**A review of the stilt-legged fly subfamily Eurybatinae (Diptera:
Micropezidae)**

by

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ABSTRACT

A REVIEW OF THE STILT-LEGGED FLY SUBFAMILY EURYBATINAE (DIPTERA: MICROPEZIDAE)

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The micropezid subfamily Eurybatinae is reviewed to include 33 species in the Australian region, 45 species in the Oriental region, one species in the Afrotropical region and two species in the Neotropical region. The subfamily is redefined to exclude the Metopochetini, and 20 of the 81 species in the subfamily are newly described. Phylogenetic trees are provided on the basis of molecular data from 26 species of Eurybatinae, representing eight genera. Eurybatinae (excluding Metopochetini) are recovered as monophyletic and sister to Taeniapterinae in all analyses. The subfamily can be arranged into two groups according to the presence or absence of a sclerotized postmetacoxal bridge. Most analyses recovered the “postmetacoxal bridge” group as monophyletic. This group, including *Crosa* Steyskal, *Nestima* Osten Sacken and *Papeza* McAlpine, is fully revised herein. The remaining members of the subfamily, which lack a sclerotized postmetacoxal bridge, fall into the following seven genera: *Anaeropsis* Bigot, *Cothornobata* Czerny, *Crepidochetus* Enderlein, *Eurybata* Osten Sacken, *Notenthes* Marshall, *Paraeurybata* Marshall and *Trepidarioides* Frey.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The subfamily Eurybatinae (Micropezidae) is a group of stilt-legged flies known from the northern Oriental region through Wallacea and into New Guinea and Australia, with outliers of one genus, *Notenthes* Marshall, in the New World (Mexico and Costa Rica) and one genus, *Paraeurybata* Marshall, in the Afrotropical region (Mauritius and Reunion Islands).

Eurybatinae occur at a wide range of elevations (from sea level to 4000 m). Oviposition often takes place in crevices or in beetle borings in fallen trees or logs (Marshall, 2012, 2019, unpublished data; Li et al., 2015). Specimens that were recently collected from Borneo were mostly collected in yellow pan traps, and specimens from the “Our Planet Reviewed - Papua New Guinea” Mount Wilhelm expedition in Papua New Guinea in 2012–2013 (Leponche et al., 2016) were collected in Malaise traps. Many specimens have also been taken individually from leaf surfaces, trees or logs, and dung baits (Marshall pers. comm.). Unlike many Taeniapterinae, most adult Eurybatinae are not attracted to dung (Marshall, 2012). The immature stages of Eurybatinae are still unknown.

Taxonomic history of Eurybatinae

Enderlein (1922) divided the Micropezidae into three subfamilies: Neriinae, Micropezinae and Calobatinae. He placed two new genera, *Crepidochetus* Enderlein and *Metopochetus* Enderlein, in the subfamily Calobatinae along with the three previously described genera *Anaeropsis* Bigot, *Eurybata* Osten Sacken and *Nestima* Osten Sacken. The subfamily Neriinae was later elevated to the family rank by Hendel (1922). Frey (1927) reclassified the Micropezidae into three subfamilies: Calobatinae, Taeniapterinae and Micropezinae. He included genera characterized by the absence of the dorsal hind tibial bristles in the Calobatinae, and placed genera with dorsal hind tibial bristles in the Taeniapterinae. Taeniapterinae *sensu* Frey (1927) thus included *Crepidochetus*, *Eurybata*, *Metopochetus*, *Nestima*, and *Trepidarioides* Frey (he omitted mention of *Anaeropsis*).

Hennig (1934), in his revision of Micropezidae, reorganized the family and restricted the subfamily Taeniapterinae to the genera with a strong vertical row of katepisternal bristles. He transferred *Crepidochetus*, *Eurybata*, *Metopochetus*, *Nestima*, *Trepidarioides* and *Cothornobata* Czerny, which lack strong katepisternal bristles, back to Calobatinae.

Anaeropsis was overlooked by Frey (1927) and Hennig (1934) and treated as a tephritid by Hennig (1936). Hennig (1938) in his later work found that *Anaeropsis* is closely related to *Trepidarioides*, thus he placed *Anaeropsis* back in the Micropezidae.

Frey (1958) followed the classification of Hennig (1934), but he divided Calobatinae into two tribes based on the distribution of the species in the subfamily. The Holarctic genus *Calobata* Meigen was placed in the tribe Calobatini, and the Indo-Australian genera were grouped in the tribe Eurybatini.

McAlpine revised the Australian Micropezidae in 1975 and, because he found no close relationship between the two tribes of Calobatinae recognized by Frey, he elevated Eurybatini (*sensu* Frey, 1958) to subfamily rank. He divided Eurybatinae into two tribes, Metopochetini and Eurybatini. The tribe Metopochetini only consisted of *Metopochetus* at that time; the apterous, ant-like, monotypic genus *Badisis* McAlpine was added in 1990. McAlpine (1998) suggested four synapomorphies of Metopochetini: (1) the presence of a supracervical tubercle below the postvertical bristles, (2) the absence of the axillary fascicle, (3) the fore coxa with everted, tooth-like anteroventral lobe and, (4) the male subepandrial sclerite with a process on each side bearing two long bristles.

The genera *Anaeropsis*, *Crepidochetus*, *Crosa* Steyskal, *Eurybata*, *Nestima*, *Trepidarioides*, *Cothornobata* and a new genus *Papeza* McAlpine were placed in the tribe Eurybatini. Marshall (2002) described *Notenthes*, the only New World genus of Eurybatinae, in the tribe Eurybatini. Within Eurybatini, McAlpine (1975) noted that *Crosa*, *Nestima*, *Papeza* and *Trepidarioides* have a postmetacoxal bridge, while the remaining genera do not. This character was first noted by Aczél (1959) in some Australian species of Eurybatinae. McAlpine (1998) suggested three synapomorphies of Eurybatini: (1) hind tibia with a bare apical area and with subapical anterodorsal bristles, (2) a straight suture with no bend marking the transition from pleural suture to anapleural suture and, (3) each fifth tarsomere at least as long as wide (Figure 1.1).

McAlpine (1975) did not explicitly recognize apomorphic characters to define the Eurybatinae including Metopochetini, and thus suspected that the subfamily as recognized at that time did not form a monophyletic group. In his revision of the Australian Micropezidae, McAlpine (1998) suggested that the triradiate shape of sternite 6 was a synapomorphy linking Metopochetini and Eurybatini, but Aczél (1959) had previously noted that this character resembles that of *Micropeza similis* Aczél (Micropezinae) as illustrated in his 1949 paper. McAlpine (1998) also found some other similarities between Metopochetini and Micropezinae: a complete transverse suture, the absence of the fascicle on the distal part of the axillary cord

and the absence of longitudinal grooving on any tibiae. Because of these similarities, McAlpine (1998) considered the possibility that Metopochetini is closely related to Micropezinae and suggested an alternative hypothesis of a close relationship between these two groups despite concluding that it is more likely that the Metopochetini belong in the Eurybatinae on the basis of the triradiate sternite 6. A recent study of Micropezidae using molecular data from multiple genes found strong support for a sister group relationship between Metopochetini and Micropezinae (Jackson, 2019). The tribe Metopochetini is here removed from Eurybatinae *sensu* McAlpine, 1975 and is treated at the subfamily rank as the Metopochetinae.

Thesis objectives

The objectives of the first part of the thesis were to use DNA sequence data to investigate the relationships of Eurybatinae and related subfamilies, to test the relationships between the genera of Eurybatinae, and to examine the relationships between species with a sclerotized postmetacoxal bridge. The second part presents the generic classification of the Eurybatinae and a revision of the monophyletic postmetacoxal bridge group. The revision includes descriptions and illustrations of 38 species from three genera in the postmetacoxal bridge clade (*Crosa* Steyskal, *Nestima* Osten Sacken and *Papeza* McAlpine), with a complete key to all the described species in that clade.

Figure 1.1: Synapomorphies of Eurybatini. A) Hind tibia and tarsus of *Crosa darlingi* sp. n. showing the apical dorsal bare area with the subapical anterodorsal bristles and the fifth tarsomere as long as wide. B) Lateral view of thorax, showing a straight suture with no bend marking the transition from the pleural suture to the anapleural suture of *Nestima necta* sp. n.

CHAPTER 2

MATERIALS AND METHODS

Depositories of material examined

Approximately 760 specimens, including dried specimens and specimens in alcohol, were examined. Specimens and type specimen images were obtained from the following collections: Australian Museum, Sydney, Australia (AMS); Australian National Insect Collection, CSIRO, Canberra, Australia (ANIC); Bishop Pauahi Museum, Hawaii, U.S.A. (BPBM); Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Ontario, Canada (CNC); Hope Entomological Collections of the Oxford University Museum of Natural History, Oxford, U.K. (OXUM); Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam (IEBR); Museo Civico di Storia Naturale ‘Giacomo Doria’, Genova, Italy (MCG); Museo Nacional de Costa Rica, San José (including the collections of INBio, the Instituto Nacional de Biodiversidad = INBC) (MNCR); Museum für Naturkunde, Berlin, Germany (MNBG); Muséum National d’Histoire Naturelle, Paris, France (MNHN); Naturalis Biodiversity Centre, Leiden, Netherlands (RMNH); Naturhistorisches Museum, Basel, Switzerland (NHMB); Oklahoma Museum of Natural History, University of Oklahoma, Oklahoma, U.S.A. (OMNH); Philippine National Museum of Natural History, Manila, Philippine (PNMNH); Royal Ontario Museum, Ontario, Canada (ROME); Senckenberg German Entomological Institute, Müncheberg, Germany (DEI); Smithsonian National Museum of Natural History, Washington, U.S.A. (USNM); The Natural History Museum, London, U.K. (BMNH); University of Guelph Insect Collection, Guelph, Ontario, Canada (DEBU); University of Michigan Museum of Zoology, Michigan, U.S.A. (UMMZ) and Zoological Museum, University of Copenhagen, Denmark (ZMUC). Specimens labelled as “IBISCA” in the specimens’ examined list are materials that were collected during the “Our Planet Reviewed - Papua New Guinea” Mount Wilhelm expedition in Papua New Guinea from 2012–2013 (Leponche et al., 2016).

Morphological terminology

Morphological terminology follows McAlpine (1998) and Marshall (2002, 2015). Parts of the male terminalia are labeled in Figures 4.15F, 4.15H and 4.23F, and female terminalia

are labelled in Figure 4.23I. The terms “basal distiphallus” and “distal distiphallus” refer to the parts of the distiphallus basal and distal to the phallic bulb (Marshall, 2015). The term “basal tubercle” follows Li et al. (2015) and refers to a protuberance at the basal third of the inner surface of the male genital fork (Figure 4.39F). Terminology for wing venation follows Cumming and Wood (2017). The descriptions for wing interference patterns characters (hereafter referred to as WIPs for the whole patterns on wing and WIP for pattern of specific wing cell) were based on Shevtsova et al. (2011). The descriptions of wing interference patterns characters (hereafter referred to as WIPs for the whole patterns on wing and WIP for pattern of specific wing cell) are based on Shevtsova et al. (2011). The WIP patterns of specific wing cell are labelled in Figures 4.12D and 4.44E.

Specimen preparation and dissection

Eurybatine wings usually wrinkle after drying, therefore they had to be removed and slide-mounted to see veins and WIPs without distortion. Wings were mounted on slides under coverslips and soaked with 70% ethanol to make the wings more supple; binder clips were used on both sides to flatten the wings. Wings were then soaked with 100% ethanol to make the wing stay flat after the slides were removed. Slide mounts were dried overnight before being photographed; the wings were then point-mounted and pinned together with the specimens. A ring light attached to a camera lens was used to photograph the wings with a white background for standard wing images and a black velvet cloth for WIP images.

Male and female terminalia were examined when possible. Abdomens were removed and soaked in hot 10% potassium hydroxide for approximately 15–30 minutes to macerate the abdomen. After maceration, the abdomens were rinsed in cold water, then soaked in 10% acetic acid to neutralize any remaining KOH. Female terminalia were stained in lignin pink when necessary. Detached abdomens and associated genitalic dissections were studied in glycerin in depression slides. Dissections were stored in glycerin capsules pinned under the specimens after study.

I have tried the enzymatic cleaning method with trypsin (0.5%) EDTA solution according to Yau and Marshall (2015), but the volume was increased to approximately 10 ml due to the larger size of eurybatine abdomen. Three abdomens were left in the solution for more than 24 hours without obtaining adequate maceration of the internal tissues. The enzymatic cleaning method was therefore not adopted for this study.

Measurements and ratios

Measurements and ratios should be treated as approximate because dried specimens vary in size due to shriveling and bending. Measurements and ratios are as follows: i) Body length (distance from the front of the head to the tip of the abdomen); ii) Wing length (maximum wing length); iii) Width of ejaculatory apodeme – (maximum blade width); iv) Halter stem length (compared to the width of the narrowest point of the halter stem); v) Basal distiphallus length (compared to the length of the shorter branch of the distal distiphallus).

Photography and illustrations

Multiple specimen images were taken using a Canon 70D camera mounted on a Stackshot motorized system (Cognisys Inc., Michigan USA) and genitalic images were taken using a Nikon D300s digital camera mounted on a Nikon compound microscope. The images were combined using HeliconFocus (Helicon Soft Ltd., Kharkiv Ukraine) stacking software, and visually enhanced in Adobe Photoshop CC (Adobe, California, U.S.A.).

Label information and Distribution Maps

Label data are mostly verbatim from the labels and are presented in a consistent manner, although obvious spelling errors are corrected, and old location names are updated where correspondence to a newer location name was unambiguous (old names are retained in parentheses). Species distribution maps were generated using SimpleMappr (Shorthouse, 2010).

CHAPTER 3

PHYLOGENETICS OF EURYBATINAE

Introduction

The micropezid subfamily Eurybatinae as defined here is equivalent to the Eurybatini *sensu* McAlpine (1975) and prior to this work included 61 species divided into the following 10 genera: *Anaeropsis* Bigot, *Cothornobata* Czerny, *Crepidochetus* Enderlein, *Crosa* Steyskal,

Eurybata Osten Sacken, *Nestima* Osten Sacken, *Notenthes* Marshall, *Papeza* McAlpine, *Paraeurybata* Marshall and *Trepidarioides* Frey. An additional 20 species are described herein.

Only a few authors have worked on the subfamily and it has never been fully revised. McAlpine (1975, 1998) revised the Australian Micropezidae including Eurybatinae. Marshall (2002) described *Notenthes*, the only New World genus of Eurybatinae. Li et al. (2015) reviewed the Oriental species of *Cothornobata*. Barraclough (1992) placed the Afrotropical species *Calobata taeniata* (Macquart) in the genus *Cothornobata* and Marshall (2019) reconsidered the same taxon as the new genus *Paraeurybata*. Otherwise, the subfamily has received very little attention.

The relationships between some of the genera remain uncertain, with several alternative hypotheses proposed by previous authors. The majority of previous studies were based on morphological characters, but a recent study of Nerioidea by Jackson (2019) used molecular evidence and included a few Eurybatinae specimens. The current study expands the sampling of Eurybatinae with available fresh or appropriately preserved specimens of 26 species, covering eight out of 10 genera. The morphology of the group is discussed against the context of molecular analyses of these taxa.

Relationships of the genera within Eurybatinae

McAlpine (1975) noted that the genera *Crosa*, *Nestima*, *Papeza* and *Trepidarioides* are closely related based on the presence of a sclerotized postmetacoxal bridge region. McAlpine noted that *Crosa*, *Nestima* and *Papeza* have a fully sclerotized region, while for *Trepidarioides*, the postmetacoxal bridge is narrow and sclerotized on the upper part only. The remaining genera, *Anaeropsis*, *Cothornobata*, *Crepidochetus*, *Eurybata*, *Notenthes* and *Paraeurybata* lack the postmetacoxal bridge.

McAlpine (1975) hypothesized that *Nestima* and *Crosa* are closely related because they both have a shallow extensive depression on the anterior third of the mesonotum. *Nestima* is diagnosed by three characters: the subscutellum longer than the scutellum, a receding anterior mesonotal margin and the ocelli closer to the posterior fronto-orbital bristle than to the postvertical bristle (Osten Sacken, 1882; McAlpine, 1975). *Crosa* is characterized by a unique synapomorphy, the male fore femur with ventral bristles on the basal half (Steyskal, 1952). Evenhuis (1989) and McAlpine (1998) treated *Crosa* as a junior synonym of *Nestima* without providing a justification for the synonymy.

The genus *Crepidochetus* is easily diagnosed with an upturned scutellum, a sloping mesonotal margin and the absence of a distal distiphallus. McAlpine (1998) noticed three species of Australian *Cothornobata*, *C. grallina* McAlpine, *C. levis* McAlpine and *C. alta* McAlpine have similar sloping mesonotal margin to *Crepidochetus*, but only two species, *C. grallina* and *C. levis* share other diagnostic feature of *Crepidochetus*, the upturned scutellum. Because of the similarities between some Australian *Cothornobata* and *Crepidochetus*, he suspected that they may be closely related. His hypothesis however was based on a limited material of the genus *Cothornobata*, especially the Oriental species. McAlpine suggested that any further reorganisation of the generic classification of the genus *Cothornobata* should be based on a detailed study of more species of the Oriental, Mascarene and Australasian *Cothornobata*. He therefore retained the Australian species in the genus *Cothornobata*, potentially rendering *Cothornobata* paraphyletic.

Li et al. (2015) pointed out that *Cothornobata* as a whole is weakly supported, and showed that the Oriental species of *Cothornobata* form a clade distinct from the Australian species and diagnosed by three characters: (1) the presence of basal and medial tubercles on the male genital fork (sternite 5), (2) a distiphallus with trifurcate terminal filaments and (3) a plate-like hypandrium. Marshall (2019) cited preliminary molecular evidence suggesting that the Afrotropical genus *Paraeurybata* is sister to the Oriental *Cothornobata* plus *Eurybata*.

The current generic relationships of the subfamily are based on adult morphological characters from previous studies. Several earlier studies have shown that molecular evidence can be useful in understanding generic relationships in other acalyptrate families, such as Conopidae and Sphaeroceridae (Gibson et al. 2010; Kits et al. 2013). This study will use DNA data to test generic concepts and hypotheses about how the genera of Eurybatinae are related.

Material and methods

Taxon sampling

A total of 38 species were used for molecular studies, including 26 species of Eurybatinae and 11 outgroup species from three subfamilies (Taeniapterinae, Metopochetinae and Micropezinae). One species of Neriidae (a close relative of Micropezidae based on Wiegmann et al. 2011), *Telostylus lineolatus* (Wiedemann), was used to root the tree. Due to the scarcity of material of Eurybatinae appropriately preserved in alcohol for molecular work, only 24 species of Eurybatinae, covering eight genera were successfully sequenced for mitochondrial

and nuclear genes in this study. Two sequences of two *Cothornobata* species, *Cothornobata paieroi* Li et al. (sequence MYCRO149-15) and *Cothornobata breviseta* Li et al. (sequence MYCRO144-15) which had previously been submitted for sequencing by our laboratory and published on BOLD (<http://www.boldsystems.org>) were included in the dataset. One species of Micropezinae (*Micropeza nitidor* Cresson), three species of Taeniapterinae (*Aristobatina rufithorax* (Enderlein), *Cardiacephala brevipennis* (Walker) and *Mimegralla splendens* (Wiedemann)) and six species of Metopochetinae (*Badisis ambulans* McAlpine, *Metopochetus bivittatus* (Macquart), *Metopochetus micidus* McAlpine, *Metopochetus freyi* McAlpine, *Metopochetus impar* McAlpine and *Metopochetus perclusus* (Walker) were also included in the dataset.

Molecular characters

Five gene regions were chosen from mitochondrial and nuclear genes, including both ribosomal and protein-coding genes: mitochondrial 12S rDNA, mitochondrial 16S rDNA, cytochrome c oxidase subunit I (COI), triose phosphate isomerase (TPI) and 28S ribosomal DNA. Genes were selected based on earlier successful use in a phylogenetic analysis of some micropezid species by Jackson (2019). Not all genes used by Jackson were successfully sequenced in this study, especially the nuclear genes (AATS, CAD and PGD genes). This is presumably due to the quality of the available preserved material. Most of the sequenced specimens were from Malaise traps, and some had apparently deteriorated prior to storage in 95% ethanol. Each specimen used is listed in Table 3.1. Sources of specimens are listed in Table 3.6. All sequences were made publicly accessible on GenBank.

Extraction

All specimens used for molecular analysis were kept in 95% ethanol and stored at -80°C for specimens in Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Ontario, Canada (CNC) and stored at -20°C for specimens in the University of Guelph Insect Collection, Guelph, Ontario, Canada (DEBU). The whole insect was used for DNA extraction using the non-destructive DNeasy® Blood & Tissue Kit (Qiagen Inc., Santa Clara, CA, USA). As recommended, a spin-column protocol was used to complete the procedure with the specimen left in the lysis solution for about 24 hours. After lysis was completed, the specimens were taken out from tubes. 4µl of RNase was added to each tube, and then the solutions were

incubated for additional 5 minutes. The final centrifugation was done by eluting 200 μ L of distilled water (pH>8.5) instead of buffer. This solution was then dried down to <5 μ L on a DNA110 SpeedVac (ThermoSavant) before the DNA was resuspended in 50 μ L of buffer AE. Since relatively few specimens of Eurybatinae have been collected into alcohol, all the extracted specimens used in this study were moved back to 95% ethanol and stored at -80°C in CNC for further use in the future.

Amplification and purification

DNA amplification was performed in 25 μ L reaction volumes using 2.5 μ L of 10X Ex-Taq buffer, 0.15 μ L of ExTaq (Takara Bio USA, Madison, WI, USA), 2.0 μ L dNTPs (10 mM), 0.65 μ L of MgCl₂ (25mM), 1.0 μ L of each forward and reverse primers (10 μ M) as listed in Table 3.2, with different volumes of DNA template (2 μ L of template was used for both mitochondrial and ribosomal genes and 3 μ L was used for nuclear gene), with the volume of H₂O reduced accordingly. PCR programs, specific to each primer program, were run in either Eppendorf epGradient S Mastercycler or Eppendorf Mastercycler Vapo.protect Pro S (Eppendorf AG, Hamburg, Germany). All products were visualized on 1% agarose electrophoresis gels mixed with (4 μ L/mL) using BioRad Gel Doc™ XR+ Gel Documentation System (Bio-Rad Laboratories Inc, California, U.S.A). PCR products were purified using CloneWell 0.8% SYBR Safe™ precast gels in the E-Gel® system (Invitrogen™, Carlsbad, CA, USA) as recommended by (Gibson et al., 2010).

Sequencing

Purified PCR products were prepared for sequencing using a BigDye® Terminator v3.1 Cycle Sequencing Kit (PE Applied Biosystems, Foster City, CA, USA), and were sequenced at the Agriculture and Agri-Food Canada Core Sequencing Facility (Ottawa, Ontario, Canada).

Sequence alignment

Sequence chromatograms were viewed and contigs were assembled in Sequencher 5.4.6. Alignment was performed in MAFFT version 7 (Katoh and Standley, 2013) using the FFT-NS-i, FFT-NS-1, or FFT-NS-2 algorithm in the MAFFT online service (Katoh et al., 2017). Data were then concatenated in Mesquite 3.6 (Maddison and Maddison, 2018) and all

alignments were then checked by eye and modified by hand as deemed necessary (fixing stop codons and misaligned gaps).

Dataset assembly and partitioning

Datasets were built in Mesquite V3.6. Partitioning strategies and evolutionary models for the concatenated dataset were determined using PartitionFinder2 (Lanfear et al., 2016) performed on the CIPRES Science Gateway V 3.3 (Miller et al., 2010) under the Akaike Information Criterion c (AICc) and using the “greedy” scheme. All datasets were partitioned by gene, with protein coding genes also partitioned by codon positions. The protein coding genes were also analysed with and without the 3rd codon position in all datasets. The best evolutionary models for each gene and partition selected by the PartitionFinder are as follows: A general time reversible model with gamma distribution and proportion of invariable sites (GTR+I+G) model for 12S, 28S, COI-5', COI-3' (1st and 3rd codon positions) and TPI (1st and 3rd codon positions) genes and a general time reversible model with gamma distribution (GTR+G) model for 16S and COI-3' (2nd codon position) and TPI (2nd codon position) genes (Table 3.3). To determine the validity of using a combined data set, a partition homogeneity test (Farris et al., 1994) was performed in PAUP version 4.0a (Swofford, 2003) to test the congruence of gene loci.

Concatenated dataset schemes

The concatenated dataset schemes analysed in this study are specified below:

ConcatenatedALL: Includes all available data from five genes (12S, 16S, 28S, COI and TPI).

ConcatenatedFOUR1: Includes all available data from combination of four genes (16S, 28S, COI and TPI).

ConcatenatedFOUR2: Includes all available data from combination of four genes (12S, 28S, COI and TPI).

ConcatenatedFOUR3: Includes all available data from combination of four genes (12S, 16S, COI and TPI).

ConcatenatedFOUR4: Includes all available data from combination of four genes (12S, 16S, 28S and TPI).

ConcatenatedFOUR5: Includes all available data from combination of four genes (12S, 16S, 28S and COI).

Phylogenetic analysis

Analyses of molecular data were performed using three methods: Maximum parsimony, Bayesian inference and maximum likelihood. First, each gene region sampled in this study was individually analyzed. Then, six concatenated datasets from different gene combinations were analyzed.

Maximum parsimony analyses were conducted in TNT 1.1 (Goloboff et al., 2008). The characters were treated as unordered and reversible, and no weighting was implied. All gaps in the molecular data were treated as missing characters. A Traditional Search was performed using 1000 replications with the TBR (tree bisection reconnection) option for branch swapping. Statistical support was obtained by bootstrap analysis with 1000 replications (Felsenstein, 1985).

Both maximum likelihood and Bayesian inference analyses were run using tools on XSEDE Restart Interface on the CIPRES Science Gateway (Miller et al., 2010), with the partition block produced by PartitionFinder2 included in the analyses file. Maximum likelihood was performed using RAxML v8.2.12 (Stamatakis, 2014), with 1000 bootstrap replications. Bayesian inference was performed in MrBayes 3.2.2., and the analysis was run with four Markov Chain Monte Carlo (MCMC) simultaneously (Ronquist and Huelsenbeck, 2003). Each run was carried out for 10,000,000 generations, sampling trees every 1,000 generations and the first 2,500 generations (250 trees) were discarded as burnin. The resulting majority-rule consensus tree with bootstrap support value and posterior probability estimation for each node was visualized in FigTree v1.4.4. Trees were edited in Adobe Illustrator CC.

Results

Sequence lengths in bp after editing and alignment were 587 for 12S, 701 for 16S, 1181 for 28S, 1437 for COI (958 without 3rd position in codons) and 475 for TPI (308 without 3rd position in codons). COI was by far the most sampled dataset with 26 species, 16S with 25 species, 12S with 23 species, 28S with 16 species and TPI was the least sampled gene with 10 species. The 3rd codon positions account for larger proportions of parsimony-informative

characters compared with their respective 1st and 2nd positions for both protein-coding genes sequenced in this study (Table 3.4).

Results from the partition homogeneity test found the complete concatenated dataset including all available data from five genes region (ConcatenatedALL) and four datasets of four genes region combined were incongruent (ConcatenatedFOUR2, ConcatenatedFOUR3, ConcatenatedFOUR4 and ConcatenatedFOUR5). Congruence was found from the partition homogeneity test in the dataset ConcatenatedFOUR1, which excluded the 12S gene (p=1.00). The results of the partition homogeneity test are presented in Table 3.5.

Independent analyses of all five individual gene regions produced unresolved trees, with most of the genera returned in a large polytomy. As a result, these trees are not reported on further.

For the complete concatenated dataset (ConcatenatedALL), maximum parsimony yielded a monophyletic Eurybatinae (2 trees, Length= 6151, CI: 43, RI: 44; Figure 3.2), but with a large polytomy within the clade. The analysis including 3rd codon positions showed *Crepidochetus*, *Eurybata* and *Papeza* returned as monophyletic. Each genus was recovered separately as a single clade within the main clade with high node support. *Crepidochetus*, *Eurybata* and *Papeza* remain monophyletic in the analysis excluding 3rd codon positions (1 tree, Length= 3023; CI: 57, RI: 56; Figure 3.3), but with lower node support. Other genera returned in a large polytomy within the clade for both datasets.

Bayesian inference analysis produced a monophyletic Eurybatinae for all datasets, with Taeniapterinae consistently returned as sister to Eurybatinae. The analysis for the complete concatenated dataset (ConcatenatedALL) with 3rd codon positions included formed two large eurybatine clades as shown in Figure 3.4. The first clade includes all but one (*Trepidarioides*) of the eurybatine genera lacking the postmetacoxal bridge, with high node support (pp=0.94). *Paraeurybata* is sister to *Eurybata* plus the Oriental *Cothornobata*. The Australian species of *Cothornobata* and *Crepidochetus* were recovered as the monophyletic sister to the previous group. The second large clade has lower node support (pp=0.72) and includes the only taxon lacking the postmetacoxal bridge, *Trepidarioides*, which is sister to a monophyletic postmetacoxal bridge (PMB) group. Within the PMB group, *Papeza* is sister to the remaining genera. Two species of *Nestima* form a single clade, with *Crosa* as the sister group.

The dataset with 12S excluded (ConcatenatedFOUR1) with 3rd codon positions included (Figure 3.8) formed polytomies of four main branches within the main clade of Eurybatinae with generally high node support. *Nestima* was returned as sister to *Crosa* with high node support (pp=0.97). *Papeza* came out in a single clade (pp=0.99), thus rendering the

PMB group non-monophyletic. All eurybatines lacking the postmetacoxal bridge except *Trepidarioides* were grouped together in one clade but with lower node support (pp=0.88).

Maximum likelihood analysis also produced a monophyletic Eurybatinae for all datasets. The analysis of the complete dataset (ConcatenatedALL) with 3rd codon positions included (Figure 3.6) yielded the same topology as the Bayesian inference analysis of ConcatenatedFOUR1 dataset, but generally with lower backbone support.

Overall, analyses of all datasets without the 3rd codon positions produced a less resolved tree topology with different arrangements and numerous unresolved polytomies (Figures 3.5, 3.7, 3.9).

Discussion

Relationships of Eurybatinae

None of the analyses suggest that Eurybatinae s.s. (Eurybatini *sensu* McAlpine, 1975) is the sister group to Metopochetinae (previously treated as Metopochetini *sensu* McAlpine, 1975). Metopochetinae is instead consistently recovered as the sister group to the Micropezinae as found by Jackson (2019) in his Nerioidea analysis.

Eurybatinae as defined here is equivalent to Eurybatini *sensu* McAlpine (1975). Eurybatinae are recovered here as sister to Taeniapterinae in all analyses. McAlpine (1998) suspected a close relationship between Eurybatinae and Taeniapterinae as he noted a resemblance between these two groups in having a longitudinal groove on the mid and hind tibiae. Despite our support for this sister group relationship between Eurybatinae and Taeniapterinae, the longitudinal groove on the mid and hind tibiae suggested by McAlpine (1998) as a possible synapomorphy of these two subfamilies is absent in some Taeniapterinae. Although this character is absent in some Taeniapterinae, it remains the only character linking Eurybatinae and Taeniapterinae as we could not find other similarities of these two subfamilies.

The subfamily Eurybatinae (in the strict sense, excluding Metopochetinae) was supported as monophyletic in all analyses. Two synapomorphies of Eurybatinae s.s. suggested by McAlpine (1998) are impractical as diagnostic features of the subfamily. The straight suture with no bend marking the transition from the pleural suture to the anapleural suture is a good defining character for Eurybatinae, but it is difficult to use as a diagnostic character because the anapleural suture is slightly bent in some species of *Crosa* and *Crepidochetus*. The synapomorphy of the length of the fifth tarsomere of each tarsus that is at least as long as wide

as suggested by McAlpine (1998) also occurs in Micropezinae, Calobatinae and Taeniapterinae.

Eurybatinae can be characterized by two synapomorphies (as mapped on the selected tree in Figure 3.10). The apical dorsal bare area on the hind tibia with subapical anterodorsal bristles (Figure 3.1A) remains a synapomorphy for the Eurybatinae as suggested by McAlpine (1975, 1998). The second uncontroverted synapomorphy is the structure of sternite 6 (S6) that is deeply V-shaped (Figure 3.1B). Aczél (1959) indicated that the structure of S6 of one species of Eurybatinae, *Crosa yapensis* (Steyskal) was similar to *Micropeza similis* (Aczél) from the subfamily Micropezinae (in Aczél 1949, Figure 12E). We found S6 of *M. similis* differs significantly from that of *C. yapensis*. Sternite 6 of *M. similis* is triangular with thick, short lateral arms compared to the distinctly narrow lateral arms of *C. yapensis*. Sternite 6 of *M. similis* is similar to several other *Micropeza* species examined. McAlpine (1998) considered Eurybatini (Eurybatinae in the current sense) to be closely related to Metopochetini (now treated as Metopochetinae) based on the structure of S6 which he described as “triradiate with asymmetrical posterior arms”. Examination of several Metopochetinae species showed that the S6 has an anteromedial apodeme and asymmetrical arms. Males of all genera of Eurybatinae except *Anaeropsis* were examined in this study, and all have S6 deeply V-shaped with narrow lateral arms. The deep V-shaped S6 is thus here considered to be an uncontroverted synapomorphy supporting Eurybatinae.

Phylogenetics and generic classification of Eurybatinae

Although all analyses recovered a monophyletic Eurybatinae, different datasets and analytic methods produced differing results within Eurybatinae. Maximum parsimony analysis (Figure 3.2 and 3.3) yielded a poorly resolved trees. This may be due to the missing data for some of the taxa as shown in Table 3.1. In maximum parsimony analysis, the phylogenetic signal can be obtained from the parsimony-informative sites only. The relatively large amount of missing data decreases the number of parsimony-informative sites in the dataset, leaving a weak phylogenetic signal in the analysis (Yang and Rannala, 2012). This results in trees that are shorter than the true ones, and recovers false relationships supported by homoplasies that are reconstructed as synapomorphies (Chase et al., 2006), thus leaving in poorly resolved trees that will not be discussed further.

Unlike parsimony, in model-based methods such as Bayesian inference and maximum likelihood, the explicit evolutionary model used for the dataset can extract the phylogenetic

information from every site, including the parsimony-informative sites and the invariable ones (Yang, 1996). The evolutionary model will make assumptions about the probability of a particular nucleotide character to each missing data based on the available data in the dataset. The obtained probabilities for the missing data will be incorporated with the available data in the analysis. Therefore, the model-based methods will have more total characters and provide better approximations of the evolutionary processes contributing to the relationships (Pybus, 2006). In this study, the results from Bayesian inference and maximum likelihood produced well resolved trees compared to maximum parsimony.

The molecular trees produced from Bayesian inference and maximum likelihood analyses are generally better resolved when 3rd codon positions are included than when they are excluded. Table 3.4 shows that 3rd codon positions contributed the highest number of parsimony-informative sites compared with their respective 1st and 2nd positions for the protein-coding genes used in this study. This suggests that these Eurybatinae genes may be evolving relatively slowly, resulting in lower saturation of 3rd codon positions, thus less homoplasy and greater phylogenetic signal being retained. Of the two trees with 3rd codon positions produced by Bayesian analysis (Figures 3.4 and 3.8) and maximum likelihood (Figure 3.7), Bayesian analysis produced a well resolved tree with generally higher node support.

Of two datasets from Bayesian analysis, the dataset including all five genes sampled in this study (ConcatenatedALL) produced a well resolved tree with high node supports (Figure 3.4) compared to the dataset of four genes (ConcatenatedFOUR1) (Figure 3.8). Although all genes in the ConcatenatedFOUR1 dataset were found to be congruent in the partition homogeneity test, the reduced dataset will not always produce a better tree because many factors can contribute to incongruence in a dataset, including inadequate sample sizes, incorrect DNA sequence alignments and missing data. Because the tree produced from ConcatenatedALL dataset produced a well resolved tree with high node supports (Figure 3.4), it was selected as the preferred representation of the evolution of Eurybatinae for purposes of further discussion on the phylogeny of Eurybatinae despite the incongruity generated by 12S.

The selected tree returned a clade characterized by a sclerotized postmetacoxal bridge (PMB) and by the absence of costagial setae (as mapped on the selected tree in Figure 3.10). This clade consists of three genera: *Crosa*, *Nestima* and *Papeza*. The results support the grouping in Eurybatinae as noted by McAlpine (1975), but *Trepidarioides* is weakly supported as sister to *Papeza* and *Nestima* plus *Crosa*. Examination of all available Eurybatinae specimens showed that of 10 genera in the subfamily, only the genera *Crosa*, *Nestima* and *Papeza* have the postmetacoxal bridge. We agree with Aczél (1959) that this character is only

found in Eurybatinae because we did not see the postmetacoxal bridge in other micropezids. McAlpine (1981) defined the postmetacoxal bridge as the metepimera that are fused together behind the bases of the hind coxae to form a bridge. According to Cumming and Wood (2017), the postmetacoxal bridge is a sclerotized area enclosed by the metepimera, the hind coxae and the first abdominal sternite. McAlpine described the postmetacoxal bridge in *Trepidarioides* as narrow and sclerotized on the upper part only, but we found that McAlpine's interpretation of the "narrow" postmetacoxal bridge in *Trepidarioides* is incorrect because the metepimera do not fuse medially to form a postmetacoxal bridge. *Trepidarioides* thus lacks the postmetacoxal bridge. This is consistent with the molecular data suggesting that it does not belong within the PMB group, but instead it is sister to the clade.

Papeza is strongly supported as monophyletic (pp=0.99) and has modest support (pp=0.72) as the sister taxon to *Nestima* plus *Crosa*. We found *Papeza* is diagnosable by the fore femur which is orange-brown on the basal third and gradually turning black distally.

Our results support McAlpine's (1975) hypothesis that *Nestima sensu stricto* and *Crosa* are closely related. McAlpine noted that they share the character of a shallow extensive depression on the anterior third of the mesonotum. We found the character does not link *Nestima sensu stricto* and *Crosa* because that depression is weakly developed in two species of *Nestima* s.s., and completely absent in three other species. The depression is distinct and extensive in *Crosa*. Both genera share other homoplastic characters: the mesonotum overhangs the pronotum and the mid and hind femora have posteroventral spines on the distal third. These characters also occur in all three described species of *Eurybata*.

Nestima and *Crosa* were treated as synonyms by Evenhuis (1989). However, our results show that *Nestima sensu stricto* is a monophyletic sister to *Crosa*. Given *Nestima* s.s. and *Crosa* are easily recognizable as independent entities based on morphology, we are inclined to treat these two groups as separate genera. The previous treatment of these genera as synonyms is rejected, and instead *Crosa* is recognized at its original generic rank.

We found that the character of the subscutellum longer than the scutellum cannot be used to diagnose *Nestima* as suggested by Osten Sacken (1882) and McAlpine (1975), because the subscutellum is equal in length to scutellum in a new species described in *Nestima*, *N. necta*. Although *N. necta* does not have the diagnostic character of *Nestima*, it shares other synapomorphies of *Nestima* (a receding anterior mesonotal margin and a long halter stem). We also found that its male genitalia is consistent with all *Nestima* species examined. *Nestima* was only represented by one species for molecular data in the analysis, and *N. necta* fell into the same clade with *N. pleuralis* with high node support. Therefore, *N. necta* is treated here as

Nestima until further evidence can be acquired. *Nestima* is redefined here to include species with three synapomorphies: the subscutellum longer than the scutellum, a receding anterior mesonotal margin and the halter stem about eight times as long as wide. The latter two characters are found in both sexes of all *Nestima* species examined. The presence of the ventral bristles on the basal half of the male fore femur remains a strong character to diagnose and define *Crosa* as suggested by Steyskal (1952). A full revision of the PMB group is included in Chapter 4.

Trepidarioides is recovered as the sister taxon to the PMB group. The rest of the eurybatine genera for which adequate material was available form a monophyletic group (the CCEP group – *Crepidochetus*, *Cothornobata*, *Eurybata* and *Paraeurybata*). Although the molecular data supports the CCEP clade, we could not find morphological character to support this clade.

Within the CCEP group, *Paraeurybata* is sister to *Eurybata* plus the Oriental *Cothornobata*. The Oriental *Cothornobata* are recovered as monophyletic with high posterior probability (pp=0.99), while the Australian *Cothornobata* species fall into a separate clade with *Crepidochetus*. This supports the hypothesis proposed by McAlpine (1998) and Li et al. (2015) that the Australian species of *Cothornobata* do not belong to the genus *Cothornobata*. We therefore exclude the Australian species from *Cothornobata* and follow the concept of *Cothornobata* s.s. defined by Li et al. (2015), which is thus restricted to the Oriental species.

Cothornobata s.s. (the Oriental *Cothornobata*) is supported by a several characters, including the unique apomorphy of basal and medial tubercles on the male genital fork (sternite 5) as suggested by Li et al. (2015). The Oriental *Cothornobata* was returned here as the sister group to *Eurybata* with high posterior probability (pp=0.99). The Oriental species of *Cothornobata* and the genus *Eurybata* share two synapomorphies: the trifurcate distal distiphallus and a broad, plate-like hypandrium. The genus *Eurybata* is supported as a monophyletic group with high node support (pp=1). We found that *Eurybata* is characterized by a tapering lower margin of the frons (Osten Sacken, 1882). This character is consistent in the three described species of *Eurybata* that we examined.

The Australian *Cothornobata* fall into a large clade with *Crepidochetus* with high posterior probability (pp=0.99). A close relationship between these two groups was suspected by McAlpine (1998) and based on the strong evidence here, we treat the Australian *Cothornobata* as *Crepidochetus*. The genus *Crepidochetus* is redefined here to include species with R_{2+3} vein that is relatively short and ending at the same level or just slightly beyond the dm-m crossvein, the scutellum directed upwards and the sloping mesonotal margin.

The relationships of the genera lacking the sclerotized postmetacoxal bridge presented here are still incompletely resolved because two genera, *Anaeropsis* and the New World genus *Notenthes*, were not included in this study due to the lack of preserved material in alcohol. *Anaeropsis* is probably closely related to the genus *Eurybata* as they both have a deep extensive depression on the anterior third of the mesonotum. Marshall (2002) found that *Notenthes* comes closest to the genus *Cothornobata* because they share some synapomorphies, but it lacks the distinctive feature of the trifurcate distal distiphallus of *Cothornobata*.

Figure 3.1: Synapomorphies of Eurybatinae. A) Hind tibia and tarsus of *Crosa darlingi* sp. n. showing the apical dorsal bare area and subapical anterodorsal bristles on the hind tibia. B) Sternites 5-8 of *Papeza funiculipes* (Enderlein) showing the deeply V-shaped sternite 6. Abbreviation: S – sternite.

Figure 3.2: Parsimony analysis of molecular dataset, 3rd codon positions included (ConcatenatedALL dataset), no weighting, strict consensus of 2 trees. Numbers beneath nodes are bootstrap support values. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.3: Parsimony analysis of molecular dataset, 3rd codon positions excluded (ConcatenatedALL dataset), no weighting, strict consensus of 1 tree. Numbers beneath nodes are bootstrap support values. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.4: Bayesian analysis of molecular dataset, 3rd codon positions included (ConcatenatedALL dataset). Numbers beneath nodes are posterior probabilities. The colour codes are as follows: green = Neriidae, the outgroup; red = Micropezinae; purple = Metopochetinae; blue = Taeniapterinae; black = Eurybatinae. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.5: Bayesian analysis of molecular dataset, 3rd codon positions excluded (ConcatenatedALL dataset). Numbers beneath nodes are posterior probabilities. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.6: Maximum likelihood analysis of molecular dataset, 3rd codon positions included (ConcatenatedALL dataset). Numbers beneath nodes are bootstrap support values. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.7: Maximum likelihood analysis of molecular dataset, 3rd codon positions excluded (ConcatenatedALL dataset). Numbers beneath nodes are bootstrap support. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.8: Bayesian analysis of molecular dataset, 3rd codon positions included (ConcatenatedFOUR1 dataset). Numbers beneath nodes are posterior probabilities. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.9: Bayesian analysis of molecular dataset, 3rd codon positions excluded (ConcatenatedFOUR1 dataset). Numbers beneath nodes are posterior probabilities. Numbers following taxon name indicate unique specimen identifiers.

Figure 3.10: Mapping of character distributions in Eurybatinae on the selected tree obtained from the Bayesian inference analysis of ConcatenatedAll dataset. The colour codes are as follows: green = Neriidae, the outgroup; red = Micropezinae; purple = Metopochetinae; blue = Taeniapterinae; black = Eurybatinae. Numbers following taxon name indicate unique specimen identifiers. Numbers above dots are character numbers. A full list of characters is attached in Appendix. Black circles indicate non-homoplastic synapomorphies. White circles indicate

homoplastic synapomorphies. Thin branches indicate the absence of a sclerotized postmetacoxal bridge. Thick branches indicate the presence of a sclerotized postmetacoxal bridge region.

Table 3.1: DNA sequences used in this study. ‘x’ represents new sequences contributed by this study. ‘*’ represents sequences contributed from other studies. Abbreviations: CNCD – CNC_DIPTERA; JSS – Jeff_Skevington_Specimen.

Species	Unique specimen identifier	12S	16S	28S	COI	TPI
<i>Telostylinus lineolatus</i> (Wiedemann)	JSS17374	*	*	*	*	
<i>Micropeza nitidor</i> Cresson	CNCD254628	*	*		*	*
<i>Mimegralla splendens</i> (Wiedemann)	CNCD254642	*	*		*	
<i>Aristobatina rufithorax</i> (Enderlein)	CNCD254643	*	*		*	*
<i>Cardiacephala brevipennis</i> (Walker)	JSS52465		*		*	
<i>Metopochetus perclusus</i> (Walker)	JSS25745	x		x	x	x
<i>Metopochetus perclusus</i> (Walker)	JSS25734	*		*	*	*
<i>Metopochetus freyi</i> McAlpine	debu01088949	x	x	x	x	x
<i>Metopochetus impar</i> McAlpine	CNC384916	x	x	x	x	x
<i>Metopochetus micidus</i> McAlpine	JSS26239	x	x	x	x	x
<i>Metopochetus bivittatus</i> (Macquart)	CNC457505	x	x	x	x	
<i>Badisis ambulans</i> McAlpine	CNCD254645	x	x	x	x	x
‘ <i>Cothornobata</i> ’ <i>grallina</i> McAlpine	CNC384920	x	x	x	x	
‘ <i>Cothornobata</i> ’ sp. n.	debu01088951		x	x	x	x
‘ <i>Cothornobata</i> ’ <i>alta</i> McAlpine	CNC384918	x	x	x	x	x

<i>Cothornobata</i> sp. n.	CNC571939	x	x		x	
<i>Paraeurybata taeniata</i> (Macquart)	CNCD254640	*	*		*	
<i>Cothornobata breviseta</i> Li et al.	debu00359247				*	
<i>Cothornobata paieroi</i> Li et al.	debu00359252				*	
<i>Crepidochetus debilis</i> Walker	debu01088940	x	x		x	
<i>Crepidochetus argenteofascia</i> Frey	debu01088939	x	x		x	x
<i>Crepidochetus pallida</i> (Steyskal)	debu01088943	x	x		x	
<i>Crepidochetus varipes</i> (Walker)	debu01088942	x	x		x	
<i>Eurybata hexapla</i> Osten Sacken	CNCD254633	*	*		*	*
<i>Eurybata hexapla</i> Osten Sacken	debu01088950		x	x	x	
<i>Crosa angusta</i> sp. n.	debu01088947	x	x		x	
<i>Crosa</i> sp. n.	JSS25727	x		x	x	
<i>Crosa splendida</i> sp. n.	debu01088869	x	x	x	x	
<i>Crosa semilauta</i> (Osten Sacken)	debu01088870	x	x	x	x	x
<i>Crosa semicolor</i> sp. n.	debu01088852	x	x	x	x	x
<i>Crosa petasibarba</i> (Enderlein)	debu01088873	x	x	x	x	
<i>Crosa tumifurca</i> sp. n.	debu01088867	x	x	x	x	
<i>Trepidarioides territa</i> (Osten Sacken)	debu01088948	x	x		x	
<i>Nestima necta</i> sp. n.	debu01088937				x	
<i>Nestima pleuralis</i> Steyskal	CNCD254647	*	*		*	
<i>Papeza funiculipes</i> (Enderlein)	debu01088890	x	x		x	

<i>Papeza szentivanyi</i> McAlpine	debu01088891	X	X	X
<i>Papeza</i> sp. n.	CNCD254639	*	*	*

Table 3.2: List of primer sequences used in this study.

Gene locus	Primer name	Sequences	References
COI-5'	LCO1490 (HebF)	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198 780-R	TAAACTTCAGGGTGACCAAAAAATCA	
COI-3'	PJ-SYR-1F	CCWGGATTYGGWATWATYTC	unpublished
	PJ-SYR-2R	GGTAATTCSGAATASCTRTG	
12S	12Sbi	AAGAGCGACGGGCGATGTGT	Simon et al. (1994)
	12Sai	AAACTAGGATTAGATACCCTATTAT	
16S	12727-12747(S)	AATTTATTGCACTAATCTGCC	Baker et al. (2001)
	13270-13290 (A)	GCTGGAATGAATGGTTGGACG	
28S	28S-SYR-1F	GGATTTTTYTKAGTAGCGGCG	unpublished
	28S-SYR-2R	GGTTCATCCCACAGCGCC	
TPI	TPI111Fb	GGNAAYTGGAARATGAAYGG	Bertone et al. (2008)
	TPI275R	GCCCANACNGGYTCRTANGC	

Table 3.3: Evolutionary model for each gene and partition data produced by PartitionFinder2.

Gene	Subset	Evolutionary Model	Partition names
12S	1	GTR+I+G	12S
16S	2	GTR+G	16S
28S	3	GTR+I+G	28S
COI	4	GTR+I+G	Barcoding_pos1
	5	GTR+I+G	Barcoding_pos2, CO1_pos2
	6	GTR+I+G	Barcoding_pos3
	7	GTR+G	CO1_pos1
	8	GTR+I+G	CO1_pos3
	9	GTR+I+G	TPI_pos1
TPI	10	GTR+G	TPI_pos2
	11	GTR+I+G	TPI_pos3

Table 3.4: Total number of sites, missing data, variable sites and parsimony-informative sites for each gene. “Missing data” represents the number of cells in the matrix represented by “?”.

Partition	No. of sites	Missing data	No. of variable sites	No. of parsimony-informative sites
12S	587	226	162	110
16S	701	241	292	139
28S	1181	219	238	142
COI	1437	960	558	497
COI position 1				89
COI position 2				14
COI position 3				394
TPI	475	85	293	149
TPI position 1				29
TPI position 2				14
TPI position 3				106
TOTAL	4381	1731	1543	1039

Table 3.5: Results of the partition homogeneity test

Dataset	Results
ConcatenatedALL	0.06
ConcatenatedFOUR1 (16S, 28S, COI, TPI)	1.00
ConcatenatedFOUR2 (12S, 28S, COI, TPI)	0.12
ConcatenatedFOUR3 (12S, 16S, COI, TPI)	0.14
ConcatenatedFOUR4 (12S, 16S, 28S, TPI)	0.27
ConcatenatedFOUR5 (12S, 16S, 28S, COI)	0.01

Table 3.6: Taxa included in molecular analysis, including data for newly sequenced specimens for this study and data and sources of sequences contributed from other studies.

Species	Unique specimen identifier	Locality	Date	Collector	Identified	Source of data
<i>Telostylinus lineolatus</i> (Wiedemann)	JSS17374	Fiji: Cakaudrove, Vanue Levu Island, Near Nauavanadi, mangroves and second growth along roadside	27.i.2006	J.H. Skevington	J.H. Skevington	Jackson (2019)
<i>Micropeza nitidor</i> Cresson	CNCD254628	USA: 25 km SW Jct 191 on hwy 366, Twilight Campsite, Mt. Graham, Piñaleno Mts, Graham Co, Arizona	30.vii-7.vii.2015	M.E. Irwin	M.D. Jackson	Jackson (2019)
<i>Mimegralla splendens</i> (Wiedemann)	CNCD254642	Mauritius: Domaine Ylang Ylang	14.xii.2016	G. Kvitte	S.A. Marshall	Jackson (2019)
<i>Aristobatina rufithorax</i> (Enderlein)	CNCD254643	Tanzania: Morogoro Region, Udzungwa Mts National Park	11-13.xi.2009	T. Pape and S.A. Marshall	S.A. Marshall	Jackson (2019)
<i>Cardiacephala brevipennis</i> (Walker)	JSS52465	Ecuador: Orellana, Yasuni Research Station., Yasuni National Park	28.iv-8.v.2009	M.D. Jackson	G.B. Ferro	Ferro (2019)
<i>Metopochetus perclusus</i> (Walker)	JSS25745	Indonesia: West Papua, Waigeo Island	25.26.x.2012	J.H. Skevington	S.A. Marshall	This study
<i>Metopochetus perclusus</i> (Walker)	JSS25734	Indonesia: West Papua, Waigeo Island	25.26.x.2012	J.H. Skevington	S.A. Marshall	Jackson (2019)
<i>Metopochetus freyi</i> McAlpine	debu01088949	Australia: New South Wales, Royal NP	7.i.2010	S.A. Marshall	S.A. Marshall	This study
<i>Metopochetus impar</i> McAlpine	CNC384916	Australia: Queensland, Wooroonooran National Park	17.xii.2014	J.H., A.M. and A.W. Skevington	N.A. Md Yusof	This study
<i>Metopochetus micidus</i> McAlpine	JSS26239	Australia: New South Wales, Oxley Highway, Ginger Creek	5.i.2010	S.A. Marshall	S.A. Marshall	This study
<i>Metopochetus bivittatus</i> (Macquart)	CNC457505	Australia: Tasmania, Franklin-Gordon Wild River National Park	11.i.2015	J.H., A.M. and A.W. Skevington	N.A. Md Yusof	This study
<i>Badisis ambulans</i> McAlpine	CNCD254645	Australia: Western Australia	1.xii.2004	S.A. Marshall	S.A. Marshall	This study
<i>Cothornobata</i>	CNC384920	Australia: Queensland, Wooroonooran	17.xii.2014	J.H., A.M. and	N.A. Md Yusof	This study

<i>grallina</i> McAlpine		National Park		A.W. Skevington		
' <i>Cothornobata</i> ' sp. n.	debu01088951	Papua New Guinea: Mount Wilhelm	26-27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
' <i>Cothornobata</i> ' <i>alta</i> McAlpine	CNC384918	Australia: Queensland, Wooroonooran National Park	17.xii.2014	J.H., A.M. and A.W. Skevington	N.A. Md Yusof	This study
<i>Cothornobata</i> sp. n.	CNC571939	Japan: Amami-Oshima Island Kinsakubaru, Virgin Forest Trail	5.vi.2016	J.H. Skevington, A.D. Young, and S. Bot	J.H. Skevington	This study
<i>Paraeurybata taeniata</i> (Macquart)	CNCD254640	Mauritius: Mare Longue, Black River Gorges	7-9.xii.2016	S.A. Marshall	S.A. Marshall	Jackson (2019)
<i>Cothornobata breviseta</i> Li et al.	debu00359247	Vietnam: Ninh Binh, Cuc Phuong National Park	30.iv.2013	S.A. Marshall and S.M. Paiero	S.A. Marshall	MYCRO Project, BOLD
<i>Cothornobata paieroi</i> Li et al.	debu00359252	Vietnam: Ninh Binh, Cuc Phuong National Park	30.iv.2013	S.A. Marshall and S.M. Paiero	S.A. Marshall	MYCRO Project, BOLD
<i>Crepidochetus debilis</i> Walker	debu01088940	Papua New Guinea: Mount Wilhelm	26-27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crepidochetus argenteofascia</i> Frey	debu01088939	Papua New Guinea: Mount Wilhelm	26-27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crepidochetus pallida</i> (Steyskal)	debu01088943	Papua New Guinea: Mount Wilhelm	26-27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crepidochetus varipes</i> (Walker)	debu01088942	Papua New Guinea: Mount Wilhelm	26-27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Eurybata hexapla</i> Osten Sacken	CNCD254633	Philippines: Los Banos, Mt. Makiling Trail	20-30.iii.2010	S.A. Marshall	S.A. Marshall	Jackson (2019)
<i>Eurybata hexapla</i> Osten Sacken	debu01088950	Philippines: Los Banos, Mt. Makiling Trail	20-30.iii.2010	S.A. Marshall	S.A. Marshall	This study
<i>Crosa angusta</i> sp. n.	debu01088947	Indonesia: Sulawesi, Minahasa, Batu	28.vii.2004	M. Kotrba	N.A. Md Yusof	This study

		Putih				
<i>Crosa</i> sp. n.	JSS25727	Indonesia: West Papua, Arfak Mountain	1.xi.2012	J.H. Skevington	N.A. Md Yusof	This study
<i>Crosa splendida</i> sp. n.	debu01088869	Papua New Guinea: Mount Wilhelm	25- 26.x.2013	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crosa semilauta</i> Osten Sacken	debu01088870	Philippines: Los Banos, Mt. Makiling Trail	20- 30.iii.2010	S.A. Marshall	S.A. Marshall	Jackson (2019)
<i>Crosa semicolor</i> sp. n.	debu01088852	Papua New Guinea: Mount Wilhelm	13- 14.v.2013	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crosa petasibarba</i> (Enderlein)	debu01088873	Papua New Guinea: Wanang 3	x-xii.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Crosa tumifurca</i> sp. n.	debu01088867	Papua New Guinea: Mount Wilhelm	13- 14.v.2013	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Trepidarioides territa</i> (Osten Sacken)	debu01088948	Philippines: Los Banos, Mt. Makiling Trail	20- 30.iii.2010	S.A. Marshall	S.A. Marshall	This study
<i>Nestima pleuralis</i> Steyskal	CNCD254647	Papua New Guinea: Wanang	1.i.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Nestima necta</i> sp. n.	debu01088937	Papua New Guinea: Mount Wilhelm	13- 14.v.2013	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Papeza funiculipes</i> (Enderlein)	debu01088990	Papua New Guinea: Mount Wilhelm	13- 14.v.2013	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Papeza szentivanyi</i> McAlpine	debu01088891	Papua New Guinea: Mount Wilhelm	26- 27.x.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study
<i>Papeza</i> sp. n.	CNCD254639	Papua New Guinea: Mount Wilhelm	1.i.2012	Gewa, Damag, Novotny and Leponce	N.A. Md Yusof	This study

CHAPTER 4

GENERIC CLASSIFICATION OF THE EURYBATINAE AND A REVISION OF THE POSTMETACOXAL BRIDGE GROUP (DIPTERA: MICROPEZIDAE)

Introduction

Phylogenetic analysis of the subfamily Eurybatinae using molecular data (Chapter 3) has provided a foundation for a revised classification of the Eurybatinae. The subfamily Eurybatinae currently comprises 81 species arranged into 10 genera (*Anaeropsis* Bigot, *Cothornobata* Czerny, *Crepidochetus* Enderlein, *Crosa* Steyskal, *Eurybata* Osten Sacken, *Nestima* Osten Sacken, *Notenthes* Marshall, *Papeza* McAlpine, *Paraeurybata* Marshall and *Trepidarioides* Frey) that can be clustered into two groups according to the presence or absence of a sclerotized postmetacoxal bridge. The group with the postmetacoxal bridge was supported as monophyletic in the molecular analyses in Chapter 3, and this clade is also supported by clear morphological synapomorphies. That group, the “postmetacoxal bridge” group, is here revised, including three genera, *Crosa* Steyskal, *Nestima* Osten Sacken and *Papeza* McAlpine. This clade consists of 38 species, of which 20 are newly described herein.

Revision of the postmetacoxal bridge group

The postmetacoxal bridge (PMB) group consists of 38 species here grouped into three genera: *Crosa*, *Nestima*, and *Papeza*. *Crosa* is the most diverse genus within the PMB group with 29 species. *Nestima* and *Papeza* include six and three species respectively. Members of the PMB group are characterized by the presence of the sclerotized postmetacoxal bridge (Fig. 4.1A) and the absence of a costagial setae on the wing base.

Distribution of the postmetacoxal bridge group

Species of the postmetacoxal bridge group are known from the Philippines to Vanuatu. *Crosa* occurs throughout that range (Figures 4.2–4.5), *Nestima* can be found throughout the island of New Guinea including the Bismarck Archipelago (Figure 4.6) and *Papeza* is only known from the eastern part of Papua New Guinea (Figure 4.7).

Biology the postmetacoxal bridge group

Marshall (2012) illustrates mating and oviposition of *Crosa* and other Eurybatinae, showing *C. semilauta* ovipositing in the burrows of woodboring beetles in decaying logs. This habit seems general for the subfamily, and it has been observed in Australia, the Philippines, India, Mauritius and Vietnam (Marshall, 2019; Li et al, 2015). Specimens of the postmetacoxal bridge group have been collected in a wide range of altitudes (between 10–4000 m), most often in yellow pan traps and Malaise traps, but also on leaf surfaces, trees or logs.

Taxonomy of the postmetacoxal bridge group

Diagnosis: Head. Two fronto-orbital bristles, one postocellar bristle, one inner vertical bristle and one outer vertical bristle (Fig. 4.44C). Clypeus glossy and smooth. Palpus broadest basally, gradually tapered distally. **Thorax.** Postmetacoxal bridge present. Cervical sclerite with a narrow, glossy anterior portion and a broad posterior portion. One postalar bristle, one supra-alar bristle, two notopleural bristles and one scutellar bristle. Costagial setae absent. **Abdomen.** Male abdomen: Genital fork (sternite 5) U-shaped; long, narrow arms with short setae, densely setose especially on inner surface and apex. Sternite 6 deeply V-shaped with narrow lateral arms. Surstylus well developed, elongate, bulbous except narrow at base, with long apical and lateral setae. Cercus rounded, setulose. Epandrium moderately elongate anteroventrally, with sparse long setae dorsally and laterally; hypandrium forming a loop through which distiphallus passes. Female abdomen: Spermathecal ducts in a long paired duct and a shorter single duct arising separately from bursa copulatrix; spermathecae (2+1) bell-shaped and similar in size (Fig. 4.9E).

Key to the genera of Eurybatinae with a sclerotized postmetacoxal bridge

1. Male fore femur with long ventral hairs on basal ½ (Fig. 4.31C). Mesonotum with an extensive depression on anterior 1/3 (Fig. 4.31C). ... ***Crosa* Steyskal** Philippines, Malaysia, Indonesia, Papua New Guinea, Yap Islands, Solomon Islands
- Male fore femur with only small setulae ventrally, without long hairs on basal ½. Mesonotum evenly elevated, without depression on anterior 1/3 (Fig. 4.8A). ... 2
2. Mesonotum receding, overhanging pronotum (Fig. 4.11A). Halter stem long, about 8 times width. ... ***Nestima* Osten Sacken** Indonesia, Papua New Guinea
- Mesonotum convex, not overhanging pronotum (Fig. 4.43A). Halter stem short, about 5 times width. ... ***Papeza* McAlpine** Papua New Guinea

***Nestima* Osten Sacken, 1881**

Nestima Osten Sacken, 1881: 457. Type species: *Nestima polita* Osten Sacken, 1881 (monotypy)

Crosa Steyskal, date and page. Type species: *Eurybata semilauta* Osten Sacken, 1882 (orig. des.). Evenhuis, 1989. Synonymy with *Nestima* here rejected.

Head: Fronto-orbital plate sometimes covered with microtrichia. Frontal vitta usually orange-brown on anterior edge, otherwise dark anterior to ocelli (posterior portion weakly differentiated), except for *N. necta* (frontal vitta yellowish on anterior edge, distinctly dark posteriorly). Arista plumose on basal $\frac{1}{2}$, bare beyond that, first flagellomere length approximately $1.5\times$ width.

Thorax: Prosternum and pleuron usually bare, *N. pleuralis* and *N. necta* with prosternum covered by white microtrichia, microtrichose area gradually broadened to meron, forming a longitudinal band on pleuron (Figs. 4.8D and 4.10C). Anterior margin of mesonotum receding, overhanging pronotum (Fig. 4.11A). Notum usually patterned, pruinose. Subscutellum usually longer than scutellum (Fig. 4.11B), except in *N. necta*, subscutellum at most equal in length to scutellum (Fig. 4.8D).

Wing: Usually uniformly infuscated, *N. nigramagnusa* with a hyaline spot. Length of halter stem about $8\times$ width.

WIPs: Height of basal $\frac{1}{4}$ of first concentric ring subequal to height of distal $\frac{1}{4}$ on cell r_{4+5} . Usually angulate anterobasally on cell m, sinuate only in *N. nigramagnusa*. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Legs: Fore femur with only inconspicuous setulae on basal $\frac{1}{2}$ (in contrast to the long-haired male fore femur of the closely related genus *Crosa*), color variable. Fore trochanter usually yellow-brown or orange-brown (black in *N. pleuralis* and *N. necta*). Fore tarsomeres whitish from tarsomere 1 to basal $\frac{1}{2}$ of tarsomere 3, usually gradually pigmented beyond that (Fig. 4.10A) but all white in *N. nigramagnusa* (Fig. 4.9A). Mid and hind tarsi black. Mid and hind femora usually with posteroventral spines on distal third, except smooth, without posteroventral spines in *N. necta*.

Abdomen: Syntergite 1+2 $2\times$ length of tergite 3, usually glossy with short setae. Male abdomen: Genital fork (sternite 5) arms asymmetrical, both arms tapered apically; with short setae, dense especially on inner surface and apex. Anteroventral epandrial arms $5\times$ as long as wide. Pregonite elongate, postgonite with rounded apical ventral lobe, both with short stout

setae (Fig. 4.12I). Basal distiphallus about 3× as long as distal distiphallus, 2.75× as long in *N. necta*; usually straight but slightly sinuate in *N. necta*; distal distiphallus bifurcated into subequal branches; phallic bulb present, length usually 1.5× width (Fig. 4.12F) but length and width equal in *N. necta* (Fig. 4.8G). Phallapodeme usually dilated distally in vertical plane, distally unmodified in *N. polita* (Fig. 4.11F). Sperm pump usually without helmet-like structure. Female abdomen: Spermathecal ducts usually membranous, except sclerotized basally for *N. nigramagnusa*; ducts sometimes with small swelling at spermathecal base; stem length of paired duct 2×–2.5× spermathecal width (Fig. 4.9E).

Comments: *Nestima* is defined by the subscutellum longer than the scutellum, a receding mesonotal margin and the halter stem about 8 times as long as wide. *Crosa* was treated as a junior synonym of *Nestima* by Evenhuis (1989). However, *Nestima* lacks the defining character of *Crosa*, the ventral hairs on the basal ½ of the male fore femur, and *Crosa* lacks the apomorphic characters of *Nestima*. *Crosa* and *Nestima sensu stricto* are thus separate clades characterized by distinct apomorphies. We here treat *Crosa* at its original generic rank, and as sister to *Nestima*.

Key to *Nestima* species

1. Fore trochanter black/dark (Fig. 4.10C). Pleuron with a white microtrichose longitudinal band, gradually broadening and extending toward meron (Fig. 4.10C). ... 2
 - Fore trochanter yellowish brown/orange-brown. Pleuron without microtrichose longitudinal band. ... 3
2. Lower frons flat. Femora uniformly yellowish, without black apex (Fig. 4.10B). Mid and hind femora with posteroventral spines on distal third. Subscutellum longer than scutellum (Fig. 4.10C). ... ***N. pleuralis* Steyskal**
 - Lower frons bulging (Fig. 4.8C). Femora yellowish brown with black apex (Fig. 4.8A). Mid and hind femora smooth, without posteroventral spines on distal third. Subscutellum at most equal in length to scutellum (Fig. 4.8D). ... ***N. necta* sp. n.**
3. Thorax with black pigmentation covering entire postpronotum and surrounding area (Fig. 4.9B). Wing with coalesced hyaline spots at distal 2/3 of cell r_{2+3} and distal ½ of cell r_{4+5} , and with a clear patch adjacent to dm–m and open to posterior wing margin (Fig. 4.9D). ... ***N. nigramagnusa* sp. n.**
 - Thorax without black pigmentation. Wing immaculate, without hyaline spot. ... 4
4. Fore femur uniformly black (according to the description by Walker 1861; see comments below species redescription below). ... ***N. prolixa* (Walker)**
 - Fore femur not as above (either with a preapical black ring OR uniformly brown). ... 5
5. Fore femur yellow-brown with a preapical dark brown ring (Fig. 4.11A). Male genital fork with right arm markedly sinuate (Fig. 4.11G). Ejaculatory apodeme blade narrower than sperm pump. ... ***N. polita* Osten Sacken**

- Fore femur uniformly brown (Fig. 4.12A). Male genital fork with right arm slightly incurved but not sinuate. Ejaculatory apodeme blade wider than sperm pump (Fig. 4.12H). ... *N. viridinsula* Steyskal

Descriptions of *Nestima* species

Nestima necta Md Yusof and Marshall new species

(Figs. 4.8A–4.8J)

Description

Body length 8.4–11.5 mm, wing length 7.5–9.0 mm.

Head: Lower frons bulging (Fig. 4.8C). Fronto-orbital plate until occiput densely covered with white microtrichia. Frontal vitta dark, darker at ocelli; slightly tapering posteriorly; width about ½ of frons width.

Thorax: Scutum with black pitchfork-like pattern, black along outer margin; pruinose (Fig. 4.8B). Prosternum with white microtrichia, microtrichose area extending and gradually broadened to katatergite, forming a longitudinal band on pleuron (Fig. 4.8D). Pleuron glossy black on dorsal third, yellowish ventrally. Subscutellum developed, at most equal in length to scutellum (Fig. 4.8D).

Legs: Trochanter dark. Femora yellowish brown with black apex; mid and hind femora smooth, without posteroventral spines on distal third. Tibia reddish-brown, darkened at apex. Tarsi black.

Wing: Uniformly tan, clear. Length of CuA+CuP 2.5× length of CuA.

WIPs: Angulated anterobasally on cell m. Cell r_{4+5} without spot above dm–m crossvein.

Male abdomen: Left arm of male genital fork longer than right arm, arms straight, tapered apically, outer margin of right arm sinuate at basal ½. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus slightly sinuate, 2.75× as long as distal distiphallus; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade 3× as wide as sperm pump, sperm pump without helmet-like structure.

Female abdomen: Ducts thin, uniformly membranous; both ducts with small swelling at spermathecal base, stem length of paired duct approximately 2× spermathecal width.

Variation: One specimen from Mount Wilhelm has a narrower ejaculatory apodeme blade, a conspicuously large sperm pump and the outer margin of the right arm of the male genital fork arcuate at the basal ½.

Etymology: The specific name refers to the pigmentation of the scutum, specifically to the connection between the lateral arms and the medial band (Latin: “bind”).

Type material: Holotype: PAPUA NEW GUINEA. Mount Wilhelm, 1700 m, 5.7209°S, 145.2695°E, 13–14.x.2013, Malaise trap, IBISCA, Gewa, Damag, Novotny and Leponce (1#m, MNHN). Paratypes: PAPUA NEW GUINEA. Mount Wilhelm, 1700 m, 5.7209°S, 145.2695°E, 13–14.x.2013, Malaise trap, IBISCA, Gewa, Damag, Novotny and Leponce (5#m, 7#f, DEBU DEBU01088935, DEBU01088936, DEBU01088937 [sequenced specimen]); Kassam, 1350 m, 48 km E. of Kainantu, 7.xi.1959, T.C. Maa (2#m, BPBM); Adelbert Mts. Wanuma, 800–1000 m, 26.x.1958, J.L. Gressitt (1#m, BPBM); Wau, 1200–1300 m, 11.ix.1965, J. Sedlacek and M. Sedlacek (1#m, BPBM); Adelbert Mts. Wanuma, 800–1000 m, 24.x.1958, J.L. Gressitt (1#m, BPBM); Sinofi, 1590 m, 30 km S. of Kainantu, 4.x.1959, T.C. Maa (1#m, BPBM); Star Mts. Sibil, Val., 1245 m, 18.x.–8.xi.1961, S. Quate and L. Quate (1#f, BPBM); Kassam Pass, 1550 m, 14–20.xi.1967, Malaise trap, P. Colman (1#f, BPBM); Morobe District Mt. Amingwiwa, 1000–2300 m, 12–13.iv.1970, J.L. Gressitt (1#f, BPBM); Wau, 1200 m, 27.x.1965, Malaise trap, J. Sedlacek and M. Sedlacek (1#m, BPBM); Adelbert Mts. Wanuma, 800–1000 m, 26.x.1958, J.L. Gressitt (1#m, BPBM); Wau, 4000 m, 29.vi.1974, S. Peck (1#f, DEBU); Wau, 1200 m, 15.xii.1965, Malaise trap, J. Sedlacek and M. Sedlacek (1#m, BPBM); INDONESIA (Irian Jaya). NETH., VOGELKOP, Bomberi, 700–900 m, 4.vi.1959, T.C. Maa (1#m, BPBM); Vogelkop, Fak Fak S. coast of Bomberi 100–700 m, 8.vi.1959, T.C. Maa (1#m, BPBM).

Other material examined: PAPUA NEW GUINEA. Mount Wilhelm, 1700 m, 5.7209°S, 145.2695°E, 13–14.x.2013, Malaise trap, IBISCA, Gewa, Damag, Novotny and Leponce (1, sex unknown, MNHN) [this specimen is not treated as type material because the abdomen is lost]

Comments: *N. necta* is the only *Nestima* with the subscutellum not exceeding the scutellum and the mid and hind femora without posteroventral spines. It is one of the two species of *Nestima* with a white microtrichose longitudinal band on the pleuron, but it differs from other *Nestima* and other Eurybatinae by its bulging lower frons. Molecular data shows that *N. necta* fell into one clade with one *Nestima* species included in the analysis, *N. pleuralis* with high node support. Although *N. necta* does not have the diagnostic feature of *Nestima*, the subscutellum longer than the scutellum as suggested by Osten Sacken (1882), it has other diagnostic features of *Nestima* (a receding anterior mesonotal margin and the halter stem about eight times as long as width). Based on the strong support from molecular data and other diagnostic features of *Nestima* possess by *N. necta*, this species is thus treated as *Nestima*.

***Nestima nigramagnusa* Md Yusof and Marshall new species**

(Figs. 4.9A–4.9H)

Description

Body length 8.9–11.6 mm, wing length 6.8–8.9 mm.

Head: Frontal-orbital plate smooth. Frontal vitta orange-brown on anterior edge, dark until before ocelli (posterior portion weakly differentiated).

Thorax: Thorax mostly orange-brown, with black pigmentation covering entire postpronotum and surrounding area. Prosternum bare.

Legs: Fore trochanter orange-brown. Basal third of fore femur orange-brown, otherwise black. Fore tarsomeres whitish. Mid and hind femora with posteroventral spines on distal third

Wing: Wing with coalesced hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{2}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. Length of $CuA+CuP$ vein $2.5\times$ of CuA .

WIPs: Sinuate anterobasally on cell m . Cell r_{4+5} with one spot just above $dm-m$ (Fig. 4.9D).

Male abdomen: Left arm of genital fork longer than right arm, right arm sinuate at basal $\frac{1}{2}$ and incurved apically. Phallapodeme dilated in vertical plane distally. Basal distiphallus about $3\times$ as long as distal distiphallus; phallic bulb length about $1.5\times$ width. Blade of ejaculatory apodeme narrower than sperm pump; sperm pump $1.5\times$ as wide as ejaculatory apodeme blade, with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Stem length of paired duct approximately $2\times$ spermathecal width. Single duct with a ring-like swelling at spermathecal base.

Variation: One specimen from New Ireland has an orange-brown fore femur that is dark on the distal third and black fourth and fifth tarsomeres.

Type material: Holotype: PAPUA NEW GUINEA. New Britain, Gazelle Peninsula, Bainings, Saint Paul's, 350 m, 4.vii.1955, J.L. Gressitt (1#m, BPBM_ENT_17845). Paratypes: PAPUA NEW GUINEA. Bismarck Archipelago, New Britain, Vudal, South of Kerevat, 13.xii.1959, T.C. Maa (1#f, BPBM_ENT_17846); New Britain, Gazelle Peninsula, Bainings, Saint Paul's, 350 m, 4.vii.1955, J.L. Gressitt (1#m, BPBM_ENT_17847).

Other material examined: PAPUA NEW GUINEA. New Britain, Gazelle Peninsula, Mount Sinewit, 900 m, 7–16.xi.1962, J. Sedlacek (1, sex unknown, BPBM) [this specimen is not treated as type material because the abdomen is lost]; New Ireland, $2^{\circ}41'06.59''S$ $150^{\circ}56'43.50''E$, x.19, Paul Zborowski (1#f) [picture of living specimen].

Etymology: *Nestima nigramagnusa* is named for its black postpronotal lobe (Latin: “black spot”).

Comment: *N. nigramagnusa* is the only species of *Nestima* with a dorsolaterally black thorax.

***Nestima pleuralis* Steyskal 1952**

(Figs. 4.10A–4.10G)

Redescription

Body length 10.5–13.5 mm, wing length 8.5–9.2 mm.

Head: Fronto-orbital plate densely covered with microtrichia from anterior to occiput. Frontal vitta orange-brown on anterior edge, dark until before ocelli (posterior portion weakly differentiated).

Thorax: Thorax dark brown on dorsal ½ and along ventral edge of anepisternum, yellowish on ventral ½. Scutum with indistinct broad central band and a narrower transverse band anterior to transverse suture. Scutellum and subscutellum with dense white microtrichia (with a gray sheen due to the microtrichia). Prosternum covered by white microtrichia, microtrichose area gradually broadened to meron, forming a longitudinal band on pleuron.

Legs: Fore trochanter black. Fore femur yellow with a preapical black ring, length of ring 2.5× width of femur. Fore tarsomeres 1 to basal ½ of tarsomere 3 whitish, gradually pigmented beyond that. Mid and hind femora with posteroventral spines on distal third

Wing: Wing uniformly infuscated without any marking. Length of CuA+CuP equal to length of CuA.

WIPs: Angulated anterobasally on cell m. Cell r_{4+5} without spot above dm–m crossvein.

Male abdomen: Left arm of male genital fork slightly longer than right arm.

Female abdomen: Ducts uniformly membranous. Stem length of paired duct approximately 2× spermathecal width. Single duct with small swelling at spermathecal base.

Type material: Holotype: NEW GUINEA. Nadzab, Markham River Valley, 14.v.1944, K.V. Krombein (1#f, USNM type #58308).

Other material examined: PAPUA NEW GUINEA. Wanang 3, 175 m, 5.2277°S 145.0797°E, 1.i.2012, Malaise trap, IBISCA, Gewa, Damag, Novotny and Leponce (1#f, DEBU01088883 sequence MYCRO374-18 [sequenced specimen], DEBU); Kalalo, 750 m, 20–30.ix.1966, Mena and G.A. Samuelson (1#m, BPBM); Finisterre Range, Saidor, Gabumi Vill, 24–30.xi.1958, W.W. Brandt (1#f, BPBM).

Comments: *N. pleuralis* is one of the two species of *Nestima* with a white microtrichose longitudinal band on the pleuron. A similar band also occurs in some species of other genera (*Crosa* Steyskal, *Cothornobata* Czerny and *Paraeurybata* Marshall). The postabdomen is lost on the only male specimen available for examination. The specimen does have a genital fork, but the right arm of the genital fork is collapsed and stripped of setae so it cannot be fully described.

***Nestima polita* Osten Sacken 1881**

(Figs. 4.11A–4.11H)

Redescription

Body length 10.5–13.0 mm, wing length 6.5–8.0 mm.

Head: Fronto-orbital plate smooth, with a blue sheen. Frontal vitta orange-brown on anterior edge, dark until before ocelli (posterior portion weakly differentiated).

Thorax: Thorax uniformly dark brown, with strong blue sheen especially on scutum and scutellum, scutum immaculate; prosternum bare, meron covered with golden microtrichia.

Legs: Fore trochanter yellow-brown. Fore femur yellow-brown with a preapical dark brown ring, length of ring $2.5\times$ width of femur. Fore tarsomeres 1 to basal $\frac{1}{2}$ of tarsomere 3 whitish, gradually pigmented beyond that. Mid and hind femora with posteroventral spines on distal third

Wing: Wing uniformly infuscated without any marking. Length of CuA+CuP equal to length of CuA.

WIPs: Angulated anterobasally on cell m. Cell r_{4+5} without spot above dm–m crossvein.

Male abdomen: Left arm of male genital fork longer than right arm, left arm slightly bent at distal third, right arm greatly bent at basal $\frac{1}{2}$. Phallapodeme quadrate, not dilated distally. Basal distiphallus about $3\times$ as long as distal distiphallus; phallic bulb length about $1.5\times$ width. Ejaculatory apodeme blade narrower than sperm pump, sperm pump $1.25\times$ as wide as ejaculatory apodeme blade, sperm pump without helmet-like structure.

Female abdomen: Ducts uniformly membranous. Stem length of paired duct approximately $2.5\times$ spermathecal width, single duct with small swelling at spermathecal base.

Type material: Syntypes: PAPUA NEW GUINEA. Andai, ix.1872, L.M.D' Albertis (1#m, MCG); PAPUA NEW GUINEA. Hatam, vii.1875, Beccari (1#m, 1#f, MCG).

Other material examined: PAPUA NEW GUINEA (Papua W.). District Oriomo Govt. Sta.,

26–28.x.1960, (no information about collector) (1#f, BPBM); Papua. Normanby I., Wakaiuna, Sewa Bay, 11–20.xi.1956, W.W. Brandt (1#m, BPBM); Papua. Kokoda-Pitoki, 400 m, 23.iii.1956, J.L. Gressitt (1#m, BPBM); Papua. Normanby I., Wakaiuna, Sewa Bay, 11–20.xii.1956, W.W. Brandt (1, sex unknown, BPBM); Mamai Pltn., east of Port Glasgow, 150 m, 13.ii.1965, R. Straatman (1#m, BPBM); Woodlark I., (Murua), Kulumadau Hill. 16.iii.1957, W.W. Brandt (1#f, BPBM); INDONESIA (EAST INDIES). Waigiou, iv.1868, W.W. Saunders (1#m, #NHMUK010862553, BMNH).

Comments: *N. polita* can be easily distinguished from other *Nestima* species by the right arm of the male genital fork, which is conspicuously bent, and by the uniformly black thorax. Walker (1861) indicated that *N. prolixa* also has a black thorax, however it differs from *N. polita* in fore femur colour. One specimen from Woodlark Island (Papua New Guinea) has a preapical ring on its fore femur, but it has heavier scutum pruinosity than specimens from other localities. We tentatively treat it as *N. polita* based on characters of the fore femur. One specimen from NHMUK collected in Waigeo, Indonesia was labeled by Czerny as ‘*Nestima prolixa*’ (#NHMUK010862553). The specimen matches Osten Sacken’s (1881) description of *N. polita* in that its fore femur has a preapical dark brown ring, and also it was collected near one of the type localities of *N. polita*, so we consider it to belong to that species. *N. polita* is the only *Nestima* that occurs throughout the island of New Guinea, including Waigeo and Woodlark Island.

***Nestima prolixa* (Walker) 1861**

Micropeza prolixa Walker 1861: 299

Nestima prolixa (Walker), McAlpine 1975: 244

Type material: Holotype: “Indonesia. Celebes, A.R. Wallace” Date not cited (#m, not seen, possibly lost).

Comments: We were unable to locate the type of *N. prolixa*. It is not in BMNH (where most of the Wallace collection is deposited). This species was described as *Micropeza prolixa* by Walker (1861) and treated as a *Nestima* by McAlpine (1975). The generic status of this species, however, is uncertain. The description by Walker (1861) suggests that it is similar in colour to *N. polita*, however it differs in having a black fore femur. Although leg coloration can be affected by the preservation or drying method, the fore femur pattern is consistent in all specimens of other species of *Nestima* that we have examined. The type locality for *N. prolixa* is Sulawesi (Celebes), Indonesia. Sulawesi has a high level of endemism, and no other species

in the postmetacoxal bridge group occurs in both Sulawesi and Papua New Guinea. Therefore, it is likely that *N. prolixa* is distinct from *N. polita* even though it is currently recognizable on nothing more substantial than femur colour. This must be reconsidered when more specimens from Sulawesi are available for study.

***Nestima viridinsula* Steyskal 1952**

(Figs. 4.12A–4.12J)

Redescription

Body length 7.3–10.8 mm, wing length 5.2–6.7 mm.

Head: Fronto-orbital plate covered with microtrichia from anterior margin to occiput. Frontal vitta orange-brown on anterior edge, dark until before ocelli (posterior portion weakly differentiated).

Thorax: Thorax mostly orange, dark brown dorsolaterally on anterior third. Notum with thin dark brown median longitudinal stripe; prosternum bare; pleuron with microtrichia, dense especially on dorsal ½ and meron, mesopleuron with a dark brown band along dorsal margin, tapering and extending to katatergite, height of the band approximately 1/3 of mesopleuron width (Fig. 4.12C).

Legs: Fore trochanter and fore femur uniformly orange-brown. Fore tarsomeres 1 to basal ½ of tarsomere 3 whitish, gradually pigmented beyond that. Mid and hind femora with posteroventral spines on distal third

Wing: Wing uniformly infuscated without any marking. Length of CuA+CuP vein 2× of CuA length.

WIPs: Angulated anterobasally on cell m. Cell r_{4+5} without spot above dm–m crossvein.

Male abdomen: Left arm of male genital fork slightly longer than right arm. Phallapodeme dilated distally in vertical plane. Basal distiphallus about 3× as long as distal distiphallus; phallic bulb length about 1.5× width. Ejaculatory apodeme with a broad blade, about 2.5× wider than sperm pump, sperm pump without helmet-like structure.

Female abdomen: Ducts uniformly membranous, very thin. Stem length of paired duct approximately 2× spermathecal width.

Type material: Holotype: PAPUA NEW GUINEA (BISMARCK ISLAND). Green Island, 1944, W.G. Downs (1#f, USNM type #58307).

Other material examined: PAPUA NEW GUINEA (BISMARCK ARCHIPELAGO). Manus I., Momote, 24.xii.1959, T.C. Maa (1#m,2#f, BPBM).

Comments: Specimens from BPBM closely match the original description by Steyskal, (1952) however the thorax is uniformly orange except for the median longitudinal stripe on the scutum. Preservation and drying methods sometimes affect color, so we are treating the BPBM specimens as *N. viridinsula*. This should be reconsidered when more specimens from the type locality are available for comparison.

***Crosa* Steyskal, 1952 gen. restit.**

Crosa Steyskal, 1952: 176. Type species: *Eurybata semilauta* Osten Sacken, 1882 (orig. des.). *Nestima* Osten Sacken, 1881: 457. Type species: *Nestima polita* Osten Sacken, 1881 (monotypy); Evenhuis 1989: 94, [as senior synonym of *Crosa* Steyskal, 1952; synonymy here rejected].

Head: Lower frons flat. Fronto-orbital plates smooth, usually flat. Frontal vitta usually velvety, width and colour variable. First flagellomere length approximately 1.5× width; arista plumose on basal 2/3, bare beyond that, longest arisal branches usually 2× length of basal aristomere.

Thorax: Scutum with a shallow extensive depression at anterior 1/3 (Fig. 4.31C). Anterior margin of mesonotum vertical, overhanging pronotum (Fig. 4.19C). Scutum usually pruinose. Prosternum usually bare, sometimes with white microtrichia; pleuron usually with white microtrichose longitudinal band. Scutellum directed posteriorly except for *C. flavifrons* with upturned scutellum. Subscutellum undeveloped (Fig. 4.31C). Usually one postsutural dorsocentral bristle but two in *C. glabra* and *C. cuneifera*. Katepisternal bristles usually scattered and thin with brown tinge; *C. densa* with conspicuously thick, whitish bristles in a distinct fan-shaped row in (as in Taeniapterinae).

Wing: Uniformly infuscated without any marking OR with hyaline spots of variable patterns. Veins R_{2+3} , R_{4+5} and M_1 usually sinuate. Length of halter stem 4× width.

WIPs: First ripple of first concentric ring bordering cell r_{2+3} . Height of basal ¼ of first concentric ring subequal to height of distal ¼ on cell r_{4+5} . Angulate or sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 variable between species.

Legs: Fore femur colour variable, male with ventral hairs on basal ½ (Fig. 4.31C). Fore

tibia usually black, luteous apically. Fore tarsomere 1 yellowish white, tarsomere 2–5 colour variable. Mid and hind femora with posteroventral spines on distal third (Fig. 4.35A), sometimes with black apex (Fig. 4.18A). Mid and hind tibia colour variable, usually darkened at apex (Fig. 4.18A).

Abdomen: Abdomen orange to dark brown, tergites pubescent. Abdominal syntergite 1+2 at least 1.5× length of tergite 3, narrow, constricted at anterior ½; usually with short setae, lateral setae longer. Male abdomen: Genital fork (sternite 5) arms usually symmetrical, with short setae, dense especially on inner surface and apex. Anteroventral epandrial arms about 3×–5× width. Pregonite elongate, with numerous short stout setae (Fig. 4.23F). Postgonite usually with apical ventral lobe with one apical seta (Fig. 4.15F). Phallapodeme usually dilated and flattened-triangular at anterior apex. Length of basal distiphallus variable, distal distiphallus bifurcated into variable length branches; phallic bulb usually present, as long as wide or about 1.5× as long as wide. Ejaculatory apodeme blade fan-shaped, blade width variable interspecifically. Sperm pump sometimes with a helmet-like structure (Fig. 4.15H). Female abdomen: Spermathecal ducts usually membranous, sclerotized basally, some species uniformly membranous, some ducts with small swelling or thickened at spermathecal base; length of stems variable interspecifically.

Comments: *Crosa* is defined by the male fore femur with ventral hairs on the basal ½. *Crosa* was treated as a junior synonym of *Nestima* by Evenhuis (1989). However, it lacks the defining characters of *Nestima*, a receding anterior mesonotum and an unusually elongate halter stem (about 8 times as long as wide). *Crosa* and *Nestima sensu stricto* are separate clades characterized by distinct apomorphies. We thus treat *Crosa* at its original generic rank, and sister to *Nestima*.

Key to *Crosa* species

1. Wing with hyaline spots (Fig. 4.31D). ... 2
 - Wing uniformly infuscated, without hyaline spot (Fig. 4.15C). ... 22
2. Wing apex clear (Fig. 4.31D). ... 3
 - Wing apex either with preapical spots (Fig. 4.38D) OR infuscated (Fig. 4.28C). ... 12
3. Mid and hind femora with black apex (Fig. 4.18A, 4.23A, 4.31B, 4.36B). ... 4
 - Mid and hind femora without black apex. ... 7
4. Wing with coalesced hyaline spots (at distal 2/3 of cell r_{2+3} and distal ½ of cell r_{4+5}) (Fig. 4.18C). Basal distiphallus with ventral keel (Fig. 4.18F). ... ***C. darlingi* sp. n.** Borneo
 - Wing with separated hyaline spots (at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5}) (Fig. 4.31D). Basal distiphallus smooth, without ventral keel (Fig. 4.31G). ... 5

5. Distal distiphallus bifurcated into subequal branches (Fig. 4.36F). Phallic bulb present, as long as wide. Left arm of genital fork bent at basal $\frac{1}{2}$ (Fig. 4.36H). ... *C. sulawesiensis* **sp. n.** Sulawesi
- Distal distiphallus bifurcated into longer right branch and shorter left branch. Phallic bulb greatly reduced (Figs. 4.23E, 4.31G). Left arm of genital fork relatively straight (Figs. 4.23G, 4.31H). ... 6
6. Scutum with a very narrow dark medial longitudinal stripe anterior to transverse suture, and a broad, reddish brown medial longitudinal stripe posterior to transverse suture (Fig. 4.31B). Postgonite tapered apically (Fig. 4.31G). ... *C. reticulata* **sp. n.** Borneo
- Scutum immaculate (Fig. 4.23B). Postgonite slightly rounded apically (Fig. 4.23F). ... *C. immaculata* **sp. n.** Borneo
7. Pleuron with a wedge-shaped white microtrichose area on anepisternum (Figs. 4.14A, 4.21A, 4.24A). ... 8
- Pleuron with a white microtrichose longitudinal band (Figs. 4.13A, 4.32A, 4.37A). ... 10
8. R_{2+3} , R_{4+5} and M_1 veins smooth (Figs. 4.21E, 4.24C). Distal distiphallus bifurcated into subequal branches (Figs. 4.21H, 4.24F). Sperm pump with helmet-like structure (Figs. 4.21I, 4.24G). ... 9
- R_{2+3} , R_{4+5} and M_1 veins sinuate (Fig. 4.14C). Distal distiphallus bifurcated into longer right branch and shorter left branch. Sperm pump without helmet-like structure (Fig. 4.14H). ... *C. borneoensis* **sp. n.** Borneo
9. Phallic bulb about 1.5 times as long as wide (Fig. 4.21H). Paired spermathecal duct long, about 4.5 times of single spermathecal duct (Fig. 4.21G). ... *C. fragilis* (Walker) Peninsular Malaysia, Borneo, Singapore, Sumatra
- Phallic bulb as long as wide (Fig. 4.24F). Paired spermathecal duct short, about 1.5 times of single spermathecal duct (Fig. 4.24E). ... *C. kuchingensis* **sp. n.** Borneo
10. White microtrichose longitudinal band on pleuron extending to vertical pleural suture (Fig. 4.13A). Frontal vitta with a very narrow tapered groove behind ocelli (Fig. 4.13C). ... *C. angusta* **sp. n.** Sulawesi
- White microtrichose longitudinal band on pleuron gradually broadened, extending to katatergite/meron (Figs. 4.32A, 4.37A). Frontal vitta broad behind ocelli, with rounded apex or tapered apex (Figs. 4.32B, 4.37B). ... 11
11. Thorax mostly brown, scutum dark brown (Fig. 4.37A). Frontal vitta widest at anterior margin, gradually tapering posteriorly (Fig. 4.37B). Basal distiphallus with ventral keel at basal $\frac{1}{2}$. Phallapodeme abruptly dilated at margin of anterior apex, thickened (Fig. 4.37H). ... *C. tenuis* (Doleschall) Ambon, Maluku
- Thorax dark brown on dorsal $\frac{1}{2}$, yellowish brown on ventral $\frac{1}{2}$ (Fig. 4.32A). Frontal vitta widest on anterior margin, gradually parallel-sided posteriorly, with rounded apex (Fig. 4.32B). Basal distiphallus smooth, without ventral keel at basal $\frac{1}{2}$. Phallapodeme quadrate and angulate anteriorly (Fig. 4.32E). ... *C. semicolor* **sp. n.** Papua New Guinea, Vanuatu
12. Wing apex uniformly infuscated. ... 13
- Wing apex with preapical hyaline spot. ... 18
13. Scutum with two pairs of dorsocentral bristles (Fig. 4.22C). ... 14
- Scutum with one pair of dorsocentral bristles. ... 15
14. Anepisternum bare, without a wedge-shaped white microtrichose area (Fig. 4.22A). ... *C. glabra* (de Meijere) Java
- Anepisternum with a wedge-shaped white microtrichose area (Fig. 4.17A). ... *C. cuneifera* (de Meijere) Java
15. Pleuron with a wedge-shaped white microtrichose area. Scutellum directed upward (Fig. 4.20C). ... *C. flavifrons* (Bigot) Papua New Guinea
- Pleuron either smooth or with a white microtrichose longitudinal band. Scutellum directed

posteriorly. ... 16

16. Distal distiphallus bifurcated into shorter right branch and longer left branch (Fig. 4.30E). Sperm pump conspicuously larger than ejaculatory apodeme blade (Fig. 4.30G). ... *C. reducta* sp. n. Papua New Guinea

- Distal distiphallus bifurcated into subequal branches (Figs. 4.28F, 4.34F). Sperm pump smaller than ejaculatory apodeme blade (Figs. 4.28H, 4.34H). ... 17

17. Thorax reddish brown. Pleuron rugose, with a white microtrichose longitudinal band (Fig. 4.34A). Genital fork smooth, without tubercle (Fig. 4.34F). ... *C. sparsa* sp. n. Papua New Guinea

- Thorax orange. Pleuron bare, without a white microtrichose longitudinal band (Fig. 4.28A). Genital fork with tubercle at basal ½ of left arm (Fig. 4.28F). ... *C. nigrifrontata* sp. n.

Solomon Islands

18. Cell r_{4+5} with three hyaline spots: adjacent to r-m, at distal 1/3 and preapically (Fig. 4.27C). ... *C. multimaculata* sp. n. Solomon Islands

- Cell r_{4+5} with two hyaline spots: at distal 1/3 and preapically (Figs. 4.16D, 4.26C, 4.33E, 4.38D). ... 19

19. Genital fork arms strongly incurved, almost flat apically (Fig. 4.38G). Thorax mostly brown (Fig. 4.38A). ... *C. tetras* (Steyskal) Solomon Islands

- Male genital fork arms relatively straight apically. Thorax mostly black (Fig. 4.26A) or reddish brown (Figs. 4.16A, 4.33B). ... 20

20. Thorax mostly black (Fig. 4.26A). Frontal vitta gradually tapering posteriorly. Phallic bulb as long as wide (Fig. 4.26E). ... *C. melanosa* sp. n. Solomon Islands

- Thorax mostly reddish brown. Frontal vitta with a very narrow tapered groove behind ocelli (Figs. 4.16C, 4.33C). Phallic bulb about 1.5 times as long as wide (Figs. 4.16F, 4.33F). ... 21

21. Mid and hind femora brown with a faint preapical black ring (Fig. 4.33A). ... *C. semilauta* (Osten Sacken) Philippines

- Mid and hind femora uniformly brown, without a preapical black ring (Fig. 4.16A). ... *C. calcarata* sp. n. Philippines

22. Pleuron bare, without white microtrichose longitudinal band. ... 23

- Pleuron with a white microtrichose longitudinal band. ... 24

23. Thorax mostly yellowish brown (Figs. 4.25A). R_{2+3} , R_{4+5} and M_1 veins straight. ... *C. meijerei* (Frey) Java

- Thorax mostly dark brown, reflecting strong blue sheen (Figs. 4.35A). Base of genital fork with long black setae ventrally (Fig. 4.35G). R_{4+5} and M_1 veins slightly sinuate. ... *C. splendida* sp. n. Papua New Guinea

24. Katepisternal bristles thick, conspicuously whitish (appear in a distinct row in fan shape as in Taeniopterinae) (Fig. 4.19C). Paired spermathecal duct thin on basal ½, gradually thickened on distal ½ (Fig. 4.19F). ... *C. densa* sp. n. Papua New Guinea

- Katepisternal bristles thin with brown tinge (appear in indefinite row) (Figs. 4.17A, 4.29A, 4.39A, 4.40A, 4.41A). Paired spermathecal duct uniformly thin (unknown for *C. vitellosa* sp. n.). ... 25

25. Distal distiphallus bifurcated into longer right branch and shorter left branch (Fig. 4.39E). Male genital fork with a tubercle at basal ½ of right arm (Fig. 4.39F). ... *C. tumifurca* sp. n. Papua New Guinea

- Distal distiphallus bifurcated into subequal branches/slightly shorter right branch. Male genital fork smooth, without tubercle on arms. ... 26

26. Thorax mostly reddish brown (Figs. 4.15A, 4.29A). Sperm pump with helmet-like structure (Figs. 4.15H, 4.29H). ... 27

- Thorax mostly orange brown (Figs. 4.40A, 4.41A). Sperm pump without helmet-like structure (Figs. 4.40G, 4.41G). ... 28

27. Distal distiphallus bifurcated into subequal branches (Fig. 4.29F). Male genital fork symmetrical, both arms relatively straight (Fig. 4.29G). Base of each spermatheca thin (Fig. 4.29E). ... *C. petasibarba* (Enderlein) Papua New Guinea

- Distal distiphallus bifurcated into slightly shorter right branch and slightly longer left branch (Fig. 4.15F). Genital fork asymmetrical, left arm distinctly longer than right arm, incurved distally (Fig. 4.15G). Base of each spermatheca distinctly thickened (Fig. 4.15E). ... *C. burgersi* (Enderlein) Irian Jaya, Papua New Guinea

28. White microtrichose longitudinal band on pleuron extending from propleuron to posterior margin of anepisternum (Fig. 4.40A). Phallapodeme dilated into fan-shape at anterior apex, apex strongly convex (Fig. 4.40E). Genital fork arms thin, tapered apically (Fig. 4.40F). ... *C. vitellosa* sp. n. Papua New Guinea

- White microtrichose longitudinal band on pleuron extending from propleuron to posterior margin of anepisternum (Fig. 4.41A). Phallapodeme slightly dilated on distal ½ and constricted before flattened-triangular anterior apex, apex straight (Fig. 4.41E). Genital fork arms thick, rounded apically (Fig. 4.41F). ... *C. yapensis* Steyskal Yap Islands

Descriptions of *Crosa* species

Crosa angusta Md Yusof and Marshall new species

(Figs. 4.13A–4.13F)

Description

Body length 12.0–12.3 mm, wing length 8.5–9.0 mm.

Head: Frontal vitta depressed, yellow on anterior margin, otherwise black; widest at anterior margin, gradually tapering until posterior fronto-orbital bristle, slightly expanded at ocelli, extending as a very narrow tapered groove behind ocelli; width of anterior margin about 1/3 of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax mostly brown, scutum with an indistinct reddish-brown narrow median vitta, vitta slightly broader beyond transverse suture. Prosternum covered by white microtrichia, microtrichose area gradually broadened to vertical pleural suture, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown with a preapical dark brown ring, length of ring 2× width of femur, fore tibia yellowish brown; fore tarsus uniformly yellow. Mid and hind femora uniformly reddish brown. Mid and hind tibia yellowish brown.

Wings: Wing with clear apex and complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins slightly sinuate at hyaline spots. Length of $CuA+CuP$ 2× of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z -

shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male: Unknown.

Female abdomen: Base of ducts sclerotized. Paired duct twice as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: INDONESIA. Sulawesi, Minahasa, Batu Putih, 28.viii.2004, M. Kotrba (1#f, DEBU01088858 sequence MYCRO347-18 [sequenced specimen], DEBU). Paratype: Same data as holotype (1#f, DEBU).

Etymology: *C. angusta* is named for its narrow frontal vitta (Latin: “narrow”).

Comments: *C. angusta* is one of the three species in *Crosa* in which the frontal vitta forms a very narrow and tapered groove behind the ocelli. However, it is easily distinguishable from the other two species by its brown colouration and the white microtrichose longitudinal band on its pleuron. Males remain unknown.

***Crosa borneoensis* Md Yusof and Marshall new species**

(Figs. 4.14A–4.14H)

Redescription

Body length 7.0–10.0 mm, wing length 4.5–6.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta yellow on anterior edge, dark posteriorly; widest at anterior margin, gradually tapering until just anterior to posterior fronto-orbital bristle, remaining width uniform with V-shaped apex; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches 2X length of basal aristomere.

Thorax: Scutum dark with strong blue sheen on anterior $\frac{1}{4}$ including postpronotum, otherwise thorax mostly brown, brighter dorsally. Prosternum bare. Anepisternum with a wedge-shaped white microtrichose area at dorsal $\frac{1}{2}$ of vertical pleural suture. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur brown basally, otherwise black, fore tibia dark, except at apex; tarsomere 2 yellowish white basally and gradually darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia dark on basal third, gradually pale apically.

Wings: Wing with clear apex and complete hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{3}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins sinuate at hyaline spots. Length of $CuA+CuP$ $1.5\times$ of length CuA .

WIPs: Sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m₄ more than ½ of cell length.

Male abdomen: Genital fork symmetrical U-shaped. Phallapodeme dilated at anterior apex, with side edges angled. Basal distiphallus 2× as long as distal distiphallus; distal distiphallus bifurcated into long right branch and short left branch; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade 3.5× width of sperm pump, sperm pump without helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct twice as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: MALAYSIA. Sarawak, Gunung Mulu National Park, Summit trail, vic Paku Waterfall in forest, 42 m, 4°2.277'N 114°49.72'E, 19–20.x.2010, Yellow pan traps, D.C. Darling (1#m, ROME). Paratypes: MALAYSIA. Sarawak (Borneo), Gunung Mulu National Park, Camp 5, forest, 165 m, 4°8.836'N 114°53.243'E, 22–23.vii.2010, Yellow pan traps, D.C. Darling (1#f, DEBU); Gunung Mulu National Park, 113 m, 4°8.187'N 114°53.509'E, 3–4.vi.2011, Pan traps (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Nightwalk trail, 67 m, 4°0.083'N 114°48.906'E, 27–28.iv.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall, in forest, 50 m, 4°2.212'N 114°49.722'E, 6–7.vii.2010, D.C. Darling (1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 29–30.v.2010, pan trap (yellow), D.C. Darling (4#m, ROME); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 23.x.2010, pan trap (yellow), D.C. Darling and B. Hubley (3#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, Headhunters trail, 140 m, 4°8.552'N 114°53.51'E, 5–8.xii.2009, pan trap (yellow), D.C. Darling and B. Hubley (2#m, ROME); Sarawak (Borneo), Gunung Mulu National Park vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 18–19.ii.2010, pan trap (yellow), D.C. Darling (4#m, ROME); Sarawak (Borneo), Gunung Mulu National Park, 113 m, 4°8.187'N 114°53.509'E, 3–4.vi.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall, in forest, 50 m, 4°2.212'N 114°49.722'E, 6–7.vii.2010, D.C. Darling (2#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, HQ, trail near intersection, with old summit trail, alluvial, 26 m, 4°2.5'N 114°48.9'E, 19–20.iv.2011, Yellow pan traps, D.C. Darling and N.F. Johnson (1#m, 1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, Melinau River gorge forest

trail, 130 m, 4°8.193'N 114°53.658'E, 5–6.v.2010, pan trap (yellow), D.C. Darling (2#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 22.vii.2010, pan trap (yellow), D.C. Darling (2#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, forest, 165 m, 4°8.836'N 114°53.243'E, 22–23.vii.2010, Yellow pan traps, D.C. Darling (1#m, 1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 22.vii.2010, pan trap (yellow), D.C. Darling (2#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, Forest, 165 m, 4°8.836'N 114°53.243'E, 16–17.xi.2010, Yellow pan traps, D.C. Darling (4#m, 1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 7–8.vii.2010, pan trap (yellow), D.C. Darling (5#m, 1#f, ROME); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 23.v.2010, pan trap (yellow), D.C. Darling (3#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, Melinau River, gorge forest trail, 130 m, 4°8.193'N 114°53.658'E, 17–18.iii.2010, pan trap (yellow), D.C. Darling (2#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail vic. Paku Waterfall in forest, 42 m, 4°2.277'N 114°49.72'E, 30.ix.2010, Yellow pan traps, D.C. Darling (3#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, along forest trail, 113 m, 4°8.187'N 114°53.509'E, 4.xii.2009, pan trap (yellow), D.C. Darling and B. Hubley (2#f, ROME); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 30.i.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 22.iv.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, Melinau River, gorge forest trail, 130 m, 4°8.193'N 114°53.658'E, 17–18.iii.2010, pan trap (yellow), D.C. Darling (2#m, DEBU01088945, DEBU01088946, DEBU); Sarawak (Borneo), Gunung Mulu National Park, vic. park HQ, under boardwalk to Deer Cave, 50 m, 4°2.487'N, 114°48.866'E, 2–6.xi.2009, pan trap (yellow), D.C. Darling and N.F. Johnson (1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 27–28.vii.2010, pan trap (yellow), D.C. Darling (1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 26–27.iv.2010, pan trap (yellow), D.C. Darling (1#f, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Camp 5, along forest trail, 113m, 4°8.187'N 114°53.509'E, 3–4.vi.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 2–7.xi.2009, pan trap (yellow), D.C. Darling and N.F. Johnson

(1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic Paku Waterfall in forest, 42 m, 4°2.277'N 114°49.72'E, 19–20.x.2010, Yellow pan traps, D.C. Darling (4#m, DEBU01088857, DEBU01088856, sequence MYCRO345-18, DEBU); Sarawak (Borneo), Gunung Mulu National Park, vic park HQ, night walk trail, 67 m, 4°2.478'N 114°48.939'E, 29–30.vi.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sabah (Borneo), Penampang District, Crocker Range, Moyog, Moyog River, 300 m, 5°53.02'N 116°14.48'E, 17.x.2011, S. Gaimari and M. Hauser (3#m, 1#f, DEBU01088854 sequence MYCRO343-18, DEBU01088855 sequence MYCRO344-18, CDFA); PHILIPPINES. Palawan, Tarumpitao Pt., Jungle clearing, 3.vi.1958, H.E. Milliron (1#f, BPBM).

Comments: Although externally similar to *C. kuchingensis*, *C. borneoensis* is characterized by a distiphallus that is distinctly bifurcated into a longer right branch and a shorter left branch (in contrast with *C. kuchingensis*, in which the arms differ only slightly in length). The anterior apex of the phallapodeme, which is dilated with the side edges slightly angled, is also a distinct character.

***Crosa burgersi* (Enderlein, 1922) new combination**

Calobata burgersi Enderlein 1922: 171

Nestima burgersi (Enderlein), Evenhuis 1989: 465

(Figs. 4.15A–4.15H)

Redescription

Body length 8.3–10.8 mm, wing length 6.3–7.6 mm.

Head: Fronto-orbital plate flat. Frontal vitta dark on anterior third, gradually reddish brown posteriorly; widest at anterior margin, gradually tapering posteriorly until posterior fronto-orbital bristle, remaining width uniform, with rounded apex; width of anterior margin about ½ of frons width, narrowest width slightly more than 1/3 of frons width. Longest arisal branches 2× length of basal aristemere.

Thorax: Anterolateral corner of mesonotum including postpronotal lobe dark, otherwise thorax reddish-brown. Prosternum covered by white microtrichia, microtrichose area extending and gradually broadened to vertical pleural suture, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur uniformly reddish brown, fore tibia dark; tarsomere 2 yellowish white

basally, gradually darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown.

Wing: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP 1.5× length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 more than ½ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm distinctly longer and incurved distally, right arm sinuate on outer margin and diverging apically. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Basal distiphallus 2× as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade 3× as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 2.5× as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: PAPUA NEW GUINEA. Lordberg, xii.1912, Burgers (1#f, MNBG).

Other material examined: INDONESIA (Irian Jaya). Neth., Vogelkop, Bomberi, 700–900 m, 7.vi.1959, T.C. Maa (3#m, 1#f, BPBM); Vogelkop, Fak Fak, south coast of Bomberai, 100–700 m, 4.vi.1959, T.C. Maa (1#m, 2#f, BPBM); PAPUA NEW GUINEA (WEST NEW GUINEA). Star Mts., Sibil Val, 1245 m, 18.x.–8.xi.1961, S. Quate and L. Quate (1#f, BPBM); Adelbert Mts: Wanuma, 800–1000 m, 26.x.1958, J.L. Gressitt (1#m, BPBM).

Comment: *C. burgersi* differs markedly from other *Crosa* by its conspicuously asymmetrical genital fork with a distinctly longer left arm that is incurved distally.

***Crosa calcarata* Md Yusof and Marshall new species**

(Figs. 4.16A–4.16I)

Description

Body length 7.8–12.0 mm, wing length 4.9–6.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta reddish-brown, darkened posteriorly; widest at anterior margin, gradually tapering until just posterior to ocelli, then extending to vertex as a very narrow tapered groove; width of anterior margin about ½ of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Scutum dark with blue sheen on anterior ¼ including postpronotum and posterior ¼,

with indistinct narrow median vitta, otherwise thorax reddish brown. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown on basal third and apically, otherwise black, fore tibia brown, slightly darkened apically; tarsomere 2 yellowish white basally, darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia pale brown.

Wings: Cell r_{2+3} with complete hyaline spot at distal 2/3 and preapical, cell r_{4+5} with complete hyaline spots at distal 1/3 and preapical, and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins sinuate at hyaline spots. Length of $CuA+CuP$ equal to length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly longer than left arm; rounded apically. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus $1.5\times$ as long as distal distiphallus; distal distiphallus bifurcated into slightly shorter right branch and slightly longer left branch; phallic bulb present, length $1.5\times$ width. Ejaculatory apodeme with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct $2.5\times$ as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: PHILIPPINES. Prov. Calamarines Norte. Mount Labo, base camp, $14^{\circ}04.456'N$ $122^{\circ}46.146'E$, 273 m, 22.v.2016, Pan traps, Cameron Siler (1#m, PNMNH #13652). Paratype: Same data as holotype (1#f, PNMNH #13653).

Etymology: *C. calcarata* is named for its posteriorly pointed frontal vitta (Latin: “spur”).

Comments: Although similar to *C. semilauta*, *C. calcarata* differs in lacking a preapical ring on the mid and hind femora. The upper part of the ejaculatory apodeme blade is missing on the only male specimen available for examination, and was probably lost during dissection. The sperm pump is intact, and is distinctly larger than in *C. semilauta*.

***Crosa cuneifera* (de Meijere, 1914)**

Eurybata cuneifera de Meijere 1914: 178

Crosa cuneifera (de Meijere), McAlpine 1975: 244

(Figs. 4.17A–4.17G)

Redescription

Body length 9.0–9.2 mm, wing length 6.0–6.3 mm.

Head: Fronto-orbital plate flat. Frontal vitta dark on anterior third, brownish posteriorly, weakly differentiated from fronto-orbital plates; widest at anterior margin, gradually tapering posteriorly; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly brown, notum with medial longitudinal stripe, and a circular patch immediately anterior to and ovoid patch posterior to transverse suture. Prosternum covered by white microtrichia, microtrichose area extending to proepimeron; anepisternum with a wedge shaped white microtrichose area at dorsal $\frac{1}{2}$ of vertical pleural suture. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with two postsutural dorsocentral bristles.

Legs: Fore femur brown on basal third and apically, otherwise black, fore tibia dark, except at apex; tarsomere 2 yellowish white, darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown (sometimes giving the impression that they are black due to black microsetulae).

Wing: Wing with complete hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{3}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ $2.5\times$ length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly longer than left arm; rounded apically. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus $4\times$ as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female: Unknown.

Type material: Holotype: INDONESIA. Java, Gunung Ungaran, xii.1909, E. Jacobson (1#m, MNBG #DIPT.0705.1).

Other material examined: INDONESIA. West Java, Djampang Mts, ix.1938, G. Besser, (1#m, B.M.1962-651, BMNH); Java, Soekaboemi, ii.1926, Purch E. Le Mout (1#m, B.M.1933-189, BMNH).

Comments: *C. cuneifera* and *C. glabra* are the only *Crosa* with two pairs of dorsocentral

bristles. Although similar to *C. glabra*, *C. cuneifera* is distinct for the presence of a wedge-shaped white microtrichose area on the anepisternum.

***Crosa darlingi* Md Yusof and Marshall new species**

(Figs. 4.18A–4.18H)

Description

Body length 8.0–11.0 mm, wing length 6.5–8.0 mm.

Head: Fronto-orbital plate flat. Frontal vitta yellow on anterior margin, dark to anterior of ocelli and indistinct reddish brown posteriorly; parallel-sided with V-shaped apex; width about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Scutum dark with blue sheen on anterior $\frac{1}{4}$, otherwise thorax reddish brown, brighter dorsally. Prosternum covered by white microtrichia, microtrichose area extending to proepimeron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur uniformly black, fore tibia dark, except at apex; tarsomere 2 yellowish white basally and gradually darkened apically. Mid and hind femora brown except for black apex. Mid and hind tibia reddish dark brown on basal third, brown apically.

Wings: Wing with clear apex and coalesced jagged edge hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{2}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ $2\times$ of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly shorter and thicker, slightly incurved apically. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus subequal in length to distal distiphallus, slightly sinuate with ventral keel near base; distal distiphallus bifurcated into long right branch and short left branch; phallic bulb greatly reduced, indistinct. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct twice as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: MALAYSIA. Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 7–8.vii.2011, pan

trap (yellow), D.C. Darling (1#m, ROME). Paratypes: MALAYSIA. Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 26–27.iv.2010, pan trap (yellow), D.C. Darling (1#m,1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 6–7.vi.2010, pan trap (yellow), D.C. Darling (8#m,1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 29–30.v.2010, pan trap (yellow), D.C. Darling (1#m,3#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 29.v.2011, pan trap (yellow), D.C. Darling (6#m, ROME); Sarawak, Borneo, Gunung Mulu National, Park Camp 5, along forest trail, 113 m, 4°8.187'N 114°53.509'E, 3–4.vi.2011, pan trap (yellow), D.C. Darling (10#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 27–28.vii.2010, pan trap (yellow), D.C. Darling (4#m,3#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, Forest, 165 m, 4°8.836'N 114°53.243'E, 12–13.i.2011, Yellow pan trap, D.C. Darling (2#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°8.083'N 114°48.906'E, 24.xi.2010, pan trap (yellow), D.C. Darling (2#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Gunung Mulu Summit trail, 50 m, 4°2.212'N 114°49.722'E, 22–23.xi.2009, Yellow pan trap, D.C. Darling and B. Hubley (1#m,2#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest. 77 m, 4°0.083'N 114°48.906'E, 1.vi.2011, pan trap (yellow), D.C. Darling (4#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, pan trap (yellow), 18.ii.2010, D.C. Darling (5#m,3#f, DEBU); Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 19.iii.2010, D.C. Darling and B. Hubley (2#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 7–8.vii.2011, pan trap (yellow), D.C. Darling (11#m,5#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 17–18.iii.2011, pan trap (yellow), D.C. Darling (15#m,2#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 22–23.iv.2010, pan trap (yellow) D.C. Darling (2#m,1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, HQ, trail near intersection with old summit trail, alluvial, 26 m, 4°2.5'N 114°48.9'E, 11–12.vii.2011, Yellow pan trap, D.C. Darling (7#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 16–17.ii.2011, pan trap (yellow), D.C. Darling (3#m, DEBU); Gunung Mulu

National Park, Camp 5, Melinau River gorge forest trail, 130 m, 4°8.193'N 114°53.658'E, 18.viii.2010, pan trap (yellow), D.C. Darling and N. Tatarnic (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 29–30.v.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 18–19.ii.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, along Deer Cave trail, near junction with small forest trail, 58 m, 4°1.525'N 114°49.481'E, 13–14.ix.2011, Yellow pan trap, D.C. Darling (1#f, DEBU); Gunung Mulu National Park, Camp 5, Forest, 165 m, 4°8.836'N 114°53.243'E, 16–17.xii.2010, Yellow pan trap, D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 16–17.ii.2011, Yellow pan trap, D.C. Darling (3#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, Melinau River gorge forest trail, 130 m, 4°8.193'N 114°53.658'E, 5–8.xii.2009, pan trap (yellow), D.C. Darling and B. Hubley (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, along forest trail, 113 m, 4°8.187'N 114°53.509'E, 16–17.iv.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N, 114°48.906'E, 22.iv.2011, pan trap (yellow), D.C. Darling (3#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 22.vii.2010, Yellow pan trap, D.C. Darling (1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, Forest, 165 m, 4°8.836'N 114°53.243'E, 27–28.xii.2010, Yellow pan trap, D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, trail along Melinau River, 113 m, 4°8.193'N, 114°53.658'E, 20–21.vii.2011, pan trap (yellow), D.C. Darling (20#m,4#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, trail along Melinau River, 113 m, 4°8.193'N, 114°53.658'E, 6–7.vii.2011, pan trap (yellow), D.C. Darling (2#m,1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N, 114°49.722'E, 19.viii.2011, pan trap (yellow), D.C. Darling (6#m,2#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Nightwalk trail, 67 m, 4°2.478'N, 114°48.939'E, 27–28.viii.2010, pan trap (yellow), D.C. Darling and N.F. Johnson (4#m,1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N, 114°49.722'E, 18–19.i.2012, pan trap (yellow), D.C. Darling (4#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, HQ, trail near intersection with old summit trail, alluvial, 26 m, 4°2.5'N 114°48.9'E, 11–12.viii.2011, D.C. Darling (12#m,1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, HQ, trail nr. intersection with old summit trail, alluvial, 26 m, 4°2.5'N, 114°48.9'E, 10–

11.i.2012, Yellow pan trap, D.C. Darling (2#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, HQ, trail near intersection with old summit trail, alluvial, 26 m, 4°2.5'N 114°48.9'E, 19–20.iv.2011, Yellow pan trap, D.C. Darling and N.F. Johnson (7#m, 1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Nightwalk trail, 67 m, 4°2.478'N 114°48.939'E, 1–2.ii.2011, D.C. Darling (2#m 1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, Melinau River gorge forest trail, 130 m, 4°8.193'N 114°53.658'E, 5–6.v.2010, pan trap (yellow), D.C. Darling (3#m, 1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 29–30.v.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 30–31.v. 2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 23.x.2010, pan trap (yellow), D.C. Darling and B. Hubley (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 27–28.vii.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Camp 5, along forest trail, 113 m, 4°8.187'N 114°53.509'E, 3–4.vi.2011, D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 17–18.iii.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall, in forest, 50 m, 4°2.212'N 114°49.722'E, 29.xii.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, 77 m. Long Lansat, in forest, 4°0.083'N 114°48.906'E, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 6–7.vii.2010, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Long Lansat, in forest, 77 m, 4°0.083'N 114°48.906'E, 24.xi.2010, D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 29–30.v.2010, D.C. Darling (1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 30–31.v.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 29.xii.2010, pan trap (yellow), D.C. Darling (1#f, DEBU); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 16–17.ii.2011, pan trap (yellow), D.C. Darling (1#m, DEBU); Sarawak, Borneo, Gunung Mulu National Park,

Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 7–8 Jul 2011, pan trap (yellow), D.C. Darling (2#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, 77 m, Long Lansat, in forest, 4°0.083'N 114°48.906'E, 13.ix.2010, pan trap (yellow), D.C. Darling (1#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 18.ii.2010, pan trap (yellow), D.C. Darling (1#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, HQ, New Trail near intersection with Old Summit Trail, 26 m, 4°2.5'N 114°48.9'E, 2–3.iii.2011, pan trap (yellow), D.C. Darling (1#m, 1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, vic. park HQ, Night Walk trail, 67 m, 4°2.478'N 114°48.939'E, 22–23 Apr 2010, pan trap (yellow), D.C. Darling (1#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 50 m, 4°2.212'N 114°49.722'E, 27.vii.2010, pan trap (yellow), D.C. Darling (1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, 77 m, Long Lansat, in forest, 4°0.083'N 114°48.906'E, 20.x.2010, pan trap (yellow), D.C. Darling and B. Hubley (1#f, ROME); Sarawak, Borneo, Gunung Mulu National Park, Summit trail, vic. Paku Waterfall, in forest, 4°2.212'N 114°49.722'E, 18.ii.2010, pan trap (yellow), D.C. Darling (1#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, 77 m, Long Lansat, in forest, 4°0.083'N 114°48.906'E, pan trap (yellow), D.C. Darling (1#m, ROME); Sarawak, Borneo, Gunung Mulu National Park, HQ, trail near intersection with old summit trail, 26 m, 4°2.5'N 114°48.9'E, 11–12.vii.2011, Yellow pan trap, D.C. Darling (3#m, DEBU); Sarawak (Borneo), Gunung Mulu National Park, Summit trail, vic. Paku Waterfall in forest, 42 m, 4°2.277'N 114°49.72'E, 19–20.x.2010, Yellow pan trap, D.C. Darling (2#m, DEBU01088857, DEBU01088863, DEBU).

Etymology: *C. darlingi* is a patronym honouring Dr. Christopher Darling, who collected the majority of the Eurybatinae specimens known from Sarawak.

Comments: *C. darlingi* is easily distinguished from other species that have a spotted-wing with a clear apex because it has coalesced hyaline spots in the distal 2/3 of cell r_{2+3} and distal 1/2 of cell r_{4+5} . This is one of four species in *Crosa* characterized by a black apex on the mid and hind femora.

***Crosa densa* Md Yusof and Marshall new species**

(Figs. 4.19A–4.19F)

Description

Body length 11.0–11.5 mm, wing length 9.2–9.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; widest on anterior margin, parallel-sided

posteriorly, with slightly tapered apex; width of anterior margin slightly more than $\frac{1}{2}$ of frons width, remaining width slightly more than $\frac{1}{3}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly dark brown with maroon tinge. Prosternum covered by silvery white microtrichia, microtrichose area extending and gradually broadened to katatergite, forming a longitudinal band on pleuron. Katepisternal bristles conspicuously thick and whitish, in a distinct row in a fan shape. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore legs missing. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown (sometimes giving the impression that they are black due to black microsetulae).

Wings: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP $1.5\times$ length of CuA.

WIPs: Sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male: Unknown.

Female abdomen: Base of ducts sclerotized, both ducts thin on basal $\frac{1}{2}$, gradually thickened on distal $\frac{1}{2}$. Paired duct $1.25\times$ as long as single duct, single duct with ring-like swelling at spermathecal base.

Type material: Holotype: PAPUA NEW GUINEA. Mount Wilhelm, 5.7209°S 145.2695°E, 13–14.v.2013, IBISCA, Gewa, Damag, Novotny and Leponce (1#f, DEBU01088867 sequence MYCRO350-18, MNHN). Paratype: Same data as holotype (1#f, DEBU01088944, DEBU).

Etymology: *C. densa* is named for its thick and conspicuous katepisternal bristles (Latin: “thick”).

Comments: *C. densa* differs markedly from all congeners in having katepisternal bristles that form a distinct fan-shaped row in (as in Taeniapterinae). Females have both spermathecal ducts thin on the basal $\frac{1}{2}$ and gradually thickened distally. Males remain unknown.

***Crosa flavifrons* (Bigot, 1886) new combination**

Eurybata flavifrons Bigot 1886: 382

Nestima flavifrons (Bigot), Evenhuis 1989: 465

(Figs. 4.20A–4.20D)

Redescription

Body length 8.4 mm, wing length 5.5–6 mm.

Head: Fronto-orbital plate flat. Frontal vitta orange on anterior margin, orange to brown posteriorly, weakly differentiated from fronto-orbital plates; widest at anterior margin, gradually tapering posteriorly; width of anterior margin slightly more than 1/3 of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Scutum orange to brown with dark medial longitudinal stripe, and a circular patch immediately anterior to and ovoid patch posterior to transverse suture. Prosternum covered by white microtrichia, microtrichose area extending to proepimeron, anepisternum with a wedge shaped white microtrichose area at dorsal ½ of vertical pleural suture. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum upturned. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur and tibia dark, except at apex; fore tarsomeres 2–3 yellowish white, darkened apically. Hind femora and tibia reddish brown.

Wing: Wing with somewhat square hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to dm–cu and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins slightly sinuate at hyaline spots. Length of CuA+CuP vein 1.5× length of CuA vein.

WIPs: Sinuate anterobasally on cell m.

Male abdomen: Not examined.

Female abdomen: Base of ducts sclerotized. The paired duct is missing from the only female specimen available for examination.

Type material: Syntypes: PAPUA NEW GUINEA. No information about date, Bigot (2#m, OXUM).

Other material examined: PAPUA NEW GUINEA. Nabire, S. Geelvink Bay, 0–30 m, 2–9.vii.1962, J.L. Gressitt (1#f, BPBM).

Comments: *C. flavifrons* is distinctive for its upturned scutellum, similar to the scutellum of *Crepidochetus* and some *Cothornobata* species. Information about male characters is from syntype pictures only, neither of which allowed for examination of terminalia because the abdomen of both specimens is broken. Osten Sacken (1881) identified one specimen collected from Ramoi, New Guinea (Irian Jaya, Indonesia) as *Nestima tenuis*. The specimen matches Bigot's (1886) description and the holotype of *C. flavifrons* because of the wing with 3 hyaline spots. For this reason, and because it was collected near the type localities of *C. flavifrons*, we consider it to belong to this species.

***Crosa fragilis* (Walker, 1856)**

Micropeza fragilis Walker 1856: 37

Crosa fragilis (Walker), McAlpine 1975: 244

Nestima fragilis (Walker), Evenhuis 1989: 465

Eurybata nigriventris Enderlein 1922: 170

Crosa nigriventris (Enderlein), McAlpine 1975: 244. **New synonym**

(Figs. 4.21A–4.21J)

Redescription

Body length 7.5–8.6 mm, wing length 5.2–6.3 mm.

Head: Fronto-orbital plate flat. Frontal vitta orange to brown; almost parallel-sided with tapered apex; width about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Scutum dark on anterior $\frac{1}{4}$ including postpronotum and postpronotal lobe. Prosternum covered by white microtrichia, microtrichose area extending to proepimeron, anepisternum with a wedge shaped white microtrichose area at dorsal $\frac{1}{2}$ of vertical pleural suture. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur dark, fore tibia dark except at apex; tarsomere 2 yellowish white basally, gradually darkened apically. Mid and hind femora uniformly orange. Mid and hind tibia orange on basal $\frac{1}{3}$, yellowish apically.

Wings: Wing with clear apex and complete hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{3}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ $2.5\times$ of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly longer. Phallapodeme dilated into fan-shaped at anterior apex. Basal distiphallus $4.5\times$ as long as distal distiphallus; distal distiphallus very short and bifurcated into subequal branches; phallic bulb present, length $1.5\times$ width and subequal in length to distal distiphallus. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct $4.5\times$ as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype of *Micropeza fragilis* Walker (1#m, BMNH type #NHMUK010579768): SINGAPORE. Date not cited, A.R. Wallace. Holotype of *Eurybata nigriventris* Enderlein (1#f, MNBG): INDONESIA. North Sumatra: Deli, Date not cited, Dr. Martin and M. Ude.

Other material examined: INDONESIA. Sumatra, Aceh, Gunung Leuser National Park, Ketambe Research Station 3°41'N 97°39'E, 1–31.iii.1990, Malaise trap with pans, D.C. Darling (1#m, ROME); Sumatra, Aceh, Gunung Leuser National Park, Ketambe Research Station, Young forest, Terrace 3, Light gap, 350 m, 3°41'N 97°39'E, 1–30.x.1989, Malaise trap with pans, D.C. Darling (1#f, ROME); MALAYSIA. Selangor, Ulu Gombak Field Studies Centre, 22.ii.1980 (2#m, DEBU); SINGAPORE. Nature Reserve, 9.x.2002, M. Kotrba (1#m, DEBU01088871, DEBU).

Comments: The holotype of *Crosa fragilis* only differs from the holotype of *C. nigriventris* in having a darker thorax. We examined material of both species from the same localities but found no further differences between them in external and internal morphology. Therefore, we here treat *C. nigriventris* as a synonym of *C. fragilis*. This species can be distinguished from all congeners by its phallapodeme, which is dilated into a fan shape distally. Some specimens have a pattern of orange-brown colouration on the frontal vitta, giving an impression of a narrower anterior margin and gradually broadened posterior part with a rounded and darkened apex.

***Crosa glabra* (de Meijere, 1914) new combination**

Eurybata glabra de Meijere 1914: 177

(Fig. 4.22A–4.22F)

Redescription

Body length 7.5–7.9 mm, wing length 6.3–6.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta black on anterior ½ and posteriorly, otherwise reddish brown; widest at anterior margin, parallel-sided posteriorly, with rounded apex; width of anterior margin slightly more than ½ of frons width, remaining width about ½ of frons. Longest arisal branches 2× length of basal aristomere.

Thorax: Scutum with medial longitudinal stripe and a patch immediately anterior to an ovoid patch posterior to transverse suture, otherwise thorax reddish brown. Prosternum bare. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly.

Scutum with two postsutural dorsocentral bristles, connected with serial rows of small dorsocentral setulae.

Legs: Fore femur brown on basal third and apically, otherwise black, fore tibia dark, except at apex; tarsomere 2 yellowish, darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown (sometimes giving the impression that they are black especially on distal ½ due to black microsetulae).

Wing: Wings with complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} and R_{4+5} smooth, and M_1 veins slightly sinuate. Length of $CuA+CuP$ 2.5× length of CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 less than ½ of cell length.

Female abdomen: Base of ducts sclerotized. Paired duct 1.5× as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype: INDONESIA. Java, Gunung Ungaran, viii.1910, E. Jacobson (1#m, MNBG #DIPT.0707.1).

Other material examined: INDONESIA. Java, Tjibodas, 400 ft., i.1936, L.E. Cheesman, (1#f, B.M.1936-89, BMNH); East Java, Tengger Highlands, Nongkodjarjar, 1100 m, 4.v.1938, K.M. Walsh (1#f, B.M.1936-99, BMNH).

Comments: *C. glabra* and *C. cuneifera* are the only *Crosa* with two dorsocentral bristles. Although similar to *C. cuneifera*, *C. glabra* can be distinguished by its bare pleuron.

***Crosa immaculata* Md Yusof and Marshall new species**

(Figs. 4.23A–4.23I)

Description

Body length 9.0–10.5 mm, wing length 7.1–7.5 mm.

Head: Fronto-orbital plate slightly elevated relative to frontal vitta. Frontal vitta black; widest at anterior margin, parallel-sided posteriorly, with V-shaped apex; width of anterior margin slightly more than ½ of frons width. Aristae missing on both specimens examined.

Thorax: Thorax orange, brighter dorsally. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur orange basally, gradually darkened apically, fore tibia dark, except at apex; tarsomere 2 luteous, pale apically. Mid and hind femora orange except for black apex. Mid and hind tibia dark.

Wings: Wing with clear apex and three clear spots: complete spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and an incomplete spot adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins sinuate at hyaline spots. Length of $CuA+CuP$ $2\times$ of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, apex of each arm bulbous and densely short setose mesally. Phallapodeme slightly dilated and angulate anteriorly. Basal distiphallus $1.5\times$ as long as distal distiphallus; distal basiphallus bifurcated into long right branch and short left branch; phallic bulb greatly reduced, indistinct. Ejaculatory apodeme blade about as wide as sperm pump; sperm pump without helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct $1.5\times$ as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype: MALAYSIA. Sabah (Borneo), Penampang District, Crocker Range, Long Gong Kugan, 1630 m, $5^{\circ}.4944'N$ $116^{\circ}.1937'E$, 21–25.x.2011, M. Hauser and S. Gaimari (1#m, CDFA). Paratype: Same data as holotype (1#f, DEBU01088853, CDFA).

Etymology: *C. immaculata* is named for its immaculate scutum (Latin: “immaculate”).

Comments: *C. immaculata* is one of the four species in *Crosa* characterized by a black apex on the mid and hind femora. Although this species is similar to *C. reticulata*, it can be distinguished by its uniformly pigmented scutum, and its uniformly wide frontal vitta. On the only two specimens available for examination, however, the flagellomere and arista are lost.

***Crosa kuchingensis* Md Yusof and Marshall new species**

(Figs. 4.24A–4.24H)

Description

Body length 6.5–10.0 mm, wing length 4.0–5.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta yellowish orange anteriorly, gradually reddish brown posteriorly, dark behind ocelli; almost parallel-sided and tapering behind ocelli, with V-shaped apex; width about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal

aristomere.

Thorax: Thorax mostly orange, brighter dorsally, except for black postpronotal lobes. Prosternum covered by white microtrichia, microtrichose area extending to proepimeron, anepisternum with a wedge-shaped white microtrichose area at dorsal ½ of vertical pleural suture. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur uniformly black, fore tibia black, except at apex; tarsomere 2 yellowish white, darkened apically. Mid and hind femora uniformly orange brown. Mid and hind tibia orange brown (sometimes giving the impression that they are black due to black microsetulae).

Wings: Wing with clear apex and complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin, R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ 2× of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than ½ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly longer and thinner, left arm slightly shorter and thicker, rounded apically. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus 2× as long as distal distiphallus; distal distiphallus bifurcated into slightly shorter left branch and slightly longer right branch; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 1.5× as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype: MALAYSIA. Sarawak, Damai Rainforest Resort, 1°45'.13.85"S, 110°19'8.04"E, 1.ix.2018, S.A. Marshall (1#m, DEBU). Paratypes: MALAYSIA. Sarawak, Damai Rainforest Resort, 1°45'.13.85"S, 110°19'8.04"E, 1.ix.2018, S.A. Marshall (1#f, DEBU); Sarawak, Bau, Pinggir Siak, 1°31'32.09"S, 110°8'22.03"E, 1.ix.2018, S.A. Marshall (1#f, DEBU); Sarawak, Bau, Mendung Escape, 1°31'15.09"S, 110°9'59.06"E, 1.ix.2018, S.A. Marshall (1#m, DEBU); Sarawak, Bau, Pinggir Siak, 1°31'32.09"S, 110°8'22.03"E, 1.ix.2018, S.A. Marshall (3#m, 1#f, DEBU).

Etymology: The specific name refers to the type locality, Kuching province in Malaysia.

Comments: Although externally similar to *C. borneoensis*, *C. kuchingensis* is characterized by a distiphallus that is bifurcated into branches that differ only slightly in length (in contrast with the long right branch and short left branch for *C. borneoensis*).

***Crosa meijerei* (Frey, 1934) new combination**

Cothornobata meijerei Frey, 1934: 333

Nestima meijerei (Frey), Li et al. 2015: 244

(Figs. 4.25A–4.25B)

Redescription

Head: Fronto orbital plate flat. Frontal vitta dark on anterior third (giving impression that the anterior is wide), brown beyond that, weakly differentiated from fronto-orbital plates; parallel-sided with slightly tapered apex; width about $\frac{1}{2}$ of frons width.

Thorax: Thorax mostly brown, scutum with a broad, pale, posteriorly tapered median vitta and a very narrow medial longitudinal stripe anterior to suture, and an ovoid patch immediately anterior to and posterior to transverse suture. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur uniformly yellowish brown, fore tibia dark; tarsomeres 2–5 darkened. Mid and hind femora yellowish brown. Mid tibia dark. Hind tibia yellowish brown.

Wing: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP $2\times$ length of CuA.

WIPs: Unknown.

Male: Unknown.

Type material: Holotype: INDONESIA. Java, Tjisaroea, vii.1931, Handschin (1#f, NHMB, only images examined).

Comments: *C. meijerei* can be distinguished from other clear-winged species by its uniformly yellowish brown colour and patterned scutum. Males remain unknown.

***Crosa melanosa* Md Yusof and Marshall new species**

(Figs. 4.26A–4.26H)

Description

Body length 9.0–10.7 mm, wing length 6.0–6.7 mm.

Head: Fronto-orbital plate flat. Frontal vitta orange on anterior margin, dark posteriorly; widest at anterior margin, gradually tapering posteriorly; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax black, scutum and scutellum pruinose and reflecting strong blue sheen (appearing grayish from some angles). Prosternum bare. Katepisternal bristles thin with brown

tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown basally and apically, otherwise black, fore tibia dark except at apex; fore tarsomere 2–4 yellowish white, dark apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown.

Wings: Wing with three hyaline spots in cell r_{2+3} , at base of cell, basal 2/3 and preapical (Fig. 4.26D) (as compared with other congeners with two spots or one spot with clear apex in cell r_{2+3}). R_{2+3} , R_{4+5} and M_1 veins sinuate at hyaline spots. Length of CuA+CuP 1.5× of length CuA.

WIPs: Sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 more than ½ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, right arm slightly straighter and longer than left arm. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Basal distiphallus 2× as long as distal distiphallus; distal distiphallus bifurcated into slightly longer right branch and shorter left branch; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade 3× as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 2.5× as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: SOLOMON ISLANDS. Kolombangara Island: Gizo, 0–140 m, xii, 1980, N.L.H. Krauss (1#f, BPBM_ENT_17848). Paratypes: SOLOMON ISLANDS. Kolombangara Island: Gizo, 0–140 m, ii, 1984, N.L.H. Krauss (1#m, BPBM_ENT_17849); SOLOMON ISLANDS. Choiseul Island, Malangona, 10 m, 2.iii.1964, P. Shahanan (1#f, BPBM_ENT_17850); Santa Yaabel, Malao, 29.vi.1960, C.W. O'Brien (1#m, BPBM_ENT_17851).

Etymology: The specific name of *C. melanosa* refers to its uniformly dark thorax and abdomen (Latin: “black”).

Comments: *C. melanosa* is similar in colour to *C. multimaculata* but differs in having only two hyaline spots in cell r_{4+5} (in contrast with three in *C. multimaculata*).

***Crosa multimaculata* Md Yusof and Marshall new species**

(Figs. 4.27A–4.27G)

Description

Body length 12.1 mm, wing length 7.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; almost parallel-sided and slightly narrower posteriorly with rounded apex; about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax uniformly black to dark brown. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown on basal $\frac{2}{3}$, gradually darkened apically, fore tibia dark; tarsomeres uniformly yellowish white. Mid and hind femora reddish brown. Mid and hind tibia reddish brown.

Wing: Wing with somewhat subquadrate hyaline spots at distal $\frac{2}{3}$ and preapical of cell r_{2+3} , adjacent to $r-m$ vein, distal $\frac{1}{3}$ and distal $\frac{2}{3}$ of cell r_{4+5} , and with a clear patch, open to posterior wing margin at adjacent to $dm-m$ and preapical of cell m (Fig. 4.27C). R_{4+5} and M_1 veins conspicuously sinuate at hyaline spots. Length of $CuA+CuP$ equal to length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, rounded apically. Phallapodeme quadrate, not dilated distally. Basal distiphallus $2\times$ as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade $1.5\times$ as wide as sperm pump, sperm pump with helmet-like structure.

Female: Unknown

Type material: Holotype: SOLOMON ISLANDS. Bougainville (S.) Kokure, 690 m, 15.vi.1956, J.L. Gressitt (1#m, BPBM_ENT_17852).

Etymology: *C. multimaculata* is named for the multiple hyaline spots on the cell r_{4+5} on the wing (Latin: “much”, “spot”).

Comments: *C. multimaculata* differs markedly from other spotted-wing species in having three hyaline spots in cell r_{4+5} (adjacent to crossvein $r-m$, distal $\frac{1}{3}$ and preapical) and a preapical clear patch in cell m . Females remain unknown.

Crosa nigrifrontata Md Yusof and Marshall new species

(Figs. 4.28A–4.28H)

Description

Body length 8.4–10.6 mm, wing length 6.5–7.2 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; very broad on anterior 2/3 (covered most of the frons) abruptly tapered and covered with white microtrichia anterior to ocelli; width of anterior 2/3 about $\frac{3}{4}$ of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax uniformly orange. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Basal $\frac{1}{2}$ of fore femur yellowish brown, gradually darkened apically, fore tibia dark except at apex; fore tarsus uniformly luteous. Mid and hind femora orange. Mid and hind tibia orange.

Wings: Wing with complete hyaline spot at distal $\frac{1}{2}$ of cell r_{4+5} , and with a clear patch adjacent to dm-m and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuA 2.5× length CuA.

WIPs: Sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped with tubercle at basal $\frac{1}{2}$ of left arm, inner surface of right arm slightly tumid at basal $\frac{1}{2}$. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus 1.5× as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, length 1.5× width. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 1.5× as long as single duct.

Type material: Holotype: SOLOMON ISLANDS. Florida Grp, Takopekope, 12.ix.1960, C.W. O'Brien (1#f, BPBM_ENT_17853). Paratypes: SOLOMON ISLANDS. Guadalcanal, Suta (Suta-Gold Ridge), Jonapau Mount, 1000 m, 29.vi.1956, J.L. Gressitt (1#f, BPBM_ENT_17854); New Georgia Group, N. Georgia I., Munda, 1–30 m, 20.vii.1959, J.L. Gressitt (1#f, BPBM_ENT_17855); New Georgia Group, N. Georgia I., Munda, 1–30 m, 20.vii.1959, J.L. Gressitt (1#m, BPBM_ENT_17856).

Etymology: *C. nigrifrontata* is named for the black and broad anterior part of the frontal vitta (Latin: “black”, “forehead”).

Comments: *C. nigrifrontata* is distinctive for its conspicuously broad frontal vitta, which covers most of the anterior 2/3 of the frons. The presence of a tubercle at the basal $\frac{1}{2}$ of the left

arm of the male genital fork is also a distinctive character.

***Crosa petasibarba* (Enderlein, 1922) new combination**

Eurybata petasibarba Enderlein 1922: 170

Nestima petasibarba (Enderlein), Evenhuis 1989: 465

(Figs. 4.29A–4.29H)

Redescription

Body length 7.8–10.8 mm, wing length 5.2–7.6 mm.

Head: Fronto-orbital plate flat. Frontal vitta dark on anterior third, gradually reddish brown posteriorly, weakly differentiated from fronto-orbital plates; widest on anterior margin, gradually parallel-sided posteriorly, with rounded apex; width of anterior margin slightly more than $\frac{1}{2}$ of frons width, remaining width slightly more than $\frac{1}{3}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly reddish brown. Prosternum covered by white microtrichia, microtrichose area extending to anepisternum, forming a longitudinal band with black-margined. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur and tibia reddish brown; fore tarsus luteous, slightly darkened apically. Mid and hind femur uniformly reddish brown. Mid and hind tibia reddish brown (sometimes giving the impression that they are black especially on basal $\frac{1}{2}$ due to black microsetulae).

Wing: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP $2\times$ length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Basal distiphallus subequal in length to distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Ducts uniformly membranous, very thin. Paired duct $1.25\times$ as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype: NEW GUINEA. Sepik Province, x.1910, Schultze (1#m, MNBG).

Other material examined: PAPUA NEW GUINEA. East Sepik Province, Amboin Patrol Post, Karawari Lodge, ii.1983, A.C. Messer (1#m, DEBU01088874 sequence MYCRO365-18, DEBU); Neth, Ifar, 300–600 m, 20.vi.1959, T.C. Maa (1#f, BPBM); Karimui, south of Goroka, 1000 m, 5.vi.1961, J.L. Gressitt and M. Gressitt (2#f, BPBM); Neth, Bodem, 100 m, 11 km SE of Oerberfaren, 7–17.vii.1959, T.C. Maa (1, sex unknown, BPBM); Amok, 6.i.1960, (1#f, BPBM); Wanang 3, 175 m, 5.2277°S 145.0797°E, x–xii.2012, IBISCA, Gewa, Damag, Novotny and Leponce (1#f, DEBU01088873 sequence MYCRO364-18 [sequenced specimen], MNHN).

Comments: *C. petasibarba* is similar in colour to *C. burgersi* but differs in having relatively straight genital fork arms (in contrast with the distinctly longer and distally incurved left arm of *C. burgersi*). The thin base of each spermatheca is also a distinctive character.

***Crosa reducta* Md Yusof and Marshall new species**

(Figs. 4.30A–4.30G)

Description

Body length 5.7 mm, wing length 5.2 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; widest at anterior margin, gradually tapering posteriorly until posterior fronto-orbital bristle, remaining width uniform, with rounded apex; width of anterior margin about $\frac{1}{2}$ of frons width, narrowest width slightly more than $\frac{1}{3}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly dark brown, scutum pruinose with pollinosity. Prosternum bare. Katepisternum with microtrichose area on dorsal $\frac{2}{3}$, katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur brown with a preapical black ring, length of ring $2.5\times$ width of femur, fore tibia dark, except at apex; fore tarsus luteous, darkened apically. Mid and hind femora uniformly yellowish. Mid and hind tibia yellowish.

Wings: Wing with complete hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{3}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ equal to length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm longer than right arm. Phallapodeme quadrate, not dilated distally. Distal distiphallus 1.5× as long as basal distiphallus; distal distiphallus bifurcated into long left branch and short right branch; phallic bulb greatly reduced, indistinct. Ejaculatory apodeme with a reduced and short blade, sperm pump 4× wider than blade, with helmet-like structure.

Female: Unknown.

Type material: Holotype: PAPUA NEW GUINEA. Papua, Brown R., 10 m, near Port Moresby, 5.x.1958, J.L. Gressitt (1#m, BPBM_ENT_17857).

Etymology: *C. reducta* is named for the reduced blade of the ejaculatory apodeme (Latin: “reduce”).

Comments: *C. reducta* is the only *Crosa* species with a reduced ejaculatory apodeme blade. Females remain unknown.

***Crosa reticulata* Md Yusof and Marshall new species**

(Figs. 4.31A–4.31I)

Description

Body length 9.5–11.0 mm, wing length 8.0–10.0 mm.

Head: Fronto-orbital plate flat. Frontal vitta yellow to orange on anterior margin, black posteriorly; widest on anterior margin, gradually tapering posteriorly; anterior margin width about ½ of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax mostly orange, scutum with a broad, pale median vitta with a very narrow medial longitudinal stripe anterior to suture, and a circular patch immediately anterior to and ovoid patch posterior to transverse suture. Prosternum covered by white microtrichia. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown basally, gradually darkened apically, fore tibia dark, except at apex; tarsomere 2 yellowish, darkened apically. Mid and hind femora reddish brown, except for black apex. Mid and hind tarsi reddish brown (sometimes giving the impression that they are black especially on distal ½ due to black microsetulae).

Wings: Wing with clear apex and complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to dm–m and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins sinuate at hyaline spots. Length of CuA+CuP 2.5× of length CuA.

WIPs: Sinuate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m₄ more than ½ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, apex of each arm bulbous and densely short setose mesally. Phallapodeme slightly dilated anteriorly. Basal distiphallus as long as distal distiphallus; distal basiphallus bifurcated into long right branch and short left branch; phallic bulb greatly reduced, indistinct. Ejaculatory apodeme with a broad blade, blade 2.5× as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. On the female specimen available for examination, the paired spermathecal duct is missing.

Type material: Holotype: MALAYSIA. Sabah, Kundasang, 1530 m, 24.viii.1983, G.F. Hevel and W.E. Steiner (1#f, USNM). Paratypes: Same data as holotype (1#m, 1#f, USNM).

Etymology: *C. reticulata* is named for its patterned scutum (Latin: “reticulate”).

Comments: *C. reticulata* is one of four species in *Crosa* characterized by a black apex on the mid and hind femora. This species is similar to *C. immaculata*, from which it can be distinguished by the patterned scutum and the posteriorly tapered frontal vitta. On the only female specimen available for examination, the paired spermathecal duct is lost.

***Crosa semicolor* Md Yusof and Marshall new species**

(Figs. 4.32A–4.32H)

Description

Body length 7.0–10.0 mm, wing length 5.5–6.0 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; widest on anterior margin, gradually parallel-sided posteriorly, with rounded apex; width of anterior margin slightly more than ½ of frons width, remaining width slightly more than 1/3 of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax dark brown on dorsal ½, yellowish brown on ventral ½, with indistinct narrow median vitta. Prosternum covered by white microtrichia, microtrichose area extending and gradually broadened and reaching to meron, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur yellowish brown with a preapical dark brown ring, length of ring 1.5× width of femur, fore tibia yellowish brown (sometimes giving the impression that it is black due to

black microsetulae); tarsomere 2 yellowish white basally, gradually darkened apically. Mid and hind femora yellowish brown. Mid and hind tibia yellowish brown (sometimes giving the impression that they are black due to black microsetulae).

Wings: Wing with clear apex and complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of $CuA+CuP$ 2× of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 less than 1/2 of cell length.

Male abdomen: Genital fork symmetrical U-shaped, bulbous apically. Phallapodeme quadrate and angulate anteriorly. Basal distiphallus 2.5× as long as distal distiphallus; distal distiphallus bifurcated into slightly longer left branch and shorter right branch; phallic bulb present, as long as wide. Ejaculatory apodeme blade about as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 1.5× as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: PAPUA NEW GUINEA. Mount Wilhelm, 1200 m, 5.720°S 145°.2695'E, 13–14.v.2013, IBISCA, Gewa, Damag, Novotny and Leponce (1#m, MNHN). Paratypes: PAPUA NEW GUINEA. Mount Wilhelm, 1200 m, 5.720°S 145°.2695'E, 13–14.v.2013, IBISCA, Gewa, Damag, Novotny and Leponce (2#m, 1#f DEBU01088851, sequence MYCRO340-18, DEBU01088852 [sequenced specimen], DEBU); 10 km north of Angoram, 10–30 m, 15.ix.1969, J.L. Gressitt (1#f, BPBM); Waris, south of Hollandia, 450–500 m, 16–23.viii.1959, T.C. Maa (2#m, BPBM); Waris, south of Hollandia, 450–500 m, 1–2.viii.1959, T.C. Maa (1#m, 1#f, BPBM); Waris, south of Hollandia, 450–500 m, 24–31.viii.1959, T.C. Maa (2#f, BPBM); VANUATU. NEW HEBRIDES. Erromango, 8 km west of Ipota, 100–200 m, iii.1970, N.L. Krauss (1#m, BPBM).

Etymology: *C. semicolor* is named for its dorsally dark brown and ventrally yellowish brown thorax (Latin: “half”, “color”).

Comments: *C. semicolor* is one of the most distinctive species in *Crosa*, easily recognized by the thorax that is dark brown on the dorsal 1/2 and yellowish brown on the ventral 1/2.

***Crosa semilauta* (Osten Sacken, 1882)**

Eurybata semilauta Osten Sacken 1882: 207

Crosa semilauta (Osten Sacken), Steyskal 1952: 177

(Figs. 4.33A–4.33I)

Redescription

Body length 7.8–12.0 mm, wing length 4.9–6.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta reddish-brown, darkened posteriorly; widest at anterior margin, gradually tapering until posterior fronto-orbital bristle, slightly expanded on ocelli, and remaining extending as a very narrow tapered groove behind ocelli; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax reddish brown, darker dorsally, with pale median vitta and a very narrow medial longitudinal stripe anterior to transverse suture, and a circular patch immediately anterior to and ovoid patch posterior to transverse suture. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown with a preapical black ring, length of ring $3\times$ of femur width, fore tibia darkened, except at base and apex; tarsomere 2 yellowish white basally, and gradually darkened apically. Mid and hind femora reddish brown with faint preapical black ring. Mid and hind tibia reddish brown.

Wings: Cell r_{2+3} with complete hyaline spot at distal $\frac{2}{3}$ and clear apex, cell r_{4+5} with complete hyaline spots at distal $\frac{1}{3}$ and preapical, and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} smooth, R_{4+5} and M_1 veins sinuate at hyaline spots. Length of $CuA+CuP$ equal to length CuA .

WIPs: Sinuate anterobasally on cell m . Length of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, rounded apically. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus $1.5\times$ as long as distal distiphallus; distal distiphallus bifurcated into slightly longer left branch and shorter right branch; phallic bulb present, length $1.5\times$ width. Ejaculatory apodeme with a broad blade, blade $2.5\times$ as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct $3\times$ as long as single duct, single duct thickened at spermathecal base.

Type material: Syntypes: PHILIPPINES. (1#m, 1#f, DEI, not examined).

Other material examined: PHILIPPINES. Laguna, Los Banos, Mount Makiling, trail, 300–500 m, $14^{\circ}8.46'N$ $121^{\circ}13.50'E$, 20–30.iii.2010, S.A. Marshall, (8#m, 9#f, DEBU00332498,

DEBU00332499, DEBU00332500, DEBU00332559, DEBU00332594, DEBU00332592, DEBU00332593, DEBU00332595, DEBU00332599, DEBU00332600, DEBU00332601, DEBU00332602, DEBU00332604, DEBU00332605, DEBU00332606, DEBU00332608, DEBU00332609, DEBU00332610, DEBU00332611, DEBU01088870 [sequenced specimen], DEBU); PHILIPPINES. Laguna, Los Banos, Mount Makiling, trail, 300–500 m, 14° .8.46'N 121° .13.50'E, 20–30.iii.2010, S.A. Marshall, (2#f, DEBU01088870 sequence MYCRO360-18 [sequenced specimen], DEBU00332498); San Jose, Mindanao, 13.iii.1945, Ross and Skinner (1#m, USNM).

Comments: *C. semilauta* differs markedly from other *Crosa* in having a preapical ring on the mid and hind femora.

***Crosa sparsa* Md Yusof and Marshall new species**

(Figs. 4.34A–4.34H)

Description

Body length 9.5–11.5 mm, wing length 6.0–7.8 mm.

Head: Fronto-orbital plate flat. Frontal vitta black; parallel-sided with V-shaped apex; width about 1/3 of frons width. Longest arisal branches approximately subequal with basal aristomere length.

Thorax: Thorax mostly reddish brown, scutum with a broad, pale, posteriorly tapered median vitta and a very narrow medial longitudinal stripe anterior to transverse suture, with circular patch immediately anterior to transverse suture. Prosternum covered by white microtrichia, microtrichose area extending and gradually broadened to posterior of meron, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown on basal ½, gradually darkened apically, fore tibia dark except at apex; distitarsus dark. Mid and hind femora reddish brown, darkened at extreme apex. Mid and hind tibia reddish brown.

Wings: Wing with coalesced laterally compressed hyaline spots at distal 2/3 of cell r_{2+3} and distal ½ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} smooth, R_{4+5} and M_1 veins slightly sinuate at hyaline spots. Length of $CuA+CuP$ vein $1.5\times$ of CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of $Z-$

shaped pattern on cell m₄ more than ½ of cell length.

Male abdomen: Genital fork symmetrical U-shaped. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus 3.5× as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 1.25× as long as single duct.

Type material: Holotype: PAPUA NEW GUINEA. NE, Eliptamin Valley, 1200–1350 m, 19–30.vi.1959, W.W. Brandt (1#m, BPBM_ENT_17858). Paratypes: PAPUA NEW GUINEA. NE, Kassam, 1350 m, 48 km East of Kainantu, 7.xi.1959, T.C. Maa (1#f, BPBM_ENT_17859); Arau, 1400 m, 48 km East of Kainantu, 16.x.1959, T.C. Maa (1#m, BPBM_ENT_17860); Mount Missim, 1199 m, 22.ii.1968, no information about collector (1#f, BPBM_ENT_17861); Aiyura, near Kainantu, 1700–1800 m, 5.i.1965, R. Straatman (1#m, BPBM_ENT_17862).

Etymology: *C. sparsa* is named for the sparse basal anteroventral bristles on the male fore femur (Latin: “sparse”).

Comments: *C. sparsa* is markedly distinct from other *Crosa* in having very short and sparse anteroventral hairs on the basal ½ of the male fore femur.

***Crosa splendida* Md Yusof and Marshall new species**

(Figs. 4.35A–4.35H)

Description

Body length 8.5–10.5 mm, wing length 7.0–8.0 mm.

Head: Fronto-orbital plate flat. Frontal vitta dark on anterior third, gradually reddish brown posteriorly with white microtrichia anterior to ocelli; widest on anterior margin, gradually parallel-sided posteriorly, with rounded apex (some specimens with tapered apex); width of anterior margin slightly more than ½ of frons width, remaining width slightly more than 1/3 of frons width. At level of inner vertical bristle and postocellar bristle with dense microtrichia. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax mostly dark brown, with indistinct median vitta, scutum with pollinosity, pleuron reflecting strong blue sheen. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur brown on basal $\frac{1}{2}$, gradually darkened apically, fore tibia black except at apex; tarsomere 2 yellowish white basally, and gradually darkened apically. Mid and hind femora reddish brown. Mid and hind tibia reddish brown.

Wing: Wing clear. R_{2+3} smooth, R_{4+5} and M_1 veins slightly sinuate. Length of CuA+CuP $2.5\times$ length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm longer than right arm, both arms tapered and diverged apically, base with long black setae ventrally. Phallapodeme dilated and flattened-triangular at anterior apex. Distal distiphallus $2.5\times$ as long as basal distiphallus; distal distiphallus bifurcated into short right branch and long left branch; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade $2.5\times$ as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Ducts uniformly membranous, without sclerotized section. Paired duct $7\times$ as long as single duct.

Type material: Holotype: PAPUA NEW GUINEA. Mount Wilhelm, 1700 m, 5.7593°S 145.2356°E , 25–26.x.2013, IBISCA, Gewa, Damag, Novotny and Leponce (1#m, DEBU01088868 sequence MYCRO358-18, MNHN). Paratypes: Same data as holotype (3#f, 1#m, DEBU01088869 sequence MYCRO359-18 [sequenced specimen], MNHN).

Etymology: *C. splendida* is named for its conspicuous glossy bluish pleuron (Latin: “luster”).

Comments: *C. splendida* is distinct from other *Crosa* species for the long and dense black setae at the base of the male genital fork.

***Crosa sulawesiensis* Md Yusof and Marshall new species**

(Figs. 4.36A–4.36H)

Description

Body length 9.0–12.1 mm, wing length 7.0–11.5 mm.

Head: Fronto-orbital plates flat. Frontal vitta orange to brown on anterior margin, black posteriorly; widest on anterior margin, gradually tapering posteriorly with a V-shape apex; anterior margin width about $\frac{1}{2}$ of frons width. Aristal branches length $2\times$ of aristemere length.

Thorax: Thorax mostly dark brown, scutum with indistinct narrow median vitta. Prosternum covered by white microtrichia, microtrichose area extending to posterior edge of anepisternum,

forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur brown on basal ½ and apically, otherwise dark, fore tibia and tarsi brown. Mid and hind femora brown with black apex. Mid and hind tibia brown.

Wing: Wing with clear apex and complete hyaline spots at distal 2/3 of cell r_{2+3} and distal 1/3 of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 smooth. Length of $CuA+CuP$ 2× of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than ½ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm bent at basal ½. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Basal distiphallus 4× as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade 2.5× as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct 2.5× as long as single duct, both ducts with small swelling at spermathecal base.

Type material: Holotype: INDONESIA. Celebes (Sulawesi), no information about date and collector (1#m, BMNH). Paratypes: INDONESIA. Sulawesi, Mak, (Makassar), no information about date and collector (1#m, 2#f, BMNH).

Etymology: The specific name refers to the type locality, Sulawesi province in Indonesia.

Comments: Although somewhat similar to *C. tenuis*, *C. sulawesensis* differs in having a black apex on the mid and hind femora (in contrast with the uniformly brown mid and hind femora for *C. tenuis*) and the absence of a ventral keel at the basal ½ of distiphallus. This species is one of four species in *Crosa* characterized by a black apex on the mid and hind femora.

***Crosa tenuis* (Doleschall) new combination**

Micropeza tenuis Doleschall 1859: 127

Nestima tenuis (Doleschall), Evenhuis 1989: 465

(Figs. 4.37A–4.37H)

Redescription

Body length 9.0–12.1 mm, wing length 7.2–12.0 mm.

Head: Fronto-orbital plate flat. Frontal vitta yellow on anterior margin with tapered dark median (giving impression that the frontal vitta tapered anteriorly), dark posteriorly; widest at anterior margin, gradually tapering posteriorly; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly brown, scutum dark brown and a medial longitudinal stripe (the stripe reflecting strong blue sheen in some angle), and a distinct black spot in the circular patch immediately anterior to and ovoid patch posterior to transverse suture. Prosternum covered by white microtrichia, microtrichose area gradually broadened to posterior edge of anepisternum and extending to katatergite, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown (sometimes giving the impression that it is black on basal third and ventral of femur due to black microsetulae), fore tibia dark, except at apex; tarsomere 2 yellowish white basally, gradually darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia reddish brown.

Wing: Wings with clear apex and complete hyaline spots at distal $\frac{2}{3}$ of cell r_{2+3} and distal $\frac{1}{3}$ of cell r_{4+5} , and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 slightly sinuate. Length of $CuA+CuP$ equal to length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, bulbous. Phallapodeme abruptly dilated at anterior apex, thickened. Basal distiphallus with ventral keel at basal $\frac{1}{2}$, basal distiphallus $2\times$ as long as distal distiphallus, distal distiphallus bifurcated into subequal branches; phallic bulb present, length $1.5\times$ width. Ejaculatory apodeme with a broad blade, blade $2.5\times$ as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct twice as long as single duct, both ducts thickened at spermathecal base.

Type material: Holotype: Not examined, possibly lost.

Other material examined: INDONESIA. Amboina (Ambon), No date cited, F. Muir (1#f, BPBM); Seram, Solea, Uncarya(?), Yellow pan, viii.1987 (2#m,3#f, BMNH); Maluku, South Seram, Waipia, $3^{\circ}17'10''S$, $128^{\circ}53'19''E$, 0.00 m, 18.viii.2018, S.A. Marshall (1#m,3#f); Maluku, Saleman-Manusela River near rest area Negeri Saleman, 28.viii.2018, S.A. Marshall (2#m,3#f) [pictures of living specimen].

Comments: Doleschall (1859) described this species from Ambon, Indonesia. We were unable to locate the type of *C. tenuis*, but we have treated one specimen from BPBM collected in Ambon as *C. tenuis* because *C. tenuis* is the only *Crosa* known from Ambon. The same species was recently photographed on Seram Island and was also collected on Seram during Operation Raleigh. Ambon is only separated from Seram by 11 km, so it is not surprising to find this species on both islands.

One specimen from RMNH identified by de Meijere (1913) as *Nestima tenuis* was apparently collected in Pulau Babi, Sumatra, Indonesia the label reads “Pulu Babi.Slm Sum. The specimen differs in the fore femur colouration from the specimens we have examined from Seram and Ambon and it is unlikely to be the same species. Since it is a single female specimen, we are tentatively treating it as undescribed species until more specimens are available. The lack of adequate material from Sumatra and elsewhere in Indonesia is a one of the greatest impediments to properly revising *Crosa* and other Eurybatinae, and it is hoped that new collections can be facilitated in the near future.

Although somewhat similar to *C. sulawesensis*, *C. tenuis* distinguished by its the uniformly brown mid and hind femora and the presence of a ventral keel at the basal ½ of the distiphallus.

***Crosa tetras* (Steyskal, 1947)**

Eurybata tetras Steyskal 1947: 2

Crosa tetras (Steyskal) 1952: 177

Nestima tetras (Steyskal), Evenhuis 1989: 465

(Figs. 4.38A–4.38H)

Redescription

Body length 8.6–10.5 mm, wing length 5.2–6.4 mm.

Head: Fronto-orbital plate flat. Frontal vitta dark anteriorly, reddish brown posteriorly; widest on anterior margin, gradually tapering posteriorly; width of anterior margin about ½ of frons width. Longest arisal branches 2× length of basal aristomere.

Thorax: Thorax uniformly brown. Prosternum bare. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown with a preapical black ring, length of ring 1.5× width of

femur, fore tibia dark, except at apex; tarsomere 2 yellowish white basally, gradually darkened apically. Mid and hind femora uniformly reddish brown. Mid and hind tibia uniformly reddish brown.

Wing: Cell r_{2+3} with laterally compressed hyaline spots at distal 2/3 and preapical, cell r_{4+5} with somewhat square hyaline spots at distal 1/3 and preapical laterally compressed spot, and with a clear patch adjacent to $dm-m$ and open to posterior wing margin. R_{2+3} , R_{4+5} and M_1 veins slightly sinuate at hyaline spots. Length of $CuA+CuP$ $2\times$ of length CuA .

WIPs: Sinuate anterobasally on cell m . Length from apex of $CuA+CuP$ to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, greatly incurved apically, almost flat. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Basal distiphallus $2\times$ as long as of distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade twice as wide as sperm pump; sperm pump with helmet-like structure.

Female: Not examined.

Type material: Holotype: SOLOMON ISLANDS. Guadalcanal. 1944, C.O. Berg (1#m UMMZI-00302918). Paratypes: Same data as holotype (1#m, 1#f, USNM): Allotype: SOLOMON ISLANDS. Guadalcanal, 1944, J. Laffoon (1#f, UMMZ).

Other material examined: SOLOMON ISLANDS. Guadalcanal, Suta-(Suta-Gold Ridge) Jonapau Mount, 1000 m, 29.vi.1956, J.L. Gressitt (1#m, BPBM); PAPUA NEW GUINEA. Bougainville, Buin, 3.vi.1956, J.L. Gressitt (1#m, BPBM).

Comments: *C. tetras* is distinct from all congeners for the greatly incurved, almost flat arms of the male genital fork.

***Crosa tumifurca* Md Yusof and Marshall new species**

(Figs. 4.39A–4.39H)

Description

Body length 9.5–11.5 mm, wing length 6.0–7.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta black, widest at anterior margin, gradually tapering posteriorly until posterior fronto-orbital bristle, remaining width uniform until tapered apex; width of anterior margin about $\frac{1}{2}$ of frons width, narrowest width slightly more than $\frac{1}{3}$ of frons width. Longest arisal branches $2\times$ length of basal aristemere.

Thorax: Anterior $\frac{1}{4}$ of scutum including postpronotal lobe dark, with strong grey sheen dorsally; scutum with pale median vitta, otherwise thorax brown. Prosternum covered by white microtrichia, microtrichose area extending and gradually broadened to posterior edge of anepisternum, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur reddish brown on basal $\frac{1}{2}$, gradually darkened apically, fore tibia dark except at apex, tarsomere 2 yellowish white basally, and gradually darkened apically. Mid and hind femora reddish brown. Mid and hind tibia reddish brown (sometimes giving the impression that they are black due to black microsetulae).

Wing: Wing clear. R_{2+3} , R_{4+5} and M_1 vein smooth. Length of CuA+CuP equal to length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 more than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm longer, right arm with rounded apex and tubercle at basal $\frac{1}{2}$. Phallapodeme dilated and flattened-triangular at anterior apex, anterior margin thickened. Distal distiphallus $2\times$ as long as basal distiphallus; distal distiphallus bifurcated into short left branch and long, slightly sinuate right branch; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade $2.5\times$ as wide as sperm pump, sperm pump with helmet-like structure.

Female abdomen: Base of ducts sclerotized. Paired duct $1.5\times$ as long as single duct.

Type material: Holotype: PAPUA NEW GUINEA. Mount Wilhelm, 1200 m, 5.7209°S 145.2695°E, 13–14.v.2013, IBISCA, Gewa, Damag, Novotny and Leponce (1#m, MNHN). Paratypes: Same data as holotype (2#m, 5#f, DEBU01088866 sequence MYCRO356-18, DEBU01088867 MYCRO357-18 [sequenced specimen], MNHN).

Etymology: *C. tumifurca* is named for the tubercle on the arm of the male genital fork (Latin: “swell”, “fork”).

Comments: *C. tumifurca* is distinctive for the presence of a tubercle at the basal $\frac{1}{2}$ of the right arm of the male genital fork.

***Crosa vitellosa* Md Yusof and Marshall new species**

(Figs. 4.40A–4.40G)

Description

Body length 7.0–10.0 mm, wing length 4.5–6.5 mm.

Head: Fronto-orbital plate flat. Frontal vitta orange to brown on anterior margin, otherwise black on anterior third and dark brown posteriorly; widest on anterior margin, gradually tapering until anterior to ocelli, and expanded at ocelli before tapering posteriorly; width of anterior margin about $\frac{1}{2}$ of frons width. Longest arisal branches $2\times$ length of basal aristomere.

Thorax: Thorax mostly orange-brown, scutum with pale median vitta, pruinose with pollinosity. Prosternum covered by white microtrichia, microtrichose area extending and gradually broadened to posterior margin of anepisternum, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in indistinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur orange with a preapical black ring, length of ring $2\times$ width of femur, fore tibia orange; tarsomere 2 yellowish white basally, slightly darker apically. Mid and hind femora orange. Mid and hind tibia orange.

Wings: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP $2\times$ length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork asymmetrical U-shaped, left arm longer than right arm; both arms thin and tapered apically. Phallapodeme dilated into fan shape at anterior apex with anterior margin prominently curved. Basal distiphallus $2.5\times$ as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme with a broad blade, blade about $2.5\times$ as wide as sperm pump, sperm pump without helmet-like structure.

Female: Unknown.

Type material: Holotype: PAPUA NEW GUINEA. Netherlands, Waris, south of Hollandia, 450–500 m, 16–23.vii.1959, T.C. Maa (1#m, BPBM_ENT_17863). Paratype: PAPUA NEW GUINEA. Netherlands, Bodem, SE of Oerberfaren, 100 m, 11 km, 7–17.vii.1959, T.C. Maa (1#m, BPBM).

Etymology: The specific name of *C. vitellosa* refers to the orange yolk colour of the whole species (Latin: “yolk of an egg”).

Comments: *C. vitellosa* is characterized by a phallapodeme that is distinctly broadly dilated into fan shape at anterior apex with anterior margin prominently curved. Females remain unknown.

***Crosa yapensis* (Steyskal, 1952)**

Crosa yapensis Steyskal 1952: 177

Nestima yapensis (Steyskal), Evenhuis 1989: 465

(Figs. 4.41A–4.41I)

Redescription

Body length 6.7–6.9 mm, wing length 4.5–4.7 mm.

Head: Fronto-orbital plate flat. Frontal vitta reddish brown parallel-sided with tapered apex; width about $\frac{1}{2}$ of frons width. Longest arisal branches approximately subequal to basal aristomere length.

Thorax: Thorax mostly orange. Prosternum covered by white microtrichia, microtrichose area extending to posterior of anepisternum, forming a longitudinal band on pleuron. Katepisternal bristles thin with brown tinge in distinct row. Scutellum directed posteriorly. Scutum with one postsutural dorsocentral bristle.

Legs: Fore femur with a preapical black ring, length of ring $2\times$ width of femur, otherwise femur orange, fore tibia orange, darkened apically; fore tarsus orange. Mid and hind femora and tibia uniformly orange.

Wing: Wing clear. R_{2+3} , R_{4+5} and M_1 veins smooth. Length of CuA+CuP $2\times$ length of CuA.

WIPs: Angulated anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 less than $\frac{1}{2}$ of cell length.

Male abdomen: Genital fork symmetrical U-shaped, rounded apically. Phallapodeme slightly dilated on distal $\frac{1}{2}$ and constricted before flattened-triangular anterior apex. Basal distiphallus $4.5\times$ as long as distal distiphallus; distal distiphallus bifurcated into subequal branches; phallic bulb present, as long as wide. Ejaculatory apodeme blade about as wide as sperm pump, sperm pump without helmet-like structure.

Female abdomen: Ducts uniformly membranous. Paired duct $2.5\times$ as long as single duct, single duct thickened at spermathecal base.

Type material: Holotype: CAROLINE ISLANDS. Yap Islands, near Yaptown, 14.vii.1946, H.K. Townes (1#m, USNM type #58984).

Other material examined: CAROLINE ISLANDS. Yap Islands, Giliman, 12.vi.1957, C.W. Sabrosky (1#f, BPBM); Map Island, Cho., 19.vi.1957, C.W. Sabrosky (1#f, BPBM); PALAU ISLANDS. Nlf. Auluptagel, 25 m, 12.xii.1952, J.L. Gressitt (1#m, BPBM); Babelthuap I. Imeliik, Netkeng, 5.vi.1957, C.W. Sabrosky (1#m, BPBM).

Comments: The phallapodeme of *C. yapensis* is slightly dilated on the distal ½ and constricted basal to the flattened-triangular at anterior apex. This species is similar to *C. nigrifrontata* in orange colouration, however it differs in having a white microtrichose longitudinal pleural band.

***Papeza* McAlpine**

Papeza McAlpine 1975: 242. Type species: *Papeza szentivanyi* McAlpine 1975 (orig. des.).

McAlpine (1975) provides a detailed description of the external morphological characters of *Papeza*. We here add details only for abdominal characters and WIPs.

WIPs: Height of basal ¼ of first concentric ring 1.5× to height of distal ¼ on cell r_{4+5} . Angulate anterobasally on cell m. Length from apex of CuA+CuP to posterior point of Z-shaped pattern on cell m_4 more than ½ of cell length (Fig. 4.44D).

Abdomen: Abdominal syntergite 1+2 at least 1.5× length of tergite 3, usually with short setae. Male abdomen: Genital fork (sternite 5) arms symmetrical, with short setae, dense especially on inner surface and apex. Anteroventral epandrial arms about 3× width. Pregonite elongate with short stout setae, slightly rounded apically. Postgonite usually with apical ventral lobe. Phallapodeme dilated and flattened-triangular at anterior apex. Basal distiphallus as long as distal distiphallus; distal distiphallus bifurcated into short left branch and long right branch; phallic bulb present, as long as wide. Ejaculatory apodeme blade fan-shaped, blade width variable. Female abdomen: Spermathecal ducts uniformly membranous, ducts with small swelling or thickened at spermathecal base; stem length subequal to spermatheca width (Fig. 4.43H).

Comment: *Papeza* is diagnosed by the fore femur which is orange-brown on basal third, gradually turning black distally. *Papeza funiculipes* and *P. szentivanyi* are very similar externally, but molecular data supports their treatment as different species. They can be distinguished with the characters as in the key.

Key to *Papeza* species

1. Fronto-orbital plate black on anterior ½, otherwise orange (Fig. 4.42). ... ***P. armillata* (Enderlein)**
- Fronto-orbital plate uniformly orange-brown. ... 2

2. Genital fork with parallel arms (Fig. 4.43F). ... ***P. funiculipes* (Enderlein)**
- Genital fork with slightly incurved arms at basal ½. (based on McAlpine, 1975, Fig. 5). ...
***P. szentivanyi* McAlpine**

Species redescriptions

***Papeza armillata* (Enderlein, 1922) new combination**

Grammicomyia armillata Enderlein 1922: 175

Nestima armillata (Enderlein), Evenhuis 1989: 465

(Fig. 4.42)

Redescription

Head: Fronto-orbital plate black on anterior ½, orange beyond that. Frontal vitta velvety yellow on anterior third, continue posteriorly in black to a point at vertex.

Legs: Fore tibia dark brown on basal third, white apically.

Wing: Wing with coalesced hyaline spots at distal 2/3 of cell r_{2+3} and distal ½ of cell r_{4+5} , and adjacent to $dm-m$.

WIPs: Unknown.

Male: Unknown.

Type material: Holotype: PAPUA NEW GUINEA. Grat, 1050 m, i.1913, Burgers (1#f, MNBG).

Comment: *Grammicomyia armillata* Enderlein was treated as *Nestima* by Evenhuis (1989). It is here removed from *Nestima* because it lacks the defining character of the clade, that is a receding anterior mesonotum and the halter stem about 8 times as long as wide. This species is here treated as *Papeza* because its mesonotum is convex (not overhanging the pronotum) and its fore femur is orange-brown on the basal third, gradually turning black distally. The redescription here is based on photographs of the holotype female. The specimen has forelegs and a mid femur but otherwise lacks legs.

***Papeza funiculipes* (Enderlein, 1922)**

Grammicomyia funiculipes Enderlein 1922: 175

Papeza funiculipes (Enderlein), Evenhuis 1989: 465

(Fig. 4.43A–4.43H)

Redescription

Body length 8.5–10.5 mm, wing length 7.0–8.0 mm.

Head: Fronto-orbital plate with slight gray sheen on anterior ½, otherwise head generally orange-brown. Frontal vitta black.

Legs: Fore tibia uniformly dark brown.

Wing: Wing uniformly tan with no hyaline spot. Length of CuA+CuP 2× length of CuA.

Male abdomen: Left arm of male genital fork bulbous apically, distal third of right arm lost. Ejaculatory apodeme with a broad blade, wider than sperm pump, blade about twice as wide as sperm pump.

Female abdomen: Ducts uniformly membranous. Spermathecal ducts arising separately from bursa copulatrix into a longer paired duct and a shorter single duct (paired duct twice as long as single duct), both ducts with small swelling at spermathecal base.

Type material: Syntypes: PAPUA NEW GUINEA. Lordsburg, 8.xii.1912, Burgers (1#f, MNBG); PAPUA NEW GUINEA. Huntsteinspitze, 4–15.iii.1913, Burgers (1#m, MNBG).

Other material examined: PAPUA NEW GUINEA. NE, Moife, 2100 m, 15 km NW of Okapa, 11–13.x.1959, T.C. Maa (1#m, BPBM); Mt. Missim, 1600 m, 7°15'S 146°48'E, 21.v.1966, Malaise trap, J.L. Gressitt (1#f, BPBM); Milne Bay Prov., Geratin Pass: Dumai Creek, 1500 m, 26.ii–5.iii.1985, at light, F.J. Radovsky (1#f, BPBM Acc #1884.164); East Highlands Aiyura, 1800 m, 10.i.1964, Malaise trap, J.L. Gressitt (1#f, BPBM); Mount Wilhelm, 1200 m, 5.7209°S, 145.2695°E, 13–14.x.2013, IBISCA, Gewa, Damag, Novotny and Leponce (1#m DEBU01088890 sequence MYCRO381-18 [sequenced specimen], DEBU).

Comment: *P. funiculipes* is very similar to *P. szentivanyi*, from which it can only be distinguished by the parallel arms of the male genital fork.

***Papeza szentivanyi* McAlpine, 1975**

(Figs. 4.44A–4.44G)

McAlpine (1975) gave a detailed description of the external morphological characters of *P. szentivanyi*. The male aedeagus is similar to *P. funiculipes*, but the ejaculatory apodeme structure differs, as described below and shown Fig. 4.44.

Male abdomen: Ejaculatory apodeme blade narrower than sperm pump, sperm pump about twice as wide as blade.

Type material: Holotype: PAPUA NEW GUINEA. Woitape, Wharton Range, 1600 m,

20.x.1963, D.K. McAlpine (1#m, AMS K70254).

Other material examined: PAPUA NEW GUINEA. NE, Barapa Sawmill 13 km WNW of Kainantu, 2300–2400 m, 8.i.1965, J.L. Gressitt (1#m, BPBM); Mount Wilhelm, 1200 m, 5.7209°S, 145.2695°E, Malaise trap, 26–27.x.2012, IBISCA, Gewa, Damag, Novotny and Leponce (1#m, MNHN), Mount Wilhelm, 1200 m, 5.7209°S, 145.2695°E, Malaise trap, 26–27.x.2012, IBISCA, Gewa, Damag, Novotny and Leponce (1#f, DEBU01088891 sequence MYCRO383-18 [sequenced specimen], DEBU).

Comment: *P. szentivanyi* is very similar to *P. funiculipes*. The male genital fork is missing on the only male specimen available for examination, but McAlpine (1975) illustrated the genital fork of this species as having slightly incurved arms at the basal ½.

Figure 4.1: Posterior view of thorax of two species of Eurybatinae illustrating the postmetacoxal bridge. A) *Crosa fragilis* (Walker). Sclerotized postmetacoxal bridge present. B) *Crepidochetus argenteofascia* Frey. Sclerotized postmetacoxal bridge absent.

Figure 4.2: Distribution of *Crosta*: *C. calcarata*, *C. semilauta*, *C. yapensis*, *C. fragilis*, *C. immaculata*, *C. cuneifera*, *C. kuchingensis* and *C. borneoensis*.

Figure 4.3: Distribution of *Crosta*: *C. darlingi*, *C. angusta*, *C. tenuis*, *C. glabra*, *C. mejerei*, *C. reticulata* and *C. sulawesiensis*.

Figure 4.4: Distribution of *Crosta*: *C. reducta*, *C. sparsa*, *C. splendida*, *C. tetras*, *C. nigrifrontata*, *C. melanosa* and *C. semicolor*.

Figure 4.5: Distribution of *Crosta*: *C. burgersi*, *C. vitellosa*, *C. multimaculata*, *C. densa*, *C. tumifurca*, *C. petasibarba* and *C. flavifrons*.

Figure 4.6: Distribution of *Nestima*.

Figure 4.7: Distribution of *Papeza*.

Figure 4.8: *Nestima necta* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, head; D, female, thorax; E, wing; F, WIPs; G, male genitalia; H, genital fork; I, ejaculatory apodeme; J, spermathecae and associated structures. Abbreviations: ss – single spermatheca, sd – single duct, ps – paired spermathecae, pd – paired duct, bc – bursa copulatrix.

Figure 4.9: *Nestima nigramagnusa* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, female, New Ireland; D, wing; E, WIPs; F, spermathecae and associated structures; G, male genitalia; H, genital fork; I, ejaculatory apodeme. Abbreviations: ss – single spermatheca, sd – single duct, ps – paired spermathecae, pd – paired duct, bc – bursa copulatrix.

Figure 4.10: *Nestima pleuralis* Steyskal. A, female, lateral habitus; B, female, dorsal habitus; C, thorax; D, spermathecae and associated structures; E, wing; F, WIPs; G, genital fork.

Figure 4.11: *Nestima polita* Osten Sacken. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.12: *Nestima viridinsula* Steyskal. A, female, lateral habitus; B, female, dorsal habitus; C, lateral habitus (holotype); D, wing; E, WIPs; F, male genitalia; G, genital fork, H, ejaculatory apodeme; I, pregonite and postgonite; J, spermathecae and associated structures.

Figure 4.13: *Crosa angusta* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, head; D, wing; E, WIPs; F, spermathecae and associated structures.

Figure 4.14: *Crosa borneoensis* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.15: *Crosa burgersi* (Enderlein). A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, genital fork; G, ejaculatory apodeme; H, male genitalia.

Figure 4.16: *Crosa calcarata* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, head; D, wing; E, WIPs; F, spermathecae and associated structures; G, male genitalia; H, genital fork; I, ejaculatory apodeme.

Figure 4.17: *Crosa cuneifera* (de Meijere). A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme.

Figure 4.18: *Crosa darlingi* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.19: *Crosa densa* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, female, thorax; D, wing; E, WIPs; F, spermathecae and associated structures.

Figure 4.20: *Crosa flavifrons* (Bigot). A, male, lateral habitus; B, male, dorsal habitus; C, female, thorax; D, spermathecae and associated structures.

Figure 4.21: *Crosa fragilis* (Walker). A, male, lateral habitus; B, male, dorsal habitus; C, head; D, head; E, wing; F, WIPs; G, spermathecae and associated structures; H, male genitalia; I, ejaculatory apodeme; J, genital fork.

Figure 4.22: *Crosa glabra* (de Meijere). A, female, lateral habitus; B, female, dorsal habitus; C, notum, showing two postsutural dorsocentral bristles; D, spermathecae and associated structures; E, wing; F, WIPs.

Figure 4.23: *Crosa immaculata* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, pregonite and postgonite, G, genital fork; H, ejaculatory apodeme; I, spermathecae and associated structures.

Figure 4.24: *Crosa kuchingensis* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, ejaculatory apodeme; H, genital fork.

Figure 4.25: *Crosa meijerei* (Frey). A, female, lateral habitus; B, female, dorsal habitus.

Figure 4.26: *Crosa melanosa* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme; H, spermathecae and associated structures.

Figure 4.27: *Crosa multimaculata* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme.

Figure 4.28: *Crosa nigrifrontata* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.29: *Crosa petasibarba* (Enderlein). A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.30: *Crosa reducta* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme.

Figure 4.31: *Crosa reticulata* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, male, thorax; D, wing; E, WIPs; F, spermathecae and associated structures; G, male genitalia; H, genital fork; I, ejaculatory apodeme.

Figure 4.32: *Crosa semicolor* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, spermathecae and associated structures; G, genital fork; H, ejaculatory apodeme.

Figure 4.33: *Crosa semilauta* (Osten Sacken). A, male and female, Philippines, Mt. Makiling; B, female ovipositing in beetle burrow; C, head; D, spermathecae and associated structures; E, wing; F, WIPs; G, male genitalia; H, genital fork; I, ejaculatory apodeme.

Figure 4.34: *Crosa sparsa* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.35: *Crosa splendida* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.36: *Crosa sulawesiensis* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, spermathecae and associated structures; F, male genitalia; G, ejaculatory apodeme; H, genital fork.

Figure 4.37: *Crosa tenuis* (Doleschall). A, female, lateral habitus; B, female, dorsal habitus; C, spermathecae and associated structures; D, wing; E, WIPs; F, genital fork; G, ejaculatory apodeme; H, male genitalia.

Figure 4.38: *Crosa tetras* (Steyskal). A, male, lateral habitus; B, male, dorsal habitus; C, postmetacoxal bridge; D, wing; E, WIPs; F, male genitalia; G, genital fork; H, ejaculatory apodeme.

Figure 4.39: *Crosa tumifurca* sp. n. A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme; H, spermathecae and associated structures.

Figure 4.40: *Crosa vitellosa* sp. n. A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme.

Figure 4.41: *Crosa yapensis* (Steyskal). A, female, lateral habitus; B, female, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, basal and distal distiphallus; G, ejaculatory apodeme; H, genital fork; I, spermathecae and associated structures.

Figure 4.42: *Papeza armillata* (Enderlein). Female, lateral habitus.

Figure 4.43: *Papeza funiculipes* (Enderlein). A, male, lateral habitus; B, male, dorsal habitus; C, wing; D, WIPs; E, male genitalia; F, genital fork; G, ejaculatory apodeme; H, spermathecae and associated structures.

Figure 4.44: *Papeza szentivanyi* (McAlpine). A, male, lateral habitus; B, male, dorsal habitus; C, head chaetotaxy; D, male genitalia; E, ejaculatory apodeme; F, wing; G, WIPs. Abbreviations: fr – fronto-orbital bristles, ivt – inner vertical bristle, ovt – outer vertical bristle, pocl – postocellar bristle.

CHAPTER 5

CONCLUSION

This thesis assesses the phylogeny and classification of the subfamily Eurybatinae using molecular data for the first time. Although the appropriately preserved material of Eurybatinae used in this study is limited and therefore only a few genes were successfully sequenced, the results from Bayesian inference analysis of complete concatenated dataset of all genes produced a well resolved tree to represent the evolutionary history of Eurybatinae.

Eurybatinae is recovered as monophyletic and sister to Taeniapterinae in all analyses. Eurybatinae are characterized by two synapomorphies: the apical dorsal bare area on the hind tibia with subapical anterodorsal bristles and the deeply V-shaped of sternite 6. Eurybatinae as defined here consists of 10 genera with 81 species divided into two large groups based on the presence or absence of a sclerotized postmetacoxal bridge.

Most analyses recovered a monophyletic postmetacoxal bridge group (PMB) including 38 species grouped into three genera: *Crosa* Steyskal, *Nestima* Osten Sacken and *Papeza* McAlpine. Besides the presence of the postmetacoxal bridge, this group is characterized by the absence of costagial setae. A full taxonomic revision of the PMB group presented in Chapter 4 of this thesis includes 20 new species of Eurybatinae, mostly in the genus *Crosa*, almost doubling the size of the group.

The relationships within the paraphyletic group lacking the postmetacoxal bridge is only partially resolved because two of the genera in this group, *Anaeropsis* Bigot and *Notenthes* Marshall, were not included in the study due to the lack of material. The results suggest that the Australian *Cothornobata* are more closely related to *Crepidochetus* Enderlein than to *Cothornobata* s.s., so they are formally moved to the genus *Crepidochetus*. *Cothornobata* Czerny is redefined to include only the Oriental species (*Cothornobata* s.s. of Li et al., 2015).

This study has improved the classification of Eurybatinae by resolving the relationships of the genera within the PMB group, which includes almost half of the described species of Eurybatinae. The new keys to the genera and species of the PMB group provided in this thesis will enable future identification of species in this group. Although the relationships within the group lacking the postmetacoxal bridge region are incompletely resolved, this thesis has resolved some of the taxonomic issues within this group. The inclusion of *Anaeropsis* and *Notenthes* in future studies would be enlightening but depends on obtaining fresh material. This is currently an issue because of restrictions on collecting and exporting material from the countries in which these taxa occur. Despite this, further taxon sampling of Eurybatinae is

necessary to move forward, especially for the resolution of the relationships of *Anaeropsis* and *Notenthes*. Material preserved appropriately for molecular work would be very useful to expand future molecular studies.

CHAPTER 6

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APPENDIX

List of synapomorphic morphological characters of Eurybatinae mapped on the selected tree.
The characters were selected from literatures and observations of specimens.

1. Hind tibia with apical dorsal bare area and subapical anterodorsal bristles.
2. Sternite 6 deeply V-shaped.
3. Distal distiphallus branches trifurcate.
4. A broad, plate-like hypandrium.
5. Tapering lower margin of frons.
6. Genital fork with basal and medial tubercles.
7. R_{2+3} vein relatively short, ending at the same level or just slightly beyond the dm-m crossvein.
8. Scutellum with more rounded apex.
9. Anterior margin of mesonotum sloping.
10. Presence of postmetacoxal bridge.
11. Absence of costagial setae.
12. Fore femur which is orange-brown on the basal third, and gradually turning black distally.
13. Mesonotum overhanging pronotum.
14. Posteroventral spines on distal third of mid and hind femur present.
15. Subscutellum longer than the scutellum
16. A receding anterior mesonotal margin.
17. Halter stem about eight times as long as wide.
18. Ventral bristles on basal $\frac{1}{2}$ of male fore femur present.

CATALOGUE OF EURYBATINAE

(**refers to manuscript names)

Genus ANAEROPSIS Bigot

ANAEROPSIS Bigot, 1866: 202. Type species: *Anaeropsis lorquini* Bigot 1866.

[=*Phytalmina guttipennis* Walker 1861] (orig. des.).

GUTTIPENNIS (Walker), 1861: 269. HT ♂ MNBG. Type locality: Indonesia, Sulawesi.
Distribution: Indonesia (Sulawesi and Maluku). *Anaeropsis lorquini* Bigot, 1866: 202.

Genus COTHORNOBATA Czerny

COTHORNOBATA Czerny, 1932: 267. Type species: *Cothornobata striatifrons* Czerny 1832 [*Trepidaria cyanea* Hendel, 1913] (monotypy).

Sphaericocephala Czerny, 1932: 291. Nomen nudum; genus-group name proposed after 1930 without designation of type species from five included species.

Sphaericocephala Steyskal, 1977a: 12. Type species: *Trepidaria cyanea* Hendel, 1913 (orig. des.). Nomen nudum; genus-group name proposed in synonymy after 1960.

ATRA Li et al., 2015: 225. HT ♂ CAU. Type locality: China, Guangxi. Distribution: China (Guangxi).

BREVISETA Li et al., 2015: 207. HT ♂ CAU. Type locality: Vietnam, Thua Thien Hue. Distribution: Vietnam.

BUBENGENSIS Li et al., 2015: 240. HT ♂ CAU. Type locality: China, Yunnan. Distribution: China (Yunnan).

CURVA Li et al., 2015: 227. HT ♂ CAU. Type locality: China, Yunnan. Distribution: China (Yunnan).

CYANEA (Hendel), 1913: 43 (*Trepidaria*). ST 16 ♀ NMW. Type locality: Taiwan, Koshun. Distribution: China and Taiwan. *Grammicomyia cyanea* Enderlein, 1922: 174. *Cothornobata striatifrons* Czerny, 1932: 267. *Trepidarioides cyanea* Hennig, 1935: 306. *Cothornobata cyanea*, Steyskal, 1977: 12.

ELEGANTULA Li et al., 2015: 229. HT ♂ CAU. Type locality: Vietnam, Ninh Binh. Distribution: Vietnam (Ninh Binh).

FUSCA Li et al., 2015: 209. HT ♂ CAU. Type locality: China, Hainan. Distribution: China (Hainan).

INGENSFURCA Li et al., 2015: 213. HT ♂ CAU. Type locality: China, Yunnan. Distribution: China (Yunnan).

LONGIFURCA Li et al., 2015: 217. HT ♂ CAU. Type locality: China, Guangxi. Distribution: China (Guangxi).

LONGIGONITEA Li et al., 2015: 229. HT ♂ CAU. Type locality: China, Yunnan.
Distribution: China (Yunnan).

MENTOGENSIS Li et al., 2015: 233. HT ♂ CAU. Type locality: China, Tibet. Distribution: China (Tibet).

NIGRIGENU (Enderlein), 1922: 173 (*Grammicomyia*). HT ♂ MNBG. Type locality: Burma, Toungoo, Karenni. Distribution: Burma, China (Yunnan), India, Laos, Sikkim, Thailand, Vietnam. *Trepidarioides nigrigenu* Hennig, 1935: 307. *Cothornobata nigrigenu*, McAlpine, 1975: 239.

PAIEROI Li et al., 2015: 219. HT ♂ IEBR. Type locality: Vietnam, Ninh Binh. Distribution: Vietnam (Ninh Binh).

PUGNOA Li et al., 2015: 221. HT ♂ CAU. Type locality: Vietnam, Thua Thien Hue. Distribution: Vietnam, (Thua Thien Hue).

SHUIMANENSIS Li et al., 2015: 211. HT ♂ CAU. Type locality: China, Hainan. Distribution: China (Hainan).

UNISETA Li et al., 2015: 238. HT ♂ CAU. Type locality: China, Yunnan. Distribution: China (Yunnan).

VIETNAMENSIS Li et al., 2015: 242. HT ♂ CAU. Type locality: Vietnam, Thua Thien Hue. Distribution: Vietnam (Thua Thien Hue).

VIRIATA (Enderlein), 1922: 174 (*Grammicomyia*). LT ♂ MNBG. Type locality: Sumatera (Deli). Distribution: Sumatra. Previous records from New Guinea (Evenhuis 1989) were in error (McAlpine, 1998). *Trepidarioides viriata* Hennig, 1935: 307. *Cothornobata viriata* Steyskal, 1977: 13.

ZHANGAE Li et al., 2015: 223. HT ♂ CAU. Type locality: China, Guangxi. Distribution: China (Guangxi).

Genus CREPIDOCHETUS Enderlein

CREPIDOCHETUS Enderlein, 1922: 172. Type species: *Crepidochetus forcipatus* Enderlein 1922 (orig. des.).

Gongylocephala Czerny, 1932b: 292. Type species: *Gongylocephala nigrifemur* Czerny, 1932.

ACZELI (McAlpine), 1998: 96. (*Cothornobata*) HT ♂ AM. Type locality: Australia, New South Wales. Distribution: Eastern Australia.

ALTA (McAlpine), 1998: 101. (*Cothornobata*) HT ♂ AM. Type locality: Australia, Queensland. Distribution: Northern Queensland, Australia.

ARGENTEOFASCIA Frey, 1958: 47. HT ♂ RMNH No. 14043. Type locality: Philippines, Los Banos. Distribution: Philippines. *Grammicomyia vittipennis* de Meijere, 1914.

ATRA Steyskal, 1947: 5 (*Gongylocephala*). HT ♂ UMMZ. Type locality: Solomon Islands, Guadalcanal. Distribution: Solomon Islands.

DEBILIS Walker, 1859: 124 (*Cardiacephala*). HT ♀ BMNH. Type locality: Indonesia, Maluku, Aru Islands. Distribution: Indonesia (Aru Islands).

FORCIPATUS Enderlein, 1922: 172. HT ♂ MNBG. Type locality: Indonesia, Sumatra. Distribution: Indonesia (Sumatra).

GRALLINA (McAlpine), 1998: 103. (*Cothornobata*) HT ♂ AM. Type locality: Australia, Queensland. Distribution: Northern Queensland, Australia.

INERMIPES (Malloch), 1935: 343 (*Grammicomyia*). HT ♂ BMNH. Type locality: Samoa, Upolu. Distribution: Samoa.

IOS McAlpine, 1998: 109. HT ♂ AMS. Type locality: Australia, Queensland. Distribution: Australia (North Queensland).

LEVIS (McAlpine), 1998: 106. (*Cothornobata*) HT ♂ AM. Type locality: Australia, Queensland. Distribution: Northern Queensland, Australia.

LINEA (McAlpine), 1998: 95. (*Cothornobata*) HT ♀ ANIC. Type locality: Australia, Norfolk Island. Distribution: Australia (Norfolk Island).

MACULA (McAlpine), 1998: 99. (*Cothornobata*) HT ♂ AM. Type locality: Australia, Queensland. Distribution: Northern Australia.

NIGRIFEMUR Czerny, 1932: 293 (*Gongylocephala*). HT ♀ (type not examined, probably lost). Type locality: Malaysia, Sarawak.

PALLIDA Steyskal, 1947: 4 (*Gongylocephala*). HT ♂ UMMZ. Type locality: Solomon Islands, Guadalcanal. Distribution: Solomon Islands.

PALLIDA LUZONICA Steyskal, 1952: 178 (*Gongylocephala*). HT ♂ USNM. Type locality: Philippines, Luzon. Distribution: Philippines (Luzon).

VARIPES Walker, 1859: 162 (*Cardiacephala*). HT ♂ BMNH. Type locality: Indonesia, Sulawesi, Makassar. Distribution: Indonesia (Sulawesi).

Genus CROSA Steyskal

CROSA Steyskal, 1952: 176. Type species: *Eurybata semilauta* Osten Sacken 1882.

ANGUSTA Md Yusof and Marshall, 2020: **. HT ♀ DEBU. Type locality: Indonesia, Sulawesi. Distribution: Indonesia (Sulawesi).

BORNEOENSIS Md Yusof and Marshall, 2020: **. HT ♂ ROME. Type locality: Malaysia, Sarawak. Distribution: Malaysia (Sarawak and Sabah).

BURGERSI (Enderlein), 1922: 171 (*Calobata*). HT ♀ MNBG. Type locality: Papua New Guinea, Lordberg. Distribution: Indonesia (Irian Jaya) and Papua New Guinea.

CALCARATA Md Yusof and Marshall, 2020: **. HT ♂ PNMNH type #13652. Type locality: Philippines, Mount Labo. Distribution: Philippines

CUNEIFERA (de Meijere), 1914: 178 (*Eurybata*). HT ♂ MNBG. Type locality: Indonesia, Java. Distribution: Indonesia (Java).

DARLINGI Md Yusof and Marshall, 2020: **. HT ♂ ROME. Type locality: Malaysia, Sarawak, Gunung Mulu National Park. Distribution: Malaysia (Sarawak).

DENSA Md Yusof and Marshall, 2020: **. HT ♀ MNHN. Type locality: Papua New Guinea, Mount Wilhelm. Distribution: Papua New Guinea.

FLAVIFRONS (Bigot), 1886: 382 (*Eurybata*). ST 2 ♂ OXUM. Type locality: Papua New Guinea, Nabire. Distribution: Papua New Guinea.

FRAGILIS (Walker), 1856: 37 (*Micropeza*). HT ♂ BMNH. Type locality: Singapore.

Distribution: Singapore, Indonesia (Sumatra), Peninsular Malaysia. *Eurybata nigriventris* Enderlein, 1922: 170. *Crosa fragilis*, McAlpine, 1975: 244. *Crosa nigriventris*, McAlpine, 1975: 244. *Nestima fragilis*, Evenhuis, 1989: 465.

GLABRA (de Meijere), 1914: 177 (*Eurybata*). HT ♂ MNBG. Type locality: Indonesia, Java. Distribution: Indonesia (Java).

IMMACULATA Md Yusof and Marshall, 2020: **. HT ♂ ROME. Type locality: Malaysia, Sabah. Distribution: Malaysia (Sabah).

KUCHINGENSIS Md Yusof and Marshall, 2020: **. HT ♂ DEBU. Type locality: Malaysia, Sarawak. Distribution: Malaysia (Sarawak).

MELANOSA Md Yusof and Marshall, 2020: **. HT ♀ BPBM_ENT_17848. Type locality: Solomon Islands, Kolombangara Island. Distribution: Solomon Islands.

MEIJEREI (Frey), 1934: 333 (*Cothornobata*). HT ♀ NHMB. Type locality: Indonesia, Java. Distribution: Indonesia (Java). *Cothornobata meijerei* Frey, 1934: 333 *Nestima meijerei*, Li et al., 2015: 244.

MULTIMACULATA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17852. Type locality: Solomon Islands, Bougainville. Distribution: Solomon Islands.

NIGRIFRONTATA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17853. Type locality: Solomon Islands, Florida Grp. Distribution: Solomon Islands.

PETASIBARBA (Enderlein), 1922: 170 (*Eurybata*). HT ♂ MNBG. Type locality: Papua New Guinea, Sepik. Distribution: Papua New Guinea.

REDUCTA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17857. Type locality: Papua New Guinea, Papua. Distribution: Papua New Guinea.

RETICULATA Md Yusof and Marshall, 2020: **. HT ♂ USNM. Type locality: Malaysia, Sabah, Kundasang. Distribution: Malaysia (Sabah).

SEMICOLOR Md Yusof and Marshall, 2020: **. HT ♂ MNHN. Type locality: Papua New Guinea, Mount Wilhelm. Distribution: Papua New Guinea.

SEMILAUTA (Osten Sacken), 1882: 207 (*Eurybata*). HT ♂ DEI. Type locality: Philippines. Distribution: Philippines.

SPARSA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17858. Type locality: Papua New Guinea, Eliptamin Valley. Distribution: Papua New Guinea.

SPLENDIDA Md Yusof and Marshall, 2020: **. HT ♂ MNHN. Type locality: Papua New Guinea, Mount Wilhelm. Distribution: Papua New Guinea.

SULAWESIENSIS Md Yusof and Marshall, 2020: **. HT ♂ BMNH. Type locality: Indonesia, Sulawesi. Distribution: Indonesia (Sulawesi).

TENUIS (Doleschall), 1859: 127 (*Micropeza*). Type not seen, possibly lost. Type locality: Indonesia, Ambon. Distribution: Indonesia (Ambon and Maluku).

TETRAS (Steyskal), 1947: 2 (*Eurybata*). HT ♂ UMMZI. Type locality: Solomon Islands, Guadalcanal. Distribution: Solomon Islands.

TUMIFURCA Md Yusof and Marshall, 2020: **. HT ♂ MNHN. Type locality: Papua New Guinea, Mount Wilhelm. Distribution: Papua New Guinea.

VITELLOSA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17863. Type locality: Papua New Guinea, Waris. Distribution: Papua New Guinea.

YAPENSIS (Steyskal), 1952: 176. HT ♂ USNM. Type locality: Yap Island, Yap town. Distribution: Caroline Islands (Yap Island).

Genus EURYBATA Osten Sacken

EURYBATA Osten Sacken, 1882b: 204. Type species: *Eurybata hexapla* Osten Sacken 1882 (orig. des.).

HEXAPLA Osten Sacken, 1882: 206. ST 1♂ 2♀ DEI. Type locality: Philippines.

Distribution: Philippines.

NIGRITIBIA Steyskal, 1952: 174. HT ♂ USNM. Type locality: Philippines, Luzon.

Distribution: Philippines.

TESELLATA Steyskal, 1952: 176. HT ♂ USNM. Type locality: Philippines, Mindanao.

Distribution: Philippines.

Genus NESTIMA Osten Sacken

NESTIMA Osten Sacken, 1881a: 457. Type species: *Nestima polita* Osten Sacken 1881 (monotypy).

NECTA Md Yusof and Marshall, 2020: **. HT ♂ MNHN. Type locality: Papua New Guinea, Mount Wilhelm. Distribution: Papua New Guinea.

NIGRAMAGNUSA Md Yusof and Marshall, 2020: **. HT ♂ BPBM_ENT_17845. Type locality: Papua New Guinea, New Britain. Distribution: Papua New Guinea.

PLEURALIS Steyskal, 1952: 179. HT ♀ USNM type #58308. Type locality: Papua New Guinea, Nadzab. Distribution: Papua New Guinea.

POLITA Osten Sacken, 1881: 458. ST 2♂1♀ MCG. Type locality: Papua New Guinea, Andai. Distribution: Indonesia (Irian Jaya) and Papua New Guinea.

PROLIXA (Walker), 1861: 299 (*Micropeza*). Type not seen, possibly lost. Type locality: Indonesia, Sulawesi.

VIRIDINSULA Steyskal, 1952: 179. HT ♀ USNM type #58307. Type locality: Papua New Guinea, Green Island. Distribution: Papua New Guinea (Bismarck Archipelago).

Genus NOTENTHES Marshall

NOTENTHES Marshall 2002: 83. Type species: *Notenthes mcalpinei* Marshall 2002 (orig. des.).

MCALPINEI Marshall 2002: 83. HT ♂ MNCR. Type locality: Costa Rica, Puntarenas.

Distribution: Costa Rica.

RUBELLA (van der Wulp) 1897: 368 (*Calobata*). LT ♂ BMNH. Type locality: Mexico, Omilteme. Distribution: Mexico.

Genus PAPEZA McAlpine

PAPEZA McAlpine 1975: 242. Type species: *Papeza szentivanyi* McAlpine 1975 (orig. des.).

ARMILLATA (Enderlein), 1922: 175 (*Grammicomyia*). HT ♀ MNBG. Type locality: Papua New Guinea, Grat. Distribution: Papua New Guinea. *Grammicomyia armillata* Enderlein, 1922: 175. *Nestima armillata*, Evenhuis, 1989: 465.

FUNICULIPES (Enderlein), 1922: 174 (*Grammicomyia*). ST 1♂1♀ MNBG. Type locality: Papua New Guinea, Lordsberg. Distribution: Papua New Guinea.

SZENTIVANYI McAlpine, 1975: 242. HT ♂ AMS. Type locality: Papua New Guinea, Woitape. Distribution: Papua New Guinea.

Genus PARAEURYBATA Marshall

PARAEURYBATA Marshall 2019: 2. Type species: *Calobata taeniata* Macquart 1843.

TAENIATA (Macquart), 1843: 401 (*Calobata*). ST 1 ♀ 1 ♂ MNHN. Type locality: La Réunion. *Calobata taeniata* Macquart, 1843: 401. *Trepidarioides taeniata* Hennig, 1935: 13. *Trepidarioides taeniatus* Steyskal, 1980: 579. *Cothornobata striatifrons* Czerny, 1932: 267. *Cothornobata taeniata*, Barraclough, 1992: 25.

Genus TREPIDARIOIDES Frey

TREPIDARIOIDES Frey 1927: 76. Type species: *Calobata territa* Osten Sacken 1882 (orig. des.).

TERRITA (Osten Sacken) 1882: 203 (*Calobata*). ST 1 ♀ 1 ♂ DEI. Type locality: Philippines, Luzon. Distribution: Philippines. [spelled as *terrirus* by Frey, 1958].