RESEARCH ARTICLE



Review of the spore-feeding Idolothripinae from China (Thysanoptera, Phlaeothripidae)

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Abstract

An illustrated key is provided to the 19 genera of the subfamily Idolothripinae from China, and a checklist given to 62 named species, of which six species are newly recorded from China, together with the genus *Bolothrips* that is represented by two un-named species. A generic diagnosis is given for each genus, along with some discussion of systematic relationship problems and species diversity. Identification keys to species of 11 genera are provided, and *Megathrips antennatus* Guo, Feng & Duan is considered as a new synonym of *Megathrips lativentris* (Heeger).

Keywords

Idolothripinae, genera, illustrated keys, species checklist, new records, China

Introduction

The insect order Thysanoptera, comprises more than 6000 species, and is classified into two suborders, Terebrantia and Tubulifera (ThripsWiki 2013). There are 14 families in the two suborders, of which five families are known only from fossil species. The suborder Tubulifera includes only one family, the Phlaeothripidae, and is the largest Thysanoptera family with nearly 3550 species in 460 genera. Adults in this family have the tenth abdominal segment tubular, and the species are grouped into two subfamilies, the Idolothripinae and Phlaeothripinae. Currently there are 81 genera and 722 species listed worldwide in the Idolothripinae (ThripsWiki 2013). Species in this subfamily have broad maxillary stylets that are more than five microns in diameter, and apparently feed on fungal spores. Mound and Palmer (1983) revised and provided a key to the world genera of Idolothripinae, but the genera from China sometimes do not fit easily into this key. Okajima (2006) provided a key to 17 genera of Idolothripinae from Japan, and Eow et al. (2011) provided a key to 31 genera of Idolothripinae from Southeast Asia. Both of these recent keys are useful when studying Idolothripinae from Southern China. However, environments within China are highly varied, with considerable floristic and faunistic differences between the temperate Palaearctic north and the southern tropical and subtropical Oriental Region. Therefore a new key to the 19 genera known from Chinese territory is presented here, particularly for the convenience of students in this country.

The present work, as part of ongoing studies on the Phlaeothripidae from China, aims at providing an identification key to the 19 genera and 62 species of Idolothripinae now recorded from China. A species checklist is included, with distributional information based on the provinces and autonomous regions of China (Table 1), and a diagnosis is provided for each genus. The genus *Bolothrips* is here newly recorded from China, and six species of Idolothripinae are also newly recorded (Table 1). Moreover, *Megathrips antennatus* Guo, Feng & Duan is here considered as a new synonym of *Megathrips lativentris* (Heeger).

Systematics of Idolothripinae

Mound and Palmer (1983) recognized two tribes within the Idolothripinae. The Chinese fauna includes nine genera that represent the tribe Idolothripini, and 10 genera that represent the Pygothripini. In species of Idolothripini the abdominal tergites usually bear two or more pairs of wing-retaining setae, the metathoracic sternopleural sutures are never developed, and the tube is relatively long and sometimes bears long lateral setae. Species of Pygothripini, in contrast, only have one pair of wing-retaining setae on each tergite, the metathoracic sternopleural sutures are present or absent, and the tube does not have long lateral setae. Within the Pygothripini, six subtribes are recognized, and these are represented in China as follows: Pygothripina (Cryptothrips; *Phaulothrips*), Allothripina (*Allothrips*), Compsothripina (*Bolothrips*; *Compsothrips*), Gastrothripina (Gastrothrips), Diceratothripina (Acallurothrips; Nesothrips), and Macrothripina (Ethirothrips; Machatothrips). Within the Idolothripini three subtribes are recognised. The Hystricothripina occurs mainly in the Neotropics, but one genus, Holurothrips, is found in China. The Elaphrothripina occurs throughout the tropics, and the following genera are recorded from China, Dinothrips, Elaphrothrips, Mecynothrips, and Ophthalmothrips. The Idolothripina occurs mainly in the Palaeotropics and Palaearctic regions, and in China includes the following four genera, Bactrothrips, Megalothrips, Megathrips and Meiothrips.

Таха	Distribution in China by Provinces or Autonomous Regions
Acallurothrips casuarinae Okajima, 1993	Taiwan
A. hagai Okajima, 1993	Taiwan
A. nonakai Okajima, 1993	Taiwan
A. tubullatus Wang & Tong, 2008	Guangdong
Allothrips bicolor Ananthakrishnan, 1964	Hainan
A. discolor Chen, 1982	Taiwan
A. taiwanus Okajima, 1987	Taiwan
Bactrothrips brevitubus Takahashi,1935	Southern China
B. elongates Dang & Qiao, 2012	Guangxi
<i>B. flectoventris</i> Haga & Okajima, 1989	Hainan
B. furvescrus Dang & Qiao, 2012	Zhejiang
B. honoris (Bagnall, 1921)	Guangxi; Yunnan
<i>B. pictipes</i> Haga & Okajima, 1989	Tibet; Guangxi; Hainan
B. quadrituberculatus (Bagnall, 1908)	Yunnan; Hainan
§Bolothrips spp.	Beijing; Inner Mongolia
Compsothrips reticulates Guo & Feng, 2006	Hebei
C. sinensis (Pelikan, 1961)	Guangdong
C. tenebronus (Han & Cui, 1991)	Sichuan
Cryptothrips nigripes (Reuter, 1880)	Inner Mongolia
C. sauteri Karny, 1913	Taiwan [known only from description]
Dinothrips hainanensis Zhang, 1982	Guangdong; Hainan
D. juglandis Moulton, 1933	Tibet; Guangdong
D. spinosus (Schmutz, 1913)	Yunnan; Hainan
D. sumatrensis Bagnall, 1908	Fujian; Guangdong; Hainan
Dinothrips sp.	Yunnan
Elaphrothrips denticollis (Bagnall, 1909)	Southern China
§E. fulmeki Priesner, 1935	Hainan
<i>E. greeni</i> (Bagnall, 1914)	Fujian; Yunnan; Hainan; Tibet
§E. insignis Ananthakrishnan, 1973	Yunnan; Hubei
E. jacobsoni Priesner, 1935	Guizhou
§E. malayensis (Bagnall, 1909)	Hubei; Guizhou; Yunnan; Hainan; Tibet
§E. procer (Schmutz, 1913)	Hubei; Yunnan; Guangdong; Hainan
E. spiniceps Bagnall, 1932	Fujian; Guangxi; Guangdong; Yunnan; Hainan; Taiwan
Ethirothrips chui (Chen, 1982)	Taiwan
E. longisetis Ananthakrishnan & Jagadish, 1970	Hainan
E. stenomelas (Walker, 1859)	Guangdong; Hainan
§§E. virgulae (Chen, 1980)	Guangxi; Taiwan
E. vitreipennis (Priesner, 1939)	Hainan
Gastrothrips eurypelta Cao et al., 2009	Hebei; Shaanxi; Shanxi
G. fulvipes Hood, 1973	Taiwan
G. fuscatus Okajima, 1979	Guangdong; Taiwan
G. mongolicus (Pelikan, 1965)	Inner Mongolia; Fujian; Zhejiang; Sichuan; Ningxia
§G. monticola Okajima, 2006	Inner Mongolia
Holurothrips morikawai Kurosawa, 1968	Guangdong; Fujian; Hainan; Taiwan
Machatothrips antennatus (Bagnall, 1915)	Guangdong; Hainan
M. artocarpi Moulton, 1928	Hainan; Taiwan
M. celosia Moulton, 1928	Hainan; Taiwan

Table 1. Idolothripinae recorded from China.

Taxa	Distribution in China by Provinces or Autonomous Regions
Mecynothrips kanoi (Takahashi, 1937)	Taiwan
M. pugilator (Karny, 1913)	Taiwan
§M. simplex Bagnall, 1912	Yunnan; Hainan
M. taiwanus Okajima, 1979	Yunnan; Hainan; Taiwan
Megalothrips roundus Guo et al., 2010	Hubei
Megathrips lativentris (Heeger, 1852)	Hebei; Henan
Meiothrips fuscicrus Dang & Qiao, 2012	Yunnan
M. menoni Ananthakrishnan, 1964	Yunnan; Hainan
M. nepalensis Kudo & Ananthakrishnan, 1974	Yunnan
Nesothrips brevicollis (Bagnall, 1914)	Henan; Shaanxi; Gansu; Taiwan
N. lativentris (Karny, 1913)	Guangxi; Taiwan
N. peltatus Han, 1991	Sichuan
Ophthalmothrips formosanus (Karny, 1913)	Henan; Taiwan
O. longiceps (Haga, 1975)	Hainan; Taiwan
O. miscanthicola (Haga, 1975)	Fujian; Guangdong; Sichuan; Hainan
O. yunnanensis Cao et al., 2010	Yunnan
Phaulothrips solifer Okajima, 1989	Taiwan

§ Newly recorded from China; §§ Newly recorded from mainland China.

Idolothripinae fauna of China

In the only available review of the Thysanoptera fauna of China, Han (1997) provided an identification key to nine genera and 16 species of Idolothripinae known at that time from China. Unfortunately, the nomenclature and generic concepts in that study are now out-of-date, and many more taxa have been added in recent years by various authors from China and Japan. As a result, Mirab-balou et al. (2011) listed 18 genera and 59 species of Idolothripinae from China, but there continues to be no identification system available to these taxa. One genus that was listed by Mirab-balou, *Neosmerinthothrips* Bagnall, is not known from China. The record is an error because the single species involved, *N. brevicollis*, is known only from the Seychelles, and the name was presumably confused with a similarly named species of *Nesothrips*. Keys have been published to the species from China in a few genera, including *Bactrothrips*, *Gastrothrips*, *Meiothrips*, and *Ophthalmothrips* (Dang and Qiao 2012a, Cao et al. 2009, Dang and Qiao 2012b, Cao et al. 2010). Recently, Dang et al. (2013) reported some changes in nomenclature, including new synonyms, new combinations and new records from China.

Methods and depositories

Descriptions and drawings are from slide-mounted specimens using Nikon Eclipse 80i & Leica DM4000B microscopes. Images were prepared with a Leica DM2500 using DIC illumination, and processed with Automontage and Photoshop software. Table 1 provides authority names and dates for all of the species discussed here, and full nomenclatural details and references for all Thysanoptera taxa are available in ThripsWiki 2013. Species that have not been studied here, and for which the information is from original descriptions, are indicated by an asterisk *. Slide-mounted specimens of all of these genera are available in the National Zoological Museum of China (NZMC), Institute of Zoology, Chinese Academy of Sciences, Beijing, China, and also the Australian National Insect Collection (ANIC), Canberra, Australia.

Field work. In China, netting and sweeping thrips living on plants and dead leaves has been the traditional collecting method. This method collects many specimens, but these are often damaged, the smaller species are not easily seen in a net, and almost no information on biology is produced. Precise field collecting methods are essential for good taxonomic research, and the best way to collect thrips in good condition is by carefully beating flowers, leaves, and dead hanging leaves and twigs, onto a white plastic plate. Thrips adhere to the plastic surface with their unique tarsal vesicle and can then be gathered into small vials of ethanol using a small brush. Furthermore, some thrips live in leaf litter, and samples of litter can be extracted through a Berlese or Tulgren Funnel into a collecting jar of ethanol. Detailed information on collecting thrips is available in ThripsWiki Website (ThripsWiki 2013).

Microscope slides. A major restraint on good taxonomic work on thrips is the large number of poorly-prepared specimens on microscope in many museum collections. In China, the method given by Han (1997) involves heating and macerating thrips in a strong NaOH solution (10%). However, this results in extensive damage and loss of colour to specimens. In contrast, Zhang et al. (2006) provided details of a method to make excellent slides, and details for slide preparation are also given in ThripsWiki (2013). Adults of the subfamily Idolothripinae have a wide range of body sizes, and many are large and dark. These dark thrips should be left in very weak NaOH solution (2%) for 12 hours or more at room temperature, but usually no more than 72 hours. It is hard work to make good slides, especially of these dark and large species, and this is one of the challenges when studying Idolothripinae.

Key to genera of Idolothripinae from China

1	Tube with prominent lateral setae (Fig. 54)	2
_	Tube smooth, without lateral setae, or lateral setae minute (Figs 11, 12)	6
2	Tube elongate, more than 10 times as long as basal width (Fig. 54)	3
_	Tube no more than 5 times as long as basal width	4
3	Head with projection in front of eyes much longer than broad, with two pairs of	of
	stout setae (Fig. 13); eyes distinctly prolonged ventrally (Fig. 13) Holurothrip	s
_	Head with projection in front of eyes broader than long, with one pair of	of
	stout setae (Fig. 16); eyes equally developed on dorsal and ventral surfaces	•
	Meiothrip	s
4	Maxillary stylets long, usually retracted to eyes, close together in middle of	of
	head) <i>s</i>

_	Maxillary stylets short and wide apart, usually V-shaped5
5	Pelta lateral lobes broadly joined to median lobe (Fig. 24); the distance between
	postocular setae less than half of head width behind eyes (Fig. 14); tergites
	II-VII each with two wing-retaining setae usually well developed; antennal seg-
	ment III usually longer than head width across eyes
_	Pelta lateral lobes narrowly joined to, or separated from, median lobe (Figs
	25, 26, 47); the distance between postocular setae about half of head width
	behind eyes; tergites II-VII of macropterae with anterior pair of wing-retain-
	ing setae small; antennal segment III much shorter than head width across
	eyes (Fig. 43)
6	Abdominal tergites III-V each with three pairs of sigmoid wing-retaining
	setae (Fig. 50)
_	Abdominal tegites III-V each with at most two pairs of sigmoid wing-retain-
	ing setae (Fig. 52)7
7	Metathoracic sternopleural sutures absent
_	Metathoracic sternopleural sutures present13
8	Eyes prolonged posteriorly on ventral surface of head (Figs 17, 41)9
-	Eyes equally developed ventrally and dorsally10
9	Antennal segment IV with 3 (rarely 2) sensoria; abdominal tergites II-VII each
	with one pair of sigmoid wing-retaining setae in macroptera Bolothrips
-	Antennal segment IV with 4 sensoria; abdominal tergites II-VII usually each
	with two pairs of sigmoid wing-retaining setae Ophthalmothrips
10	Female with inner margin of fore femur with row of about 4 tubercles at least
	(Figs 34, 35) Machatothrips
_	Fore femur of female without tubercles on inner margin11
11	Abdominal tegites III–V each with one pair of sigmoid wing-retaining setae
	(Fig. 52)Ethirothrips
-	Abdominal tegites III-V each with two pairs of sigmoid wing-retaining
	setae
12	Pelta divided into three lobes (Fig. 31); mesothoracic spiracular area of male
	produced into prominent process (Fig. 36)
-	Pelta not divided into three lobes (Figs 29, 30); mesothorax of male normal
1.0	Elaphrothrips
13	Metathoracic sternopleural sutures complete (Fig. 53); eyes distinctly pro-
	longed ventrally
-	Metathoracic sternopleural sutures incomplete; eyes usually not prolonged
1/	Ventrally
14	Maxillary palp with a large stout terminal sensorium (Fig. 45)Allothrips
-	Maxillary palp without stout terminal sensorium, or small
15	Maxillary stylets close together medially (Figs 42, 44) 16
-	Iviaxiliary stylets wide apart, almost v-shaped (Figs 1, 2, 3, 40)
16	Antennal segment IV with 2 sensoriaPhaulothrips

_	Antennal segment IV with 3 sensoria	Cryptothrips
17	Antenna 7-segmented, segment VII with an incomplete suture	e Acallurothrips
-	Antenna 8-segmented, but segments VII and VIII sometim	es broadly joined
	(Fig. 46)	
18	Antennal segment IV with 3 sensoria	Gastrothrips
_	Antennal segment IV with 4 sensoria	Nesothrips

Acallurothrips Bagnall

http://species-id.net/wiki/Acallurothrips

Remarks. There are 22 species listed in this genus, of which five are recorded from China: *tubullatus* from Guangdong (Wang and Tong 2008), and *casuarinae*, *hagai*, *hanatanii* and *nonakai* from Taiwan (Okajima 2006), of which paratypes were studied in ANIC.

Diagnosis. Head usually broad; postocular setae usually longer than eye, and pointed at apex; stylets long and wide apart; antennae 7-segmented, VII and VIII usually joined with incomplete or complete suture, III with 2 sensoria, IV with 4; pronotum with 4 or 5 pairs of acute setae, sometimes anteroangular setae reduced; notopleural sutures incomplete or complete; basantra present, mesopraesternum reduced a small plate or absent; sternopleural sutures present; fore tarsal tooth present in both sexes; fore wings broad, usually without duplicated cilia; pelta irregular, usually eroded at posterior margin medially; tergites II–VII with 1 pair of wing-retaining setae; tube usually with sides convex, maximum width more than twice apical width; anal setae much shorter than tube.

Key to Acallurothrips species from China

1	Tube longer, more than 1.3 times as long as the widest part (Fig. 4)2
_	Tube broad, about as long as the widest part (Figs 5, 6)
2	Pronotal notopleural sutures incomplete (Fig. 1); accessory setae S2 on ab-
	dominal tergite IX well-developed hanatanii
_	Pronotal notopleural sutures complete; accessory setae S2 on abdominal ter-
	gite IX minute (Fig. 4)nonakai
3	Accessory setae S2 on abdominal tergite IX minute; postocular setae about as
	long as eyes (Fig. 3) casuarinae
_	Accessory setae S2 on abdominal tergite IX well-developed (Fig. 5); postocu-
	lar setae much longer than eyes
4	Head broad, about 1.6 times as broad as long; postocular setae about 2.0
	times as long as eyestubullatus*
_	Head about 1.2 times as broad as long; postocular setae about 1.4 times as
	long as eyes (Fig. 2)



Figures 1–6. Acallurothrips spp. 1–3 Head & pronotum: 1 hanatanii 2 hagai 3 casuarinae 4–6 Abdominal tergites IX–X: 4 nonakai 5 hagai 6 casuarinae.

Allothrips Hood

http://species-id.net/wiki/Allothrips

Remarks. There are 24 species listed in this genus, of which three are recorded in China: *bicolor* from Hainan (Han 1997), *discolor* and *taiwanus* from Taiwan (Chen

1982, Okajima 1987). Species of this genus are usually wingless, and are distinguish from other Idolothripinae by the unusually large terminal sensorium on the maxillary palp (Fig. 45), and the 7-segmented antennae.

Diagnosis. Head slightly longer than broad; dorsum of head usually with 3 or 4 pairs of well developed capitate setae; maxillary palp terminal sensorium stout, stylets long and wide apart; antennae 7-segmented, morphological VII and VIII completely fused, III with 2 sensoria, IV with 2; pronotal major setae usually expanded, notopleural sutures incomplete or complete; basantra present, mesopraesternum reduced; sternopleural sutures present; fore tarsal tooth usually absent in female, present in male; usually aptera; pelta broad, with obviously lateral lobes; tube straight sided, usually shorter than head; anal setae usually slightly longer than tube.

Key to Allothrips species from China

1	Dorsal surface of body fully reticulated	taiwanus*
_	Dorsal surface of body smooth or simply sculptured	2
2	Postocular cheek setae small, much shorter than postoculars	discolor*
_	Postocular cheek setae well developed, length more than 0.5	of postocular
	setae, with apex expanded	bicolor

Bactrothrips Karny

http://species-id.net/wiki/Bactrothrips

Remarks. Currently there are 53 species listed in this genus, of which seven have been recorded from China: *brevitubus, elongatus, flectoventris, furvescrus, honoris, pictipes* and *quadrituberculatus*. Dang and Qiao (2012a) provided an identification key to these seven species, based on morphological and DNA barcoding data. The genus *Bactro-thrips* is closely related to *Megathrips*, and differs from *Megalothrips* in usually having shorter maxillary stylets.

Diagnosis. Head much longer than width across eyes, usually prolonged in front of eyes; eyes usually equally developed ventrally and dorsally, sometimes obviously prolonged on ventral surface (*B. flectoventris*); dorsum of head usually with 4 pairs of well-developed setae; stylets short and far apart, or long and close together; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotum usually with 5 pairs of well-developed major setae, sometimes epimeral accessory setae also well-developed, notopleural sutures incomplete or complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings usually fully developed with numerous duplicated cilia, sometimes apterous; fore tarsal tooth absent in both sexes; pelta broad, with two lobes; abdominal tergites II–VII each with 2 pairs of sigmoid wing-retaining setae; tergites V–VIII of male with or without lateral tubercles; tube surface with numerous fine setae; anal setae much shorter than tube.

Bolothrips Priesner

http://species-id.net/wiki/Bolothrips

Remarks. There are 17 species listed in this genus, although none have previously been recorded from China. However, specimens from Northern China representing two unidentified species of this genus are available in NZMC.

Diagnosis. Head usually longer than wide, projecting in front of eyes; eyes strongly prolonged ventrally; postocular setae well-developed; stylets V-shaped; antennae 8-segmented, segment III with 2 or 1 sensoria, IV with 3 or 2; pronotal major setae pointed or blunt, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings, if present, with numerous duplicated cilia; fore tarsal tooth present in male; pelta broad, rounded triangular; abdominal tergites II–VII each with 1 pair of sigmoid wing-retaining setae in macroptera; tube surface smooth, without prominent setae; anal setae about as long as tube.

Compsothrips Reuter

http://species-id.net/wiki/Compsothrips

Remarks. There are 27 species listed in this genus, of which three are recorded from China: *reticulates, sinensis* and *tenebronus* (Guo and Feng 2006, Pelikan 1961, Han and Cui 1991). Dang et al. (2013) transferred *Ophthalmothrips tenebronus* Han & Cui to *Compsothrips* as a new combination, and also placed *Cryptothrips furvus* Reyes from Philippines as a new synonym of that species. Pelikan (1961) described *C. sinensis* from Guangdong, China based on a single female specimen, and indicated that the holotype was deposited in NZMC, Institute of Zoology, Chinese Academy of Sciences. However, that specimen has not been found in NZMC, nor is it in the Pelikan collection in Slovakia, and it is possibly lost. From the original description, *sinensis* cannot be distinguished with *tenebronus*, and they may represent the same species, so *sinensis* is here excluded from the key below.

Diagnosis. Head much longer than wide, projecting in front of eyes; eyes strongly prolonged ventrally; postocular setae well-developed, one pair of ocellar setae developed; stylets V-shaped; antennae 8-segmented, segment III with 2 or 1 sensoria, IV with 2, sensoria small; pronotal major setae expanded, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures complete; usually apterous; fore tarsal tooth present in both sexes; pelta broad, round-ed triangular; abdominal tergites usually without sigmoid wing-retaining setae; tube surface smooth, without prominent setae; anal setae shorter or a little longer than tube.

Key to Compsothrips species from China

1	Antennal segment III wi	th one sensorium	reticulates*
_	Antennal segment III wi	th two sensoria	tenebronus

Cryptothrips Uzel

http://species-id.net/wiki/Cryptothrips

Remarks. There are 12 species listed in this genus, of which only one, *C. nigripes*, is known from China, this Palaearctic species having been recorded from Inner Mongolia by Dang et al. (2013). Also *C. sauteri* was described from Taiwan, but judging from the original description it was based on a single specimen that lacks antennae. This species cannot be recognized, and even its generic relationship remains unknown. The original specimen is not in the Senckenberg Museum, Frankfurt, where so many of Karny's specimens are deposited, and is probably lost. The references in Mirab-balou (2011) are simply bibliographic quotations.

Diagnosis. Head longer than wide; eyes equally developed ventrally and dorsally; postocular setae well-developed, ocellar setae usually small; stylets long and close together medially; antennae 8-segmented, segment III with 2 sensoria, IV with 3; pronotal major setae usually pointed or blunt, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures present; wings, if present, with duplicated cilia; fore tarsal tooth present in male, absent in female; pelta broad, with two slender lobes; abdominal tergites III–VI with 1 pair of sigmoid wing-retaining setae; tube surface smooth, without prominent setae; anal setae usually shorter than tube.

Dinothrips Bagnall

http://species-id.net/wiki/Dinothrips

Remarks. This genus comprises six Asian species, of which four are recorded from southern China, *hainanensis*, *juglandis*, *spinosus* and *sumatrensis*. Species of this genus can be recognised by the pelta divided into three separate parts, and the males with the mesothoracic spiracular area curiously expanded into a prominent process (Mound and Palmer 1983). Species differ in the shape of this process in males, but females cannot be identified to species with any certainty. The spiracular process of males varies with body size within *spinosus*, and the shape also varies in slide-mounted specimens due to cover-slip pressure. As a result, it seems likely that *hainanensis* is the same species as *spinosus*. Here, the key to three species of *Dinothrips* from China excludes *hainanensis*.

Diagnosis. Head much longer than wide, projecting slightly in front of eyes, cheeks with numbers of stout setae; eyes equally developed ventrally and dorsally; postocular setae well developed, interocellar setae usually developed; stylets V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotal major setae usually pointed or blunt, notopleural sutures complete; basantra present; mesothoracic spiracular area of male usually prolonged into prominent process; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings, if present, with duplicated cilia; fore tarsal tooth present in both sexes, a series tuber-

cles present on inner margin of fore tibiae in large males; pelta divided into one large median lobe, 2 small lateral lobes; abdominal tergites III–VI with 2 pairs of sigmoid wing-retaining setae; tube surface smooth, without prominent setae; anal setae usually shorter than tube.

Key to Dinothrips species from China

1	Antennal segment III largely yellow with brown apexjuglandis
_	Antennal segment III largely yellow but brown at apex and base2
2	Antennal segment III short, about 3 times as long as apical brown part
	sumatrensis
_	Antennal segment III elongate, more than 4 times as long as apical brown
	partspinosus

Elaphrothrips Buffa

http://species-id.net/wiki/Elaphrothrips

Remarks. Species of this genus can be found in all tropical countries, and 141 species are currently listed, with eight recorded from China: *denticollis, jacobsoni, greeni, spiniceps, fulmeki, insignis, malayensis* and *procer*. The last four are here newly recorded from China, but there are also several undescribed species represented in NZMC. The species *denticollis* is widespread in Southern China, and shares most characters with *malayensis*, especially fore tarsi elongate. There is no satisfactory differentiation between these two species, although Palmer and Mound (1978) distinguished *denticollis* from *malayensis* by antennal segments IV–V being uniformly brown or with the basal stem light brown. This is difficult to assess in many specimens that have been slightly bleached. There is a similar problem with *fulmeki* and *malayensis* that are distinguished only by antennal segment VI with the basal 1/5 brown or pale. Currently, the identification of some *Elaphrothrips* species is not satisfactory.

Diagnosis. Head much longer than wide, projecting in front of eyes, cheeks usually with numbers of stout setae; eyes equally developed ventrally and dorsally, or a little prolonged ventrally; postocular setae well-developed, interocellar setae well developed, and one pair of median dorsal setae usually developed; stylets short and V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotal major developed setae usually pointed or blunt, notopleural sutures complete or nearly complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings, if present, with duplicated cilia; fore tarsal tooth present in male, absent in female, fore femur of large males usually with sickle-shaped seta on external apical margin; pelta broad, two lateral lobes broadly joined with middle one; abdominal tergites III–VI with 2 pairs of sigmoid wing-retaining setae; tube surface smooth, without prominent setae; anal setae usually shorter than tube.

Key to Elaphrothrips species from China

1	Head with cheek setae dark2
_	Head with cheek setae yellow or pale
2	Head only slightly produced in front of eyes, length about 1/8 as long as
	width; inner margin of male fore femora with tubercles (Fig. 37); pelta broad-
	ly joined to lateral wings (Fig. 29)insignis
_	Head strongly produced in front of eyes, length about 1/2 as long as width;
	inner margin of fore femora without tubercles in both sexes; pelta narrowly
	jointed to lateral wings or separatedjacobsoni*
3	Head process in front of eyes short, width 3-5 times its length; tibiae uni-
	formly dark brown
_	Head process in front of eyes long, width 1-3 times its length; tibiae some-
	times pale in the apical half5
4	Head produced process very short, width about 5 times as long as length (Fig.
	22); antennal segment III stout and short, about twice as long as apical brown
	part; pelta narrowly jointed with lateral wings, joint slenderspiniceps
_	Head produced process short, width about 3 times as long as length; antennal
	segment III more than 4 times as long as apical brown part; pelta narrowly
	jointed with lateral wings, joint short (Fig. 30)procer
5	Tibiae largely yellow, with sub-basal 1/3 brown (head produced process
	about as long as width) (Fig. 23)greeni
_	Mid tibiae uniformly brown at least
6	Antennal segments IV-V uniformly brown, sometimes a little shallow at base;
	fore tarsal elongate, about 3 times as long as width (Fig. 38) denticollis
_	Antennal segments IV-V brown with basal pedial pale; fore tarsal various 7
7	Antennal segment III longer than IV; VI brown with basal 1/5 yellow
	(Fig. 32) <i>fulmeki</i>
-	Antennal segment III as long as IV; VI uniform brown malayensis

Ethirothrips Karny

http://species-id.net/wiki/Ethirothrips

Remarks. This genus currently comprises 37 species, of which eight are recorded from China: *brevis, indicus, obscurus, chui* and *virgulae* from Taiwan, *longisetis* and *vitreipennis* from Hainan, and *stenomelas* from Guangdong and Hainan. However, *virgulae* is here newly recorded from mainland China at Guangxi. In this study, type-specimens of two species of Chen (Taiwan Agricultural Research Institute, Taichung) were checked, but unfortunately they are so poor that most characters could not be studied.

Diagnosis. Head usually longer than width across eyes; eyes small, equally developed ventrally and dorsally; postocular setae well-developed; stylets long, V-shaped or sub-parallel; antennae 8-segmented, segment III with 2 sensoria, IV 4; pronotal major setae pointed or blunt, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings, if present, with numerous duplicated cilia; fore tarsal tooth present in male; pelta broad, with two broad lateral lobes; abdominal tergites II–VII each with 1 pair of sigmoid wingretaining setae in macroptera; tube surface smooth, without prominent setae; anal setae shorter than tube.

Key to Ethirothrips species from China

1	Antennal segment IV with five sensoriastenomelas
_	Antennal segment IV with four sensoria2
2	Postocellar setae elongate, longer than diameter of posterior ocelli (Figs 7, 8) 3
_	Postocellar setae reduced, much shorter than diameter of posterior ocelli (Fig. 9)
3	Antennal segments IV–VIII uniformly brown, at least IV darker than III; ab- dominal segment IX with posteromarginal setae shorter than tube (Fig. 11) <i>indicus</i>
-	Antennal segment IV as yellow as III, V–VIII brown; abdominal segment IX with posteromarginal setae longer than tube (Fig. 12)
4	Major setae blunt at apex
_	Major setae acute at apex
5	Metanotum without campaniform sensillachui
_	Metanotum with pair of campaniform sensilla (Fig. 10) brevis
6	Major setae well developed, postocular setae about 230 micronslongisetis*
_	Major setae relatively shorter, postocular setae about 100 microns7
7	Body uniformly brown to dark brownvirgulae
_	Body bicolored, largely yellow except brown tubevitreipennis

Gastrothrips Hood

http://species-id.net/wiki/Gastrothrips

Remarks. There are 38 species listed in this genus, of which five are recorded from China: *fuscatus, fulviceps, mongolicus, eurypelta*, also *monticola* that was described from Japan by Okajima (2006) but is here newly recorded from Inner Mongolia, China. One species, *fulviceps*, was described by Hood (1937) from Peru with the head and antennae colored distinctively, and this species was recorded from Taiwan by Kudo (1974) as *Nesothrips fulviceps* (Hood). *G. mongolicus* which was described by Pelikan (1965) based on two females, was first recorded from China by Cao et al. (2009) together with a new species *eurypelta*. However, Cao et al. (2009) indicated in a key that the postocular setae of *mongolicus* are pointed at the apex, and was the only difference given from *eurypelta*. However, the description of *mongolicus* stated



Figures 7–12. *Ethirothrips* spp. 7–9 Head, pronotum & foreleg: 7 *indicus* 8 *obscurus* 9 *vitreipennis* Mesonotum & metanotum: 10 *brevis* 11–12 Female abdominal tergites IX–X: 11 *indicus* 12 *obscurus*.

that these setae are blunt, also the pronotal major setae. Furthermore, although the description of *eurypelta* did not mention the ventral shape of the eyes, the illustration indicated the eyes are slightly prolonged ventrally, as is illustrated for *mongolicus* by

Okajima (2006). Thus *eurypelta* is probably a synonym of *mongolicus*, and is excluded from the key below.

Diagnosis. Head usually as long as broad, or a little longer; eyes normal, usually equally developed ventrally and dorsally; postocular setae well-developed; stylets usually V-shaped; antennae 8-segmented, segment III with 1 or 2 sensoria, IV with 3; pronotal major setae pointed or blunt, notopleural sutures complete or incomplete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures present; wings, if present, with or without numerous duplicated cilia; fore tarsal tooth present in male; pelta triangular, or with two broad lateral lobes; abdominal tergites II–VII each with 1 pair of sigmoid wing-retaining setae in macroptera; tube surface smooth, without prominent setae; anal setae shorter than tube.

Key to Gastrothrips species from China

1	Antennal segment III with one sensorium
_	Antennal segment III with two sensoria
2	Head uniformly brown, concolorous with thorax; antennal segments uni-
	form brown, concolorous with head, except III yellow; postoculars and pro-
	notal major setae nobbed at apex <i>fuscatus</i> *
_	Head bicolored, the front yellow, sides and basal part brown; antennal seg-
	ments I-VI largely golden yellow; postoculars and pronotal major setae
	pointed at apex <i>fulviceps</i> *
3	Postoculars and pronotal major setae pointed at apexmonticola
_	Postoculars and pronotal major setae blunt at apexmongolicus

Holurothrips Bagnall

http://species-id.net/wiki/Holurothrips

Remarks. There are four species listed in this genus. Only *morikawai* is recorded from China, and this species is here newly recorded from Taiwan.

Diagnosis. Head much longer than broad, with elongate projection in front of eyes; eyes obviously prolonged ventrally; 2 pairs of postoculars, 2 pairs of interocellars and 1 pair of postocellars well developed; cheeks with 1 pair of stout setae; stylets V- or U-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 2 or 4; pronotal with 5 pairs of major developed setae, anteroangulars close to midlaterals, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings, if well developed, with duplicated cilia; fore tarsal tooth absent in both sexes, femur with a few stout setae; pelta wide, with two broad lobes; abdominal tergites II–VII each with 2 or 3 pairs of sigmoid wing-retaining setae; tube elongate, with prominent lateral setae; anal setae much shorter than tube.

http://species-id.net/wiki/Machatothrips

Remarks. Of the 14 species included in this genus, three are recorded from China: *antennatus, artocarpi* and *celosia*. Several specimens of *antennatus* and *artocarpi* have been studied in ANIC, and these were identified from the types. The third species, *celosia*, was described from Taiwan and is added to the key below based on the key to 14 species by Palmer and Mound (1978).

Diagnosis. Head much longer than broad; eyes normal; 1 pair of postoculars welldeveloped, also 1 pair of interocellars and 1 pair of vertex setae; stylets V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotum usually with 5 pairs of major setae, notopleural sutures complete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; fore wings with duplicated cilia; fore tarsal tooth present in both sexes; females with fore femur bearing a row of tubercles on inner margin; pelta broadly triangular; abdominal tergites II–VII each with 1 pair of sigmoid wing-retaining setae; tube longer than head, without prominent lateral setae; anal setae shorter than tube.

Key to Machatothrips species from China

- 1 Pronotal anteromarginal setae longer than anteroangulars......*celosia**

- rior margin without setae except anteromarginal setae (Fig. 21); pronotal anter fore femora with 4–6 stout teeth in different size in female (Fig. 35)....*artocarpi*

Mecynothrips Bagnall

http://species-id.net/wiki/Mecynothrips

Remarks. The 14 species included in this genus involve some of the largest Thysanoptera, and in the proventriculus of adults there is a prominent basket-like structure that is probably involved in crushing the fungus spores on which these species feed (Tree et al. 2010). A similar structure also occurs in species of *Elaphrothrips*. Four species are recorded from China: *kanoi*, *pugilator*, *simplex* and *taiwanus*, of which *simplex* is here newly recorded from China based on four females and eight males from Yunnan and Hainan Provinces. Okajima (1979) described *taiwanus* from Taiwan, and this can be distinguished from *pugilator* by having a longer preocular projection from base of



Figures 13–19. 13–17 Idolothripinae head: 13 Holurothrips 14 Bactrothrips 15 Elaphrothrips 16 Meiothrips 17 Ophthalmothrips 18 Mecynothrips simplex, head & pronotum 19 Mecynothrips pugilator, head, pronotum & foreleg.

antennal segment I to anterior margin of eyes about 1.5 times as long as wide, whereas in *pugilator* this is about as long as wide. The species *kanoi* was described from Taiwan, but the depositary of the syntypes is unknown, and no useful characters can be taken from the simple original description. Therefore, *kanoi* is excluded in the following key to Chinese species of *Mecynothrips*.

Diagnosis. Head much longer than broad, with prominent projection in front of eyes; eyes normal; 2 pairs of postoculars developed, also 1 pair of anterocellars well-developed, and 1 pair of postocellars; stylets short, V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotal major setae pointed or blunt, notopleural sutures usually complete, often incomplete; basantra present; mesopraesternum devel-

19



Figures 20–23. 20–21 Machatothrips, head & pronotum: 20 antennatus 21 artocarpi 22–23 Elaphrothrips, head, pronotum & foreleg: 22 spiniceps 23 greeni.

oped; metathoracic sternopleural sutures absent; fore wings with duplicated cilia; fore tarsal tooth present in male, absent in female, fore tibiae sometimes with seta-bearing apical tubercle in male, fore femur with a tumor or tubercles on inner margin in large

male; pelta broad, with two prominent lateral lobes; abdominal tergites II–VII each with 2 or 3 pairs of sigmoid wing-retaining setae; tube smooth, without prominent lateral setae; anal setae shorter than tube.

Key to Mecynothrips species from China

1	Pronotal epimeral accessory setae well-developed, as long as epimeral setae
	(Fig. 18); two pairs of postocular setae developed, as long as or longer than
	interocellar setae (Fig. 18)simplex
_	Pronotal epimeral accessory setae minute (Fig. 19); two pairs of postocular
	setae minute, much shorter than interocellar setae (Fig. 19)2
2	Preocular projection shorter, about as long as wide (Fig. 19) pugilator
_	Preocular projection longer, about 1.5 times as long as wide taiwanus*

Megalothrips Uzel

http://species-id.net/wiki/Megalothrips

Remarks. Of the eight species included in this genus, only *roundus* is recorded from China. The significance of four genera in the subtribe Idolothripina, *Bactrothrips, Megalothrips, Megathrips, and Meiothrips,* remains problematic (Dang and Qiao 2012a), and further studies are needed on the inter-relationships between the Holarctic and tropical faunas. The species of *Megalothrips* are identified by their remarkably elongate stylets which are close together medially, but they share other character states with *Bactrothrips* and *Megathrips* species.

Diagnosis. Head much longer than broad, without prominent projection in front of eyes; eyes small; 1 pair of postoculars short, 1 pair of interocellars well-developed, and 1 pair of vertex setae usually longer than postoculars; stylets elongate, reaching eyes and close together; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotal setae vary, anteroangulars close to midlaterals, notopleural sutures reduced; basantra present; mesopraesternum developed; metathoracic sternopleural sutures absent; fore wings with duplicated cilia; fore tarsal tooth absent in both sexes; pelta hat-shaped, with two slender lateral lobes narrowly fused; abdominal tergites II–VII each with 2 pairs of sigmoid wing-retaining setae; tergite VI with a pair of tubercles laterally in male; tube with prominent lateral setae; anal setae shorter than tube.

Megathrips Targioni-Tozzetti

http://species-id.net/wiki/Megathrips

Remarks. There are seven species listed in this genus, of which two, *lativentris* and *antennatus*, are recorded from northern China. The original description of *antennatus*



Figures 24–31. Idolothripinae Pelta: 24 Bactrothrips sp 25–26 Megathrips lativentris 27 Nesothrips brevicollis 28 Nesothrips peltatus 29 Elaphrothrips insignis 30 Elaphrothrips procer 31 Dinothrips sp.

states that it differs in having the pelta divided into three parts in contrast to the European species *lativentris* that has the two lobes narrowly joined to the median one (Figs 25, 26). However, we studied the types of *antennatus*, and in one paratype the left lobe of the pelta is separated from median one but the right lobe is narrowly joined to the median one. Furthermore, a female and a male from England studied in ANIC show that the lateral lobes of pelta slightly joined to the median one, or close to separate (Fig. 47). As a result, *Megathrips antennatus* Guo, Feng & Duan (2005) is here considered to be a new synonym of *Megathrips lativentris* (Heeger). Mound and Palmer (1983) indicated that *Megathrips* could be distinguished from *Bactrothrips* only by the slightly larger head and more deeply retracted stylets. However, in China, *Megathrips* and *Bactrothrips* species are similar in having the stylets short and V-shaped, but the lateral lobes of the pelta are broadly fused to the median lobe in *Bactrothrips* species whereas these lateral lobes are separate or narrowly joined in *Megathrips* species (Dang and Qiao 2012a).

Diagnosis. Head usually longer than width across eyes, slightly prolonged in front of eyes; eyes normal; interocellar, postocellar, postocular and mid-dorsal setae usually well-developed; stylets far apart; antennae 8-segmented, segment III shorter than head

width across eyes, segment III with 2 sensoria, IV with 4; pronotal major setae usually well developed, anteroangulars close to midlaterals, notopleural sutures incomplete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings usually fully developed with numerous duplicated cilia; fore tarsal tooth absent in both sexes; pelta always broad, lateral lobes narrowly joined to median major lobe, or separated; abdominal tergites II–VII each with 2 pairs of sigmoid wingretaining setae in macroptera; tergite VI with a pair of long lateral tubercles in male, tubercles on VIII small; tube usually shorter than head, with numerous lateral setae; anal setae shorter than tube.

Meiothrips Priesner

http://species-id.net/wiki/Meiothrips

Remarks. Dang and Qiao (2012b) provided a key to the five known species of *Meio-thrips*, of which three are recorded from China: *fuscicrus, menoni* and *nepalensis*. Moreover, *Meiothrips baishanzuensis* Duan & Li from Henan Province was synonymised with *Bactrothrips brevitubus* Takahashi by Dang and Qiao (2012a).

Diagnosis. Head much longer than width across eyes, prolonged in front of eyes, usually shorter than broad except in one species (*M. kurosawai*) about twice as long as broad; eyes normal or clearly prolonged on ventral surface; interocellar, postocellar, postocular, mid-dorsal and posterior-dorsal setae usually well-developed, sometimes small; stylets short and far apart; antennae 8-segmented, very slender, segment III usually more than twice head width across eyes, segment III with 2 sensoria, IV with 4; pronotal major setae usually well developed, sometimes as small and epimeral accessory setae always minute, notopleural sutures incomplete; basantra present; mesopraesternum boat-shaped; metathoracic sternopleural sutures absent; wings usually fully developed with or without numerous duplicated cilia; fore tarsal tooth absent in both sexes, femora with several spine-setae; pelta always broad, lateral lobes broadly joined to median lobe; abdominal tergites II–VII each with 2 pairs of sigmoid wing-retaining setae; male tergites V–VIII without lateral tubercles; tube much longer than head, with numerous lateral setae, sometimes with 2 rows of stout tubercles and many large and small tubercles or denticles on dorsal surface; anal setae much shorter than tube.

Nesothrips Kirkaldy

http://species-id.net/wiki/Nesothrips

Remarks. There are 28 species listed in this genus, of which three are recorded from China: *brevicollis, lativentris* and *peltatus*. A further species, *atropoda* Duan et al. (1998) from Henan Province, was treated by Dang et al. (2013) as a synonym of the wide-spread Asian species *brevicollis*.



Figures 32–39. 32–33 Elaphrothrips fulmeki: 32 antennae 33 mid-leg 34–35 Machatothrips foreleg: 34 antennatus 35 artocarpi 36 Dinothrips sumatrensis, male mesothoracic spiracular process 37 Elaphrothrips insignis, male foreleg 38 Elaphrothrips denticollis, male fore tarsi 39 Ophthalmothrips miscanthicola, female fore tarsal tooth.



Figures 40–46. Idolothripinae genera. 40 *Gastrothrips*, head, pronotum & foreleg 41 *Bolothrips*, ventral view of head 42 *Phaulothrips*, head 43 *Megathrips*, head, pronotum & foreleg 44 *Cryptothrips*, head & pronotum 45 *Allothrips*, maxillary palps with stout terminal sensoria 46 *Gastrothrips*, antennal segments III–VIII.

Diagnosis. Head various, usually wider than long; eyes normal, sometimes prolonged ventrally; 1 pair of postoculars well-developed, sometimes postocellar setae elongate; stylets V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 4; pronotal major setae pointed or slightly blunt, notopleural sutures complete; basantra present; mesopraesternum developed; metathoracic sternopleural sutures present; fore wings, if well developed, with duplicated cilia; fore tarsal tooth present in male, absent in female; pelta broadly hat-shaped; abdominal tergites II–VII each with 1 pair of sigmoid wing-retaining setae in macroptera; tube smooth without lateral setae; anal setae usually slightly shorter than tube.

Key to Nesothrips species from China

1	Head clearly longer than wide	lativentris
_	Head about as long as width	2
2	Pelta rectangle, without lateral wings (Fig. 28)	peltatus
_	Pelta median rounded, with slender lateral wings (Fig. 27)	brevicollis

Ophthalmothrips Hood

http://species-id.net/wiki/Ophthalmothrips

Remarks. Of the 11 species included in this genus, four are recorded from China: *formosanus, longiceps, miscanthicola* and *yunnanensis.* This last species was based on one female and three males, and the description indicates that it is unusual in having the tergal wing-retaining setae small and straight in macropterae (Cao et al. 2010). *O. formosanus* is here newly recorded from mainland China, in Henan Province.

Diagnosis. Head longer than broad, projecting in front of eyes; eyes distinctly prolonged ventrally; 1 pair of postoculars well developed, 1 pair of interocellar setae elongate; stylets short, V-shaped; antennae 8-segmented, segment III with 2 sensoria, IV with 2 or 4; pronotum usually with 4 pairs of major setae, anteromarginals short, notopleural sutures complete; basantra present; mesopraesternum developed; metathoracic sternopleural sutures absent; fore wings, if well developed, with duplicated cilia; fore tarsal tooth present or absent; pelta broadly triangular; abdominal tergites II–VII usually each with 2 pairs of sigmoid wing-retaining setae; tube smooth without lateral setae; anal setae various.

Key to Ophthalmothrips species from China

1	Abdominal segments with wing-retaining setae small and straight in macrop-
	tera yunnanensis*
_	Abdominal segments with wing-retaining setae well developed and sigmoi-
	dal2
2	Fore tarsal tooth present in both sexes (Fig. 39)miscanthicola
_	Fore tarsal tooth absent in both sexes
3	Postocular setae shorter than interocellar setae longiceps
_	Postocular setae longer than interocellar setae (Fig. 17) formosanus



Figures 47–54. Idolothripinae genera. 47 *Megathrips lativentris*, pelta 48 *Ethriothrips*, pelta 49 *Gastrothrips*, pelta 50 *Mecynothrips*, abdominal tergite IV 51 *Megathrips*, male abdominal tergites VI–X 52 *Ethirothrips*, abdominal tergites IV–V 53 *Compsothrips*, ventral view of thorax 54 *Meiothrips*, male abdominal tergites IX–X.

Phaulothrips Hood

http://species-id.net/wiki/Phaulothrips

Remarks. There are 20 species listed in the genus, of which 16 are known only from Australia. *P. solifer*, described from Taiwan, is the only member of the genus known from China. A paratype female and male on loan from Japan have been studied here.

Diagnosis. Head much longer than broad; eyes normal, sometimes prolonged dorsally; 1 pair of postoculars well developed, close together, anterocellar setae usually elongate; cheeks with 1 pair of stout setae just behind eye; stylets long, close together medially; antennae 8-segmented, segments III–IV each with 2 sensoria; pronotal major setae pointed or slightly blunt, notopleural sutures complete; basantra present; mesopraesternum developed; metathoracic sternopleural sutures present; fore wings, if well-developed, with duplicated cilia; fore tarsal tooth present in both sexes; pelta broad, with two slender lateral lobes; abdominal tergites II–VII each with 1 pair of sigmoid wing-retaining setae in macroptera; tube smooth without lateral setae; anal setae shorter than tube.

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RESEARCH ARTICLE



Review of the Parasa undulata (Cai, 1983) species group with the first conifer-feeding larva for Limacodidae and descriptions of two new species from China and Taiwan (Lepidoptera, Limacodidae)

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Abstract

Although the caterpillars are well-known for the stings and magnificent coloration, the systematics of Limacodidae is historically neglected and chaotic due to the difficulty in matching the larval with adult stages as well as the very conservative and convergent adult morphology. One of the biggest taxonomic problems surrounds a collective group from Southeastern Asia, termed the "green limacodid moths", which harbours at least 90 species placed in the genus *Parasa* Walker, 1859 and 14 "subunits". The *P. undulata* group was previously composed of 3 species from China and Taiwan, and characterized only by wing pattern. This species group is extensively studied herein with two new species described, i.e. *P. viridiflamma* **sp. n.** (Taiwan) and *P. minwangi* **sp. n.** (S. China), and discovery of female genitalia of three species, presenting new phylogenetic insights in this potentially paraphyletic genus. In addition, one limacodid larva was found to be feeding exclusively on *Picea* (Pinaceae) in Taiwan. Its identity, *Parasa pygmy* Solovyev, 2010 in *P. undulata* group, is confirmed through matching its COI sequence to the adult. This discovery is also biologically significant because the previous known host breadth of *Parasa* was of polyphagy on various angiosperm plant families. This case, therefore, represents the first record of conifer-feeding behavior in this family as well as

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the first of specialized herbivory in the genus. Meanwhile, the background match between *Picea* leaves and larval coloration is shared with other *Picea*-feeding insects. This phenomenon is worth of further investigation in the aspect of convergent evolution of crypsis associated with a particular plant.

Keywords

Conifer-feeder, Limacodidae, Parasa, new species, Picea, Pinaceae, Taiwan

Introduction

(1) Systematic problems surrounding the genus Parasa Moore, 1859 and its relatives.

The southeastern Asian limacodid moths comprise about 90 species of "green limacodids", that are green at least on some parts of wings and thorax (Holloway 1986; Solovyev 2011). These species were hitherto all embedded in the genera *Parasa* Moore, 1859 (based on a New World species, *chloris* Herrich-Schäffer, [1854]) and *Latoia* Guérin-Ménéville, 1844 (based on a Madagascan species, *albifrons* Guérin-Ménéville, 1844) according to interpretation of morphology, including known female and immature characters (Seitz 1913; van Eecke 1925; Inoue et al. 1982, 1992; Cai 1983; Wu and Fang 2009, 2010; Wu 2011). The taxonomic history of these groups has been detailed in several studies, i.e. Holloway (1986), Holloway et al. (1987) and Solovyev (2011) and the current generic name *Parasa* has been adopted and generally accepted for the Southeast Asian green limacodids since Holloway (1986).

Though a subgrouping of *Parasa* into 14 subunits was proposed by Solovyev and Witt (2009) and Solovyev (2010, 2011) based on the diversity of wing color patterns and differences in genitalia, the potential paraphyly of this genus indicated by Holloway (1986) has not yet been elucidated. This is mainly due to the conservative male genitalia, except in the *P. bicolor* species group, as well as limited taxon sampling of female and immature characters. Futhermore, the green pigmental appearance is not only present in *Parasa* and *Latoia*, but also in nine more genera according to Solovyev (2011). In addition, the presence of four black dorsal patches at the posterior marginal scoli of the larva seems to be a potential synapomorphy for *Parasa* (Holloway, 1986). The concatenation of morphological characters (Holloway 1986) and molecular data (Solovyev 2011) are expected to illuminate taxonomic problems surrounding the genus *Parasa*.

(2) Discovery of conifer-feeding habits with unique larval morphology and two additional new species in the *Parasa undulata* species group.

Recently, a single limacodid larva was discovered on the conifer tree Taiwan Spruce (*Picea morrisonicola* Hayata, 1908, Pinaceae), at mid-elevation (ca. 2600 m) of the central mountain range of Taiwan. This presents unusual ground maculation and an external appearance similar to the stomatal band of conifer leaves that is described and discussed in detail below.

Since this larva failed to pupate successfully after the prepupal stage in an indoor rearing environment, we sequenced its mitochondrial COI for comparison to that of two other limacodid moths. These two moths, *Parasa pygmy* Solovyev, 2010 and *P. martini* Solovyev, 2010, only occur in mid to high elevation montane regions of Taiwan. These data deposited in Genbank (KF595045, KF595046, KF595047) reveal zero divergence between the collected larva and the adult of *P. pygmy*, but ca. 6.3% p-distance divergence to *P. martini*, thus confirming the identity of the first known conifer-feeding limacodid (although not unique among zygaenoids, e.g. *Psycharium* Herrich-Schäffer, 1856, Somabrachyidae feeds on *Pinus*: Epstein et al. 1999). Accompanying our larval discovery, we also describe two additional montane species, *P. viridiflamma* sp. n. and *P. minwangi* sp. n. The above four moth species all belong to the *P. undulata* species group as defined by Solovyev (2010, 2011). In addition, the female genitalia have been regarded as including important characters to separate the genus *Parasa* and the Madagascan *Latoia*. In the present study, all females and the genitalia of Taiwanese species are described for the first time. These results provide new evidences to reassess the relationships between the species groups of *Parasa* or the so-called "green limacodids" globally.

Materials and methods

Specimen acquisition

The studied specimens were examined in or borrowed from the following institutions and private collections:

BMNH	The Natural History Museum, London
CCMF	Collection of Chien-Ming Fu, Taichung
CVAK	Collection of Valentin A. Kalinin, Moscow
ESRI	Taiwan Endemic Species Research Institute, Nantou
NMNS	National Museum of Natural Science, Taichung
NSMT	National Museum of Nature and Science, Tsukuba
SCAU	Entomological Department, South China Agricultural University, Guangzhou
TFRI	Insect collection of Taiwan Forestry Research Institute, Taipei

Genitalia preparations for morphological studies

Genitalia were prepared following the general method described e.g. by Holloway et al. (1987) with slight modification. After maceration of the abdomen in 10% KOH and subsequent cleaning, male genitalia were carefully removed from the abdomen and abdominal segments 1–8 were opened along the caudocephalic axis from the right side. Female genitalia were removed entirely from the abdomen, cleaned and mounted with the ventral side uppermost. All the chitinuous genital tubes, including bursae, derived from the genital openings were preserved. Genitalia and abdominal skins of both sexes

were stained with pen ink (Pilot), preserved in 70% ethanol then transferred in 99.5% ethanol before mounting in Euparal on slides. Specimens were photographed using a Nikon D300 digital camera.

Terminology

The terminology of wing patterns and genital structures follows that of Solovyev (2011), that of immature morphology follows Epstein (1996).

Molecular analysis

Genomic DNA was extracted from fragments of adult legs and part of larval tissues using an ALS Tissue Genomic DNA Extraction Kit (Kaohsiung, Taiwan). A partial COI sequence was amplified by a polymerase chain reaction (PCR) with a set of universal primers (LCO1490 and HC02198) (Folmer et al. 1994). The PCR was initiated at 95°XC for 5 min, followed by 35 cycles at 95°C for 1 min, 40°C for 1 min, and 72°XC for 1 min, with a final extension at 72°XC for 7 min. The PCR products were separated by electrophoresis in 1.5% agarose gels and sequenced. The 636 nucleotide base pairs of high quality COI sequences were aligned using CLUSTALX 2.0.10 (Thompson et al. 1997). Pairwise genetic distances were calculated using MEGA 4.0.2 (Tamura et al. 2007). Three newly sequenced COI data were deposited in the GenBank database (numbers mentioned above) (http://www.ncbi.nlm.nih.gov/genbank/). The voucher specimens were preserved in the Insect collection of Taiwan Forestry Research Institute, Taipei, Taiwan.

Systematics

Parasa undulata species group

- P. viridiflamma sp. n. (Taiwan)
- P. undulata (Cai, 1983) (central and southern China)
- P. pygmy Solovyev, 2010 (Taiwan)
- P. minwangi sp. n. (S. China)
- P. martini Solovyev, 2010 (Taiwan)

The definition and diagnosis of the *Parasa undulata* species group given in Solovyev (2010, 2011) regarded the median green patch as a likely apomorphic character. Here we re-define this group by following characters:

 Forewing with median green patch surrounded by two white longitudinal stripes, i.e. a short basal stripe and another long one along outer margin of the patch (see Figs 1–9). Notes. The combined pattern of forewings of the resting moths is similar to the needle leaves and stomatal band of several conifer genera, e.g. *Pinus, Tsuga* and *Abies* (Pinaceae), thus revealing a potentially adult adaptation to such a resting environment (see Figs 26, 27).

- Corpus bursae with only one transverse signum (see Figs 20–25), rather than two in other species groups of the genus *Parasa*.
- Mature larva, at least that of *Parasa pygmy*, with green ground coloration, white longitudinal stripes and without dorsal abdominal scolus structures. See description part of immature stage of *P. pygmy* in detail.

Key to the species of Parasa undulata species group

1	Forewing green patch wide, extended over approximately half of discal area2
_	Forewing green patch narrow, covering less than half of discal area; a pale
	ochreous stripe arising between vein R3 and R44
2	Outer margin of green patch distinctly sinuous
_	Outer margin of green patch smoothly curved P. undulata
3	Outer margin of green patch deeply incised between cubitals and anal vein
_	Outer margin of green patch slightly incised between cubitals and anal vein
4	Forewing white stripes wide, terminal and anal areas of forewing with wider
	ochreous band; anal field of hindwing ochreous
_	Forewing stripes slender, terminal and anal areas of forewing with narrower
	ochreous band; anal field of hindwing brown, without ochreous coloration

Parasa viridiflamma sp. n.

http://zoobank.org/0F20787E-FA13-480F-87C4-9DBC99F06263 http://species-id.net/wiki/Parasa_viridiflamma Figs 1–3, 10, 11, 20, 21

Type material. Holotype: ♂, TAIWAN, Hualien County, Tayuling, 2550 m, 25-VI-2008, leg. H. H. Lin (coll. ESRI); paratypes: 3♂, Taichung County, Tashuehshan Mts., Anmashan, 2230 m, 14-16.VI.1989, leg. M. Owada; 1♂, same collecting data, slide NSMT-SW131; 1♀, Taichung County, Anmashan, 2300 m, 30-VII-1997, leg. T. Mano, slide NSMT-SW132 (coll. NSMT); 1♂, Taichung County, Anmashan, 2600 m, 23-V-1998, leg. C. M. Fu; 1♂, Taitung County, Yenping, 31-VII-1992, leg. Shiau & Yang (coll. NMNS); 1♂, Nantou County, Renluen, 1400 m, 21-VIII-1991, leg. Y. B. Fan, slide TFRI00061358; 1♂, Nantou County, Tatajia, 2610 m, 6-VII-2011, leg. S. Wu & W. C. Chang (coll. TFRI).



Figures 1–9. Dorsal views of *Parasa* spp. from China and Taiwan. 1 *P. viridiflamma* sp. n., male, paratype, Taiwan 2 *ditto*, male, paratype, Taiwan 3 *ditto*, female, paratype, Taiwan 4 *P. undulata* (Cai, 1983), male, Guangxi Province, S. China 5 *P. pygmy* Solovyev, 2010, male, Taiwan 6 *ditto*, female, Taiwan 7 *P. minwangi* sp. n., male, holotype, Guangdong Province, S. China 8 *P. martini* Solovyev, 2010, male, Taiwan 9 *ditto*, female, Taiwan. Bar scale= 10 mm. Specimens by courtesy of: NSMT (1–3, 8); CVAK (4); TFRI (5, 9); ESRI (6); SCAU (7). Photo by Shipher Wu (1–3, 5–9); Alexey Solovyev (4).

Diagnosis. The new species is externally similar to *P. undulata* from central and southern China and *P. pygmy* from Taiwan but it can be easily distinguished by the forewing green patch strongly incised between cubitals and anal veins. In the male genitalia the basal part of aedeagus (coecum) is long, strongly extending toward ventral side in *P. viridiflamma*. Females of all three Taiwanese species of the *P. undulata* group are recorded in the present study, they can be distinguished by the shape of the single signum, that of *P. viridiflamma* is short, irregular in shape, that of *P. pygmy* is saddle-shaped and that of *P. martini* is straight and long in transverse axis.

Description. Adult (Figs 1–3).

Measures. Wingspan 23-24 mm in male (n= 7); 26 mm in female (n= 1).

Head. Antennae bipectinate in male, rami longer at basal part and gradually shortening to absent at 5/6 from base; filiform in female. Eyes black, round. Frons, vertex, labial palpi fringed with long, chestnut hair-like scales, 3rd labial palpal segment short.

Thorax. Thoracic segments green with chestnut dorsal stripe. Forewing ground coloration chestnut with median large green patch delimited externally by white line which is in turn lined by brown border, all these pattern elements strongly incurved between cubitals and anal veins, less so towards termen; marginal scales ochreous. Hind wings chestnut, marginal scales ochreous.

Abdomen. Abdominal segments fringed with long chestnut hair-like scales.

Male genitalia (Figs 10, 11). Uncus robust, wide with hook-like apex. Gnathos. Gnathos large, sclerotized, apically narrowed; juxta plate-like with two lateral sides extending dorsally. Valva short, apex tongue-like. Aedeagus long, tubular, coecum strongly bent ventrally.

Female genitalia (Figs 20, 21). Apophyses elongated, length of anterior and posterior ones equal; ductus bursae long; corpus bursae small, about 3.5 times shorter than ductus bursae, signum small, irregular-shaped.

Distribution and bionomics. This species is endemic to Taiwan. The adults occur in May and mid June to late August in mid-elevation mountain areas (1400–2610 m). The fresh individuals appear earlier in the season. Possibly univoltine. Hostplant unknown.

Etymology. The new species is named through the combination of *viridis* (green) and *flamma* (flame), according to its flame-shaped green median patch on forewing.

Parasa pygmy Solovyev, 2010

http://species-id.net/wiki/Parasa_pygmy Figs 5, 6, 12, 13, 22, 23, 26–33

Parasa pygmy Solovyev, 2010, 89 (11): 1358, figs. 1, 5; 2, 5; Solovyev 2011, 91(1): 100, figs. 1, 5; 2, 5. (Type locality: Taiwan)

Material examined. TAIWAN, 2d, Chiai Hsien [Nantou County], Luhlin Lodge, [ca. 2600 m], 16-VIII-1990, leg. B. S. Chang (coll. NMNS); 33, Miaoli County, Guanwu, 2000 m, 27-IX-2010, S. Wu leg.; 13, Nantou County, Black Water Cottage, 2757 m, 7-IX-2012, S. Wu & W. C. Chang leg.; 1Å, Nantou County, Chen-gong Lodge, 2853 m, 10-IX-2012, leg. S. Wu & W. C. Chang; 73, Nantou County, Piluchi, 2000 m, 3-IX-1986, leg. Y. J. Chang; 4Å, same locality, 4-IX-1986, Y. J. Chang leg.; 18Å, same locality, 14-IX-1986, Y. J. Chang leg.; 5Å, same locality, 15-X-1987, Y. B. Fan (coll. TFRI); 1Å, Nantou County, Hohuanshan, 3006 m, 14-IX-2009, L. C. Shih leg., slide ESRI A12-20090914-037 (coll. ESRI); 13, Nantou County, Yuanfeng, 2700 m, 11-IX-2012, leg. S. Wu, slide TFRI00148804; 1Å, Nantou County, Xiaofengko, 3002 m, 13-VIII-2012, leg. S. Wu & W. C. Chang; 13, Ilan County, Jianchin, 1930 m, 8-X-2012, leg. S. Wu; 8, Hualien County, Guanyuan, 2400 m, 13-IX-2012, leg. S. Wu (coll. TFRI); 13 Hualien County, Kuanyan (=Guanyuan), 2370 m, 13-IX-2012, leg. M. Owada & S. Wu (coll. NSMT); 1 Mature larva, Hualien County, 820 Logging Trail, 2600 m, 26-V-2012, leg. S. Wu & W. C. Chang (coll. TFRI); 1♀, Hualien County, Jinma Tunnel, 2400 m, 23-IX-2009, leg. L. C. Shih, slide ESRI A09-20090923-127 (coll. ESRI); 1 2, Hualien County, Biluishenmu, 2150 m, 22-VIII-1991, leg. H. Y. Wang (coll. NMNS).

Diagnosis. This species represents the insular sister species of *P. undulata* from China. It can be easily distinguished from *P. undulata* by its broader forewing medial



Figures 10–19. Male genitalia of *Parasa* spp. from China and Taiwan. 10, 11 *P. viridiflamma* sp. n., holotype, Taiwan 12, 13 *P. pygmy* Solovyev, 2010, Taiwan 14, 15 *P. undulata* (Cai, 1983), Guangxi Province, S. China 16, 17 *P. minwangi* sp. n., holotype, Guangdong Province, S. China 18, 19 *P. martini* Solovyev, 2010, Taiwan 10, 12, 14, 16, 18 Male genital apparatus 11, 13, 15, 17, 19 Aedeagi. Bar scale= 1 mm. Specimens by courtesy of: ESRI (10, 11, 12, 13); CVAK (14, 15); SCAU (16, 17); TFRI (18, 19). Photo by Shipher Wu (10–13, 16–19); Alexey Solovyev (14, 15).

green patch and its longer coecum. The comparison of the female genitalia is given under the diagnosis of the preceding species.

Description. The female and mature larva are described for the first time.

Female (Fig. 6).

Measures. Wingspan 24–25 mm (n= 3).

Head. Antennae filiform. Eyes black, round. Frons, vertex, labial palpi fringed with long, chestnut hair-like scales, 3rd labial palpal segment short.

Thorax. Thoracic segments green with chestnut dorsal stripe. Forewing ground coloration chestnut with large median green patch delimited externally by thin white line which is in turn lined by brown border; marginal scales ochreous. Hind wings chestnut, marginal scales ochreous.

Abdomen. Abdominal segments fringed with long chestnut hair-like scales.
Female genitalia (Figs 22–23). Apophyses elongated, length of anterior and posterior ones equal; ductus bursae long; corpus bursae small, about 3.5 times shorter than ductus bursae, signum saddle-shaped in transverse axis.

Immature stages.

Mature instar (Figs 28–33). Body spindle-like, length 20 mm when fully extended. Legs very small, largely reduced. Prolegs fully absent; adhesive, sucker-like regions on abdomen present. Head and body ground coloration green; a pair of prominent conical dorsal scoli arising from the dorsal part of mesothorax and on the 9th abdominal segment, respectively, the remaining parts smooth. 10 fresh red spots, circled by light blue ring, arranged longitudinally along mid-dorsum; two cream yellow subdorsal lines running parallel adjacent to the red spots; dorso-lateral, lateral and ventro-lateral lines wide; regions between subdorsal and dorso-lateral lines pale green; small subdorsal scoli, arising from mesothorax, metathorax and abdominal segment A2 to A8, orange, along on lateral lines and reduced as small scobinate patches; spiracles orange.

COI sequence. Two new COI sequences (identical) from adult male and mature larva, respectively, were deposited in the GenBank database (KF595046, KF595047).

Distribution and bionomics. *P. pygmy* is endemic to Taiwan. The adults occur from mid August to early October in mid to high elevation mountains of central Taiwan (~2000–3000 m), where they match the distribution range of the presently known hostplant, *Picea morrisonicola* Hayata (Pinaceae). The single mature larva was taken in late May, the leaf flushing period of *P. morrisonicola*. This observation suggests a univoltine life cycle for *P. pygmy* and the overwintering stage is inferred to be the egg. The patterns of the adult and mature larva are similar to the needle leaves of Pinaceae, especially the hostplant species. This potential evolutionary adaptation is detailed in results and discussion.

Parasa undulata (Cai, 1983)

http://species-id.net/wiki/Parasa_undulata Figs 4, 14, 15

Latoia undulata Cai, 1983, 4 (26): 449, fig. 10. (Type locality: Dukou, Sichuan [China]) *Parasa undulata*: Solovyev 2010, 89 (11): 1358; Wu and Fang 2010: 43, pl. 18, fig. 1–36; Solovyev 2011: 100.

Material examined. CHINA, 1³, Guangxi Province, Dayao Shan Mts. Jingxiu, 100 km SE Liuzhou, 24°07'N, 110°14'E, 1700 m, VII-2008, leg. V. Siniaev (coll. CVAK).

Diagnosis. This species is closely related to *P. pygmy*, their comparison is given under the diagnosis of preceding species.

Distribution and bionomics. According to Wu and Fang (2010), this species is widely distributed in China (Henan, Anhui, Hubei, Sichuan, Yunnan, Shaanxi and Gansu). It is recorded in Guangxi Province for the first time. Hostplant unknown.



Figures 20–25. Female genitalia of *Parasa* spp. from Taiwan. 20, 21 *P. viridiflamma* sp. n., paratype 22–23 *P. pygmy* Solovyev, 2010 24–25 *P. martini* Solovyev, 2010 21, 23, 25 Magnified images of signa. Bar scale= 1 mm. Specimens by courtesy of: NSMT (20–21); ESRI (22–23); TFRI (24–25). Photo by Shipher Wu.

Parasa minwangi sp. n.

http://zoobank.org/F5D21EB2-EB61-42D4-953C-48F8478E2EB5 http://species-id.net/wiki/Parasa_minwangi Figs 7, 16, 17

Type material. Holotype: 3° , CHINA, Guangdong Prov., Shaoguan, Nanling, 700-1200 m, 22-25-IV-2005, leg. K. Horie, slide NSMT-SW133 (coll. SCAU); paratypes: 43° , Guangdong Prov., Shaoguan, Nanling, 600–1400 m, 11-18-V-2005 (coll. NSMT); 43° , same collecting data (coll. SCAU); 13° , same collecting locality, 21-28-VI-2008 (coll. NSMT); 23° , same collecting locality, 1-6-VIII-2006 (coll. NSMT); 13° , same collecting data (coll. SCAU); 1 male, same collecting locality, 31-VIII-1IX-2003 (coll. NSMT); 13° , same collecting data (coll. SCAU); 1 male, same collecting locality, 26-27-IX-2005, leg. M. Wang et al. (coll. NSMT); 1 male, same collecting data (coll. SCAU), all leg. Wang et al.

Diagnosis. This species is closely related to the allopatric species *P. martini* from Taiwan. Externally its forewing white stripes are more slender. In the male genitalia the aedeagus has a more slender coecum and bears a separated, sclerotized dorsal process at the apex, the latter structure being absent in other species of the same group.

Description. Adult (Fig. 7).

Measures. Wingspan 21–22 mm (n= 21).

Head. Antennae bipectinate in male, rami longer at basal part and gradually shortening to absent at 5/6 from base; filiform in female. Eyes black, round. Frons, vertex, labial palpi fringed with long, chestnut hair-like scales, 3rd labial palpal segment short.

Thorax. Thoracic segments green with chestnut dorsal stripe. Forewing ground coloration chestnut with ochreous stripe situated between vein R4 and R5 and a large median green patch delimited by slender white lines and subsequent wide brown border; marginal scales ochreous. Hind wings chestnut, marginal scales pale chestnut fringed with ochreous.

Abdomen. Abdominal segments fringed with long chestnut hair-like scales.

Male genitalia (Figs 16, 17). Uncus robust, wide with hook-like apex. Gnathos large, sclerotized, apically narrowed; juxta sclerotized with two lateral sides extending dorsally. Valva short, apex tongue-like. Aedeagus long in straight distal part and down-curved basal part, respectively, and with a distal sclerotized dorsal process.

Distribution and bionomics. This species is recorded only from mid-elevation (600–1400 m) of Nanling mountain areas, S. China. The adults occur in April, May, June, August and September. Possibly bivoltine. Hostplant unknown.

Etymology. This species is dedicated to Dr. Min Wang (SCAU), who represents the main collector of most of the type material of this new species in Nanling mountain areas, S. China.



Figures 26–33. Photos of alive *Parasa pygmy* Solovyev, 2010 in Taiwan. 26, 27.Adult male on *Abies kawakamii* (Pinaceae) 26 Lateral side 27 Dorsal side 28–33 Mature instar on hostplant, *Picea morrisonicola* (Pinaceae) 28 Resting posture on ventral side of hostplant 29 *ditto*, dorsal view, denoted by red arrow 30 Magnified image 31–33 Larva feeding on leaf. Photo by Shipher Wu.

Parasa martini Solovyev, 2010

http://species-id.net/wiki/Parasa_martini Figs 8, 9, 18, 19, 24, 25

Parasa martini Solovyev, 2010, 89(11): 1358, figs. 1, 6; 2, 6; Solovyev 2011, 91(1): 100, figs. 1, 6; 2, 6. (Type locality: Taiwan)

Material examined. Type material: Holotype. ♂, "TAIWAN, Taichung County., He-ping, Dayueshan National Forest Recreation Area, N24°15.315 E121°00.374, 28-V-2007, 2223 m, At MV light, leg. G. Martin & D.L.J. Quicke, BMNH (E) 2007-43","BMNH (E) # 820958","BMNH genital slide 1422" (coll. BMNH), paratypes: 2♂, same collecting data as holotype (coll. BMNH)

Other material: TAIWAN, 1, Miaoli County, Guanwu, 2000 m, 29-VI-2010, leg. S. Wu & W. C. Chang; 1, same collecting data, slide TFRI00143030 (coll. TFRI); 1, Taichung County, Anmashan, 2100 m, 19-VIII-1996, leg. C. M. Fu; 4, same collecting locality, 13-IX-1996, leg. C. M. Fu; 1, 1, same collecting locality, 200 m, 29-VII-1997, leg. C. M. Fu (CCMF); 1, same collecting locality, 2200 m, 29-VII-1997, leg. C. M. Fu; 1, Baxianshan, 1000 m, 26-VII-1997, leg. C. M. Fu (coll. CCMF); 3, 3, 1, Taichung County, Chingshan, 1400 m, 9-10-IX-1993, leg. W. T. Yang & M. L. Chan (coll. NMNS); 3, Taichung County, Wushihken, 950 m, 23-V-2012, leg. L. C. Shih (ESRI); 1, Nantou County, Piluchi, 2000 m, 12-VIII-1987, leg. Y. B. Fan, slide TFRI00061365; 1, Hualien County, Ci'en, 1950 m, 13-IX-2012, leg. S. Wu (coll. TFRI); 1, Hualien County, Cien, 2039 m, 20-VII-2009, leg. L. C. Shih (coll. ESRI); 1, Hualien County, Tsuen (=Ci'en), 2000 m, 13-IX-2012, leg. M. Owada & S. Wu (coll. NSMT).

Diagnosis. This species is the allopatric sister-species of *P. minwangi* sp. n. from southern China. Their comparison is given under the diagnosis of the preceding species.

Description. The female is described here for the first time.

Female (Fig. 9).

Measures. Wingspan 24–25 mm (n= 3).

Head. Antennae filiform. Eyes black, round. Frons, vertex, labial palpi fringed with long, chestnut hair-like scales, 3rd labial palpal segment short.

Thorax. Thoracic segments green with chestnut dorsal stripe.

Forewing ground coloration chestnut with ochreous stripe situated between vein R4 and R5 and one median longitudinal green patch delimited by white lines and subsequent wide brown border; marginal scales ochreous. Hind wings chestnut, anal margin and marginal scales ochreous.

Abdomen. Abdominal segments fringed with long chestnut hair-like scales.

Female genitalia (Figs 24, 25). Apophyses elongated, length of anterior and posterior ones equal; ductus bursae long; corpus bursae small, about 3.5 times shorter than ductus bursae, signum transverse, long with medial part more expanded.

COI sequence. A new COI sequence was deposited in the GenBank database (KF595045).

Distribution and bionomics. This species is endemic to Taiwan. The adults occur from late May to late June, mid and late July then mid August to mid September in mid-elevation mountain areas with primary vegetation (ca. 950–2223 m). Possibly bivoltine. Hostplant unknown.

Results

The present study reports on the first record of a conifer-feeding limacodid moth on the Taiwan Spruce (*Picea morrisonicola*) in Taiwan, describing the specialised morphology of the last larval instar. The larval identity is confirmed through COI sequence (636 bp) comparison between *P. martini* and *P. pygmy*. The sequences of adult and larval *P. pygmy* are identical but about 6.3% divergent to *P. martini*.

The conifer-feeder, *P. pygmy* (Taiwan), together with *P. undulata* (central and southern China), *P. martini* (Taiwan), and the newly described *P. viridiflamma* sp. n. and *P. minwangi* sp. n., form the *P. undulata* species group sensu Solovyev (2011). The female and genital structures of the Taiwanese species are firstly illustrated and described before discussing the phylogenetic affinity with congeneric species.

Discussion

Previously known Parasa larvae are mostly regarded as being polyphagous, often as agricultural pests on broad-leaved trees (Robinson et al. 2001, 2002) and possess the potentially synapomorphic character of four black dorsal scolus patches on their posterior margin (Holloway 1986). The presence of dorsal and dorsal-lateral scoli places them in the first limacodid group as defined by Solovyev and Witt (2009: 40). In the present study, the first record of a conifer-feeding limacodid moth, *P. pygmy*, together with description of the particular morphology of the mature instar is reported. This finding does not likely represent an occasional circumstance of a much broader host plant repertoire since external patterns of the adult and mature larva of *P. pygmy* are similar to the needle leaves of Pinaceae species, especially that of its hostplant Picea morrisonicola, revealing the tight specialization of the larva at least on Pinaceae. Conifer-feeding macrolepidopteran species in temperate regions that have larval patterns matching those of their hostplants were also reported and illustrated in several studies, e.g. the Japanese Sphinx caliginea (Butler, 1877) (Sphingidae) (Nakatomi 1987; Miyata 2011), Alsophiloides acroama (Inoue, [1944]) (Geometridae) (Nakajima 2011), the northern American Lithophane lemmeri (Barnes & Benjamin, 1929), Xestia badicollis (Grote, 1873) and Feralia comstocki (Grote, 1874) (Noctuidae) (Maier et al. 2011). This phenomenon is worth of further investigation in the aspect of convergent evolution of crypsis associated with a group of particular plants.

Additionally, the larval habits of *P. pygmy* are also interesting. The observed larva always moves and feeds on the ventral side of needle leaf and branches, thus, its patterns and behavior can be regarded as a case of countershaded crypsis on Pinaceae to prevent predation by high mountain birds (lizard species occur more rarely in this high altitude biotope of Taiwan). Although it is cryptic, the prominent red spots of the mid-dorsal line of the mature larva, in contrast to its green ground coloration, act as a potentially aposematic signal (a similar pattern occurs in some *Pinus* feeding Bombycoidea, such as *Lapara bombycoides* Walker, 1856, Sphingidae). The combination of visual crypsis and aposematism was reported in previous studies, e.g. Edmunds (1974), Rothschild (1975), Papageorgis (1975), Endler (1978); Ruxton et al. (2004); Tullberg et al. (2005) and Gamberale-Stille et al. (2009), and this kind of function can be modulated according to the distance between prey (signal) and predator (observer).

In addition to the descriptions of new species and the discovery of conifer-feeding larval habits, the female of three representatives of the *P. undulata* species group in Taiwan are reported for the first time. Their genitalia are different to those of other *Parasa* species groups by the presence of only one signum rather than two. The number of signa is hitherto regarded as a significant character state to distinguish a broad sense pantropical *Parasa* from Madagascan *Latoia*. The latter has no signum.

Though the known immature and female characters of the *Parasa undulata* species group show remarkable differences compared to the other *Parasa* species groups, the characters of wing venation and male genitalia are typical for the genus. Therefore, we hesitate to treat this lineage as an independent taxonomic unit until the mentioned characters can be comprehensively analyzed in all green limacodid groups.

In addition, the species richness and distribution of the *Parasa undulata* species group is extensively reviewed in this study, comprising wide-distributed *P. undulata* and local-ranged *P. minwangi* sp. n. in Asian continental region (China) and three endemic species found in a mountainous island (Taiwan). Assuming that no more or a few undescribed species may be discovered in the mainland in future studies, their distribution patterns show a rather higher species diversification in a small biogeographic unit. Though Holloway and Hebert (1979) claimed the lower opportunities for specialization of conifer-feeding lepidopteran larvae compared to angiosperm-feeding ones, the hostplant selection of different conifer genera is still regarded as a potential key to speciation of this lineage which would be interesting to further investigate.

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RESEARCH ARTICLE



Redescription of *Mymarilla* Westwood, new synonymies under *Cremnomymar* Ogloblin (Hymenoptera, Mymaridae) and discussion of unusual wings

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Abstract

The monotypic genus *Mymarilla* Westwood is known only from St. Helena, a remote island in the South Atlantic Ocean. The peculiar species *M. wollastoni* Westwood (Mymaridae) is redescribed and illustrated from non-type material. *Mymarilla* is compared with *Cremnomymar* Ogloblin spp. from the Juan Fernández Islands in the South Pacific Ocean. *Stephanodes* Enock is shown to be the most likely sister genus to *Mymarilla. Nesopolynema* Ogloblin, **syn. n.**, *Oncomymar* Ogloblin, **syn. n.**, *Scolopsopteron* Ogloblin, **syn. n.**, are placed in synonymy under *Cremnomymar* and their species transferred as *Cremnomymar caudatum* (Ogloblin 1952), **comb. n.**, *C. dipteron* (Ogloblin 1957), **comb. n.**, and *C. kuscheli* (Ogloblin 1952), **comb. n.** Wing shape and wing reductions in Mymaridae are discussed in relation to biogeography, particularly with respect island faunas and to four genera, *Cremnomymar, Mymarilla, Parapolynema* Fidalgo, and *Richteria* Girault, some or all of whose species have more or less convex fore wings.

Keywords

Mymaridae, Mymarilla wollastoni, Cremnomymar, Richteria, Parapolynema, wing modifications, island faunas

Introduction

The small, remote South Atlantic island of St. Helena contains a high proportion of endemic species but among the Hymenoptera only the Formicidae have been systematically studied (Wetterer et al. 2007). Among the insects, one of the most remarkable is *Mymarilla wollastoni* Westwood (Hymenoptera: Mymaridae). Although the species was described briefly from both sexes (Westwood 1879), it is instantly recognizable from the original illustrations that show the peculiar, strongly convex fore wings. Annecke and Doutt (1961) redescribed the species in greater detail, designated a lecto-type, and cleared up the confusion by previous authors over what species should be included in *Mymarilla* Westwood. Subba Rao (1976) illustrated the species with a habitus drawing. *Mymarilla* is redescribed from material other than the original type series and is compared with new material of *Cremnomymar* Ogloblin and its synonyms (proposed below) from the Juan Fernández Islands, about 600 km W. of Chile in the South Pacific Ocean. Wing shape, and wing reduction and/or convexity is discussed in relation to geographical distribution of Mymaridae.

Methods

Morphological terms follow Gibson (1997) and Huber (2012). Measurements are in micrometres (μ m). Photographs of critical point dried and card mounted specimens were taken with a ProgRes C14^{plus} digital camera attached to a Nikon Eclipse E800 compound microscope, and the resulting layers combined electronically using Auto-Montage[®] or Zyrene Stacker[®] and retouched as needed with Adobe[®] Photoshop CS6[®]. Specimens of *Cremnomymar* were gold coated for scanning electron micrography, using the techniques described in Bolte (1996).

Specimens are in the following institutions.

BMNH	The Natural History Museum (formerly British Museum [Natural History]),
	London, England (G. Broad).
CNC	Canadian National Collection of Insects, Ottawa, Canada.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium (E. de Coninck).
OUMNH	Oxford University Museum of Natural History.

Systematics

Mymarilla Westwood

http://species-id.net/wiki/Mymarilla

Mymar: Westwood 1879: 585 (*M. wollastoni* included, together with another, correctly placed species).

- *Mymarilla* Westwood, 1879: 585 (footnote) + figs 8, 9 (recommended as a new genus group name for *M. wollastoni* "if it should be deemed necessary to separate this species from the genus *Mymar*").
- Mymar: Dalla Torre 1898: 427 (Mymarilla treated as a synonym).
- *Mymarilla*: Schmiedeknecht 1909: 495 (treated as valid genus with one [incorrectly placed] species but no mention of *M. wollastoni*).
- *Mymar*: Schmiedeknecht 1909: 496 (listed *M. Wollastoni* [*sic*] together with three other species [one other of which is also incorrectly placed generically]).

Mymarilla: Ferrière 1952: 43 (treated as valid name for Mymar of authors, not Curtis).

- *Mymarilla*: Doutt 1955: 11 (key), 12 (treated as valid genus, but noted that American authors used *Mymar* as the name for species included under *Mymarilla* by previous workers).
- *Mymarilla*: Heqvist 1960, 432 (treated as valid genus with one [incorrectly placed] species but no mention of *M. wollastoni*).

Mymarilla: Annecke and Doutt 1961: 31 (discussion of past confusion with Mymar).

Type species. *Mymarilla wollastoni* Westwood, by monotypy. Transferred (as geno-type) to *Mymarilla* by Heqvist (1960: 432).

The confusion in the use of the name *Mymarilla* and which species should be placed in the genus continued for over 80 years. Heqvist (1960) was the first to treat *M. wollastoni* as the genotype of *Mymarilla*, even as he incorrectly placed *Mymar* species under it, as did previous authors. As Annecke and Doutt (1961) clarified, wherever previous authors use *Mymarilla* it was clearly in the sense of *Mymar*, because the species names mentioned are typical *Mymar* species.

Diagnosis. The combination of smooth, shiny black body, extremely short mesocutum compared to much longer pronotum, and extraordinary convex and densely setose fore wing distinguish the genus and species from any other Mymaridae.

Mymarilla belongs clearly to the Polynema Haliday group of genera within Mymarini sensu Annecke and Doutt (1961). They suggested that Mymarilla was most similar to Oncomymar Ogloblin from the Juan Fernández Islands. Superficially, the most similar genus is Cremnomymar Ogloblin (including Oncomymar Ogloblin and Scolopsopteron Ogloblin, see below), some of whose species also have a convex fore wing and reduced mesoscutum. The two genera are not closely related; their resemblance is due to adaptations to life on remote, presumably wind-swept, oceanic islands.

I propose instead that *Mymarilla* is derived from *Stephanodes* Enock, likely the most closely related genus. Four features, shared with *Stephanodes*, suggest this: first, the extremely smooth body without trace of microscupture on the mesosoma (Figs 1, 3, 4, 6, 9, 10); second, the slightly advanced mesothoracic spiracle about midway between the anterior apex of a notaulus and posterolateral angle of the mesoscutum (Figs 3, 4); third, the presence of a metapleural pit (Figs 9, 10); fourth, the fore wings that are held more or less horizontally. In dead specimens of *Stephanodes*, the fore wings are often horizontal, crossed scissor-like and covering the body, unlike other, related genera in the *Polynema*-group where the wings (in dead specimens) are almost always

vertical, directed away from the body. The strong convexity of the fore wings of *Mymarilla* would appear to prevent them from being crossed scissor-like over the body. Yet they are presumably capable of enveloping the metasoma, as pointed out by Westwood who noted ". . . when shut [the fore wings] form a semiglobular dome over the abdomen" when the wasp is at rest. The densely hairy wing membrane with dark base around each microtrichia would allow for maximum heat absorption and retention.

Mymarilla wollastoni (Westwood)

http://species-id.net/wiki/Mymarilla_wollastoni Figs 1–10

Mymar wollastoni: Westwood 1879: 585 (original desciption). Mymar wollastonii [sic]: Dalla Torre 1898: 427 (catalogue, unjustified emendation). Mymarilla wollastoni: Annecke and Doutt 1961: 31 (redescription). Mymarilla wollastoni: Subba Rao 1976: 90 (diagnosis), 91 (figure).

Remarks. Lectotype female in OUMNH (not examined), designated by Annecke and Doutt (1961), with catalogue number HYME0029 and labeled: "Holotype", "det. D.P. Annecke 25.vii.1960".

Description. Because only one species of *Mymarilla* is known, the generic and specific features are both described in the species description. Female. Body length 2125 (n=1). Body entirely smooth and shiny except for a few small punctures on pronotum. Colour. Head black except mandibles, mesosoma, metasoma medially, and clava; flagellum, and metasoma basally and apically dark brown; scape, pedicel, mandibles, legs, petiole, and ovipositor brownish yellow; all body setae almost white; wings brown behind venation, membrane beyond venation translucent but membrane around each microtrichia back, so wings generally appearing dark. Head. (Figs 3–6) $1.46 \times$ as wide as long, and $1.17 \times$ as wide as high (406/227/347) (n=1), in lateral view with anterior surface slightly depressed between toruli then, at level of ventral margin of eye, receding to mouth (Fig. 5). Face measured from eye to eye below toruli about as long as wide, flat above toruli but forming a shallow circular depression medially below toruli; subantennal groove and pits between toruli absent. Torulus about 1.5× its diameter from thin transverse trabecula and about mid height of eye. Preorbital groove against eye almost to ventral margin of eye (Fig. 5), then extending almost straight to anterolateral angle of mouth margin. Eye (Fig. 5) in lateral view 0.75× as long as high, not extending to back of head dorsally and separated by more than its own length from back of head ventrally. Malar sulcus absent and malar space almost 0.6× eye height. Gena narrow dorsally, very wide ventrally. Vertex in lateral view almost flat, sloping anteriorly, forming an obtuse angle to face (separated by transverse trabecula), smoothly merging posteriorly with occiput. Mid ocellus flat in shallow depression, not projecting above surface of vertex and 2× diameter of small lateral ocellus. Ocelli in high triangle, with POL (168),



Figures I, 2. *Mymarilla wollastoni*. I female dorsolateral **2** male antennae (pedicel + flagellum). Scale line = 1000 μm.

1.9× LOL, and LOL (89) 3.0× OOL (30). Mandibles normal, overlapping medially when closed, with 3 teeth. **Antenna.** Scape about 3.9× as long as wide, with both inner and outer surfaces apparently smooth, and with radicle short but distinct; pedicel slightly shorter than fl_1 , about 0.41× scape length; funicle 6-segmented; clava unsegmented, slightly longer than scape. Number of mps of funicle segments and clava uncertain (not clearly visible on card mounted specimen). Measurements (n=1) length/width: scape 267/69, pedicel 109/50, fl_1 129/20, fl_2 267/20, fl_3 198/30, fl_4 149/30, fl_5 149/30, fl_6 149/30, clava 317/80. **Mesosoma.** About 2.67× as long as wide, about 1.80× as long as high, and 1.48× as wide as high (n=1). Pronotum (Fig. 3) in dorsal view clearly visible, shorter than wide (218: 267), strongly convex, with almost vertical sides flaring outward ventrally and almost horizontal at junction with propleura; pronotum in lateral view strongly triangular. Propleura (Fig. 4) in dorso-



Figures 3, 4. *Mymarilla wollastoni*. 3 mesosoma, dorsal 4 head and mesosoma, dorsolateral. Scale line = $200 \ \mu m$.

lateral view tightly pressed to pronotum laterally and anteriorly, and fused to each other at neck, and, in dorsal view (Fig. 3), slightly extending lateral to pronotum. Neck long (90), clearly separating head from pronotum. Prosternum triangular, strongly appressed laterally to propleura, without median longitudinal line, anterior apex not visible but perhaps closed anteriorly. Mesonotal spiracle (Fig. 6) small, at



Figures 5, 6. *Mymarilla wollastoni*. **5** head and prothorax, lateral **6** head and thorax, anterolateral. Scale line = 200 µm.

end of short tube, midway between posterolateral angle of mesoscutum and anterior apex of notaulus. Mesoscutum (Fig. 3) smooth and shiny, in lateral view slightly convex, in dorsal view short (99), about $0.4 \times$ as long as pronotum and $0.4 \times$ as long



Figures 7, 8. *Mymarilla wollastoni.* **7** mesosoma, petiole and wings posterodorsal **8** fore and hind wing bases, dorsal. Scale line = $200 \mu m$.

as wide, with slightly diverging, almost straight notauli, each ending anteriorly in a distinct pit. Axillae not advanced (Figs 3, 4, 9, 10). Mesoscutellum (Fig. 3) almost as long as pronotum (267: 246), slightly overlapping metanotum, without trace of frenal line (frenum therefore not distinguishable). Prepectus (Figs 6, 9, 10) triangular, about $3 \times$ as long as dorsal width. Mesopleuron tightly appressed to prepectus, convex, not divided by suture into mesepisternum and mesipimeron. Metanotum small, triangular, separated from propodeum by wide groove. Metapleuron with a

large metapleural pit at junction with mesoepisternum. Propodeum (Figs 3, 4, 7, 10) evenly convex, without carinae, with a large pit at anterior margin just anterior to spiracle, with a slightly upturned nucha covering anterior apex of petiole, and with propodeal seta almost at posterior margin. Spiracle small, round, separated by several diameters from anterior margin of propodeum. Wings. Fore wing (Figs 1, 7, 8) deeply convex, with the anterior and posterior margins strongly curving downward, the wing *height* in lateral view about $0.7 \times$ wing width in dorsal view. Wing behind submarginal vein very narrow, with strongly convex hind margin, abruptly widening beginning at parastigma, generally oval in dorsal view. Entire surface to wing base covered in long microtrichia, those behind venation appressed and those beyond venation semi-erect to erect. Fore wing length 1792 (n=1), width 640, length/width 2.8, venation length 287, about 0.18× forewing length. Submarginal vein black basally, brown apically, and much wider basally than apically; parastigma + stigma black, oval about 1.7× as wide as base of submarginal vein. Costal cell extremely narrow. Hind wing (Fig. 1) flat to slightly convex, with long marginal setae and erect microtrichia similar to those on forewing, and wing membrane extending almost to base of wing but very narrow behind venation. Hind wing length ca. 1535, width 77, venation black, length about 0.3× wing length. Legs. Long and slender (Figs 1, 7). Metasoma. Petiole length 180, slightly longer than metacoxa, about 6× as long as wide. Gaster (Fig. 1) smooth and shiny, narrowly oval in cross section (as seen in posterior view), wider dorsally, almost knife-like ventrally at ovipositor. Gt, about 0.57× gaster length (870) and almost completely covering gs, so petiole apparently attached to tergum, gt,-gt, progressively shorter, gt, and syntergum (gt₇ + gt₈) each about as long as gt₂. Spiracle present on gt₆, small. Ovipositor length ca. 770, slightly down turned apically, as long as gaster but not exserted beyond gaster, about 1.2× metatibia length (640).

Male. Colour as in female but body dark brown (possibly due to fading), scape brownish yellow, pedicel light brown, flagellum dark brown. Body length 1843–1894 (n=2). Fore wing length 1664 (hind wing not measurable on pinned specimens), with the edges almost meeting ventrally in one specimen, giving the appearance of a hirsute cigar when seen end on in posterior view (Fig. 7). **Antenna.** Scape about 3.8× as long as wide, with both inner and outer surfaces apparently smooth. Measurements (n=1) length/width or length for flagellomeres: scape 218/59, pedicel 99/45, fl₁ 277, fl₂ 267, fl₃ 248, fl₄ 248, fl₅ 223, fl₆ 228, fl₇ 198, fl₈198, fl₉ 178, fl₁₀ 198, fl₁₁ 198; total flagellum 2461. Fl₆ length/width about 6.0, with perhaps 8 mps (not clearly visible on card mounted specimen). **Metasoma.** Gaster length 742–793 (n=2), in lateral view truncate apically.

Material examined. SAINT HELENA. Centre. High Central Ridge, Cabbage Tree Road, 2500', iii.1967, J. Decelle, N. & J. Leleup (2 males, MRAC); High Peak, 15°58.7'S, 5°44.0'W, ca.752m, xii.2005–1.2006, N.P. & M.J. Ashmole, H. Mendel, E.A. Thorpe, pitfall trap (1 female, BMNH).

Habitat. Westwood (1879) stated that the specimens were swept from low herbage.

Annecke and Doutt (1961) suggested that the wings may be used for floating on air currents. Whether individuals are capable of this, let alone normal flight, is uncertain.



Figures 9, 10. *Mymarilla wollastoni*. 9 mesosoma lateral 10 mesosoma, lateral, SEM. Scale line = 200 µm.

The greatly reduced mesoscutum suggests that the flight muscles are so reduced they would be incapable of powered flight. The collection of one female in a pitfall trap suggests that *M. wollastoni* lives near the ground.

Cremnomymar Ogloblin

http://species-id.net/wiki/Cremnomymar Figs 11–14, 20–38

- *Cremnomymar* Ogloblin, 1952: 120 (generic description, two species described, based on males); Ogloblin 1957: 418 (two species described, based on females); Annecke and Doutt 1961: 6 (key), 31 (comments); Fidalgo, 1982: 98 (comparison with *Parapolynema*);
- Scolopsopteron Ogloblin, 1952: 127 (generic description, one species based on two males); Annecke and Doutt, 1961: 6 (key), 30 (comments). syn. n.
- Nesopolynema Ogloblin, 1952: 132 (generic description, one species based on a male); Annecke and Doutt 1961: 6 (key), 30 (comments). syn. n.
- *Oncomymar* Ogloblin, 1952: 132 (generic description, one species based on a female); Annecke and Doutt 1961: 6 (key), 30 (comments). **syn. n.**

Remarks. Ogloblin (1952, 1957) described seven species of Mymaride based on eight specimens from the Juan Fernández Islands, all but one from Masatierra Island (Robinson Crusoe Island). Three were described from females only and four from males only. *Scolopsopteron dipteron* Ogloblin (Ogloblin 1952) has a fore wing of normal length but unusually narrow and a rudimentary hind wing. *Oncomymar kuscheli* Ogloblin (Ogloblin 1957) has a fore wing of normal width and length but strongly convex (spoon-shaped) and a rudimentary hind wing. *Nesopolynema* has a normal fore wing (hind wings missing in Ogloblin's specimen).

It is improbable that the Juan Fernández Islands would have four endemic genera of Mymaridae, as treated by Ogloblin (1952, 1957). Above the species category similarities must be used to define collective groups, not differences. If differences are used, then how different must something be to be placed in a different genus? "Different enough" is not an acceptable answer. If it were, the placement of species in genera of finer and finer difference would be the norm, with the result that the genus category would become almost synonymous with the species category, and each genus would contain only one or two species. Unfortunately, Ogloblin sometimes defined genera based on obvious but superficial differences that resulted in oversplitting. I am confident that all seven of Ogloblin's species from the Juan Fernández Islands represent at most different species within a single genus. Indeed some of them have likely been described twice, once from females and once from males.

I examined forty-three specimens (not the types) of *Cremnomymar* (including the synonyms proposed above), all from Masatierra, the largest of the Juan Fernández Islands. In some of the species the fore wing is fully developed and flat (Fig. 11) but in others it is more or less reduced and convex (Figs 12–14). Depending on the extent of wing reduction the mesothorax is also reduced but the placoid sensilla on the scutellum are always widely separated. The pronotal structure varies from entire, sometimes with indication of a mediolongitutinal line, to being apparently completely divided medially by a complete longitudinal carina. The propodeum in



Figure 11. Cremnomymar sp., macropterous female, dorsal (fore wing flat). Scale line = 1000 µm.

short-winged specimens changes in ways that I consider to be at most of species-level significance, from strongly carinate and with a large, sublateral tooth bearing the propodeal seta, as in fully winged *Cremnomymar* (Figs 11, 12, 32) to almost smooth (Fig. 14) but still with the propodeal seta on a bump or tooth. Therefore, I propose the above generic synonymies and transfer the included species to *Cremnomymar* as *C. caudatum* (Ogloblin 1952), comb. n., *C. dipteron* (Ogloblin 1957), comb. n., and *C. kuscheli* (Ogloblin 1952), comb. n.



Figure 12. *Cremnomymar* sp., slightly brachypterous male, dorsal (forewing slightly convex, hind wing brachypterous). Scale line = 1000 µm.

Biogeography

St. Helena, with a land area of 122 km², is a remote island of volcanic origin in the South Atlantic Ocean at 15°54'–16°01'S, 5°37'–5°47'W, about 1920 km W. of Africa, the nearest continent (Ashmole and Ashmole 2000). The highest elevation is 823 m and the island's age is estimated to be 14.3 \pm 1.0 million years. It has a tropical climate moderated by the Benguela Current and southeast trade winds. Two distinct physiographic zones are defined, a wet well-vegetated area above 450 m and an arid, poorlyvegetated zone below. A considerable proportion of the plant species are endemic.

The Juan Fernández islands with a total land area of 124 km², almost identical in size to St. Helena, are in the South Pacific Ocean about 600 km west of Chile. Masatierra Island (Robinson Crusoe Island), at 33°38'S, 78°51'W with a land area of about 51 km² and a 916 m high point is 3.8–4.2 million years old. Masafuera Island (Alejandro Selkirk Island) at 33°46'S, 80°47'W with a land area of 50 km² and a 1319 m high point is 1.0–2.4 million years old. Santa Clara, the smallest island is 1 km SW



Figure 13. *Cremnomymar* sp., moderately brachypterous male, dorsal (forewing distinctly convex, hind wing micropterous). Scale line = $1000 \mu m$.



Figure 14. *Cremnomymar* sp., strongly brachypterous male, dorsal (forewing slightly convex, hind wing absent). Scale line = $1000 \mu m$.



Figure 15. *Cremnomymar* sp., macropterous female, dorsolateral (fore wing convex, hind wing brachypterous). Scale line = 1000 µm.

of Robinson Crusoe and 5.8 million years old (Haberle 2009). Over half of the native plants species (126 of 209) are endemic. The climate is subtropical and its climate is affected by the cold Humboldt Current.

Despite being two to three times the age of Santa Clara, the oldest of the Juan Fernández Islands, the remoteness of St. Helena from the nearest continent is likely the main reason why it has only one endemic species of Mymaridae. In contrast, the Juan Fernández Islands have several endemic species, diverse enough to have been placed in separate genera by Ogloblin, who was swayed by the most notable structural differ-



Figure 16. *Richteria ara*, female, lateral. Scale line = 1000 µm.

ences among species of three of the four genera, i.e., wing reduction with concomitant modifications of the mesosoma. Another reason for the difference in faunas of the two groups of islands is the harsher climate on the Juan Fernández Islands (subtropical)



Figures 17, 18. *Richteria ara*, male. **17** lateral, wings dorsoposterior **18** fore wing detail. Scale line = 500 μm.

compared to St. Helena (tropical), causing a greater selection pressure on any terrestrial organism established there and therefore a greater likelihood of diversification into several species. Two other reasons are: 1) there is greater chance of continental species reaching the Juan Fernández Island than St. Helena, so multiple introductions could



Figure 19. Parapolynema sp., female, dorsolateral. Scale line = 1000 µm.

account for the diversity of *Cremnomymar* species on Masatierra; and 2) the fauna (and flora) of St. Helena has been much more affected by human activity, possibly resulting in the disappearance of other species of Mymaridae that may have existed there, leaving only *M. wollastoni* among the endemic Mymaridae.

One specimen of *Parapolynema* Fidalgo was seen, collected in Bolivia, La Paz, Sorata environs, 3200m, 20.iv.1997, L. Masner, sweeping open scrub (1 female, CNC). Fidalgo (1982, 1991) stated that *Parapolymema* is most similar to *Cremnomymar*, based on fore wing structure (Fig. 15) and propodeal seta set on a similar (as in some *Cremnomymar*), distinct protuberance. But the fore wing also is remarkably similar to that of *Richteria* Girault (Figs 16–18). The endemic Mymaridae on the Juan Fernández Islands are probably derived from specimens of *Parapolynema* that arrived there from southern South America but there seems to be a link to the New Zealand/Australian fauna and all three genera may be Gondwanan remnants.



Figures 20–25. *Cremnomymar* sp. (macropterous), micrographs. **20** head, anterior **21** head, lateral **22** head, posterior (sculpture hidden by glue except laterally and dorsally) **23** head, dorsal **24** head, ventral **25** mouthparts. Scale lines = 20 μm.



Figures 26–31. *Cremnomymar* sp. (macropterous), micrographs. **26** mesosoma (pronotum missing), dorsal **27** mesosoma, lateral **28** mesosoma, ventral **29** petiole, dorsal **30** petiole, lateral **31** petiole, ventral. Scale lines for $26-28 = 50 \ \mu\text{m}$; for $29-31 = 20 \ \mu\text{m}$.

Wing modification in Mymaridae

The wings of Mymaridae vary considerably in shape, perhaps more than in most other families of Chalcidoidea. In a normal, fully developed (macropterous) wing the surface is flat, with the length several times greater than width and with a more or less rounded apex. Variations in shape are due partly to changes in length and width and partly to changes in outline, particularly of the posterior margin and wing apex. Depending on the genus and species a full length fore wing may become narrower so that length becomes even greater relative to width. The extremes are 2.5× as long as wide in *Paranaphoidea* Girault (Lin et al. 2007, fig. 206) and 30× as long as wide in *Cleruchus biciliatus* (Ferrière) (Ferrière 1952). Hind wing shape varies only slightly because it is generally linear to begin with. Variation in a full length hind wing is therefore mainly in width, from extremely narrow, thread-like, e.g., *Mymar* (Huber et al. 2009, fig. 55) to wide, e.g., *Par*-



Figures 32–38. *Cremnomymar* sp. (macropterous), micrographs. **32** frenum + propodeum, dorsal **33** mesosoma, ventroanterior **34** metasoma, dorsal **35** metasoma, lateral **36** metasoma, ventral **37** apex of gaster, dorsal **38** apex of gaster, lateral. Scale lines for **34–36** = 100 μm; for **32, 33, 37, 38** = 20 μm.

anaphoidea (Lin et al. 2007, fig. 206); rarely the hind wing may be curved, with the anterior and posterior margins distinctly convex and concave, respectively. Despite all this variation the wings remain two dimensional. Most of the range of wing shapes and sizes is illustrated in generic treatments of Mymaridae by Subba Rao (1983) for the Oriental region, Noyes and Valentine (1989) for New Zealand, Yoshimoto (1990) for the Western Hemisphere, Huber (1997) for North America, Lin et al. (2007) for Australia, Huber et al. (2009) for the Arabian Peninsula, and Luft Albarracin et al. (2009) for Argentina.

Wing reduction (brachyptery, microptery) or complete loss (aptery) usually occurs where there a strong selection pressure against having fully developed wings. Reduction in length may be slight shorter than normal, to extremely short, at least in one sex (usually the female) of at least one species of a genus. Species with wings reduced or absent occur on all continents, mostly in species that search for host eggs in confining places where wings would be a hindrance, e.g., in soil, leaf litter, or in tubules of bracket fungi (some *Cleruchus* spp.) or in windy places, e.g., small, remote oceanic islands and high elevations on mountains. All three species (100%) of Mymaridae found on small islands (Campbell I., Auckland I., South Georgia) at more than 45° south are wingless or micropterous. Each species is placed in its own genus and each genus is evidently related to a genus on the nearest mainland or is a wingless species with winged congeners in New Zealand, and South America, respectively. For example, on South Georgia (at or near sea level) *Notomymar* is completely wingless, whereas at 4100 m in Ecuador (Yoshimoto 1990) the species there is micropterous, and at low altitude in Chile, the species (undescribed?) is/are fully winged.

On remote oceanic islands between 30°–45° S Mymaridae are reported so far only from the Juan Fernández Islands (*Cremnomymar*, 7 described spp., but some probably synonyms), Norfolk Island (*Cybomymar* Noyes & Valentine [Lin et al. 1997], 1 sp.), and Lord Howe Island (*Anagroidea* sp., new record). Wingless or short-winged species represent at least 20% of the fauna, excluding genera/species likely introduced over the past few hundred years by humans. In contrast, Mymaridae from continents south of 30° S contain a low percentage of short winged or wingless species. The exception is New Zealand (a large continental island) with 17 of 42 genera that contain at least one flightless species (Noyes and Valentine 1989: 8).

Between the tropics of Cancer and Capricorn no wingless or short winged species have yet been recorded on the relatively well studied but still poorly known (for Mymaridae) Pacific oceanic islands: Micronesia (Doutt 1955), Fiji (Huber 2009), Galapagos Islands (Huber, unpublished), Hawaiian Islands (Beardsley and Huber 2000) and, in the Atlantic Ocean, the Cape Verde Islands (Viggiani and Jesu 1995). Northern Hemisphere islands north of the tropic of Cancer are almost all in the North Atlantic Ocean. They are either too close to continents to develop endemic faunas that include short-winged or wingless species or they are too far north and therefore too cold for most insects to survive. They have generally been poorly explored, except Madeira (Graham 1979, 1983, 1988).

Curvature of the fore wing so it becomes convex or dome-shaped, i.e., it is no longer flat but clearly three-dimensional, occurs in at least one species of four genera: *Cremnomymar* Ogloblin (Figs 12, 13), *Mymarilla* (Figs 1, 7), *Parapolynema* Fidalgo (Fig. 15), so far known from Argentina and Bolivia, and *Richteria* (Figs 16–18), so far known from Australia and New Zealand. On wind-swept islands convex wings may perhaps have survival value by enveloping the posterior part of the mesosoma and the metasoma, either for greater heat absorption and retention or to reduce the chance of

being blown away. But species of *Parapolynema* and *Richteria* do not necessarily occur in harsh environments so there evidently are other reasons for having a more or less convex fore wing. Interestingly, the fore wings of both genera have a double dome, in contrast to the single dome of *Mymarilla* and some *Cremnomymar*.

It would be interesting to find out if Mymaridae occur on other remote Southern Hemisphere islands, particularly those south of 30°. Collecting in a diversity of microhabitats using yellow pan traps or sifting of soil and whatever vegetation is present is required because any Mymaridae present are almost certain to be wingless or short winged.

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RESEARCH ARTICLE



The Chinese species of the genus Ontsira Cameron (Hymenoptera, Braconidae, Doryctinae)

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Abstract

The Chinese species of the genus *Ontsira* Cameron, 1900 (Hymenoptera: Braconidae, Doryctinae) are reviewed. Eleven species are recognized, of which four new species are described from China and South Korea: *O. abbreviata* **sp. n.**, *O. henana* **sp. n.**, *O. robusta* **sp. n.**, and *O. rugivertex* **sp. n.** Two species, *O. ignea* (Ratzeburg) and *O. neantica* Belokobylskij et Maetô, are recorded in China for the first time. A key to the Asian species of the genus *Ontsira* is provided.

Keywords

Ectoparasitoid, Braconidae, Doryctinae, Ontsira, new species, new record, key, Asia

Introduction

The genus *Ontsira* Cameron, 1900 is not a species-rich genus and is one of the less specialised taxa of the large tribe Doryctini (Hymenoptera: Braconidae, Doryctinae) (Belokobylskij 1992, 1998a). Twenty-nine species are known, including the new taxa described here. They are distributed in the Holarctic (18 species), Oriental (9 species), Australasian (1 species) and Afrotropical (1 species) regions, but no species have yet been found in the Neotropics. Members of *Ontsira* are known as ectoparasitoids of mainly xylophagous beetle larvae of the families Anobiidae, Bostrichidae, Buprestidae, Cerambycidae (prevalently), Curculionidae, Scolytidae, Eucnemidae, Nitidulidae and Tenebrionidae (Shenefelt and Marsh 1976; Belokobylskij and Maetô 2009; Yu et al. 2012), but the records of the last three families need confirmation.

After recent morphological and molecular studies (Belokobylskij 1998a, 2008; Zaldivar-Riverón et al. 2008; Belokobylskij and Maetô 2009), some species formerly belonging to *Ontsira* have been moved to other existing genera, such as *Dolopsidea* Hincks, 1944 and *Neurocrassus* Šnoflak, 1940 (Belokobylskij 1982, 1998a; Belokobylskij and Maetô 2009) or to new genera established by Belokobylskij (1998b, 2008), such as *Rhacontsira* Belokobylskij, 1998 and *Cryptontsira* Belokobylskij, 2008.

Only three species of this genus were previously described from China (Chen and Shi 2004). However, according to Belokobylskij and Maetô (2009), *O. brachytes* Chen & Shi, 2004 is a junior synonym of *O. apposita* Belokobylskij, 1998 and *O. retina* Chen & Shi, 2004 a junior synonym of *Hypodoryctes fuga* Belokobylskij & Chen, 2004. In this study, another four new species of *Ontsira* are described from China and South Korea, and two species, *O. ignea* (Ratzeburg, 1852) and *O. neantica* Belokobylskij & Maetô, 2009, are recorded for the fauna of China for the first time.

Material and methods

This study is based on specimens from the Parasitic Hymenoptera Collection of the Institute of Insect Sciences, Zhejiang University, Hangzhou, China (ZJUH) and Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP); material from other museums was not available in the period of our investigation. The terms of wing venation are used as defined by Belokobylskij and Maetô (2009). The following abbreviations are used: POL – postocellar line; OOL – ocular-ocellar line; Od – maximum diameter of lateral ocellus. In the key, additional features useful for separating species are listed after the dash "–".

The descriptions and measurements were made under a Micromed MC–2 ZOOM stereomicroscope, and all figures were made by a digital camera (Q-Iming, Micropublisher, 3.3 RTV) attached to a stereomicroscope (Leica MZ APO, Germany) and Auto-Montage Pro version 5.0 software. Type specimens and other materials are deposited in the collection of ZISP and ZJUH.

Taxonomic part

Genus Ontsira Cameron, 1900

http://species-id.net/wiki/Ontsira

- *Ontsira* Cameron, 1900: 89; Shenefelt and Marsh 1976: 1322; Belokobylskij and Tobias 1986: 41; Belokobylskij 1998a: 464; 1998c: 54; Chen and Shi 2004: 27; Belokobylskij and Maetô 2009: 363.
- Doryctes (Doryctodes) Hellen, 1927: 40 [type species: Rogas (Doryctes) imperator Haliday, 1836]; Shenefelt and Marsh 1976: 1322.

Doryctodes: Telenga, 1941: 389; Shenefelt and Marsh 1976: 1322.

Wachsmannia Szépligeti, 1900: 217 (type species: W. maculipennis Szépligeti, 1900); Shenefelt and Marsh 1976: 1332; Belokobylskij 1992: 908; van Achterberg 1995: 131; Belokobylskij 1998a: 462.

Type species. Ontsira reticulata Cameron, 1900.

Key to the Asian species of the genus Ontsira Cameron

(Update from Belokobylskij and Maetô 2009)

1 Second tergite with more or less smooth basomedian area separated by furrow or different type of sculpture. Body usually with contrasted pale and dark colouration. Upper tentorial pits (latero-posteriorly from antennal sockets) present, small or very small Neurocrassus Šnoflak Second tergite without smooth basomedian area. Body usually without contrasted colouration. Upper tentorial pits completely absent......2 2 Second metasomal tergite sculptured at least basally7 First metasomal tergite shorter, not longer than its apical width. Mesoscutum 3 mostly smooth or finely granulate in anterior part4 First metasomal tergite longer, 1.15–1.30 times as long as its apical width. 4 Ovipositor shorter, its sheath 0.5-0.7 times as long as metasoma, 0.65-0.80 times as long as mesosoma, 0.30–0.35 times as long as fore wing. Transverse diameter of eye 1.0-1.1 times as long as temple. Propodeum with distinct lateral tubercles. First metasomal tergite shorter, 0.8-0.9 times as long as its apical width. Body length 3.0–4.5 mm. – China (Heilongjiang); Russia, Caucasus, Turkey, Central and West Europe, USA...... O. antica (Wollaston) Ovipositor longer, its sheath 0.9–1.0 times as long as metasoma, distinctly longer than mesosoma, about 0.5–0.6 times as long as fore wing. Transverse diameter of eye 0.9 times as long as temple. Propodeum almost without lateral tubercles. First metasomal tergite longer, its length equal to its apical width. Body length 3.1–5.3 mm. – China (Heilongjiang); Japan O. neantica Belokobylskij & Maetô

5 Parallel vein arising almost from middle of distal margin of brachial cell. Second radial abscissa 0.8 times as long as third abscissa. Second radiomedial cell 2.7 times as long as its maximum width. Basolateral areas of propodeum granulate. Median length of second tergite 1.4 times as long as median length of third tergite. - First tergite entirely striate. Nervulus of fore wing strongly postfurcal. Ovipositor sheath 0.4 times as long as fore wing. Body length 3.6 Parallel vein arising from posterior 0.25-0.30 of distal margin of brachial cell. Second radial abscissa 0.50-0.65 times as long as third abscissa. Second radiomedial cell 2.3-2.4 times as long as its maximum width. Basolateral areas of propodeum entirely or mainly smooth, sometimes rugulose posteriorly. Median 6 Nervulus of fore wing almost interstitial. Ovipositor sheath 0.7 times as long as fore wing. Hind coxa smooth dorsally. First metasomal tergite longer, 1.25 times as long as its apical width. Hind coxa and femur mainly dark reddish brown. Frons without pit between antennal sockets. Body length 5.6 mm. -India......O. reticulata Cameron Nervulus of fore wing distinctly postfurcal. Ovipositor sheath 0.4 times as long as fore wing. Hind coxa distinctly sculptured dorsally. First metasomal tergite shorter, 1.15 times as long as its apical width. Hind coxa and femur entirely yellow. Frons with distinct elongate pit between antennal sockets. Body length 3.0 mm. – China (Shaanxi)...... O. abbreviata sp. n. 7 Second tergite entirely or almost entirely sculptured, but sometimes sculpture in apical half fine and interrupted17 8 Temple very short, transverse diameter of eye 3.3-3.8 times as long as temple. Acrosternite of first tergite rather distinctly elongate. Apical segments of antenna white. Body length 3.0-3.7 mm. - China (Fujian, Zhejiang); Viet-Temple longer, transverse diameter of eye 1.0-1.6 times as long as temple. Acrosternite of first tergite shorter. Apical segments of antenna dark9 9 Mesoscutum and basolateral areas of propodeum completely smooth. Mesosoma 1.5 times as long as its maximum height. Eyes glabrous. Radial vein arising slightly before middle of pterostigma. Body length 2.1 mm. - Vietnam O. tayi Belokobylskij Mesoscutum and basolateral areas of propodeum more or less granulate or sometimes finely granulate and with distinct punctation. Mesosoma 1.7-2.0 times as long as its maximum height. Eyes often (except O. henana sp. n.) rather densely and shortly setose. Radial vein arising more or less behind middle of pterostigma or sometimes from its middle.....10 10Ovipositor sheath not longer than metasoma. Mesoscutum and scutellum distinctly and densely granulate. Parallel vein of fore wing arising slightly

before or almost from middle of distal margin of brachial cell. First abscissa of mediocubital vein of hind wing almost equal to second abscissa11 Ovipositor sheath longer than metasoma, almost as long as body. Mesoscutum finely granulate; scutellum almost smooth. Parallel vein of fore wing arising from posterior 0.25–0.30 of distal margin of brachial cell. First abscissa of 11 Vertex almost entirely and finely granulate-reticulate; frons at least partly rugulose-granulate. Eyes distinctly setose. Antennal segments thick, first flagellar segment 3.4-3.5 times as long as its apical width. Third tergite without transverse furrow. Vertex and mesoscutum with long setae. Body length 2.8-3.1 mm. - Russia (Far East)...... O. eugeniae Belokobylskij Vertex and most part of frons smooth. Eyes glabrous. Antennal segments slender, first flagellar segment 4.3 times as long as its apical width. Third tergite with transverse furrow. Vertex and mesoscutum with short setae. Body length 2.8 mm. - China (Henan) O. henana sp. n. 12 First metasomal tergite shorter, 0.9–1.1 (rarely 1.2) times as long as its apical width. Hind femur wide, 3.4-4.0 times as long as wide. Penultimate segment First metasomal tergite longer, 1.2–1.7 times as long as its apical width. Hind femur slender, 4.0-5.3 times as long as wide. Penultimate segment 2.1-2.4 times as long as wide......14 Vertex entirely or mostly and temple almost entirely smooth. Mesoscutum 13 (except rugose-striate in medioposterior area) mainly smooth, partly finely granulate. Body length 2.5–7.5 mm. – China (Taiwan); Japan, Korea, Mongolia, Russia, Kazakhstan, Iran, Caucasus, Central and Western Europe, Vertex almost entirely or mostly and temple at most part distinctly striate. Mesoscutum (except rugose-striate in medioposterior area) almost entirely, very densely and finely granulate with sparse punctation. Body length 6.0-7.2 mm. – China (North-east part); South Korea O. robusta sp. n. 14 Hind femur 4.0-4.5 times as long as its maximum width. First metasomal tergite 1.2-1.3 (rarely 1.15 or 1.40) times as long as its apical width. Second metasomal tergite shorter, 0.5–0.8 times as long as its basal width. Hind tibia Hind femur 4.9-5.3 times as long as its maximum width. First metasomal tergite 1.4-1.7 times as long as its apical width. Second metasomal tergite longer, 0.9 times as long as its basal width. Hind tibia dorsally with sparse setae......16 15 Vertex entirely smooth. Mesoscutum rather finely punctate-reticulate, partly with fine granulation. Second tarsal segment of hind leg shorter, 1.4–1.5 times as long as its fifth segment (without pretarsus) and about 0.4 times as long as basitarsus. First flagellar segment longer, 4.0-4.5 times as

long as wide. Body length 5.0-7.4 mm China (Shaanxi, Fujian, Guang-
dong); Japan, Korea, Russia, Caucasus, Turkey, Israel, Europe
Vertex entirely or almost entirely coarsely rugose-striate. Mesoscutum coarse-
ly rugose-granulate. Second tarsal segment of hind leg longer, 1.5–1.7 times
as long as its fifth segment (without pretarsus) and about 0.5 times as long as
basitarsus. First flagellar segment shorter, 3.4–3.6 times as long as wide. Body
length 5 5–7 0 mm – China (Henan, Shaanxi) O. rugivertex sp. n.
Brachial cell of fore wing distinctly widened medially Basolateral areas of
propodeum without carinae Pterostigma and radial cell longer: pterostigma
4.8 times and radial cell 3.9-4.0 times as long as their maximum width Body
length 7.5 mm Japan O amamioshima Belokobylskii & Maeta
Brachial cell of fore wing not widened medially. Basolateral areas of propo
down with distinct carinas. Deprestigme and radial call shortery properties
4.4.4.6 times and radial call 3.4.3.6 times as long as their maximum width
4.4–4.6 times and radial cell $5.4–5.6$ times as long as their maximum width.
Body length 5.4–8.4 mm. – China (Zhejiang, Fujian, Guangdong)
0. macer Chen & Shi
Itennae $1/-19$ -segmented. Female body length 2.5–5.0 mm
Antennae 30–40-segmented. Female body length $4.0-7.0$ mm
Recurrent vein of fore wing almost as long as second abscissa of medial vein.
Antenna 1/-segmented. Head pale brown, mesosoma and metasoma dark
brown. Body length 2.5 mm. – Vietnam O. bistriata (Kieffer)
Recurrent vein of fore wing 0.3–0.5 times as long as second abscissa of me-
dial vein. Antenna 19-segmented. Head and all body brownish yellow. Body
length 3.0 mm. – Vietnam O. brevipetiolata (Kieffer)
Ovipositor sheath 0.8 times as long as metasoma. Third metasomal tergite
submedially with transverse furrow. Transverse diameter of eye 2.8 times as
long as temple. Seven apical segments of antenna white. Parallel vein of fore
wing arising weakly behind middle of distal margin of brachial cell. Body
length 3.3 mm. – Vietnam O. alboapicalis Belokobylskij
Ovipositor sheath much longer than metasoma. Third metasomal tergite
without transverse sculptured furrow. Transverse diameter of eye 1.0-1.3
times as long as temple. Apical segments of antenna dark. Parallel vein of fore
wing arising strongly behind middle of distal margin of brachial cell20
Third metasomal tergite entirely smooth. Second tergite sometimes finely and
interruptedly striate in posterior 0.3. Body length 5.0–7.5 mm. – Japan
Third metasomal tergite basally with semi-circular striae. Second tergite al-
ways completely striate. Body length 4.0-6.2 mm Russia (Far East)
O. kasparyani Belokobylskij

Review of Chinese species

Ontsira abbreviata sp. n.

http://zoobank.org/C79C62F9-32ED-4F77-8457-4B7D1142975D http://species-id.net/wiki/Ontsira_abbreviata Fig. 1

Type material. Holotype: female, China, Shaanxi, Huoditang, 5.VI.1998 (Du Yuzhou), N 982455 (ZJUH).

Etymology. From Latin "abbreviatae", meaning "shortened", after the shortened second radiomedial cell of the fore wing

Description. Female. Body length 3.0 mm; fore wing length 2.7 mm.

Head width 1.6 times as long as its median length, 1.2 times as long as width of mesoscutum. Frons without carina, with distinct elongate pit between antennal sockets. Head behind eyes (dorsal view) regularly roundly narrowed; transverse diameter of eye 1.2 times as long as temple. Ocellar triangle situated behind middle of head (dorsal view), its anterior ocellus situated almost on level of anterior margins of eyes. Ocelli small, in almost equilateral triangle. POL 1.2 times as long as Od, 0.3 times as long as OOL. Eye sparsely and shortly setose, without emargination opposite antennal sockets, 1.2 times as high as broad. Face along eyes without carinae, with small shallow depressions above clypeus; width of face 1.4 times height of eye and 1.4 times height of face and clypeus combined. Diameter of antennal socket almost equal to distance between sockets and distance between socket and eye. Malar suture indistinct. Malar space about 0.6 times height of eye and 0.9 times basal width of mandible. Clypeus with distinct lower flange. Clypeal suture distinct and complete. Hypoclypeal depression oval, its width almost equal to distance from edge of depression to eye, 0.4 times width of face. Occipital carina ventrally fused with hypostomal carina at upper base of mandible. Maxillary palpi long, 1.5 times as long as head height.

Antennae rather slender, filiform, 25-segmented, as long as body. Scape 1.9 times as long as its maximum width. First flagellar segment 5.0 times as long as its apical width, and 1.4 times as long as second segment. Penultimate segment 2.7 times as long as wide, 0.5 times as long as first flagellar segment, and 0.9 times as long as apical segment; the apical segment distinctly pointed apically.

Mesosoma. Length 1.8 times its height. Pronotum not convex dorsally (lateral view), with distinct pronotal carina. Median lobe of mesoscutum (dorsal view) weakly protruding forward, with wide median furrow. Notauli deep, narrow, crenulate-rugulose. Prescutellar depression rather deep, with three median carinae, finely rugulose to smooth between carinae, 0.4 times as long as scutellum. Scutellum convex, without lateral carinae. Metanotum (dorsal view) with two strongly convergent and fused posteriorly lateral carinae, without median carinae; with short and obtuse metanotal tooth. Subalar depression rather shallow, wide, sparsely rugose-striate. Sternaulus deep, straight, finely crenulate, connected with prepectal carina anteriorly, running along anterior 0.6 of the lower part of mesopleuron. Metapleural flange long, wide, rounded apically. Propodeum with short, thick lateral tubercles.



Figure 1. *Ontsira abbreviata* sp. n. (female). **A** habitus, lateral view **B** head, front view **C** head, dorsal view **D** metasoma, dorsal view **E** mesosoma, lateral view **F** basal segments of antenna **G** fore and hind wings **H** mesosoma, dorsal view. Scale bar 0.5 mm.

Wings. Fore wing 3.1 times as long as maximum width. Radial vein arising weakly behind middle of pterostigma, from its basal 0.55. Radial cell not shortened; metacarp 1.25 times as long as pterostigma. First radial abscissa 0.5 times as long as maximum width of pterostigma. Second radial abscissa 4.5 times as long as first abscissa, 0.5 times as long as the straight third abscissa, and 1.15 times as long as first radiomedial vein. Second radiomedial cell 2.4 times as long as its maximum width, and 1.7 times as long as brachial cell. First medial abscissa weakly sinuate. Mediocubital vein almost straight. Recurrent vein distinctly antefurcal. Distance from nervulus to basal vein about 0.5 times as long as nervulus. Parallel vein arising distinctly behind middle of distal margin of brachial cell. Hind wing 4.5 times as long as maximum width. First costal abscissa 0.7 times as long as second abscissa. Mediocubital cell large, weakly widened toward apex, 7.0 times as long as wide, and 0.4 times as long as wing. Recurrent vein weakly curved, strongly antefurcal, unsclerotized.

Legs. Fore tibia with rather numerous slender spines arranged in almost single line. Hind coxa without dorsal tooth, 1.6 times as long as wide. Hind femur 4.2 times as long as wide. Hind tarsus 0.9 times as long as hind tibia. Hind basitarsus 0.7 times as long as second-fifth segments combined. Second segment of hind tarsus 0.45 times as long as basitarsus, 1.1 times as long as fifth segment (without pretarsus).

Metasoma about as long as head and mesosoma combined. First tergite with distinct dorsope, with small spiracular tubercles in basal 0.3, rather distinctly and almost linearly widened from base to apex. Maximum width of first tergite about twice its minimum width; length 1.15 times as long as its apical width. Second tergite without basomedian area; length of tergite 0.7 times as long as its basal width, almost equal to length of third tergite. Second suture very shallow and straight. Third tergite without additional transverse furrow. Ovipositor sheath 0.8 times as long as metasoma, as long as mesosoma, and 0.4 times as long as fore wing.

Sculpture and pubescence. Vertex and temple smooth; frons mostly smooth, finely coriaceous anterolaterally; face mostly smooth, finely rugulose-striate on upper part and on clypeus. Sides of pronotum smooth ventrally, coarsely crenulate medially, rugulose dorsally. Mesoscutum densely and distinctly granulate, rugulose anteriorly. Scutellum entirely finely granulate. Mesopleuron mostly smooth. Propodeum with distinctly areas delineated by carinae; basolateral areas large, smooth, but rugose in posterior 0.3 and along carinae; areola long and narrow, twice as long as wide; dorsal carina rather long, about twice as long as areola fork. Hind coxae coarsely striate in dorsal half, finely rugulose to smooth in ventral half. Hind femur smooth. First tergite with high complete sub-parallel dorsal carinae, rather distinctly striate, but smooth mediobasally (between dorsal carinae) and lateroapically. Second and the following tergites smooth. Vertex with rather sparse, long and semi-erect pale setae, glabrous in anterior half. Mesoscutum with dense, rather long and semi-erect pale setae, glabrous in rather wide submedian areas on lateral lobes. Hind tibia dorsally with rather long, sparse semi-erect setae basally and densely apically, length of these setae 0.7–1.0 times as long as maximum width of hind tibia.

Colour. Body dark reddish brown, metasoma behind first tergite reddish brown, malar area of head yellowish brown. Antennae dark brown, light reddish brown basally. Palpi yellow. Legs entirely yellow. Ovipositor sheath black. Forewing membrane faintly infuscate. Pterostigma brown, paler basally and apically.

Male unknown.

Distribution. China (Shaanxi).

Diagnosis. The new species is similar to *O. reticulata* Cameron (India), but differs in having the second radiomedial cell and the second radial abscissa short, the nervulus postfurcal, the ovipositor shorter, the hind coxa sculptured dorsally, the legs entirely yellow, the first tergite shorter, and the frons with distinct elongate pit between antennal sockets. It also resembles *O. gratia* Belokobylskij (from Taiwan), but differ in having the parallel vein arising distinctly behind middle of distal margin of brachial cell, the occipital carina fused below with hypostomal carina, the basolateral areas of propodeum without granulation, the radial vein arising weakly behind middle of pterostigma, and the second radial abscissa and the second radiomedial cell shorter.

Ontsira antica (Wollaston, 1858)

http://species-id.net/wiki/Ontsira_antica

Clinocentrus anticus Wollaston, 1858: 24; Yu et al. 2012. *Ontsira antica*: Marsh, 1973: 71; Shenefelt and Marsh 1976: 1322. *Doryctes gallicus* Reinhard, 1865: 248; Shenefelt and Marsh 1976: 1322; Yu et al. 2012.

Material examined. China: 1 female, Heilongjiang, Daiceng, 24.VII.1977 (He Junhua), N 771882 (ZJUH).

Distribution. China (Heilongjiang) (**new record**); Russia, Caucasus, Central and Western Europe, North America.

Ontsira apposita Belokobylskij, 1998

http://species-id.net/wiki/Ontsira_apposita

Ontsira apposita Belokobylskij, 1998: 466; Yu et al. 2012. *Ontsira brachytes* Chen & Shi, 2004: 27; Belokobylskij and Maetô 2009: 363.

Material examined. China: 1 male, Zhejiang, Gutianshan, 19.VII.1992 (Chen Xuexin), N 923661 (ZJUH).

Distribution. China (Zhejiang, Fujian); Vietnam.

Remark. The male of *O. apposita* is recorded for the first time. It differs from females in the following characters: the parallel vein of the fore wing arises slightly behind middle of distal margin of brachial cell, the recurrent vein of fore wing antefurcal, the first abscissa of mediocubital vein of hind wing not shorter than second abscissa, and the acrosternite of first metasomal segment weakly elongate.

Ontsira henana sp. n.

http://zoobank.org/E6BFCC07-1F4E-435B-876F-4B53E4752EF9 http://species-id.net/wiki/Ontsira_henana Fig. 2

Type material. Holotype: female, China, Henan, Neixiang, Baotianman, 15.VII.1998 (Chen Xuexin), N 989014 (ZJUH).

Etymology. Named after the locality of the holotype, Henan province.

Description. Female. Body length 2.8 mm; fore wing length 2.7 mm.

Head width 1.5 times as long as its median length, 1.15 times as long as width of mesoscutum. Frons without carina, with very shallow median furrow. Head behind eyes (dorsal view) regularly roundly narrowed; transverse diameter of eye 1.6 times as long as temple. Ocellar triangle situated on middle of head (dorsal view), its anterior ocellus situated weakly behind middle level of eyes. Ocelli small, in almost equilateral triangle. POL 1.3 times as long as Od, 0.4 times as long as OOL. Eye glabrous, without emargination opposite antennal socket, 1.1 times as high as broad. Face along eyes without carinae, with small shallow elongate depressions above clypeus; width of face 1.4 times as long as height of eye and 1.4 times as long as height of face and clypeus combined. Diameter of antennal socket 1.4 times as long as distance between sockets and 1.4 times as long as distance between socket and eye. Malar suture indistinct. Malar space 0.5 times as long as height of eye and equal to basal width of mandible. Clypeus with distinct lower flange. Clypeal suture distinct and complete. Hypoclypeal depression round, its width 0.8 times as long as distance from edge of depression to eye and 0.35 times as long as width of face. Occipital carina ventrally not fused with hypostomal carina. Maxillary palpi long, 1.4 times as long as head height.

Antennae rather thick, almost filiform, 26-segmented, 1.3 times as long as body. Scape 1.5 times as long as its maximum width. First flagellar segment 4.3 times as long as its apical width, 1.1 times as long as second segment. Penultimate segment 2.5 times as long as wide, 0.5 times as long as first flagellar segment, and 0.9 times as long as apical segment; the apical segment shortly pointed apically.

Mesosoma. Length 1.8 times as long as high. Pronotum not convex dorsally (lateral view), with rather distinct pronotal carina. Median lobe of mesoscutum (dorsal view) not protruding forward, without median furrow. Notauli deep, narrow and distinctly crenulate with rugosity partly. Prescutellar depression rather deep, with three median carinae, entirely rugulose, 0.3 times as long as scutellum. Scutellum convex, without lateral carinae. Metanotum (dorsal view) with two strongly convergent and fused posteriorly lateral carinae and without median carinae; with distinct and pointed metanotal tooth. Subalar depression rather shallow, wide, rugose-reticulate. Sternaulus deep, straight, entirely smooth, connected with prepectal carina anteriorly, running along anterior 0.6 of the lower part of mesopleuron. Metapleural flange long, wide, rounded apically. Propodeum with very short, thick lateral tubercles.



Figure 2. Ontsira henana sp. n. (female). A habitus, lateral view B head, dorsal view C head, front view D fore and hind wings E basal segments of antenna F mesosoma, lateral view G metasoma, dorsal view H mesosoma, dorsal view. Scale bar 0.5 mm.

Wings. Fore wing 3.0 times as long as its maximum width. Radial vein arising from middle of pterostigma. Radial cell not shortened. Metacarp 1.2 times as long as pterostigma. First radial abscissa 0.8 times as long as maximum width of pterostigma. Second radial abscissa 4.4 times as long as first abscissa, 0.7 times as long as the straight third abscissa and 1.3 times as long as first radiomedial vein. Second radiomedial cell 3.2 times as long as its maximum width, 2.4 times as long as brachial cell. First medial abscissa weakly curved. Mediocubital vein almost straight. Recurrent vein interstitial to first radiomedial vein. Distance from nervulus to basal vein almost equal to nervulus length. Parallel vein arising almost from middle of distal margin of brachial cell. Hind wing 5.0 times as long as its maximum width. First costal abscissa 0.6 times as long as second abscissa. First abscissa of mediocubital vein almost as long as second abscissa. Mediocubital cell large, distinctly widened toward apex, 7.5 times as long as wide, 0.4 times as long as whole length of wing. Recurrent vein straight, weakly antefurcal, unsclerotized.

Legs. Fore tibia with rather numerous slender spines arranged in almost single line. Hind coxa without dorsal tooth, 1.6 times as long as wide. Hind femur 3.6 times as long as wide. Hind tarsus 0.9 times as long as hind tibia. Hind basitarsus 0.6 times as long as second-fifth segments combined. Second segment of hind tarsus 0.6 times as long as basitarsus, 1.6 times as long as fifth segment (without pretarsus).

Metasoma 0.8 times as long as head and mesosoma combined. First tergite with distinct dorsope, without spiracular tubercles, rather weakly and almost linearly widened from base to apex. Maximum width of first tergite about twice its minimum width; length 1.1 times as long as its apical width. Second tergite without basomedian area, 0.7 times as long as its basal width, 1.2 times as long as length of third tergite. Second suture straight and shallow. Third tergite with shallow submedian transverse furrow. Ovipositor sheath 0.7 times as long as metasoma, 0.75 times as long as meso-soma and 0.3 times as long as forewing.

Sculpture and pubescence. Vertex and temple smooth; frons mostly smooth, finely granulate-coriaceous anterolaterally; face finely striate with dense fine granulation between striae, almost smooth laterally. Sides of pronotum entirely coarsely rugose-striate. Meso-scutum densely and coarsely granulate, coarsely rugose in narrow area on medioposterior half. Scutellum entirely densely granulate. Mesopleuron mostly smooth, finely granulate posteriorly. Propodeum with distinctly delineated by carinae areas; basolateral areas large, entirely coarsely granulate, additionally rugulose posteriorly; areola long and rather narrow, 1.7 times as long as wide; dorsal carina long, about 1.7 times as long as areola fork. Hind coxa dorsally coarsely rugose with granulation, densely granulate with fine rugosity laterally, almost smooth ventrally. Hind femur mostly smooth, finely rugulose-granulate dorsally. First tergite entirely densely, coarsely and linearly striate. Second tergite mostly rather finely and densely striate-rugulose, smooth posteriorly. Remaining tergites smooth. Vertex entirely with rather dense, short and semi-erect setae; mesoscutum entirely with dense, short and semi-erect setae, length of these setae 0.6–0.8 times maximum width of hind tibia.

Colour. Body dark reddish brown with almost black spots, head brownish yellow below. Antennae brownish yellow in basal half, brown to dark brown in apical half. Palpi pale yellow. Legs yellow or brownish yellow, infuscate distally. Ovipositor sheath black. Fore wing membrane faintly infuscate. Pterostigma brown, yellow in basal 0.3 and apically.

Male unknown.

Distribution. China (Henan).

Diagnosis. This new species is similar to *O. eugeniae* Belokobylskij (Russian Far East), but differs in having the vertex and most part of frons smooth, the eyes glabrous, the second tergite widely sculptured, the antennal segments slender, the third tergite with transverse furrow, and the vertex and mesoscutum with short setae. It differs from *O. gratia* Belokobylskij in having the second tergite widely sculptured, the second suture distinct, the third tergite with transverse submedian furrow, the hind femur wider, and the sternaulus smooth.

Ontsira ignea (Ratzeburg, 1852)

http://species-id.net/wiki/Ontsira_ignea

Bracon igneus Ratzeburg, 1852: 36.

Doryctes igneus: Reinhard 1865: 250.

Doryctodes igneus: Telenga 1941: 91.

Ontsira ignea: Shenefelt and Marsh 1976: 1323; Belokobylskij and Tobias 1986: 43 (as synonym of *O. imperator*); Belokobylskij and Maetô 2009: 370.

Material examined. China: 1 female, Shaanxi, Ningshan, Huoditang, 1580 m, 17.VIII.1998 (Yuan Decheng) (ZJUH); 1 female, Fujian, Sangang, X.1979 (Huang Juchang), N 20003927 (ZJUH); 1 male, Guangdong, Meizhou, 29.VII.2003 (Chen Jujian), N 20048483 (ZJUH).

Distribution. China (Shaanxi, Fujian, Guangdong) (**new record**); Japan Caucasus, Turkey, Israel, Central and Western Europe.

Ontsira imperator (Haliday, 1836)

http://species-id.net/wiki/Ontsira_imperator

Rogas (Doryctes) imperator Haliday, 1836: 46; Yu et al. 2012.

Doryctodes imperator: Hellen, 1940: 26; Telenga 1941: 91.

Ontsira imperator: Marsh 1973: 71; Shenefelt and Marsh 1976: 1324; Belokobylskij and Tobias 1986: 43; Belokobylskij 1998a: 56; Chen and Shi 2004: 29; Yu et al. 2012; Belokobylskij and Maetô 2009.

Material examined. China: 1 female, Jilin, Changchun, 8.X.1985 (Bai Hongyu), N 861610 (ZJUH).

Distribution. China (Jilin, Taiwan); Japan, Korea, Mongolia, Russia, Kazakhstan, Iran, Caucasus, Central and Western Europe, North America.

Ontsira macer Chen & Shi, 2000

http://species-id.net/wiki/Ontsira_macer

Ontsira macer Chen & Shi 2004: 30; Belokobylskij and Maetô 2009: 370.

Material examined. China: 1 female, Zhejiang, Qingyuan, Baishanzu, 3.X.1993 (Wu Hong), N 945613 (ZJUH); 1 female, Zhejiang, Longquan, Fengyangshan, 29–31.VII.2007 (Liu Jingxian), N 200804390 (ZJUH); 1 female, Fujian, Wuyishan, 7.IX.1989 (Wang Jiashe), N 964392 (ZJUH); 1 female, Fujian, Jiangle, Longqishan, 16.VII.1991 (Liu Changming), N 20007069 (ZJUH); 1 female, Fujian, Erliping, XI.1979 (Huang Juchang), N 20003841 (ZJUH); 1 female, Guangdong, Shixing, Chebaling, 25.V.2002 (Xu Zaifu), N 20051526 (ZJUH).

Distribution. China (Zhejiang, Fujian, Guangdong).

Ontsira neantica Belokobylskij & Maetô, 2009

http://species-id.net/wiki/Ontsira_neantica

Ontsira neantica Belokobylskij & Maetô, 2009: 379.

Material examined. China: 13 females, 5 males, China, Heilongjiang, Yichun, Daiceng, 29.V.1956 (Shi Zhenhua), N 5710.1(18) (ZJUH, ZISP).

Description of male (first record). Body length 3.2–3.8 mm; fore wing length 3.0–3.4 mm. Transverse diameter of eye 0.9–1.0 times as long as temple. Frons mostly smooth. Antennae rather thick, 33-segmented. First flagellar segment 3.2–3.4 times as long as its apical width, 1.1–1.3 times as long as second segment. Prescutellar depression almost smooth, with three carinae. Second radial abscissa of fore wing 2.4–2.6 times as long as first abscissa, 0.4–0.5 times as long as third abscissa. Second radiomedial cell 2.2–2.4 times as long as its maximum width, 1.2–1.3 times as long as brachial cell. First abscissa of mediocubital vein of hind wing 1.2–1.4 times as long as second abscissa. Hind femur 3.3–3.6 times as long as wide. Metasoma 1.1–1.2 times as long as head and mesosoma combined.

Distribution. China (Heilongjiang) (new record); Japan. **Remarks.** Vertex of females is usually striated on it sides.

Ontsira robusta sp. n.

http://zoobank.org/6266B6AA-1976-40FE-83EB-D59D4A208237 http://species-id.net/wiki/Ontsira_robusta Fig. 3

Type material. Holotype: female, "Korea, Kyonggi-do, Suwon-shi, Sodun-dong, Mt. Yogi, 23–29.VI.1994, Malaise trap" (ZISP).

Paratypes. 1 female, "Korea, Kyonggi-do, Suwon-shi, Sodun, Mt. Yogi, 16–23. VI.1994, Malaise trap" (ZISP); 1 female, China, North-East, 195(7?), N 5703.10 (ZIUH).

Etymology. After Latin "robustus", meaning "strong", because of the first metasomal tergite short and wide.

Description. Female. Body length 6.0–7.2 mm; fore wing length 4.8–5.4 mm.

Head width 1.2-1.3 times as long as its median length, about 1.1 times as long as width of mesoscutum. Frons without carina, with shallow or very shallow median furrow. Head behind eyes (dorsal view) weakly convex anteriorly, roundly narrowed posteriorly; transverse diameter of eye almost equal to temple. Ocellar triangle situated before middle of head (dorsal view), its anterior ocellus situated almost on middle level of eyes. Ocelli medium-sized, in triangle with base 1.2–1.3 times as long as its sides. POL 1.0-1.3 times Od, 0.4-0.5 times OOL. Eye rather densely and shortly setose, with very shallow or indistinct emargination opposite antennal sockets, 1.3–1.4 times as high as broad. Face along eyes without distinct carinae, with short and shallow elongate depressions above clypeus; width of face 1.15–1.20 times as long as height of eye and 1.3–1.4 times as long as height of face and clypeus combined. Diameter of antennal socket 1.1–1.4 times as long as distance between sockets and 1.4–1.6 times as long as distance between socket and eye. Malar suture indistinct. Malar space 0.40-0.45 times as long as height of eye, almost equal to basal width of mandible. Clypeus with wide flange ventrally. Clypeal suture complete, deep laterally and very shallow dorsally. Hypoclypeal depression round, its width 1.1–1.2 times as long as distance from edge of depression to eye, 0.45-0.50 times as long as width of face. Occipital carina ventrally fused with hypostomal carina at upper base of mandible. Maxillary palpi long, 1.1–1.2 times as long as head height.

Antennae rather thick, weakly setiform, 36–37-segmented, 0.75–0.80 times as long as body. Scape 1.7–1.9 times as long as its maximum width. First flagellar segment 2.7–3.0 times as long as its apical width, 1.15–1.30 times as long as second segment. Penultimate segment 1.7–1.9 times as long as wide, about 0.4 times as long as first flagellar segment, 0.7–0.8 times as long as apical segment; the apical segment distinctly pointed apically.

Mesosoma. Length about twice as long as its height. Pronotum weakly convex dorsally (lateral view), with fine pronotal carina in anterior 0.4. Median lobe of mesoscutum (dorsal view) rather distinctly protruding forward, with shallow and wide median furrow. Notauli deep anteriorly and shallow posteriorly, wide, densely coarsely crenulate-rugulose with granulation partly. Prescutellar depression rather deep, long, with one to three carinae, rather coarsely rugose entirely, about 0.5 times as long as scutellum. Scutellum weakly convex, without lateral carinae. Metanotum (dorsal view) with two strongly and curvedly convergent and fused posteriorly with large rugulose area lateral carinae, without median carinae; with short and obtuse metanotal tooth. Subalar depression shallow, wide, coarsely striate-rugose. Sternaulus deep, weakly curved or straight, oblique, densely and coarsely crenulate and with fine or very fine granulation, connected with prepectal carina anteriorly, running along anterior 0.6–0.7 of



Figure 3. *Ontsira robusta* sp. n. (female). **A** habitus, lateral view **B** head, dorsal view **C** mesosoma, lateral view **D** head, front view **E** basal segments of antenna **F** fore and hind wings **G** metasoma, dorsal view **H** mesosoma, dorsal view. Scale bar 0.5 mm.

lower part of mesopleuron. Metapleural flange rather short, wide, rounded apically. Propodeum with rather distinct, short, thick lateral tubercles.

Wings. Fore wing 3.5–3.6 times as long as its maximum width. Radial vein arising behind middle of pterostigma, inner basal part of pterostigma 1.2–1.3 times as long as its inner apical part. Radial cell not shortened; metacarp 1.3 times as long as pterostigma. First radial abscissa 0.6-0.8 times as long as maximum width of pterostigma. Second radial abscissa 3.6-4.0 times as long as first abscissa, 0.6 times as long as the straight third abscissa, 1.3-1.5 times as long as first radiomedial vein. Second radiomedial cell 2.3–2.5 times as long as its maximum width, 1.1 times as long as brachial cell. First medial abscissa almost straight or weakly sinuate. Mediocubital vein weakly curved. Recurrent vein 3.0–3.3 times second abscissa of medial vein. Distance from nervulus to basal vein 0.7–1.0 times as long as nervulus. Parallel vein arising from posterior 0.25 of distal margin of brachial cell. Hind wing 4.7-5.2 times as long as its maximum width. First costal abscissa 0.6-0.7 times as long as second abscissa. First abscissa of mediocubital vein 1.5-1.8 times as long as second abscissa. Radial cell weakly narrowed posteriorly. Mediocubital cell large, widened toward apex, 6.5–6.7 times as long as wide, 0.45–0.50 times as long as whole length of wing. Recurrent vein straight or weakly curved, oblique, more or less distinctly postfurcal, unsclerotized but distinctly pigmented.

Legs. Fore tibia with numerous slender spines arranged in rather narrow stripe. Hind coxa without dorsal tooth, 1.3–1.5 times as long as wide (with tubercle). Hind femur 3.5–3.6 times as long as wide. Hind tarsus 0.85–0.90 times as long as hind tibia. Hind basitarsus 0.80–0.85 times as long as second-fifth segments combined. Second segment of hind tarsus 0.40–0.45 times as long as basitarsus, 1.20–1.25 times as long as fifth segment (without pretarsus).

Metasoma 1.1–1.2 times as long as head and mesosoma combined. First tergite with large dorsope, with small spiracular tubercles in basal 0.3, rather weakly and almost linearly widened from base to apex. Maximum width of first tergite 1.7 times its minimum width; length 0.9–1.1 times as long as its apical width. Second tergite without basomedian area, 0.5–0.6 times as long as its basal width, 0.85–0.90 times as long as third tergite. Second suture straight, shallow, complete. Third tergite without transverse furrow. Ovipositor sheath 0.8–1.1 times as long as body, 1.5–2.2 times as long as metasoma, 2.4–3.3 times as long as mesosoma, 1.1–1.4 times as long as fore wing.

Sculpture and pubescence. Vertex entirely or mostly more or less coarsely or (rarely) rather finely curvedly striate; frons entirely coarsely and partly undulately rugosestriate, with granulation between striae; face distinctly and rather densely transverse striate-rugose with dense and fine granulation, clypeus smooth with rugulosity below; temple rather coarsely or rather finely vertically striate, smooth on more or less narrow part near eye. Sides of pronotum entirely coarsely rugose, with crenulate median furrow. Mesoscutum densely and rather finely punctulate-rugulose entirely, with dense and rather fine granulation between rugae, coarsely rugose in wide area on medioposterior half. Scutellum mostly smooth. Mesopleuron rather coarsely or sometimes finely rugose, with two-three small smooth areas. Propodeum with rather distinctly delineated by carinae areas, entirely coarsely rugose-reticulate; basolateral areas large, entirely coarsely rugose-reticulate with dense granulation at least in anterior half; areola long and narrow, 1.6–1.8 times as long as wide; dorsal carina long, 1.1–1.7 times as long as areola fork. Hind coxae almost entirely and densely rugose-reticulate with dense and fine granulation between rugae. Hind femur rugulose-areolate with dense fine granulation dorsally and laterally, almost smooth ventrally. First tergite densely, coarsely linearly or curvedly striate, rugose-reticulate in mediobasal 0.3–0.7, without distinct ground sculpture between striae. Second tergite sparsely striate in basal 0.2–0.3, sometimes (holotype) with three semicircular striae or with curved striae basomedially, smooth on remaining part. Remaining tergites smooth. Vertex with rather sparse, short and semi-erect setae; mesoscutum entirely with very dense, short and semi-erect pale setae. Hind tibia dorsally with short, dense and almost erect or semi-erect setae, length of these setae about 0.5 times as long as maximum width of hind tibia.

Colour. Body black, metasoma behind first tergite dark reddish brown, yellowish brown or reddish brown ventrally, sometimes metasoma light reddish brown medially. Antennae dark reddish brown to black. Palpi reddish brown or sometimes dark reddish brown. Legs reddish brown, partly yellowish, all tibiae basally yellow. Ovipositor sheath black. Fore wing membrane rather distinctly infuscate. Pterostigma brown, sometimes very shortly paler basally and apically.

Male unknown.

Distribution. China (North East); Korea.

Diagnosis. This new species is very similar to *O. imperator* (Haliday), but differs in having the vertex almost entirely or mostly and temple at most part distinctly striate, and the mesoscutum almost entirely, very densely and finely granulate with sparse punctation. It is also similar to *O. rugivertex* sp. n., but differs in having the antennae rather distinctly shorter than body, the first abscissa of mediocubital vein of hind wing longer, the hind femur wider, the second segment of hind tarsus shorter, the first tergite shorter and wider, the second tergite shorter, and the palpi dark.

Ontsira rugivertex sp. n.

http://zoobank.org/E349C77C-E5BB-4A7E-B1E0-3BF3B2AB5D88 http://species-id.net/wiki/Ontsira_rugivertex Fig. 4

Type material. Holotype: female, China, Henan, Neixiang, 14.VII.1998 (Chen Xuexin), N 988629 (ZJUH).

Paratype. China: 1 female, Shaanxi, Zhouzhi, Houzhenzi, 13.VI.1998 (Ma Yun), N 981419 (ZJUH).

Etymology. After Latin "rugae" meaning "wringle" and "vertex" meaning "vertex, top" because of the vertex almost entirely and coarsely undulately striate.

Description. Female. Body length 5.5–7.0 mm; fore wing length 5.0–6.2 mm.

Head width 1.2–1.3 times as long as its median length, 1.1 times as long as width of mesoscutum. Frons without carina, with shallow or very shallow median furrow.



Figure 4. *Ontsira rugivertex* sp. n. (female). **A** habitus, dorsal view **B** head, dorsal view **C** mesosoma, dorsal view **D** head, front view **E** fore and hind wings **F** mesosoma, dorsal view **G** basal segments of antenna **H** metasoma, dorsal view. Scale bar 0.5 mm.

Head behind eyes (dorsal view) weakly convex anteriorly, roundly narrowed posteriorly; transverse diameter of eye 1.0-1.1 times as long as temple. Ocellar triangle situated distinctly behind middle of head (dorsal view), its anterior ocellus situated behind middle level of eyes. Ocelli medium-sized, in triangle with base 1.2–1.3 times as long as its sides. POL 1.0-1.2 times Od, 0.35-0.40 times OOL. Eye rather densely and shortly setose, with shallow or very shallow emargination opposite antennal sockets, 1.3 times as high as broad. Face along eyes without distinct carinae, with distinct small shallow elongate depressions above clypeus; width of face 1.2 times as long as height of eye and 1.20–1.25 times as long as height of face and clypeus combined. Diameter of antennal socket 1.0-1.3 times as long as distance between sockets and 1.5-1.7 times as long as distance between socket and eye. Malar suture indistinct. Malar space 0.45-0.50 times as long as height of eye and 0.8-0.9 times as long as basal width of mandible. Clypeus with wide flange ventrally. Clypeal suture distinct and complete. Hypoclypeal depression round, its width almost equal to distance from edge of depression to eye, 0.45 times as long as width of face. Occipital carina ventrall fused with hypostomal carina at upper base of mandible. Maxillary palpi long, 1.3–1.4 times as long as head height.

Antennae rather thick, almost filiform, 37–43-segmented, almost as long as body. Scape 1.8–2.0 times as long as its maximum width. First flagellar segment 3.6–3.8 times as long as its apical width, 1.2–1.3 times as long as second segment. Penultimate segment 2.0–2.2 times as long as wide, 0.4 times as long as first flagellar segment, 0.7 times as long as apical segment; the apical segment distinctly pointed apically.

Mesosoma. Length 1.8–1.9 times as long as high. Pronotum not convex dorsally (lateral view), with fine pronotal carina in posterior 0.4. Median lobe of mesoscutum (dorsal view) rather distinctly protruding forward, without or with shallow median furrow. Notauli deep, wide, densely coarsely crenulate and partly with rugosity. Prescutellar depression rather deep, without median carina, with several striae, coarsely rugose entirely, about 0.5 times as long as scutellum. Scutellum convex, without lateral carinae. Metanotum (dorsal view) with two strongly convergent and fused posteriorly lateral carinae, without median carinae; with short and obtuse metanotal tooth. Subalar depression shallow, wide, coarsely rugose-reticulate. Sternaulus deep, almost straight, densely and coarsely crenulate, connected with prepectal carina anteriorly, running along anterior 0.60–0.65 of the lower part of mesopleuron. Metapleural flange rather short, wide, rounded apically. Propodeum with distinct, short, thick lateral tubercles.

Wings. Fore wing 3.4 times as long as its maximum width. Radial vein arising weakly behind or from middle of pterostigma. Radial cell not shortened; metacarp 1.3–1.4 times as long as pterostigma. First radial abscissa 0.6–0.7 times as long as maximum width of pterostigma. Second radial abscissa 3.5–3.7 times as long as first abscissa, 0.5–0.6 times as long as the straight third abscissa, 1.3–1.5 times as long as first radiomedial vein. Second radiomedial cell 2.2 times as long as maximum width, 1.1–1.2 times as long as brachial cell. First medial abscissa almost straight. Mediocubital vein not curved. Recurrent vein 2.5–3.0 times as long as second abscissa of medial vein. Distance from nervulus to basal vein 0.4–1.0 times as long as nervulus. Parallel

vein arising from posterior 0.15–0.25 of distal margin of brachial cell. Hind wing 4.5–4.8 times as long as its maximum width. First costal abscissa 0.7 times as long as second abscissa. First abscissa of mediocubital vein 1.2–1.5 times as long as second abscissa. Radial cell weakly narrowed posteriorly. Mediocubital cell large, distinctly widened toward apex, about 6.5 times as long as wide, 0.40–0.45 times as long as whole length of wing. Recurrent vein weakly and evenly curved, interstitial, sclerotized.

Legs. Fore tibia with rather numerous slender spines arranged in narrow stripe. Hind coxa without dorsal tooth, 1.6 times as long as wide. Hind femur 4.5 times as long as wide. Hind tarsus equal to hind tibia. Hind basitarsus 0.70–0.75 times as long as second-fifth segments combined. Second segment of hind tarsus 0.5 times as long as basitarsus, 1.6–1.8 times as long as fifth segment (without pretarsus).

Metasoma 1.1 times as long as head and mesosoma combined. First tergite with large dorsope, with small spiracular tubercles in basal quarter, rather weakly and almost linearly widened from base to apex. Maximum width of first tergite about twice as long as its minimum width; length 1.3–1.4 times as long as its apical width. Second tergite without basomedian area, 0.75–0.80 times as long as its basal width, 1.2 times as long as third tergite. Second suture straight, very shallow, almost absent medially. Third tergite without transverse furrow. Ovipositor sheath 1.1–1.2 times as long as body, 2.1–2.4 times as long as metasoma, 3.1–3.4 times as long as mesosoma, 1.2–1.4 times as long as fore wing.

Sculpture and pubescence. Vertex entirely or mostly more or less coarsely undulately striate, almost smooth near ocellar triangle; frons entirely coarsely rugosereticulate; face distinctly and rather densely transverse striate, rugose medially, almost smooth below; temple coarsely rugose in upper 0.20-0.25, smooth on remaining part. Sides of pronotum entirely coarsely rugose-striate. Mesoscutum densely and distinctly rugose with dense fine granulation between rugae, coarsely and sparsely rugose in medioposterior half. Scutellum rather densely punctate, sometimes with very fine granulation between punctulae. Mesopleuron coarsely rugose-striate, rather narrowly smooth medially. Propodeum with distinctly delineated by carinae areas; basolateral areas large, entirely coarsely rugose-areolate; areola short and rather narrow, 1.4-1.5 times as long as wide; dorsal carina rather long, about twice as long as areola fork. Hind coxae almost entirely rugose-striate, partly with fine granulation, sculpture below fine. Hind femur dorsally and laterally rugose with fine granulation, almost smooth ventrally. First tergite densely, coarsely and linearly striate with fine rugulosity between striae. Second tergite densely striate in basal 0.3. Remaining tergites smooth. Vertex with rather dense, short and semi-erect setae; mesoscutum entirely with dense, short and semi-erect pale setae. Hind tibia dorsally with short, very dense and semi-erect setae, length of these setae about 0.5 times as long as maximum width of hind tibia.

Colour. Body black; metasoma medially or behind first tergite reddish brown. Antennae black, dark reddish brown basally. Palpi pale yellow. Legs light reddish brown, all coxae, trochanters and tibiae basally yellow, the remaining tibiae and tarsi sometimes reddish brown to dark reddish brown. Ovipositor sheath black. Fore wing membrane faintly infuscate. Pterostigma brown, shortly paler basally and apically. Male unknown.

Distribution. China (Henan, Shaanxi).

Diagnosis. The new species is similar to *O. ignea* Ratzeburg, but differs in having the vertex coarsely rugose-striate entirely or almost entirely, the first flagellar segment shorter, the second tarsal segment of hind leg distinctly longer than fifth segment (without pretarsus), and the mesoscutum coarsely rugose-granulate. It resembles *O. robusta* sp. n., but their differences are listed after the description of *O. robusta*.

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RESEARCH ARTICLE



Taxonomy, distribution, and natural history of flying foxes (Chiroptera, Pteropodidae) in the Mortlock Islands and Chuuk State, Caroline Islands

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Abstract

The taxonomy, biology, and population status of flying foxes (Pteropus spp.) remain little investigated in the Caroline Islands, Micronesia, where multiple endemic taxa occur. Our study evaluated the taxonomic relationships between the flying foxes of the Mortlock Islands (a subgroup of the Carolines) and two closely related taxa from elsewhere in the region, and involved the first ever field study of the Mortlock population. Through a review of historical literature, the name Pteropus pelagicus Kittlitz, 1836 is resurrected to replace the prevailing but younger name P. phaeocephalus Thomas, 1882 for the flying fox of the Mortlocks. On the basis of cranial and external morphological comparisons, Pteropus pelagicus is united taxonomically with P. insularis "Hombron and Jacquinot, 1842" (with authority herein emended to Jacquinot and Pucheran, 1853), and the two formerly monotypic species are now treated as subspecies—P. pelagicus pelagicus in the Mortlocks, and P. p. insularis on the islands of Chuuk Lagoon and Namonuito Atoll. The closest relative of P. pelagicus is P. tokudae Tate, 1934, of Guam, which is best regarded as a distinct species. Pteropus p. pelagicus is the only known resident bat in the Mortlock Islands, a chain of more than 100 atoll islands with a total land area of <12 km². Based on field observations in 2004, we estimated a population size of 925-1,200 bats, most of which occurred on Satawan and Lukunor Atolls, the two largest and southernmost atolls in the chain. Bats were absent on Nama Island and possibly extirpated from Losap Atoll in the northern Mortlocks. Resident Mortlockese indicated bats were more common in

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the past, but that the population generally has remained stable in recent years. Most *P. p. pelagicus* roosted alone or in groups of 5–10 bats; a roost of 27 was the largest noted. Diet is comprised of at least eight plant species, with breadfruit (*Artocarpus* spp.) being a preferred food. Records of females with young (April, July) and pregnant females (July) suggest an extended breeding season. *Pteropus p. pelagicus* appears most threatened by the prospect of sea level rise associated with global climate change, which has the potential to submerge or reduce the size of atolls in the Mortlocks. Occasional severe typhoons probably temporarily reduce populations on heavily damaged atolls, but hunting and ongoing habitat loss are not current problems for the subspecies.

Keywords

Pteropus phaeocephalus, P. pelagicus, P. insularis, P. tokudae, Mortlock Islands, Chuuk, Micronesia, atoll, taxonomy, distribution, status, natural history, climate change, sea level rise

Introduction

Many islands of the west-central Pacific Ocean remain poorly known biologically, particularly the numerous, small, low-lying, coralline atolls and atoll-like islands of Micronesia. Their inaccessibility and relatively depauperate biotas (compared with those of larger and higher islands) have contributed to a paucity of visiting biologists. However, an understanding of the biogeography and biodiversity of Oceania remains incomplete without knowledge of the species that inhabit these miniscule lands.

The genus *Pteropus* is comprised of about 65 species of flying foxes, making it by far the largest genus in the family Pteropodidae (Simmons 2005; Helgen et al. 2009). Primarily island-dwelling, the genus is widespread through the Indo-Pacific region westward to the islands off eastern Africa. Much taxonomic work is still needed in the genus. Additionally, many species of *Pteropus* remain poorly known in terms of their population status, biology, and specific conservation needs. In particular, few studies of atoll-dwelling populations have been conducted (Dolbeer et al. 1988, Wiles et al. 1991, Holmes et al. 1994). The need for such studies is especially pressing in Pacific archipelagos, where larger bats have suffered considerable declines, extirpations, and extinctions over the past 200 years (Flannery 1995; Wiles et al. 1997; Helgen 2005; Helgen et al. 2009; Wiles and Brooke 2009, Nakamoto et al. 2012).

Although *Pteropus phaeocephalus* Thomas, 1882 was originally described as a distinct species endemic to the Mortlock Islands, a group of atolls in central Micronesia, there has long been recognition of the similarity between this form and *P. insularis*, which is restricted to the neighboring main islands and barrier reef islands of Chuuk Lagoon and Namonuito Atoll located 171 km to the northwest (Oustalet 1895, Andersen 1912, Rainey and Pierson 1992, Kepler 1994, Flannery 1995). This has resulted in suggestions that *P. phaeocephalus* may be better regarded as a subspecies or synonym of *P. insularis* (Oustalet 1895; Koopman 1993; K. Helgen, in Simmons 2005). Information on the distribution, relative abundance, and ecology of *P. phaeocephalus* is almost nonexistent, and the lack of comparative material from these islands, hitherto limited to the holotype, has impeded taxonomic appraisal. Specimens obtained from Namoluk and Satawan Atolls during this study provide material for new comparisons and a taxonomic reappraisal. Our field observations together with information provided by Mortlockese islanders furnish new data on the distribution, abundance, and biology of flying foxes in the Mortlocks. In light of the many threats to biodiversity on Pacific islands (Helgen et al. 2009, Wiles and Brooke 2009, Woinarski 2010), we also discuss conservation concerns relating to these bats.

Study area

The Mortlock Islands (07°00'N, 152°35'E to 05°17'N, 153°39'E) are a part of Chuuk (formerly Truk) State, one of four states comprising the Federated States of Micronesia (FSM), the others being Yap, Pohnpei, and Kosrae. The FSM together with the Republic of Belau (Palau) make up the Caroline Islands in the tropical western Pacific Ocean. The Mortlocks are a chain of five atolls and one low, coral island spanning 224 km (Figure 1). Land area totals 11.9 km², distributed among more than 100 islands; Ta, Satawan Atoll, is the largest island (Table 1). Maximum elevations are only 3–5 m asl. Over the years, a confusing array of alternative names and spellings has been proposed for different islands and island groups in the Mortlocks and Chuuk Lagoon (Baker 1951, Bryan 1971, Berg 1993). We use the names Northern Mortlocks for Nama Island and Losap Atoll, Central Mortlocks for Namoluk Atoll, and Southern Mortlocks for Ettal, Lukunor, and Satawan Atolls.

The Mortlocks fall within the equatorial rainbelt and are wet enough to support mesophytic vegetation (Mueller-Dombois and Fosberg 1998), though some of the smaller islets that lack a fresh water lens are more xeric. Coconut (Cocos nucifera L.) forest is the predominant vegetation type, with breadfruit (Artocarpus spp.) being a codominant tree in the interior of the larger islands. Other common forest and forest edge trees include Barringtonia asiatica (L.) Kurz, Ficus spp., Guettarda speciosa L., Hernandia sonora L., Neisosperma oppositifolia (Lam.) Fosb. & Sachet, Pandanus spp., and Terminalia samoensis Rech. Forest canopy height ranges from 10 to 20 m. The forest abuts the beach or merges abruptly with a narrow zone of coastal scrub or thicket dominated by Tournefortia argentea L. f. and Scaevola taccada (Gaertn.). Large community-maintained taro patches occupy much of the interior of Nama, Namoluk, Satawan, Kuttu, Moch, Oneop, and Lekinioch Islands. More detailed accounts of island vegetation and physiognomy exist for Losap Atoll (Severance 1976, Manner and Sana 1995), Namoluk Atoll (Marshall 1975), Ettal Atoll (Nason 1970), Lukunor Atoll (Borthwick 1977, Tolerton and Rauch n. d. [1949?]), and Kuttu Island, Satawan Atoll (Reafsnyder 1984).

All six island groups comprising the Mortlocks are inhabited, but only 1–4 islands in each group have permanent settlements (Table 1). The other islands are visited by atoll residents with varying degrees of frequency to cultivate taro or to gather coconuts, crabs, and other forest and coastal commodities. A total of 6,911 people lived in the Mortlocks in 2000, representing a density of 581 people per km².



Figure 1. Location map for the Mortlock Islands and Chuuk Lagoon, Micronesia. Inset **A** location of islands in the west-central Pacific Ocean, G = Guam, K = Kosrae, NG = New Guinea, Pa = Palau, Po = Pohnpei, Y = Yap; inset **B** southern end of Satawan Atoll, solid circles indicate beach sites where interisland movement of flying foxes was assessed (see Table 5) and the open star indicates the airport station count site on Ta Island.

Methods

Museum specimens utilized in this study are deposited in the collections of the American Museum of Natural History, New York, USA (AMNH), the Academy of Natural Sciences, Drexel University, Philadelphia, USA (ANSP), the Natural History Museum,

Island group	Land area (km²)ª	Number of islands	Largest island (km ²) ^a	Number of inhabited islands	Number of residents ^b	Distance to next atoll (km) ^c	Observation days ^d
Northern							
Mortlocks							
Nama Island	0.75	1	Nama (0.75)	1	995	14	7
Losap Atoll	1.03	10	Lewel (0.56)	2	875	110	1
Central							
Mortlocks							
Namoluk Atoll	0.83	5	Namoluk (0.31)	1	407	53	11
Southern							
Mortlocks							
Ettal Atoll	1.89	20 ^e	Ettal (0.97)	1	267	7	3
Satawan Atoll	4.59	65 ^f	Ta (1.55)	4	2,935	8	70
Lukunor Atoll	2.82	18	Lekinioch ^g (1.28)	2	1,432	_	26

Table 1. Statistical data for the Mortlock Islands, Chuuk State, Federated States of Micronesia.

^a From Bryan (1971).

^b Based on the 2000 national census (Division of Statistics 2002).

° Measured reef to reef.

^d Total number of days spent on the island(s) by DWB while conducting faunal surveys for flying foxes, birds, lizards, butterflies, and dragonflies.

^e Number of islands counted by DWB while walking on the reef flat, but Bryan (1971) recorded 18.

^f Based on information given DWB by residents of Satawan Atoll, but exact number uncertain. Bryan (1971) indicated "approximately" 49 islands in the summary section for "Truk District," but mentioned at least 80 named and unnamed islands in the atoll and described one area in the northeast part of the atoll as having "numerous small cays on edge of reef" without naming or numbering them.

^g Formerly Lukunor Island, and known also as Likinioch, Lukinoch, and Lukunoch Island.

London, UK (BMNH), Brigham Young University-Hawaii Campus, Laie, Hawaii, USA (BYUH), College of Micronesia-FSM, Kolonia, Pohnpei, Federated States of Micronesia (COM), the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and the Museum für Naturkunde, Humboldt University, Berlin, Germany (ZMB).

Measurements of specimens are in millimeters and grams. Cranial and forearm measurements were taken on museum specimens (skins, skulls, and fluid preserved specimens) using dial calipers. Cranial measurements (see Figure 2) are abbreviated (and defined) as follows: GLS (greatest length of skull; distance from posterior midpoint on occipital crest to anterior midpoint of premaxillae); PL (palate length; distance from anterior midpoint of premaxillae to posterior midpoint of bony palate); ZW (greatest width across the zygomatic arches); IOB (width of interorbital constriction); BBC (breadth of braincase, measured across the braincase at squamosal bases);



Figure 2. Cranial measurements employed in this study. See Methods for abbreviations.

MTR (length of maxillary toothrow, alveolar distance from anterior root of canine to posterior root of last molar); CC (external, alveolar distance across upper canines); M1M1 (external, alveolar distance across upper first upper molars). Head-body length (snout to rump) and ear length were measured with a millimeter ruler on fresh material or recorded from museum specimen labels. Body mass was obtained from fresh specimens using Pesola scales or recorded from specimen labels. Immatures are defined as neonates to young weighing ≤ 100 g. Subadults are defined as adult-sized or nearly adult-sized young with incompletely fused skull sutures/synchondroses (cf. Helgen 2004) and some indication of cartilaginous epiphyseal swellings in the bones of the wing. Because sexual dimorphism is negligible in these bats, measurements for both sexes are pooled in our comparisons. Statistical methods included a two-sample *t*-test processed by Excel 2000 data analysis.

Standard descriptive statistics (mean, standard deviation, and observed range) were calculated for the samples of populations and species listed in the tables. Only cranial and dental measurements were incorporated in the multivariate analyses. Principal component analyses were computed using the combination of cranial and dental measurements indicated in tables and in the text. All measurement values were transformed to natural logarithms prior to multivariate analysis. Principal components were extracted from a covariance matrix. Variables for multivariate analyses were selected judiciously to maximize sample sizes for comparison by allowing for inclusion of partially broken skulls in some cases. The software program Statistica 8.0 (Statsoft Inc., Tulsa, Oklahoma, USA) was used for multivariate analysis.

Field work for this study began as part of a biological survey of terrestrial vertebrates and selected insect groups on Satawan Atoll, but was expanded in 2004 to include broader population assessments of flying foxes and other wildlife in the Mortlocks. Field surveys were conducted on Satawan Atoll during 17–26 December 2002, 7 July–1 August 2003, 30 March–9 April 2004, 22 June–6 July 2004, and 1–5 August 2004. The five other groups of islands were visited in 2004: Nama Island, 7–14 July; Losap Atoll, 10 July; Namoluk Atoll, 19–29 July; Ettal Atoll, 30 July–1 August; and Lukunor Atoll (Lekinioch Island only), 2–3 August. In 2012, incidental observations were made at Lukunor Atoll, 20 June–15 July, and Satawan Atoll, 15–17 July. All field work was conducted by DWB.

Information on the abundance and biology of bats came from a combination of sources. Station counts of flying bats were conducted on Satawan Atoll at two types of locations providing relatively unobstructed views of the sky: the Ta airport and six beach sites where interisland movement of bats was assessed (Figure 1). These counts were made by a single person at sunrise or sunset, lasted 25–95 minutes, and were made once or twice per time period at each station except for multiple counts at the Ta airport.

Flying foxes (and other wildlife) were also counted during walks conducted from mid-morning to mid- to late afternoon. These were made along pre-existing trails or by following a compass bearing through the center of less frequently visited islands, usually along the long axis of an island, but occasionally at right angles to it. Each route was surveyed only once. Care was taken to avoid double counting bats flushed by the observer. An undetermined, but probably substantial, proportion of roosting bats was hidden from view by the relatively dense forest canopy. Roosting flying foxes were viewed with 10x binoculars to observe behavior and search for the presence of young. Other information on bats was obtained from incidental observations and atoll residents. We did not search for feeding evidence of bats (i.e., discarded fruit, chewed pellets, fecal splats). An estimate of the number of flying foxes on each atoll was made based on: 1) overall numbers of bats seen, 2) percentage of each atoll covered by the observer, 3) the quality and amount of forest on an atoll, and 4) information provided by island residents, especially for Namoluk, Ettal, and Lukunor Atolls.

Results

Taxonomy

Pteropus pelagicus Kittlitz, 1836

Taxonomic history

The Russian research vessel Senyavin, under command of Friedrich [Feodor] Lütke, and with F. H. von Kittlitz as one of the ship's naturalists, was in the eastern Caroline Islands early in 1828 (Nozikov 1946). After leaving Ualan (= Kosrae), the Senyavin spent approximately the first two weeks of February in the southern Mortlocks (Lütke 1835). Although the ship traveled along the coasts of all three southern atolls, the only anchorage and the base of scientific operations was the harbor at Lukunor Atoll (Lütke 1835). Remarking on the fauna of Lukunor, Kittlitz (1836) stated "Nous prîme, comme à Ualan, deux mammifères dont l'un est un Pteropus (Pteropus pelagicus m.) qui sans aucun doute diffère de celui de cette île, tant par sa taille qui est beaucoup moindre, que par une tache blanche de forme circulaire qu'il a sur l'abdomen [We found, as on Kosrae, two mammals, one of which is a Pteropus (Pteropus pelagicus mihi) that without any doubt differs from the one of that island by its much smaller size and by a round white patch on its abdomen]." Although Kittlitz's description is brief and unaccompanied by illustration, clearly he was referring to the same species that Thomas (1882: 756) named Pteropus phaeocephalus. The zoological specimens that Kittlitz obtained during this expedition were deposited in the Russian Academy of Sciences in St. Petersburg (Baker 1951, Hume 2001), but the only flying foxes in the St. Petersburg collection today are two *P. pselaphon* Say from the Bonin Islands, Japan (V. Loskot, pers. comm.). We thus regard Pteropus pelagicus as the earliest name for the flying fox currently known as *P. phaeocephalus*, and advocate its usage (see Taxonomic Conclusions, below).

Thomas (1882) described *P. phaeocephalus* from the Mortlock Islands based on "a gravid female in alcohol" collected by Dr. [John = Johann = Jan] Kubary for the Godeffroy Museum, Hamburg, Germany, and subsequently transferred to the Natural History Museum, London (BMNH 82.10.27.4). Andersen (1912: 299) considered the holotype as "perfectly similar to *Pt. insularis* [from Chuuk Lagoon islands] in skull, dentition, palate-ridges, and all external characters, except much paler colour of the fur, particularly on the back." He (Andersen 1912: 299) concluded "the evidence is in favour of the assumption that *Pt. phaeocephalus* (Mortlock group) is specifically distinct from *Pt. insularis* (Ruck [= Chuuk] group)." This opinion has prevailed in the literature until relatively recently. Koopman (1993) remarked that *P. phaeocephalus* is probably better recognized as a subspecies of *P. insularis*, and Simmons (2005) concurred in referring to the Mortlock population as *P. i. phaeocephalus*.

The holotype of *P. phaeocephalus* is labeled as collected by Kubary in the Mortlock Islands, but the date and the name of the island are unstated. Kubary traveled widely in the Pacific while employed as a naturalist and ethnographer by the Godeffroy Museum

(Spoehr 1963). He visited the Mortlock Islands apparently on two occasions. Hezel (1979: 33, revised online as of 2002 and unpaged) stated that the brig *Iserbrook* put in at Ta, Satawan Atoll on 16 February 1873 and "returned in July or August with John Kubary aboard from Palau." Referring to the same voyage, Paszkowski (1971: 48) stated that "in May, 1873, Kubary sailed on the *Iserbrook* [from Palau] and visited the islands of Ngulu, Ulithi, Woleai, Nukuoro, and Mortlock...[and] landed at Ponape [= Pohnpei] in August, 1873." Little is known of Kubary's activities in the Mortlocks during this visit, which may have been very brief, and Kubary did not allude to it in his ethnography of the Mortlocks (Kubary 1880). Also, any specimens that may have been collected at this time may have been among those lost in a subsequent shipwreck at Jaluit, in the Marshall Islands, in September 1874, when only a small part of Kubary's collections of the previous five years were saved (Paszkowski 1971, 1987).

Kubary returned to the Mortlocks in 1877. In a separate and anonymously written introduction to the ethnography that Kubary apparently sent to L. Friederichsen, editor of Mittheilungen der Geographischen Gesellschaft in Hamburg, the author (L. Friederichsen?) or authors (in Kubary 1880) stated "Kubary verweilte auf den Mortlock-Inseln während der Monate März bis Ende Mai 1877 und zwar speciell auf der Inseln Tä, Uoytä und Aliar [Kubary visited the Mortlock Islands, particularly the islands Ta, Weito, and Aliar during the months of March through the end of May 1877]." Westwood (1905: 89, 112) saw Kubary also on Satawan Island (immediately to the east of Ta) during his visit in 1877. In light of this information, the holotype of *P. phaeocephalus* probably was collected on Satawan Atoll sometime during March– May 1877 and very likely on Ta Island, where flying foxes are now common and where Kubary seems to have spent most of his time during his three months in the Mortlocks (Nason 1970: 363).

Matschie (1899) discussed a specimen he referred to as *Pteropus phaeocephalus* from Pohnpei in the Caroline Islands, obtained by Otto Finsch (ZMB A4065), but this is actually a specimen of a *Pteropus* allied to *P. mariannus* (Andersen 1912), previously discussed as a specimen of *P. ualanus*, otherwise known only from Kosrae (Wiles et al. 2008) but in fact most closely resembling *P. pelewensis* of Palau (confirmed by KMH). The source of Finsch's specimen was possibly mislabeled or the specimen may represent a population of *P. pelewensis* (or a closely related taxon) that has become extinct on Pohnpei, where only *Pteropus molossinus* occurs today (Flannery 1995).

Morphological comparisons

External comparisons

Among the 11 specimens from Satawan Atoll, the mantle ranges from creamy white to deep buff or tawny in adults and subadults, and is grayish brown (without yellowish or reddish highlights) in immatures. It averages darker (more tawny, less pale buff) in the six adults from Namoluk Atoll. In all Mortlock specimens, the mantle is bisected



Figure 3. (**A**) Scanned image of Plate LIV from original description of *Pteropus phaeocephalus* Thomas 1882, which is presumably based on the holotype (**B**) dorsal view and (**C**) ventral view of *Pteropus p. pelagicus* from Satawan Atoll (**D**) ventral view and (**E**) dorsal view of *P. p. insularis* from Weno, Chuuk Lagoon.

by a narrow to broad area of darker (brown) pigmentation, which, in some cases, gives the appearance of having pale shoulder patches. In specimens from both Namoluk and Satawan, the back and rump are dark brown (occasionally tinged with reddish brown in Satawan specimens), with scattered pale-tipped hairs; Namoluk specimens average slightly darker than those from Satawan. In both the Namoluk and Satawan material, the face is dark brown to nearly black and with varying amounts of grizzling. The top of the head is brown or grayish brown. The venter is usually light brown to pale reddish brown anteriorly (on throat and chest) and dark brown posteriorly; subadults are more uniformly light brown. A large prominent white or pale yellowish white patch, 20–40 mm wide, occurs midventrally in most specimens (Figure 3C); it is occasionally slightly reduced or nearly obsolete.

Mortlock Islands specimens generally match the color descriptions of the holotype of *phaeocephalus* as described by Thomas (1882) and Andersen (1912), although the pale-tipped hairs on the dorsum described as "nearly white" by Thomas (1882) and "golden cream buff" by Andersen (1912) are much sparser in the new material and visible only upon close inspection. Mortlock specimens, especially some of the paler and brighter individuals from Satawan, closely resemble the illustration (Plate LIV) in Thomas (1882) (see Figure 3A). DWB observed an unusually pale individual through binoculars from a distance of 30–40 m on Toimon Island, Namoluk Atoll, on 27 July 2004. The venter and sides were entirely creamy white. Only the top of the head, neck, a small part of the mantle middorsally, and most of the back and rump were dark brown.

Compared with a sample of five specimens of *P. insularis*, all presumably from Chuuk Lagoon (four from Weno, one [MCZ 7023] of uncertain origin), the Mortlock Islands bats tend to show greater contrast between the paler coloration of the mantle and the darker pigmentation on the back and rump. The midventral pale patch is consistently larger in the Mortlock specimens that we examined, although Andersen (1912: 296) stated "the size of this bright pectoral patch varies greatly individually [in P. insularis from Chuuk Lagoon], but in none is it wanting...." The cotype of P. insularis from Chuuk Lagoon illustrated in Hombron and Jacquinot (1844: plate v) shows a prominent mid-ventral patch as large as any seen in specimens from the Mortlocks (George Glazer Gallery web page at www.georgeglazer.com/archives/prints/animals/ durvillebat.html). Hair length was measured only on the mantle and averaged slightly shorter in Chuuk Lagoon specimens than in those from the Mortlocks-14.7 mm long in three specimens from Weno, Chuuk Lagoon, and 15.0 and 16.0 mm in four from Namoluk and nine from Satawan, respectively. In body size, bats from Chuuk Lagoon are similar to those from the Mortlocks. One skin and skull (AMNH 249954) dated 26 May 1987 and 13 other skulls (AMNH 249955-67) dated 3 July 1986 were shipped from Chuuk State and intercepted by customs officials in Guam; the specimens were prepared by G. Wiles. Whether the AMNH series consists entirely of specimens from Chuuk Lagoon, which is likely, or whether it includes material from the Mortlocks or other Chuuk outliers, is unknown. During the 1980s, bats commercially hunted in the Mortlocks were transshipped to Weno for transfer to Guam and the Commonwealth of the Northern Mariana Islands together (but apparently unsegregated) with bats collected on islands in Chuuk Lagoon. In external measurements, the AMNH specimens are similar to samples from both Weno and those from the Mortlocks (Table 2). Chromatically, the lone AMNH skin more closely resembles those from Satawan in the Mortlocks than it does the small sample from Weno.

The type series of *Pteropus laniger*, originally described as *Pteropus lanigera* [sic] by H. Allen (1890), and now regarded as a synonym of *P. p. insularis* (Andersen 1912;

				Mortlock Islands		
Character	Sex	"Truk"ª	Chuuk Lagoon islands	Namoluk Atoll	Satawan Atoll	
TT 11 1 1 .1	1		168.0-186.0 (2)	150.0 (1)	150.0-170.0 (2)	
Head-body length	0		177.0 ± 12.73	158.0 (1)	160.0 ± 14.0	
	0	165.0(1)	131.0(1)	155.0–170.0 (5)	155.0–170.0 (4)	
	Ť	105.0 (1)	131.0 (1)	163.0 ± 6.08	161.3 ± 6.29	
Forearm length	2		101.0(1)	103.0(1)	102.0–108.7 (2)	
	0		101.0 (1)	105.9 (1)	105.4 ± 4.74	
	Q	104.8 (1)		102.3–107.3 (5)	103.2–108.0 (5)	
	+			104.6 ± 2.18	105.3 ± 1.78	
Ear length	8		20.0-22.0(2) 21.0 ± 1.41	23.0 (1)	24.0 (1)	
	0			23.0-24.0 (3)	22.0-23.0 (2)	
	Ť			23.7 ± 0.58	22.5 ± 4.74	
Body mass	8		148.0-200.0 (2)	175.0 (1)	142.0-203.0 (2)	
BOUY IIIass			174.0 ± 36.76	1/ 5.0 (1)	172.5 ± 43.1	
	0	170.0(1)	150.0(1)	190.0-225.0 (5)	153.0–187.0 (4)	
	+	170.0 (1)	1)0.0 (1)	211.0 ± 13.87	171.8 ± 12.28	
Greatest skull	2	43.9–46.1 (5)	44.6 (1)	45.0 (1)	47.2 (1)	
length (GLS)		44.8 ± 0.18	1110 (1)		1/.2 (1)	
	Q	44.0–45.4 (5)	44.1 (1)	45.3–46.1 (2)	45.0–46.6 (4)	
		44.7 ± 0.53		45.7 ± 0.57	45.7 ± 0.59	
Palate length (PL)	8	22.6–24.0 (5)	22.2 (1)	23.3 (1)	22.0-24.4 (2)	
		23.0 ± 0.59			$23.2 \pm 1./0$	
	₽ P	22.0-24.0(6)	22.9 (1)	23.0-24.0(2)	23.2-24.1(3)	
Maxillary		22.0 ± 0.73	15 1 15 2 (2)	25.5 ± 0.71	25.9 ± 0.39	
toothrow (MTR)	8	14.0 - 17.2(5) 15.1 + 0.17	15.1 - 15.2(2) 15.2 + 0.70	15.5 (1)	15.2 - 19.8(2) 15.6 + 0.50	
		15.0-15.5.(6)	19.2 ± 0.70	148-155(3)	15.0-15.5.(4)	
	Ŷ	15.2 ± 0.19	14.8 (1)	15.2 ± 0.36	15.2 ± 0.24	
Breadth of	4	17.2–17.6 (5)			17.6–18.2 (2)	
braincase (BBC)	ð	17.4 ± 0.15	17.3 (2)	18.0 (1)	17.9 ± 0.42	
		17.0-17.8 (6)	17.0 (1)	17.9–18.1 (2)	17.5-18.1 (4)	
	Υ	17.5 ± 0.33	1/.0(1)	18.0 ± 0.14	17.9 ± 0.26	
Breadth across	7	10.0-11.0 (5)	10.8-11.1 (2)	11.1.(1)	10.7-11.9 (2)	
canines (CC)	0	10.4 ± 0.44	11.0 ± 0.21	11.1 (1)	11.3 ± 0.85	
		9.6–10.8 (6)	99(1)	11.0–11.4 (3)	10.9–11.1 (4)	
	Ť	10.4 ± 0.41).) (1)	11.2 ± 0.21	11.0 ± 0.10	
Breadth across M ¹	2	12.0–12.5 (4)	12 2 (2)	12.0 (1)	12.3–12.9 (2)	
(M1M1)	0	12.3 ± 0.22	12.2 (2)	12.0 (1)	12.6 ± 0.42	
	Ŷ	12.1–12.8 (5)	12.0 (1)	11.9–12.3 (3)	12.3–12.8 (3)	
	+	12.3 ± 0.29		12.1 ± 0.21	12.6 ± 0.26	
Interorbital	3	7.0-7.4 (4)	7.5 (1)	7.5 (1)	7.1-7.6 (2)	
breadth (IOB)		7.2 ± 0.17		7780(2)	7.4 ± 0.5	
	Ŷ	7.0 - 7.4(0)	7.2 (1)	7.7 = 0.0(5) 7.8 + 0.15	7.8 + 0.06	
Zygomatic width	3	23.0-25.4 (4)	24.0-27.0 (2)	/.0 ± 0.17	23.9-27.1 (2)	
(ZW)		24.1 ± 0.95	25.5 ± 2.21	25.6 (1)	25.5 + 2.26	
		23.6–25.4 (5)		25.7-26.0 (2)	25.2–25.6 (3)	
	¥	24.5 ± 0.65		25.9 ± 0.21	25.4 ± 0.20	

Table 2. Mensural data for samples of flying foxes from Chuuk Lagoon islands and the Mortlock Islands; data sets include range, n in parentheses, and mean \pm SD; all measurements are in millimeters or grams.

^a Specimens confiscated on Guam, but originated from Chuuk State. Most were probably collected on islands in the Chuuk Lagoon, but some may have come from outer atolls, including the Mortlocks.
Helgen et al. 2009) (USNM 37815, lectotype, and MCZ 7023, paralectotype), was stated by Allen (1890) to have come from Samoa, but this was later emended to the Caroline Islands (see Andersen 1912; Helgen and McFadden 2001). These specimens match well with BYUH specimens from Weno in being nearly uniformly brown with less contrasting areas of coloration, and having a reduced midventral pale patch, and probably originated from one of the main islands of Chuuk Lagoon.

Overall pelage coloration of the two available skins of *P. tokudae* (e.g. Figure 4; see further discussion below) is generally similar to that of *P. p. insularis*, perhaps averaging somewhat darker overall (Tate 1934; Flannery and Schouten 2001: 172).

Craniometric comparisons

Our study of essentially all available museum specimens of *Pteropus* from the islands of Chuuk Lagoon, Namonuito Atoll, and the Mortlocks, including the newly collected Mortlock material reported here, allowed us to examine patterns of multivariate craniometric variation in Pteropus from these archipelagos using Principal Component Analyses (PCA). We also included in these comparisons the three available skulls of *Pteropus tokudae* Tate, 1934, of Guam (a species that apparently became extinct in the late twentieth century: Wiles 1987a), which appears to be the closest relative of P. pelagicus. Pteropus tokudae and P. pelagicus share most qualitative morphological features but purportedly differ in that *P. tokudae* is darker brown in coloration and smaller in body size (Tate 1934; Flannery 1995); Tate (1934) indicated in the original description of *tokudae* that, "It may well be merely a race of insularis." We included P. tokudae in these comparisons because no study has yet explored the consistency of differences between P. tokudae and P. pelagicus, and because, as noted above, the largest available sample of *Pteropus* specimens supposedly originating from Chuuk State was seized in Guam, such that we wanted to evaluate whether these specimens showed closer craniometric relationship with P. p. insularis of Chuuk Lagoon, or with P. tokudae of Guam. Demonstration of the precise phylogenetic relationships of P. pelagicus and P. tokudae awaits a more detailed molecular phylogenetic review of the genus Pteropus than has yet been published (Giannini et al. 2008), but we regard P. pelagicus and P. tokudae to be closely related species that constitute a small radiation of relatively small-bodied flying-foxes from islands of the remote Central Pacific.

The type of *pelagicus* can no longer be traced (see above), and the skulls of the surviving type specimens for the other relevant taxa in this group (*insularis* [MNHN 1996-2112, syntype of *insularis*, designated here as the lectotype of *insularis* based on being the only skull available from the type series], *phaeocephalus* [BMNH 82.10.27.4, holotype], *laniger* [USNM 37815, lectotype], and *tokudae* [AMNH 87117, holotype] are all somewhat broken. Consequently, we based our PCA comparisons on a relatively small number of five variables (Table 4, Figure 5) to allow for the inclusion of these various type specimens, as well as various other museum specimens (adult skulls at



Figure 4. Holotype skin of *Pteropus tokudae*. AMNH 87117, adult male, from Guam, collected 10 Aug 1931 by W.F. Coultas. Scale bar = 25 mm.

AMNH, ANSP, BMNH, COM, MNHN, USNM, and ZMB), many of which are also partially broken.

Our craniometric comparisons (Figure 5, Table 4) indicate that skulls from the Mortlock Islands (*pelagicus*), from the islands of Chuuk Lagoon and Namonuito At-

				10	
Character	Chuuk Lagoon ^₀	Mortlock Islands	t	df	P
Greatest skull length	44.8 ± 0.63 (12)	45.9 ± 0.80 (6)	-3.37	18	0.003
Palate length	22.8 ± 0.64 (13)	23.5 ± 0.82 (8)	-2.22	19	0.039
Maxillary toothrow	15.1 ± 0.18 (14)	15.3 ± 0.32 (10)	-1.93	22	0.066
Breadth of braincase	17.4 ± 0.26 (14)	17.9 ± 0.24 (9)	-4.88	21	0.000
Breadth across canines	10.5 ± 0.44 (14)	11.1 ± 0.34 (10)	-3.93	22	0.001
Breadth across M ¹	12.4 ± 0.30 (12)	12.3 ± 0.36 (9)	0.21	19	0.834
Interorbital breadth	7.2 ± 0.16 (12)	7.7 ± 0.26 (9)	-4.83	19	0.000
Zygomatic width	24.5 ± 1.07 (11)	25.6 ± 0.89 (8)	-2.21	17	0.041

Table 3. Cranial measurements (mean \pm SD, in millimeters, *n* in parentheses) for pooled samples of flying foxes from Chuuk Lagoon islands versus Mortlock Islands^a.

^a Unpooled sample statistics are in Table 2.

^b Includes AMNH specimens confiscated on Guam.

Table 4. Factor loadings, eigenvalues, and percentage of variance explained by illustrated components (Figure 5) from Principal Components Analysis of 27 adult skulls of *Pteropus pelagicus* and *P. tokudae* (see "specimens examined"). Principal components are extracted from a covariance matrix of 5 log-transformed cranial measurements (see Figures 2 and 5, Tables 2–3).

Variable	PC1	PC2
Interorbital width	-0.587	0.798
Breadth of braincase	-0.869	-0.121
Maxillary toothrow length	-0.911	-0.163
Breadth across canines	-0.972	-0.105
Breadth across M ¹ s	-0.711	-0.368
Eigenvalue	0.013	0.003
Percent variance	71.4%	17.9%

oll (*insularis*), and from Guam (*tokudae*), separate primarily along the first principal component (representing 71% of the variance), mainly reflecting differences in overall skull size between these insular populations/taxa.

Several points are of special note. First, specimens of *tokudae* separate cleanly from *pelagicus/insularis*, chiefly on the basis of their consistently smaller size (showing no overlap with *P. pelagicus* in most skull measurements). *Pteropus tokudae* has a markedly smaller skull (greatest length 41.2–42.2 mm) with a relatively shorter and narrower rostrum compared to *P. pelagicus* (Figure 6).

Second, some overlap in morphometric space characterizes samples of *pelagicus* (skulls generally larger) and *insularis* (skulls generally smaller), especially with regard to the holotype of *P. phaeocephalus*, which associates more closely with Chuuk Lagoon and Namonuito specimens than with more recent Mortlock samples. Chuuk Lagoon and Namonuito specimens tend to average slightly smaller in most measurements than Mortlock specimens (Table 2), but sample sizes are small. Statistically significant differences (p < 0.05) were found in six of eight cranial measurements when samples from different localities were pooled and sexes combined (Tables 2–3); ranges overlap in all measurements.



Figure 5. Morphometric separation (first two principal components of a Principal Components Analysis) of 27 adult skulls of Pteropus pelagicus and P. tokudae. These comparisons involve 5 measurements (maxillary toothrow length, breadth of braincase, external breadth of rostrum across canines, external breadth of palate across first upper molars, and least interorbital breadth). The first principal component mainly reflects distinctions in overall skull size, which increases from right to left. Specimens of Pteropus pelagicus pelagicus from the Mortlock Islands are denoted by red symbols (including the red triangle, the holotype of phaeocephalus from "Mortlock Islands"; red circles, Satawan Atoll; and red squares, Namoluk Atoll). Specimens of *Pteropus pelagicus insularis* are denoted by black symbols; closed black symbols indicate samples of known geographic origin (including the closed black triangle, the holotype of *insularis* from "Ruck"; closed black circles, specimens labeled "Ruck"; closed black square, specimen labeled "Uala" (= Weno); and black cross, specimen from Namonuito Atoll) and open symbols indicate specimens of imprecise geographic origin (including the large open triangle, the lectotype of *laniger*, erroneously attributed to the "Samoa Islands" in the original description; open black circle, an unprovenanced specimen from ANSP; and open black diamonds, specimens at AMNH seized on Guam but originating from Chuuk State). Specimens of the closely related species Pteropus tokudae from Guam are denoted by pink symbols (including the pink triangle, the holotype of tokudae from Guam, and the pink squares, other specimens from Guam).

The only available skull from Namonuito Atoll (BMNH 15.1.18.1) shows closest association with specimens from Chuuk Lagoon (Figure 5), an indication that the flying fox population of Namonuito, the taxonomic position of which has not previously been analyzed and has been considered uncertain (Rainey and Pierson 1992, Flannery 1995), is best referred to *P. p. insularis* (but its taxonomic status should ideally



Figure 6. Skulls of *Pteropus pelagicus* (**A** *P. p. insularis*, USNM 151563, unsexed adult, from Uala [= Weno]; note last lower premolars missing in lower jaw) and *P. tokudae* (**B** AMNH 87117, holotype of *tokudae*, adult male, from Guam). Scale bar = 25 mm.

be re-evaluated once additional comparative material is available). The lectotype of *laniger* also associates craniometrically with specimens of *P. p. insularis* (Figure 5), supporting the suggestion that the type series of *laniger* originated from Chuuk Lagoon (Andersen 1912, Helgen and McFadden 2001, Helgen et al. 2009) and that *laniger* can be regarded as a synonym of *P. p. insularis*. The majority of specimens at AMNH that were seized on Guam and said to originate from Chuuk State fall within the range

of morphometric variation for specimens known to have come from Chuuk Lagoon (Figure 5), supporting the idea that they likely originated from Chuuk Lagoon, and their taxonomic identification as *P. p. insularis*. However, the AMNH series, along with an unprovenanced specimen from the ANSP (ANSP 6196), expand the range of variation in *P. p. insularis* along the second principal component (representing 18% of the variance), suggesting a slightly greater range of cranial shape variation within *P. p. insularis* than documented by firmly localized samples. The possibility that some of these unprovenanced AMNH and ANSP specimens might have originated from the Mortlocks, or other outlying island populations of Chuuk State, cannot be ruled out.

Our search for museum material of P. p. pelagicus and P. p. insularis uncovered one additional very interesting and largely overlooked museum specimen. This is a broken skull of a flying fox much larger than P. p. insularis, received from Otto Finsch, probably in 1880 (when he was in the Caroline Islands during his first Pacific expedition), and labeled "Ruck" (= Chuuk). This specimen (ZMB 5697) was misidentified as Pteropus insularis by Matschie (1899), who figured the skull (Matschie 1899: Plate 5, numbers 11-12), but was correctly identified by Andersen (1912) as a member of the remote Pacific group of flying foxes allied taxonomically with P. mariannus (including the named forms *pelewensis*, *yapensis*, and *ualanus*). This specimen, examined by KMH, most closely resembles P. pelewensis of Palau and provides an indication that, like Guam (the original fauna of which included P. mariannus and P. tokudae), the islands of the Chuuk Lagoon may have supported both a smaller species of flying fox (P. p. insularis) and P. cf. pelewensis. No other collections or reports from Chuuk State give any indication of a larger species of flying fox in the archipelago, suggesting that any larger taxon that may have inhabited these islands is now extinct. However, the possibility that it could still exist in an outlying island group in Chuuk State should be kept in mind by future fieldworkers in these regions. Similarly, and as noted above, Finsch's overlooked nineteenth century Pacific collections in Berlin reveal that the fauna of Pohnpei also may have included both a small species, P. molossinus, which survives, and a larger species, also most closely resembling *P. pelewensis*, unknown today in Pohnpei. Alternatively, we cannot fully discount the possibility that the two anomalous specimens (one from Chuuk, the other from Pohnpei) are specimens of P. pelewensis from Palau that have been mislabeled. Both were obtained by Finsch and deposited in the collections of the Berlin Museum (ZMB). Finsch visited Pohnpei in 1880 (Finsch 1881), but we found no mention of his having travelled to Chuuk or Palau. However, while on Pohnpei, he visited with Johann Kubary, who resided at Pohnpei at the time and who had collected zoological specimens extensively throughout the Caroline Islands, including in Chuuk and Palau. Finsch (1880) published many new locality records of birds from Chuuk State based on Kubary's specimens that he (Finsch) examined during this visit. Possibly the enigmatic specimen of flying fox from "Ruck" originated from Kubary's collections. The likelihood of mislabeling in the cases of these two specimens is further enhanced by the tendency of the curators at the Berlin Museum at that time to remove collectors' labels when attaching uniformly standardized museum labels (Frahnert and Buden 2010).

Taxonomic conclusions

The name *Pteropus pelagicus* Kittlitz, 1836 is a senior synonym of the younger but prevailing name *Pteropus phaeocephalus* Thomas, 1882. Kittlitz's name is listed in Sherborn's (1929) Index Animalium (Part XIX: 4818), which Gardner and Hayssen (2004) included in a list of important nomenclators in mammalogy. It is also used in a similar context in Kramer's (1935) report on the results of the German 1908–1910 South Seas Expedition. Inasmuch as the name *P. pelagicus* appears in at least these two post-1899 publications, it is not a "forgotten name" (*nomen oblitum*) sensu ICZN (1999: Article 23.9 and glossary), and we find no compelling reason to maintain use of the younger name under special provisions of the Code (ICZN 1999: Article 23.9.3). The species known largely by its junior synonym, *P. phaeocephalus*, has a very limited distribution, has until now been known by a single museum specimen, and has been rarely discussed in the literature. In a strict application of the Principle of Priority, the name *Pteropus pelagicus* Kittlitz, with type locality Lukunor Atoll in the Mortlock Islands, is resurrected here to replace the younger synonym, *P. phaeocephalus*.

In view of the very close similarity in body size and cranial features and measurements between specimens from Chuuk Lagoon islands (P. insularis) and those from the Mortlocks Islands (P. pelagicus), we include P. insularis Jacquinot and Pucheran, 1853 (herein emended from Hombron and Jacquinot, 1842 - see remarks on authorship, this account) in *P. pelagicus* and treat the two former monotypic species as subspecies - P. p. pelagicus Kittlitz, 1836 in the Mortlock Islands (synonym phaeocephalus Thomas, 1882) and P. p. insularis Jacquinot and Pucheran, 1853 on Chuuk Lagoon islands and Namonuito Atoll (synonym laniger Allen, 1890). Nomenclatorial issues notwithstanding, this arrangement follows in principle that of Simmons (2005), who referred to the Mortlock population as P. i. phaeocephalus. The nominate subspecies (P. p. pelagicus) is distinguished from P. p. insularis chiefly, and on average, by its brighter coloration, more contrastingly colored (paler) mantle, larger white or pale buff midventral patch, and larger cranial size. The euphonious English vernacular name "Pelagic flying fox" would logically stem from the binomen, but we suggest the name "Chuuk flying fox" for this species following a tendency to use geographic-based names for the pteropodids endemic to the Caroline Islands (e.g. Flannery 1995, Wilson and Cole 2000, Simmons 2005, Wiles 2005).

Remarks on the authority of *P. insularis*

"Hombron and Jacquinot, 1842" has long been the recognized authority for the name *Pteropus insularis* (e.g. Andersen 1912, Wilson and Reeder 1993, Flannery 1995), but a recent review of the early literature indicates this to be an error perpetuated over the years. The name was proposed in the results of a 19th century French expedition to Antarctica and Oceania known in abbreviated form as "*Voyage au Pole Sud*," or in a longer and more complete form as "*Voyage au pôle sud et dans l'Océanie sur les corvettes l'Astrolabe*

et la Zélée exécuté par ordre du roi pendant les années 1837–1838–1839–1840 sous le commandement de M. Dumont-d'Urville." This work was published in seven parts (Histoire du Voyage, Zoologie, Botanique, Anthropologie, Géologie, Physique, and Hydrographie) in 23 volumes with six atlases. Many authors and editors contributed to the work and publication dates range from 1842–1854 for the different components. *Pteropus insularis* was described in Part II (Zoologie), volume 3, which was edited by Hombron and Jacquinot and divided into 3 sections under different authors. The first section, *Mammiferes et Oiseaux* by H. Jacquinot and Pucheran (pp. 1–166), contains the description of *P. insularis* on page 24. The two other sections are *Reptiles et Poissons* by H. Jacquinot and Guichenot (pp. 1–56) followed by *Crustacés* by H. Jacquinot and Lucas (pp. 1–107). Clark and Crosnier (2000) remark that the earliest verifiable date for volume 3 is 1854 (although 1853 appears on the title page), but Holthuis (2002: 419) pointed out that "as there is no evidence to prove that the volume was published after 1853…the date on the title page [see Holthuis 2002: figure 7] has to be accepted as correct."

The description of *P. insularis* by Jacquinot and Pucheran (1853) includes a reference to plate v, which was published in a separate Atlas d'Histoire Naturelle, Zoologie, edited by Hombron and Jacquinot. The plate is a composite of dorsal and ventral views of the body and dorsal, ventral, lateral, and frontal views of the skull of one of the two cotypes (skin 53 A, skull A. 6770) of *P. insularis* in the Paris Museum (Andersen 1912). The plate is undated but the title page of the atlas bears the range of dates 1842–1853. However, a detailed study of the atlas by Clark and Crosnier (2000) revealed that the 40 plates were distributed in 28 livraisons, and that plate v was included in the 11th livraison, the earliest verifiable date of which is 1844, according to British Library records. But the date of the plate is seemingly irrelevant as it identifies the species with a French vernacular name, Rousette Insulaire, not a scientific binomen. On the other hand, Jacquinot and Pucheran (1853: 24) give the name as "Rousette insulaire.-Pteropus insularis Homb. et Jacq." Although Jacquinot and Pucheran (1853: 25) remarked "La Rousette insulaire a été trouvée par MM. Hombron et Jacquinot dans l'île d'Hogoleu [The island flying fox was found by MM. Hombron and Jacquinot in Chuuk.]", and attributed authorship to them, there is no indication that Hombron contributed directly to the description. The authority of *P. insularis* should revert to Jacquinot and Pucheran (1853). It is also noteworthy that Sherborn's Index Animalium, which lists original sources of species names up to 1850, does not include P. insularis.

Distribution and status of P. p. pelagicus

Northern Mortlocks

Records of flying foxes from the northern Mortlocks are scanty, lacking in substantive detail, and confined to Losap Atoll; no records exist for Nama Island. Severance (1976) remarked that bats were present on Losap during his anthropological investigations in the late 1960s and early 1970s, but the information may have been based on hearsay from local residents as he did not later recall definitely seeing bats on the atoll (C. Severance, pers. comm.). Kachusy Silander, whom Severance first met on Pis Island, Losap Atoll, and who lived there until the early 1970s, stated in a telephone conversation (fide C. Severance, pers. comm.) that he never saw bats on the atoll, but recalled that the traditional chief at that time claimed that flying foxes lived on his parcel of land at the southeastern end of Pis. In 2004, DWB spoke with two former Losap Island residents who had relocated to Pohnpei. Tasiro Leg (pers. comm.) recalled occasionally seeing bats and throwing stones at them as a boy during the 1980s. Scaima Pamar (pers. comm.), age 78 in 2004, recalled seeing his mother and grandmother preparing bats to eat on Pis during the time of the Japanese administration in the 1930s or early 1940s. DWB also received a report from another former Losap resident, age 76 in 2004, who remembered a large group of bats arriving together at Losap shortly after World War II (fide Tridell Elitok, pers. comm.). They resided in a no longer present stand of mangroves and were caught and eaten by the islanders because of the scarcity of food at the time. H. Manner (pers. comm.), who spent one week collecting plants on Losap Island and adjacent islets in July 1988 (Manner and Sana 1995), did not remember seeing flying foxes then.

In the late 1980s, government officials on Weno, Chuuk Lagoon, reported bats present on Losap Atoll and said that a Losap islander was among several Mortlockese shipping bats to Weno for export to the Mariana Islands (Wiles 1992a), but whether any of the bats originated from Losap Atoll is unknown. Joakim Peter (pers. comm., College of Micronesia, Weno) informed DWB that the exporter from Losap resided on Weno at the time and worked mainly for his brother-in-law, who was from Ettal and also resided on Weno. J. Peter (pers. comm.) went on to say that the exporter from Losap may have been more involved with transportation and management operations than in collecting bats. Attempts to contact this exporter in 2004 were unsuccessful. Rainey and Pierson (1992), citing M. Henry and C. Glover in Chuuk Lagoon as sources, also reported bats from Losap but gave no additional details.

DWB saw no bats on Losap Atoll during a one-day visit that included 2–3 hrs each on Pis, Losap, and Lewel Islands in July 2004. Lewel, the largest island in the atoll, has extensive breadfruit-coconut forest typical of bat habitat elsewhere in the Mortlocks. It is used as a garden island by the people of Losap Island, but has no permanent settlement or resident families. He walked the length of Lewel through the center and returned via a shore route without seeing bats. None of the several Losap and Pis residents interviewed during his visit knew of bats occurring on the atoll.

DWB spent one week on nearby Nama Island without seeing any bats or encountering any resident islanders who had seen them. Mitaro Chosa (pers. comm.), deputy mayor of the island and age 58 in 2004, was firm in his conviction that bats had not occurred on Nama during his lifetime.

These few, and in some cases questionable, records together with the lack of sightings during this study suggest that flying foxes are absent from Nama Island, and are either recently extirpated or possibly still present in such small numbers as to be unknown to many islanders on Losap Atoll.

Central Mortlocks

Girschner (1912) recorded flying foxes on Namoluk Atoll in about 1910, but gave no indication of their abundance. Bats were present on all of the atoll's islands during the late 1960s and early 1970s and reportedly numbered "in the hundreds" (Marshall 1972:17; 1975). During that time, bats were most common on the uninhabited islands of Amwes and Toinom (M. Marshall, pers. comm.).

DWB observed small numbers of bats on all the islands in July 2004. The encounter rate on Namoluk Island averaged four per hour during six 45-minute walks in the least disturbed parts of the coconut-breadfruit forest on four different days. Overall, an estimate of 150–200 bats was made for the atoll. However, Maikawa Setile (pers. comm.), deputy mayor of Namoluk, claimed that bats were more abundant at certain times, especially when breadfruit was in season. He recalled seeing large numbers of bats in the settlement earlier in 2004, with as many as 50 in one tree.

Southern Mortlocks

There are few historical accounts of flying foxes in the southern Mortlocks. J. Nason (pers. comm.) reported "scores of fruit bats.....possibly 100+" on Ettal Island, Ettal Atoll, during the late 1960s.

Wiles (1992b) reported bats on Ettal and Satawan Atolls being harvested for export in the late 1980s. A resident of Lukunor Atoll told us that he shot 50 bats on the atoll and another 150 bats on other southern Mortlock islands for this purpose during a 5-month period in 1986. These were sold to a Palauan man operating a trading boat, who provided the hunter with a .22 caliber air rifle and .410 gauge shotgun. The bats were steeped in boiling water (but not cooked), wrapped individually in plastic bags, and packed in ice prior to shipment.

During field surveys in 2004, DWB found bats to be uncommon on Ettal Atoll and estimated 75–100 to be present. He saw only five or six bats flying in and out of several breadfruit trees in the village on Ettal Island at sunset on 30 and 31 July, and observed only one bat during several walks elsewhere on the island and none on three of the atoll's smaller outlying islands. One resident stated that he occasionally saw as many as 20–30 bats together in breadfruit trees in the settlement.

DWB judged bats to be common on Lekinioch Island, Lukunor Atoll, in 2004. He counted 53 bats in flight over the central taro patch and adjacent forest during 30 minutes near sunset on 2 August. No other station counts were made and no bats were seen during daytime walks among breadfruit and coconut trees in the settlement. However, the less disturbed areas of the island where bats were more likely roosting were not visited. DWB was unable to visit other islands in the atoll in 2004, but many of the people interviewed on Lekinioch, as well as former Lukunor residents living on Pohnpei at the time, reported bats on Oneop and many of the smaller islands. An overall estimate of 300–400 bats was made for the atoll. In 2012, DWB visited all of the islands in Lukunor Atoll except Lekinioch. Small numbers of bats were recorded on eight of the 17 islands visited, as follows: Oneop, 5 bats; Piafa, 1; Kurum, 1; Pienemon, 4; Fanamau, 1; Sapull, 6; Sopotiw, 2; and Fanafeo, 1. Seven bats were noted flying between Sapull and Sopotiw Islands. No colonies were found and no population estimate was made for the atoll.

Surveys on Satawan Atoll in 2004 indicated that bats were common and regularly encountered, with an estimated 400–500 present. The largest numbers of bats observed during the study were on this atoll, with the greatest concentrations seen on Satawan and Ta, the two largest and southernmost islands in the Mortlocks. The encounter rate on Ta was eight per hour during walking surveys totaling 2.2 hours through breadfruit and coconut forest. The maximum number of bats observed during station counts was 81 in 25 min at Ta airport at sunset on 4 April. The largest aggregation observed during this study was 27 on Satawan Island (see Roosting below). One to 10 bats (usually less than five) were encountered per visit on other islands in the atoll, including Weito in the south; Kuttu, Orin, Pike, Mariong, Apisson, Lemasul, and Alengarik in the northwest; and Faupuker, Pononlap, and Fatikat in the east. Numbers of bats noted on Ta in 2012 matched or exceeded those recorded in 2004, and included many flying to or from Satawan Island.

Natural history of P. p. pelagicus

Roosting

Pteropus p. pelagicus characteristically roosted singly or in small, loose aggregations of 5–10 individuals, usually in the crowns of coconut and breadfruit trees in closed or nearly closed canopy forest outside of settlements. A maximum of 27 was seen together in the crowns of two adjacent coconut trees at the northern end of Satawan Island on 2 July 2004, with seven roosting along the rachis of a single palm frond and separated from each other by one or two body lengths. Bats were frequently observed hanging from tree branches and palm fronds, and occasionally clinging to the trunks of coconut trees a short distance below the crowns. Roosting bats were noted to occasionally stretch their wings and reposition themselves, or awake and relocate to another site. Some were seen crawling on the petiole bases of palm fronds and disappearing from view among the leaf axils.

Diet

Ripe breadfruit is apparently one of the most preferred food items of *P. p. pelagicus*. DWB saw bats active in breadfruit trees at night on all the atolls having bats, and resident islanders invariably mentioned the fruit of breadfruit at the top of their lists of foods eaten by bats. Other foods reported by islanders were banana (*Musa* sp.; fruit),

Station ^a	Date	Time	Number of bats	Direction of flight
1 Fatikat	26 June	1745–1815	0	
1 Fatikat	27 June	0515-0545	0	
2 Satawan (east end)	2 July	0500–0530	0	
2 Satawan (east end)	2 July	1730-1830	1	Fatikat to Satawan
2 Satawan (east end)	3 July	0430-0545	0	
3 Satawan (west end)	1 July	1725–1850	7	Ta to Satawan
4 Ta (east end)	25 June	1730-1830	0	
5 Ta (west end)	24 June	1715-1830	0	
6 Weito (east end)	3 July	1700-1835	8	Weito to Ta

Table 5. Numbers of bats observed flying between islands during six sunset and three sunrise counts at six different stations on Satawan Atoll, Mortlock Islands, 24 June–3 July 2004.

^a See Figure 1 for locations.

coconut (parts eaten unknown), papaya (*Carica papaya* L.; fruit), *Calophyllum inophyllum* L. (fruit), *Crataeva speciosa* Volkens (fruit), *Pandanus* cf. *tectorius* Parkinson (fruit), and *Ficus tinctoria* G. Forster (fruit). The only observation of bats feeding was on Weito Island, Satawan Atoll, at sunset on 3 July 2004, when three or four bats repeatedly flew in and out of the dense foliage of a pandanus tree. One flew away with a segment of ripe fruit and another dropped a segment while flying over the beach.

Flight activity

Flying foxes were observed flying at all hours, including midday, although some daytime activity was doubtless caused by the observer's passage. Flight activity was greatest near sunset and sunrise (Figure 7) when bats moved between day roosts and foraging sites. Fewer bats were encountered at sunrise than at sunset, suggesting that some animals returned to roosts before daylight. The direction of evening flights probably was associated with the location of food resources, often ripe breadfruit according to local residents. During April and June 2004, with the exception of a few individuals settling in nearby trees, all bats observed during evening flights at the Ta airport station moved toward the western end of the island; in July and August, 19–40% of bats flew from west to east. Interisland flights within atolls occurred regularly near sunset, but none were recorded at other times (Table 5). No bats were seen flying between atolls.

Reproduction

At least 50% of the bats observed on Namoluk Atoll in July 2004 appeared to be females with young. In some cases, young were evident only as a bulge beneath a



Figure 7. Mean number of bats observed per 10-minute count period during (**a**) five early morning counts from 23 June–6 July 2004 and (**b**) five evening counts from 22 June–3 August 2004 at the airport on Ta Island, Satawan Atoll, Mortlock Islands.

female's wing. Large volant young were occasionally seen in close proximity to or in body contact with their presumed mothers. Among five females collected on Namoluk Atoll on 21–22 July 2004, two contained single fetuses (crown-rump length 68 mm,

mass 27 g, but with part of the brain case shot away; crown-rump length 42 mm) and a third had an immature male (forearm 78 mm, head-body length 110 mm) clinging to its ventral surface. Two females collected on Satawan Atoll in April 2003 each had a large young (head-body length 100, 100 mm; mass 62, 65 g) clinging to their ventral surface. Two adults were observed copulating in the crown of a coconut tree on Ta Island on 24 December 2002.

Discussion

Taxonomy

Our examinations and analyses of craniometric and pelage variation in the flying foxes of Chuuk State demonstrate minor but largely consistent morphological distinctions between flying foxes of the Mortlock Islands and those from the islands of Chuuk Lagoon and Namonuito Atoll. We regard these differences as indicating no more than subspecific distinction between these two regional groupings, which we refer to P. pelagicus (P. p. pelagicus and *P. p. insularis*, respectively). A specimen from Namonuito Atoll, the enigmatic type series of Pteropus laniger, and a series of seized bats said to originate from Chuuk State, are all best referred to P. p. insularis. The closest relative of P. pelagicus is the recently extinct P. tokudae of Guam, which based on its consistently smaller size, shorter and narrower rostrum, darker coloration, and considerable geographic isolation from *P. pelagicus*, is best regarded as a distinct species (cf. Tate 1934). An overlooked nineteenth century specimen in the Berlin Museum provides an indication that the islands of Chuuk Lagoon may have originally supported a second, larger species of flying fox (i.e., in addition to P. p. insularis), similar to P. pelewensis, which may now be extinct in the archipelago. The possible historical extinction of this species, and those of *P. tokudae* on Guam and *P. pilosus* in Palau, highlights the vulnerability of remote Pacific Pteropus populations to insular extirpation and extinction, and the importance of further clarifying studies of the taxonomic status, ecology, and current conservation standing of flying fox populations from remote Pacific archipelagos (Wiles et al. 1997, Helgen et al. 2009).

The subspecific status of flying foxes in the northern Mortlocks remains unresolved. The nearest neighboring populations are comprised of *P. p. insularis* on the islands of Chuuk Lagoon 66 km to the northwest and *P. p. pelagicus* on Namoluk Atoll 110 km to the south. Both distances are perhaps within the flight capabilities of the species. However, based on its nearer distance and much larger land area that would support a larger bat population producing potentially more dispersing individuals, Chuuk Lagoon would appear to be a more likely source of animals colonizing Losap Atoll and Nama Island. Interisland movements of up to 119 km and corresponding genetic exchange have been reported in *P. mariannus* in the Mariana Islands (Wiles and Glass 1990, Brown et al. 2011), but this species is substantially larger (forearm 134–154 mm), and perhaps a more powerful flier, than *P. pelagicus*.

Status and natural history

The entire population of *P. p. pelagicus* is probably currently restricted to the four atolls comprising the southern and central Mortlock Islands, which total 10.1 km² in size. A few additional bats may be present on Losap Atoll in the northern Mortlocks, but it is unclear which subspecies these might represent. Our study provides the first population estimate for *P. p. pelagicus*, with approximately 925–1,200 bats present in 2004. About 75% of the population occurs on the two atolls with the largest land areas: Satawan and Lukunor. Resident islanders in the southern and central Mortlocks reported that bats were more common in the past, but that numbers appeared to have remained relatively stable in recent years. Residents also stated that bat abundance seems to fluctuate with the seasonal availability of food, especially breadfruit, but this impression likely comes from the bats' strong attraction to villages during the peak fruiting season of breadfruit.

Some double-counting of flying foxes may have occurred during our survey due to movements of bats between atolls. However, this problem was probably minor because our primary survey period when all six island groups in the Mortlocks were visited was limited to a 6-week period from 22 June to 5 August 2004, thus reducing the likelihood of significant inter-atoll flights.

Recent data are lacking on the status of *P. p. insularis.* The main population in Chuuk Lagoon probably numbered in the mid-thousands in the early 1980s, but was reduced in abundance by commercialized hunting in the latter part of that decade (Wiles 1992b, 1992c). The only records from Namonuito Atoll are two specimens (BMNH 15.1.18.1, 15.1.18.2) collected in 1914. DWB did not sight any bats while visiting Onoun (Ulul) Island in this atoll on 3–7 January 2003, and none of the local residents queried reported seeing bats. However, no information was obtained for the islands on the eastern and northern sides of the atoll.

Our survey efforts, including conversations with islanders, failed to confirm the presence of two other bat species in the Mortlock Islands, both of which are based on questionable early records. Thomas (1882) and Andersen (1912) listed P. molossinus Temminck (originally reported under the name P. breviceps; see Thomas 1887) as present in the Mortlocks, based on a single specimen collected by Kubary that supposedly originated from the island group. Pteropus molossinus is otherwise recorded only from Pohnpei and nearby Ant and Pakin Atolls (Wiles 1992d, Buden 1996a, 1996b). Our findings support Rainey and Pierson's (1992) belief that this record is erroneous, though it is also possible that P. molossinus was more widespread in the recent past and is now extinct or extremely rare in the Mortlocks. We also did not detect the insectivorous emballonurid *Emballonura semicaudata sulcata* Miller, which is firmly recorded only from Chuuk Lagoon's main islands and Pohnpei (Koopman 1997). Schmeltz and Krause (1881: 298), in listing the mammals that Kubary recorded in the Mortlocks, remarked about "...noch einen von Ruk her eingefuhrten Hund, von wo auch ab und an eine *Emballonura* hierher verweht wird [...a dog imported from Chuuk and sometimes an *Emballonura* blown in from that same place]." Further along

in the same text, and in comparing the fauna of Nukuoro Atoll, Pohnpei State, with that of the Mortlocks, Schmeltz and Krause (1881: 331) stated, with respect to Nukuoro, "...von Säugetieren kommt nur die Ratte vor; *Pteropus* und *Emballonura* fehlen [...of the mammals, there is only the rat; *Pteropus* and *Emballonura* missing.]." These unconfirmed allusions to *E. semicaudata* in the Mortlocks are probably best treated as hypothetical or indicative of occasional vagrant occurrence.

Atoll-dwelling populations of *Pteropus* are of ecological interest because of their occurrence on islands with impoverished and often highly human-altered floras (see Mueller-Dombois and Fosberg 1998). Our study of *P. p. pelagicus* supports the findings of others (Dolbeer et al. 1988, Wiles et al. 1991, Holmes et al. 1994) that although flying fox diets appear to comprise relatively few plant species on atolls, these islands nevertheless can support sizeable population densities approaching or exceeding 100 bats per km². The fact that atoll habitats have experienced widespread conversion to coconut-dominated forest and that a number of cultivated fruit-producing tree species has been introduced may enhance the productivity of these islands for flying foxes (Wiles and Brooke 2009).

Most species of *Pteropus* are seasonal breeders with births synchronized over a period of several months (O'Brien 1993). Contrary to this pattern, our limited observations suggest that births in *P. p. pelagicus* occur over a longer time frame and that females with dependent young are present for at least 8 months of the year. Two other Micronesian taxa, *P. yapensis* in Yap and *P. mariannus* on Guam, are among the few species of flying fox known to breed continuously (Wiles 1987b, Falanruw 1988).

Threats to populations of P. p. pelagicus

With a small population size and a geographic range comprised of many small low-lying islands totaling <12 km², flying fox populations in the Mortlock Islands are highly vulnerable to environmental changes and certain human activities. The apparent depletion or possible extirpation of bats on Losap Atoll in the northern Mortlocks during the past 60 years underscores this vulnerability.

Sea level rise associated with climate change may represent the greatest long-term threat to *P. p. pelagicus* and other populations of atoll-dwelling *Pteropus* (Rainey 1998). One of the most recent climate models forecasts a rise in sea level of 0.57–1.10 m by 2100 and 1.84–5.39 m by 2500, although much uncertainty exists over the latter estimate (Jevrejeva et al. 2012). Rises of this magnitude certainly have the potential to submerge atolls throughout the world or greatly reduce atoll land areas and change vegetation patterns, and therefore put *P. p. pelagicus* at considerable risk of extinction within this or the next several centuries. Lukunor Atoll in the Mortlocks and some other Micronesian atolls experienced several extreme high tides between 2007 and 2009 that flooded islets for several hours per event (Fletcher and Richmond 2010, Keim 2010). At Lukunor Atoll, the resulting salinated soil from the initial flooding in 2007 damaged or killed 78% and 55% of the breadfruit trees on Oneop and Lekinioch

islands, respectively (Keim 2010), substantially reducing an important food for *P. p. pelagicus* on the atoll. Despite this, some experts believe that some atoll islands may be more resilient to sea level rise than previously thought and may be able to maintain their land area through continued sediment accretion as long as geomorphic processes are not substantially altered in the future by ocean warming and acidification, changes in storm occurrence, and reductions in atoll vegetation (Woodroffe 2008, Webb and Kench 2010). However, even if atoll islands persist in the future, it is unknown what type of vegetation may remain and whether it could support populations of flying foxes.

The negative impacts of severe cyclonic storms on *Pteropus* populations are well documented and occasionally include significant population declines (e.g., Cheke and Dahl 1981, Pierson et al. 1996, McConkey et al. 2004, Esselstyn et al. 2006, Wiles and Brooke 2009). The vast majority of bat mortalities occur in the aftermath of storms following depletion of food resources, loss of protected roosting sites, and in some cases increased post-storm hunting pressure. The Mortlock Islands are positioned along the southern edge of the typhoon belt present in the western North Pacific Ocean. Records since the early twentieth century suggest that individual islands in the Mortlocks experience devastating typhoons and massive damage to plant communities two to four times per century (Nason 1970, Marshall 1975, 1976, Joint Typhoon Warning Center 1980–2011, Reafsnyder 1984). However, even the largest storms rarely inflict serious habitat damage across the entire archipelago (e.g., Marshall 1979) and typically leave flying foxes and other wildlife with habitat refugia on some islands.

In 1976, Typhoon Pamela killed most of the tree crops (e.g., breadfruit, coconut, and banana trees) on the islands of Ettal, Namoluk, Kuttu, Oneop, Moch, and Nama (Marshall 1976, 1979), including 95% of the breadfruit on Kuttu (Reafsnyder 1984) and all breadfruit, coconuts, and bananas on Ettal, where breadfruit trunks and limbs were stripped bare (M. Marshall, *fide* J. Nason, pers. comm.). In contrast, the islands of Losap, Ta, Satawan, Pis, and Lukunor experienced much lower losses of these trees. Ettal, Namoluk, and Kuttu were also entirely submerged by high sea surge for 15–18 hrs during this typhoon (Marshall 1979). During Typhoon Phyllis in 1958, nearly 75% of all trees at Namoluk Atoll were fully uprooted with the remaining trees being mere stumps 5–7 m tall (Davis 1959, in Marshall 1975).

Current model projections suggest that typhoon intensity will increase, but frequency may decrease, in the western Pacific as climate change progresses over the next century (Knutson et al. 2010). Typhoon impacts on atolls may be exacerbated when combined with projected rises in sea level.

The extent that Mortlock bat populations have been affected by severe typhoons in the past is undocumented. However, Marshall (1976) remarked that although few birds were encountered on the hardest hit islands 6–10 days after Typhoon Pamela, flying foxes appeared to survive the storm fairly well, with good numbers seen flying about searching in vain for food and shaded roosting sites. *Pteropus p. pelagicus* has doubtless had a long history of exposure to intense typhoons and has been able to adjust to these periodic environmental disruptions and presumed population reductions, possibly via recruitment from surrounding islands or simply by population renewal by survivors.

Centuries of human occupation have greatly altered the vegetation of the Mortlocks, but anthropogenic disturbance is now low despite the atoll's high human population density. The coconut-breadfruit-pandanus forests where bats roost and feed are economically important to islanders, and they manage this resource sustainably. Cutting and clearing of the undergrowth occurs sporadically and is usually done on small, family-owned plots, but widespread cutting of forest does not occur. Additionally, a high emigration rate of Mortlockese to the larger islands of Micronesia and to overseas locations for better job opportunities (Marshall 2004) has reduced human population growth and stress on the environment.

Overhunting has contributed to declines in flying fox populations in many areas of the Indo-Pacific region (e.g., Wiles et al. 1989, 1997, Craig et al. 1994, Brooke and Tschapka 2002, Lee et al. 2005, Wiles and Brooke 2009, Harrison et al. 2011) and may have done so in the Mortlocks in the past. Between 1986 and 1989, large numbers of Pteropus pelagicus were harvested in Chuuk State and exported to meet the demands of the commercial markets for bats on Guam (5,108 bats; Wiles 1992b) and in the Commonwealth of the Northern Mariana Islands (229 bats; Stinson et al. 1992). An unknown, but possibly sizable, number of these bats originated from the Mortlocks (Rainey 1990, Wiles 1992a, 1992b). Some of the bat exporters and/or hunters involved in this trade were from Losap, Ettal, Satawan, and Lukunor Atolls (Wiles 1992a, this study). The impacts of this harvest on bat populations in the Mortlocks were never quantified. The listing of all Micronesian species of *Pteropus* on Appendix I of the Convention on Trade in Endangered Species of Wild Flora and Fauna (CITES) in 1989 halted, or at least greatly reduced, commercial hunting of bats in the Federated States of Micronesia for export to the Marianas (Wiles 1992b, Wiles and Brooke 2009). It is uncertain to what extent illegal shipments of bats from Chuuk State may have occurred since then, but the amount is probably insignificant.

Like the vast majority of islanders from Chuuk, Pohnpei, and Kosrae states, Mortlockese almost universally disdain flying foxes as food. From the late 1960s to 1980, anthropological researchers noted that bats were not hunted or eaten on Ettal Island (Nason 1970), Namoluk Atoll (Marshall 1972), Losap Atoll (Severance 1976), Lukunor Atoll (Borthwick 1977), and Kuttu Island, Satawan Atoll (C. Reafsnyder, pers. comm.). Marshall (1972) remarked that mention of consuming bats, as done by residents of the Marianas, brought expressions of revulsion to Namoluk islanders. He also noted that bats were disliked in part because of their habit of urinating on themselves while roosting and their depredation of breadfruit, papayas, and bananas. J. Nason (pers. comm.) stated that in the Mortlockese ethnotaxonomy, bats were essentially considered as rats with wings and were never eaten. Paraphrasing a folktale told to DWB by M. Setile of Namoluk Atoll,

Once, long ago, the rat was envious of the bat's wings. The rat asked the bat if he could borrow his wings for a short time just to have a brief experience of flying; he promised to return them soon. The bat allowed the rat to use his wings. But the rat lied and flew away with no intention of returning the wings. Now, what was rat is bat and the original bat is the rat. Flying foxes may have been a part of the Mortlockese diet in the past, when reliance on local foods was greater and food supplies from Chuuk Lagoon and Pohnpei were not so readily available, and bats may still be utilized on occasion especially when other foods become scarce, such as after typhoons. Girschner (1912) included bats among the foods eaten by Namoluk islanders, and elders from Pis and Losap Islands told DWB of bats being eaten during the 1930s or 1940s. During our visits to the Mortlocks, no evidence was observed of bats being hunted, eaten, or killed to limit crop damage. Conversations with resident islanders throughout the central and southern Mortlocks indicated that local consumption of bats was apparently confined to a few individuals, who ate them from time to time, and to occasional visitors (largely friends and relatives) who acquired a taste for bats elsewhere.

Potential predators of flying foxes in the Mortlocks include four non-native species: cats (Felis catus Linnaeus), rats (Rattus exulans (Peale) and R. rattus complex; Wallace et al. 1972), and Pacific monitor lizards (Varanus indicus (Daudin)). Cats and rats are widely distributed among all major island groups, though not necessarily on every island. Although both may prey opportunistically on bats, Rainey (1998) noted that bats roosting in tree canopies have managed to coexist with these predators in most settings. At Namoluk Atoll, M. Setile (pers. comm.) once observed cats on the roof of a cooking shed keeping close watch on bats feeding on fruits of an adjacent Crataeva speciosa tree, but the bats kept a safe distance away. On another occasion, he saw a cat carrying the wing of a bat, but did not know how it was acquired. Monitor lizards are localized in distribution, occurring on only a few islands in the southern Mortlocks, including Lekinioch and Satawan islands (Buden 2007), where bat populations are large relative to elsewhere in the Mortlocks. Monitor lizards are opportunistic predators that consume a variety of invertebrate and smaller vertebrate prey, and are effective climbers. Flying foxes have not been reported in their diet (Dryden 1965, Losos and Greene 1988, McCoid and Witteman 1993, Dryden and Ziegler 2004, Philipp et al. 2007), but monitor lizards have been observed climbing in trees and approaching roosting P. mariannus on Guam (D. Janeke, pers. comm.).

Specimens examined

Pteropus pelagicus pelagicus

Mortlock Islands: Namoluk Island, Namoluk Atoll (4 skins and skulls and 2 fluid preserved adults, field numbers 12–17, plus two unnumbered fetuses and one unnumbered young, all COM collections); Satawan Island, Satawan Atoll (11 skins and 9 skulls, COM field numbers 1–11); "Mortlock Islands" (in fluid with skull extracted, BMNH 82.10.27.4 [holotype of *phaeocephalus*]).

Pteropus pelagicus insularis

Chuuk Lagoon islands and Namonuito Atoll: "Ruck" (skull, MNHN 1996-2112 (apparently originally A6770 *fide* Andersen 1912) [lectotype of *insularis*]; 2 skulls, ZMB

5698 and an unnumbered specimen collected in 1907; skull extracted from fluid specimen, BMNH 98.1.2.1); Uala (= Weno) (4 skins and skulls, USNM 151563–151566); Moen (= Weno) (4 skins and skulls, BYUH 248, 249, 253, 254); Namonuito (skull, BMNH 15.1.18.1); "Truk" (1 skin and skull plus 13 skulls [confiscated in Guam, probably all from Chuuk Lagoon, but possibly also outlying islands; all tentatively identified as *P. p. insularis*], AMNH 249954–249969); "Samoa" (emended to Caroline Islands [probably Chuuk Lagoon islands]) (skin and skull, USNM 37815 [lectotype of *laniger*], and skin, MCZ 7023); no locality (ANSP 6196, skull).

Pteropus tokudae

Guam (2 skins and skulls, AMNH 87117 [holotype of *tokudae*] and 87118, and 1 skull, AMNH 256558).

Pteropus cf. pelewensis

"Ruck" (skull, ZMB 5697); Pohnpei (skull, ZMB A4065).

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