outside the archipelago. Despite agreeing more or less in color pattern of coxae and foreleg spines with the types (Figs 27-28), Sundaian specimens have comparatively shorter pronota (length/width 1.3-1.4 vs. 1.5-1.6 in the Philippine specimens) and more elongate wings (tegmen length/width 3.4-3.7 vs. 3.1-3.2 in males, and 2.5 vs. 2.3 in females). The tegmen of the female type, now slightly damaged, had a more pointed apex (SJÖSTEDT 1930, Fig. 26a), and its costal field is less sinuate than in Sundaian specimens. The wings of the male type (Fig. 26b) and of the Samar specimen are much broader than of Sundaian specimens, and with a broader and less sinuate costal field. A male from Palawan shows intermediate features (pronotum length/width 1.4, tegmen length/ width 3.1). A revision of the whole tosta complex is needed to clarify the situation. The genitalia of Sundaian T. tosta, T. borneana, and T. burmeisteri have been figured by Bragg (2010).

The following specimens have been used for comparison:

T. tosta: \Diamond holotype and \heartsuit allotype, Philippines, SEMPER leg. (NRM). \Diamond , Magellanes Point, Homonhon Island, East Samar, Philippines; lux; VII.2001, H.-G. PFEIFFER leg. (SMNK).

T. cf. *tosta*: \mathcal{J} and \mathcal{Q} , Mt. Deleng Bubun, N Sumatra, Indonesia; 23.VII.2004, ded. B. DE GROOF XII.2004 (TSC). \mathcal{Q} , Malay Peninsula, MY; road from Tapah to Tanah Rata, Cameron Highlands; IX.2005, ded. WONG TET SENG (TSC). \mathcal{Q} , same as before, I.2006, leg. S. MATERNA, J. MEHL, M. BORER & J. SOMMERHALDER (TSC). 2 $\mathcal{J}\mathcal{J}$, Maliau Basin Conservation Area, SAFE Project Camp, Sabah, Borneo MY; III.2012, O. KONOPIK leg. (CSC). \mathcal{J} , Sabah, Borneo, MY; lux; II.-III.2003, leg. M. HELMKAMPF & J. BECK (CSC). \mathcal{J} , Salakot Falls, vic. Puerto Princesa, Palawan, Philippines; 9°44' N, 118°43' E, 330 m; 16.VII.1998, ded. M. STIEWE (TSC).

T. servillei: 3° and 9° , Mt. Argapura, E Java, Indonesia; I.2004, aq. at Frankfurt Insect Fair (CSC). 9° , same as before, XI.2003, ded. B. DE GROOF (TSC). 3° , same as before, XII.2003 (TSC). 9° , Java, Indonesia; IX.2006, ded. S. MUNSTER (CSC). 5° 3° and 4° 9° , Java, Indonesia; captive bred 2007–2008; C. Schwarz leg. (CSC).

T. borneana: 2 \Im , Malay Peninsula, MY; road from Tapah to Tanah Rata, Cameron Highlands; IX.2005, ded. WONG TET SENG (TSC). \Im , Batang Ai NP, Trail No. 1, Sarawak, MY; 250 m; 24.XI.2000, leg. F. STEUERWALD & R. ZEITZ (SMNK).

T. burmeisteri: \eth and \bigcirc , Java, Indonesia; aq. 2015 at Frankfurt Insect Fair (TSC).

T. ophthalmica: photos of the holotype of *T. blanchardi* Wood-Mason, 1891 published at https://science.mnhn.fr/ institution/mnhn/collection/ep/item/ep2705?lang=en_US.

The species of the genus *Theopompa* may be distinguished with the following key (after BRAGG 2010, modified):

Key to the *Theopompa* species

- 3 Antero-ventral spines of fore-femora with black apex only... *T. ophthalmica*
- 4 Fore-coxae testaceous, only slightly marked subapically ... 5

Life history

In contrast to the preceding taxon, *Theopompa* species prefer larger and higher trees. Even though they might be found at lower heights at forest edges or in disturbed habitats (pers. obs.), in closed primary forests they inhabit the canopy, avoiding the shady understorey. Males of this genus are known to be sampled by light trapping (HELMKAMPF et al. 2007, SCHWARZ & KONOPIK 2014), but despite such efforts, no male of this new species could be collected on Panay so far. *T. schulzeorum* seems to be rather rare on the island, with only two females encountered over the course of seven years.

The peculiar morphology exhibited by all *Theopompa* species conceals the specimens very well on the bark of the inhabited trees. Flattening is the primary defense mechanism of choice in this taxon. The broad wings with their angled costal field minimize betraying shadows and hide the walking legs beneath them. In addition, the dorsal margin of the fore-femora fits the contour of the lateral pronotal margin when the specimen is flattened against the bark, while the protruding juxta-ocular bulges fit to the anterior margin of the pronotum. This aids in concealing the betraying insect outline when the head is held in prognathous position (EDMUNDS 1976, EDMUNDS & BRUNNER 1999, WIELAND 2013).

The mottling pattern is very variable, to an extent that there are no two specimens of this genus looking exactly the same. Disruptive markings are common. Thus, the pronotum and parts of the tegmina are often much darker than the remaining specimen. This bark mantis ecomorph is also remarkable in succeeding to produce an asymmetrical color pattern in spite of symmetrical markings. This is achieved by partial overlap of two symmetrically colored body parts, in this case the wings. For instance, the costal field of the holotype of *T. schulzeorum* (Fig. 29)



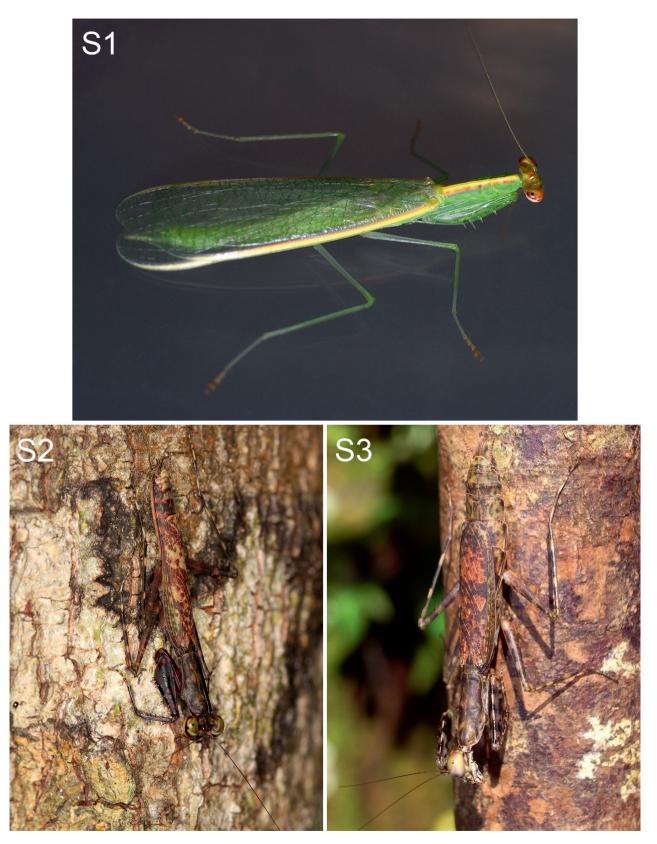
Figures 29. *Theopompa schulzeorum* **n. sp.**, life appearance of holotype.

shows, besides smaller spots, a large dark spot which continues into an oblique line traversing the discoidal field. Another oblique line, parallel to the previous one, crosses the discoidal field anteriorly of it, reaching the posterior end of the tegmen at the same distance from the wing base as the starting point of the distal band. When the wings are closed, the anterior line continues into the costal field spot of the opposite tegmen. Thus, the resulting pattern is an oblique and irregular one. Comparable patterns are exhibited by its congeners.

The ecological counterparts of *Theopompa* in other parts of the world are: *Paratheopompa* Schwarz & Ehrmann 2017 sympatric in Indochina, *Theopompella* Giglio-Tos, 1917 in Africa, *Majanga* Wood-Mason, 1891 in Madagascar, and *Gonatista* Saussure, 1869 and *Hagiomantis* Saussure & Zehntner, 1894 in the Neotropics (KROMBEIN 1963, EDMUNDS 1976, LADAU 2003, EDMUNDS & BRUNNER 1999, SCHWARZ 2018).

4 Discussion

The three new taxa presented here add to the ever increasing number of Western Visayan endemics already



Supplementary Figures. S1. *Pliacanthopus (Malayamantis) visayanus* n. sp., life appearance of holotype. S2–3. *Compsogusa rheae* n. gen. n. sp., life appearance of dark phenotype, S2 ♂, S3 ♀.

demonstrated in other groups (HUTTERER 2007, KREHEN-WINKEL et al. 2009, KOCH et al. 2010, SILER et al. 2011, 2012, LOWRY & COLEMAN 2012, GIUPPONI & MIRANDA 2012, JAKOSALEM et al. 2018). The reasons for this are both methodological and biogeographic. First, Panay, even though the fourth largest island of the archipelago, is the least sampled one, although things started to change recently. Secondly, the Greater Negros-Panay PAIC is relatively isolated with respect to the remaining archipelago. While the Greater Luzon and the Greater Mindanao PAIC are today separated from adjacent SE Asian mainland (and from each other) by only one oceanic barrier, a second oceanic barrier separates the Western Visayas, acting as an additional dispersal filter and promoting endemism.

However, regarding Panay just as a part of the Greater Negros-Panay PAIC is an oversimplification, since speciation in most investigated taxa seems to be older than the PAICs created by glacial cycles and to reflect more the Miocene to Pliocene geologic history of the archipelago than Pleistocene sea level changes (STEPPAN et al. 2003, SILER et al. 2010, 2011, 2012). There is, for example, a biogeographic link between Panay and Luzon, demonstrated by species or species groups shared between these two islands which do not occur in other parts of the archipelago, e.g. the monitor lizard subgenus Philippinosaurus Mertens, 1959, the snake Calamaria bitorques Peters, 1872, and the mantodeans Tagalomantis manillensis Saussure, 1870 and Compsogusa n. gen. (GAULKE & VOGEL 2005, ZIEGLER et al. 2005, GAULKE 2010, SCHWARZ 2017). On the other hand, the closest relative of Walden's Hornbill, Rhabdotorrhinus waldeni (Sharpe, 1877) is the Writhed Hornbill, Rh. leucocephalus (Vieillot, 1816) from the southern Philippines.

This picture is supplemented (and further complicated) by biogeographic oddities like Pliacanthopus visavanus **n. sp.**, which has (as far as it is known today) no relatives on other islands of the archipelago. Compsogusa, while related to the Sundaian and Philippine genus Compsomantis Saussure, 1872, has evolved into a bark mantis ecotype common in the Afro- and Neotropics, but not found in the southern Philippines, or in the Sunda archipelago, for that matter. The nearest congener of Pliacanthopus visayanus is P. flavus Giglio-Tos, 1915 from Borneo. Neither Palawan nor Mindanao, both potential step-stones for the genus to reach Panay, is currently known to harbor species of this genus. However, only one specimen was encountered during seven years of extensive field research, despite great efforts to acquire additional specimens. If the rarity of the species is typical for Philippine populations, specimens from other islands may have gone undetected so far.

In contrast to the two preceding species, *Theopompa* schulzeorum **n. sp.** has relatives on the archipelago. *Theopompa tosta* Stål, 1977, is known to occur, variability aside, on both Palawan and the oceanic Philip-

pines. While the exact origin of the types is unknown, the SMNK *T. tosta* specimen from Homonhon suggests that they might have originated from an island of the Greater Luzon or Greater Mindanao PAIC, as was the case with other Philippine species described by STAL (1877). As far as is known today, in the Western Visayas *T. schulzeorum* solely represents the genus.

T. schulzeorum is the first new *Theopompa* species described for more than a century. That a species of this size has gone undetected to the present day epitomizes the fact that the mantodean fauna of the Philippines is far from being known to an even moderately satisfactory degree. This prevents for now a deeper assessment of the complex biogeographic histories which shaped the dispersal and diversification of praying mantids across the archipelago. Unfortunately, habitat loss continues at an alarming rate, and since bureaucratic obstacles are virtually preventing representative sampling across the archipelago as a whole, this task will not be completed anytime soon.

5 References

- BEIER, M. (1931): Neue und seltene Mantodeen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg. – Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg 45: 1–21.
- BEIER, M. (1966): Noona Dan Papers No. 29. Die Mantiden der Noona Dan Expedition nach den Philippinen und Bismarck Inseln. – Entomologiske Meddelelser 34: 361–370, 3 pls.
- Béthoux, O. & WIELAND, F. (2009): Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. – Zoological Journal of the Linnean Society 156: 79–113.
- BRAGG, P. E. (2010): A review of the Liturgusidae of Borneo (Insecta: Mantodea). – Sepilok Bulletin 12: 21–36.
- BRANNOCH, S. K. & SVENSON, G. J. (2016): A new genus and species (*Cornucollis* gen. n. *masoalensis* sp. n.) of praying mantis from northern Madagascar (Mantodea, Iridopterygidae, Tropidomantinae). – Zookeys 556: 65–81.
- BRUNER, L. (1915): Preliminary catalogue of the orthopteroid insects of the Philippine Islands. – University Studies 15: 195–281.
- EDMUNDS, M. (1976): The defensive behaviour of Ghanaian praying mantids with a discussion of territoriality. – Zoological Journal of the Linnean Society **58**: 1–37, 2 pls.
- EDMUNDS, M. & BRUNNER, D. (1999): Ethology of defenses against predators. – In: PRETE, F. R., WELLS, H., WELLS, P. H. & HURD, L. E. (eds.): The praying mantids, pp. 276– 299; Baltimore & London (Johns Hopkins University Press).
- FREUDENSCHUSS, M., GRABOLLE, A. & KREHENWINKEL, H. (2016): A new species of *Gambaquezonia* from the Philippine Island of Panay (Aranae: Salticidae). – Arachnology **17** (1): 25–27.
- GAULKE, M. (2010): Overview on the present knowledge on *Varanus mabitang* Gaulke and Curio, 2001, including new morphological and meristic data. Biawak 4 (2): 50–58.
- GAULKE, M. (2011): The herpetofauna of Panay Island, Philippines, 390 pp.; Frankfurt am Main (Edition Chimaira).
- GAULKE, M. & VOGEL, G. (2005): Verbreitungsnachweis und Längenrekord für *Calamaria bitorques* Peters, 1872. – Sauria **27** (1): 15–19.

- GIGLIO-TOS, E. (1921): Orthoptera, Fam. Mantidae, Subfam. Eremiaphilinae. – Genera Insectorum 177: 36 pp., 2 pls.
- GIUPPONI, A. P. L. & MIRANDA, G. S. (2012): A new species of *Sarax* Simon, 1892 from the Philippines (Arachnida: Amblypygi: Charinidae). – Anais da Academia Brasileira de Ciências (Annals of the Brazilian Academy of Sciences) 84 (1): 165–173.
- HEANEY, L. R. (1985): Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. – Modern Quaternary Research in Southeast Asia 9: 127–144.
- HEBARD, M. (1920): Studies in Malayan, Papuan, and Australian Mantidae. – Proceedings of the Academy of Natural Sciences of Philadelphia 71: 14–82, 2 pls.
- HELMKAMPF, M., SCHWARZ, C. J. & BECK, J. (2007): A first look at the biodiversity of praying mantids (Insecta: Mantodea) in Sabah, Borneo. – Sepilok Bulletin 7: 1–13.
- HILL, P., HOLWELL, G. I., GÖTH, A. & HERBERSTEIN, M. (2004) Preference for habitats with low structural complexity in the praying mantid *Ciulfina* sp. (Mantidae). – Acta Oecologica 26: 1–7.
- HOLWELL, G. I. (2014): Four new species of *Ciulfina* Giglio-Tos, 1915 (Mantodea: Liturgusidae, Liturgusinae) from the Northern Territory, Australia. – Zootaxa **3797** (1): 29–38.
- HOLWELL, G. I., GINN, S. G. & HERBERSTEIN, M. E. (2007): Three new species of *Ciulfina* Giglio-Tos (Mantodea: Liturgusidae) from north-eastern Australia. – Zootaxa 1583: 23–35.
- HUTTERER, R. (2007): Records of shrews from Panay and Palawan, Philippines, with the description of two new species of *Crocidura* (Mamnalia: Soricidae). – Lynx, n. s. 38: 5–20.
- INGER, R. F. (1954): Systematics and zoogeography of Philippine Amphibia. – Fieldiana: Zoology **33** (4): 183–531.
- JAKOSALEM, P. G. C., PAGUNTALAN, L. J., KINTANAR V. L., TAN, S. K. M., QUISUMBING, R. J., QUEMADO, R. D. & OSAWA, T. (2018): Photographic guide to the birds of Negros, Panay & Cebu, 471 pp; Bacolod City (Philippines Biodiversity Conservation Foundation, Inc.).
- JAVIER, S. N. & COLEMAN, C. O. (2010): *Talitrus curioi* (Crustacea, Amphipoda, Talitridae), a new species of landhopper from the rainforests of the Philippines. – Zoosystematics and Evolution 86 (1): 41–48.
- KALKMAN, V. J. & VILLANUEVA, R. J. T. (2011): A synopsis of the genus *Rhinagrion* with description of two new species from the Philippines (Odonata: Magapodagrionidae). – International Journal of Odonatology **14** (1): 11–31.
- KOCH, A., GAULKE, M. & BÖHME, W. (2010): Unravelling the underestimated diversity of Philippine water monitor lizards (Squamata: *Varanus salvator* complex), with the description of two new species and a new subspecies. – Zootaxa 2446: 1–54.
- KREHENWINKEL, H., CURIO, E., TACUD, J. & HAUPT, J. (2009): On *Telyphonoides panayensis* gen. et sp.n. (Arachnida: Uropygi: Telyphonidae), a new genus and a new species of whip scorpions from Panay Island (Philippines). – Arthropoda Selecta 18 (3–4): 139–143.
- KROMBEIN, K. V. (1963): Behavioral notes on a Floridian mantid, Gonatista grisea (F.) (Orthoptera, Mantidae). – Entomological News 74 (1): 1–2, 1 pl.
- LADAU, J. (2003): Prey capture in a mantid (Gonatista grisea): Does geotropy promote success? – Canadian Journal of Zoology 81: 354–356.
- LOURENS, H. J. (2011): Six new Philippine species of the genus Cyana Walker, 1854 and a review of the geminopunctagroup, with emphasis on endemic develop lines in various islands (Lepidoptera: Arctiidae, Lithosiinae). – Nachrichten des Entomologischen Vereins Apollo 32: 69–96.

- LOWRY, J. K. & COLEMAN, C. O. (2012): A new terrestrial talitrid genus from the Philippine Islands (Crustacea, Amphipoda, Talitrida, Talitridae) and the designation of two informal subgroups. – Zootaxa 3400: 64–68.
- LOXTON, R. G. (1979): On display behaviour and courtship in the praying mantis *Ephestiasula amoena* (Bolivar). Zoological Journal of the Linnean Society **65**: 103–110.
- PARK, K.-T. & BYUN, B.-K. (2008): A new genus *Pectinimura* (Lepidoptera, Gelechioidea, Lecithoceridae), with four new species from Thailand and the Philippines. – Florida Entomologist **91** (1): 110–115.
- Roy, R. (2011): Les Amorphoscelinae Indo-Malais (Mantodea, Amorphoscelidae). – Revue française d'Entomologie (N. S.) 32 (1–2): 65–92.
- SCHMIDT-RHAESA, A. & SCHWARZ, C. J. (2016): Nematomorpha from the Philippines, with description of two new species. – Zootaxa 4158 (2): 246–260.
- SCHWARZ, C. J. (2003): Diets and habitat preferences of neotropical praying mantids (Dictyoptera: Mantodea, Burm. 1838), 114 pp; Diploma thesis at the University of Würzburg.
- SCHWARZ, C. J. (2017): Update on *Tagalomantis manillensis* (Saussure, 1870), with description of the female and comments on its systematic placement and life history (Insecta: Mantodea: Deroplatyinae). – Stuttgarter Beiträge zur Naturkunde A, Neue Serie 10: 19–39.
- SCHWARZ, C. J. (2018): Von Asthockern und Rindenläufern. Reptilia 134: 24–29.
- SCHWARZ, C. J. & KONOPIK, O. (2014): An annotated checklist of the praying mantises (Mantodea) of Borneo, including the results of the 2008 scientific expedition to Lanjak Entimau Wildlife Sanctuary, Sarawak. – Zootaxa 3797 (1): 130– 168.
- SCHWARZ, C. J. & EHRMANN, R. (2017): A new genus and species of bark mantis from Thailand, with an updated key to the bark mantis genera of the Oriental region (Insecta: Mantodea). – Zootaxa 4291 (3): 581–587.
- SCHWARZ, C. J. & ROY, R. (2019): The systematics of Mantodea revisited: an updated classification incorporating multiple data sources (Insecta: Dictyoptera). – Annales de la Société entomologique de France (N. S.) 55: 101–196.
- SILER, C. D., DIESMOS, A. C., ALCALA, A. C. & BROWN, R. M. (2010): Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. – Molecular Phylogenetics and Evolution 55: 699–710.
- SILER, C. D., DIESMOS, A. C., ALCALA, A. C. & BROWN, R. M. (2011): Phylogeny of Philippine slender skinks (Scincidae: *Brachymeles*) reveals underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification. – Molecular Phylogenetics and Evolution 59: 53–65.
- SILER, C. D., OAKS, J. R., WELTON, L. J., LINKEM, C. W., SWAB, J. C., DIESMOS, A. C. & BROWN, R. M. (2012): Did geckos ride the Palawan raft to the Philippines? – Journal of Biogeography 39: 1217–1234.
- SJÖSTEDT, Y. (1930): Orthopterentypen im Naturhistorischen Reichsmuseum zu Stockholm. – Arkiv för Zoologi **21A**: 1–43.
- STAL, C. (1877): Orthoptera nova ex insulis Philippinis descripsit. – Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 34 (10): 33–58.
- STEPPAN, S. J., ZAWADZKI, C. & HEANEY, L. R. (2003): Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic

archipelago. – Biological Journal of the Linnean Society **80**: 699–715.

- SVENSON, G. J. (2014): Revision of the Neotropical bark mantis genus *Liturgusa* Saussure, 1869 (Insecta, Mantodea, Liturgusini). – ZooKeys **390**: 1–214.
- SVENSON, G. J. & WHITING, M. F. (2009): Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the role of Gondwanan vicariance and morphological convergence. – Cladistics 25: 468–514.
- VORIS, H. K. (2000): Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. – Journal of Biogeography 27: 1153–1167.
- WERNER, F. (1922): Philippine mantids, or praying insects. Philippine Journal of Science **21**: 147–157, 1 pl.

- WERNER, F. (1924): Dritter Beitrag zur Kenntnis der Mantodeen von Niederländisch-Indien. – Treubia 5 (1–3): 259–266.
- WERNER, F. (1926): Zur Kenntnis der Mantodeen der Philippinen. – Konowia 5: 227–232.
- WIELAND, F. (2013): The phylogenetic system of Mantodea (Insecta: Dictyoptera). – Species, Phylogeny, and Evolution 3 (1): 1–306.
- YAGER, D. D. & SVENSON, G. J. (2008): Patterns of praying mantis auditory system evolution based on morphological, molecular, neurophysiological, and behavioural data. – Biological Journal of the Linnean Society 94: 541–568.
- ZIEGLER, T., GAULKE, M. & BÖHME, W. (2005): Genital morphology and systematics of *Varanus mabitang* Gaulke & Curio, 2001 (Squamata: Varanidae). – Current Herpetology 24 (1): 13–17.

Author's address:

Dr. Dipl.-Biol. Christian J. Schwarz, Ruhr University Bochum, Department of Biology and Biotechnology, Conservation Biology Unit, ND 1, 44780 Bochum, Germany; E-mail: christianschw@gmx.de

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Integrative Systematics: Stuttgart Contributions to Natural History

Jahr/Year: 2020

Band/Volume: 3

Autor(en)/Author(s): Schwarz Christian J.

Artikel/Article: <u>Three new praying mantises from Panay Island, Philippines (Insecta: Mantodea)</u> <u>35-56</u>