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# Review of the *Phyllium* Illiger, 1798 of Wallacea, with description of a new subspecies from Morotai Island (Phasmatodea: Phylliidae: Phylliinae)

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- ZooBank : <http://zoobank.org/651FCCFA-271B-48A3-A58E-A30FDC739493>

## Keywords:

Phasmatodea ; Morotai ;  
Phasmida ; *tobeloense* ;  
Phylliidae ; *bhaskarai* ;  
Phylliini ; description ;  
*Phyllium* ; new subspecies ;  
Wallacea ; distribution ;  
Indonesia ; biogeography.

**Abstract.** – The Phylliidae of Wallacea are here reviewed, with notes on species distributions. *Phyllium* (*Phyllium*) *tobeloense* Größer, 2007 is also here recorded as having a new subspecies from Morotai Island, *Phyllium* (*Phyllium*) *tobeloense bhaskarai* Cumming, Le Tirant, and Hennemann **ssp. nov.** based largely upon the distinct egg morphology. To conclude a key to all known *Phyllium* from Wallacea is presented with most features illustrated for ease in identification.

Cumming R. T., Le Tirant S. & Hennemann F. H., 2019. – Review of the *Phyllium* Illiger, 1798 of Wallacea, with description of a new subspecies from Morotai Island (Phasmatodea: Phylliidae: Phylliinae). *Faunitaxys*, 7(4) : 1 – 25.

ZooBank : <http://zoobank.org/CEC3E930-3E5D-4B2A-AE4D-51A198FD9E9E>

## Introduction

Members of the genus *Phyllium* Illiger, 1798 are well known as “Leaf Insects” or “Walking Leaves” and their still poorly understood systematics, phylogeny, and distributions have been studied more comprehensively during the past ten years. It has been shown that the actual biodiversity of these fascinating insects is far larger than previously suggested and several papers by the authors and various colleagues have described 30 new species of *Phyllium* from throughout Southeast Asia since 2009 (Brock *et al.*, 2018). The Phylliidae of Wallacea are particularly interesting but have not yet been studied in any detail, with only some of the species described before 2009 covered by Hennemann *et al.* (2009). In addition, two new species from Wallacea have recently been described from the islands of Peleng (Cumming & Teemsma, 2018) and Lombok (Cumming, Valero & Teemsma, 2018). Examination of extensive fresh material that has recently become available from various islands of Wallacea has revealed interesting facts concerning the synonymies and distributions of the species concerned and are summarized in the present paper. This includes a new subspecies from the Island of Morotai north of Halmahera, Maluku Islands, which is described herein. Still however, many questions concerning the true distributional ranges of some species throughout the very complex Wallacea subregion remain unanswered and the authors are aware of further still undescribed species, that will hopefully sometime become available for scientific recognition in order to clarify the biogeographic and phylogenetic facts and help to complete our knowledge of Wallacean Phylliidae.

## Biogeography

Wallacea is a group of several thousand islands of various sizes, which cover a total land area of roughly 338,500 km<sup>2</sup> located between Sundaland in the west, the Philippines in the north as well as New Guinea and Australia in the east and southeast. Recent studies suggest that also the Philippines need to be considered as part of the Wallacea (e.g. Vallejo, 2011), but for covering the Phylliidae of this particular region Wallacea is here treated in its traditional definition that excludes the Philippines. All islands are located almost entirely within the borders of Indonesia and include the island of Sulawesi, the Maluku Islands (also called Moluccas), the Kai Islands, Banda Islands and the Lesser Sunda Islands (except Bali). The largest of these islands is Sulawesi. The Lesser Sunda Islands attributed to the Wallacea are located south of Sulawesi and include Lombok, Sumba, Sumbawa, Flores and Timor, as well as several hundred smaller intervening islands. The Maluku Islands include several hundred islands in the northern portion of Wallacea, the largest being Halmahera in the north and Seram in the south. The most northern islands of the Maluku Islands are the Sangihe Islands and Talaud Islands, the most southeastern ones are the Kai Islands and Banda Islands, situated west of New Guinea.

Principally, Wallacea is a transition zone between the Oriental region and the Australian region with the fauna showing influences from both these regions (Dickerson, 1928). The western border of Wallacea is represented by Wallace’s line (named by Huxley in 1868), which runs between Borneo and Sulawesi in the north and Lombok and Bali in the south (Fig. 1). The eastern border of Wallacea has been disputed by

geologists and biogeographers and attempts to draw a definite line have produced a number of different lines (Simpson, 1977). The most accepted of these lines is Lydeker's line which follows the Sahul shelf, that runs between Seram and the Banda Islands in the west and New Guinea in the east (Fig. 1). Another well-known and much discussed line is Weber's line, which roughly runs between Sulawesi and the Maluku Islands (Gressitt, 1982). Mayr (1944) regarded Weber's line as a line of faunal balance, east of which the Papuan faunistic elements have a numerical superiority over Oriental elements.

Wallacea is regarded as a biodiversity hotspot although the subregion contains fewer known species overall compared to e.g. Sundaland, the Philippines, or the Australian region. However, Wallacea contains a very high percentage of endemic species, i.e. species that are only found in Wallacea or on single islands within this subregion, which is explained by several factors. First of all, the subregion contains a large number of different islands and geographic isolation is one of the major factors which leads to diversification and formation of endemic species. Wallace's line marks the position of deep ocean straits and separates shallow waters in the west from deep waters in the east. The sea-level dropped by an estimated 120 meters during the last ice-age and while the shallow waters in the west disappeared and formed land connections between the Large Sunda Islands (Sumatra and Java), Borneo, and the remaining portions of Sundaland, there were no such land bridge connections towards Wallacea.

## Materials and Methods

Photos of specimens were taken by René Limoges of the Montreal Insectarium (IMQC) using a Nikon D810 DSLR camera with Nikon Micro-Nikkor 200mm f/4 lens on Manfrotto 454 micrometric positioning sliding plate. Lighting was provided by two Nikon SB-25 flash units with a Cameron Digital diffusion photo box. Adobe Photoshop Elements 13 was used as post processing software. Measurements of specimens were made to the nearest 0.1 mm using digital calipers. The *Phyllium* (*Phyllium*) *tobeloense bhaskarai* **ssp. nov.** holotype and allotype specimens are deposited in the Montreal Insectarium Quebec, Canada (IMQC) type collection.

Photographs of specimens within the Frank Hennemann personal collection were taken by himself using a Nikon D7000 camera equipped with a Nikon DX AF-S Micro 40mm lens and a wireless Nikon SU-800 dual speed light system. Background lightning was provided by a 18W 6000K LED panel light plate. The photographs of the female holotype *Phyllium* (*Pulchriphyllium*) *suzukii* Gröber, 2008 was taken by Mandy Schröter under direction of Stephan Blanke at the Senckenberg German Entomological Institute Müncheberg using a Nikon D7200 digital camera and a Nikon Micro Nikkor 105mm f/2.8 G ED objective. Lightning was from the Yongnuo Digital Speedlight YN 560 IV reflected by the inner surface of a styrofoam box set up around the specimen. A grey card was used for white balance. Composite images with an extended depth of field were created using the software StackShot Macro Rail Package (Cognisys Inc., U.S.A.) and Zerene Stacker (release November 7, 2017; Zerene Systems LLC, U.S.A.).

## Abbreviations

- **AMSA**: Australian Museum, Sydney, NSW / Australia.
- **BPBM**: Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
- **BYU**: Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah / U.S.A.
- **CASC**: California Academy of Sciences, San Francisco, California / U.S.A.

- **IMQC**: Insectarium de Montréal, Montréal, Québec / Canada.
- **IRSN**: Institut Royal des Sciences Naturelles, Brussels / Belgium.
- **LEMQ**: Lyman Entomological Museum, McGill University, Québec, Canada.
- **MNHN**: Muséum National d'Histoire Naturelle, Paris / France.
- **MNHU**: Museum für Naturkunde der Humboldt-Universität, Berlin / Germany.
- **MZSF**: Muséum Zoologique, Université de Strasbourg, Strasbourg / France.
- **NHMUK**: The Natural History Museum, London / United Kingdom.
- **NHMW**: Naturhistorisches Museum Wien, Vienna / Austria.
- **NMR**: Natuurhistorisch Museum, Rotterdam / Netherlands.
- **RMNH**: Nationaal Natuurhistorisch Museum Naturalis, Leiden / Netherlands.
- **SDEI**: Senckenberg Deutsches Entomologisches Institut, Müncheberg / Germany.
- **SDNHM**: San Diego Natural History Museum, San Diego, California / U.S.A.
- **SFMF**: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M. / Germany.
- **SMNS**: Staatliches Museum für Naturkunde, Stuttgart / Germany.
- **UCRC**: University of California, Dept. of Entomology, Riverside, California / U.S.A.
- **UZZM**: Uppsala University Zoological Museum, Linnean collection, Uppsala / Sweden.
- **ZSMC**: Zoologische Staatssammlung, Munich / Germany.
- **AB**: Private collection of Alexander Banko / Canada.
- **EB**: Private collection of Edy Bhaskara / Indonesia.
- **FH**: Private collection of Frank H. Hennemann / Germany.
- **MO**: Private collection of Maxime Ortiz / France.
- **OC**: Private collection of Oskar V. Conle / Germany.
- **RTC**: Private collection of Royce T. Cumming / U.S.A.
- **SLT**: Private collection of Stéphane Le Tirant / Canada.
- **ST**: Private collection of Sierra Teemsma / U.S.A.
- **TM**: Private collection of Tetsuo Miyashita / Japan.

## Note on Locality Spelling Changes

With a number of historic data labels listed within, it is important to note the various spellings of localities which have changed throughout the years. Although not all those listed below are used within this work, we have noted additional spellings from throughout Wallacea to assist others who may be reviewing historic Wallacean specimens.

### Present Common Name = Known Historic Names

- **Ambon Island** = Ambonia / Amboina
- **Bacan Island** = Bachans / Bachians / Batchians
- **Banggai Islands** = Bangai / Bankei / Bangkei
- **Buru Island** = Bouru / Boro / Boeroe
- **Buton Island** = Button / Boeton / Butung
- **Halmahera** = Jilolo / Gilolo / Jailolo
- **Kai / Kei Islands** (both commonly used at present) = Key Islands
- **Maluku Province** = Moluccas / Maluku Province
- **Sanana Island** = Sula Besi / Xulla Besi
- **Seram Island** = Ceram / Seran / Serang
- **Sulawesi** = Celebes
- **Taliabu Island Regency** = Taliaboe

## Treatment of Species

### Subgenus *Phyllium* (*Pulchriphyllium*) Griffini, 1898

**Type species:** *Phyllium pulchrifolium* Audinet-Serville, 1838, 292, by original designation.

**Remarks.** – Only two species currently in this subgenus and attributed to the *frondosum* species group defined by

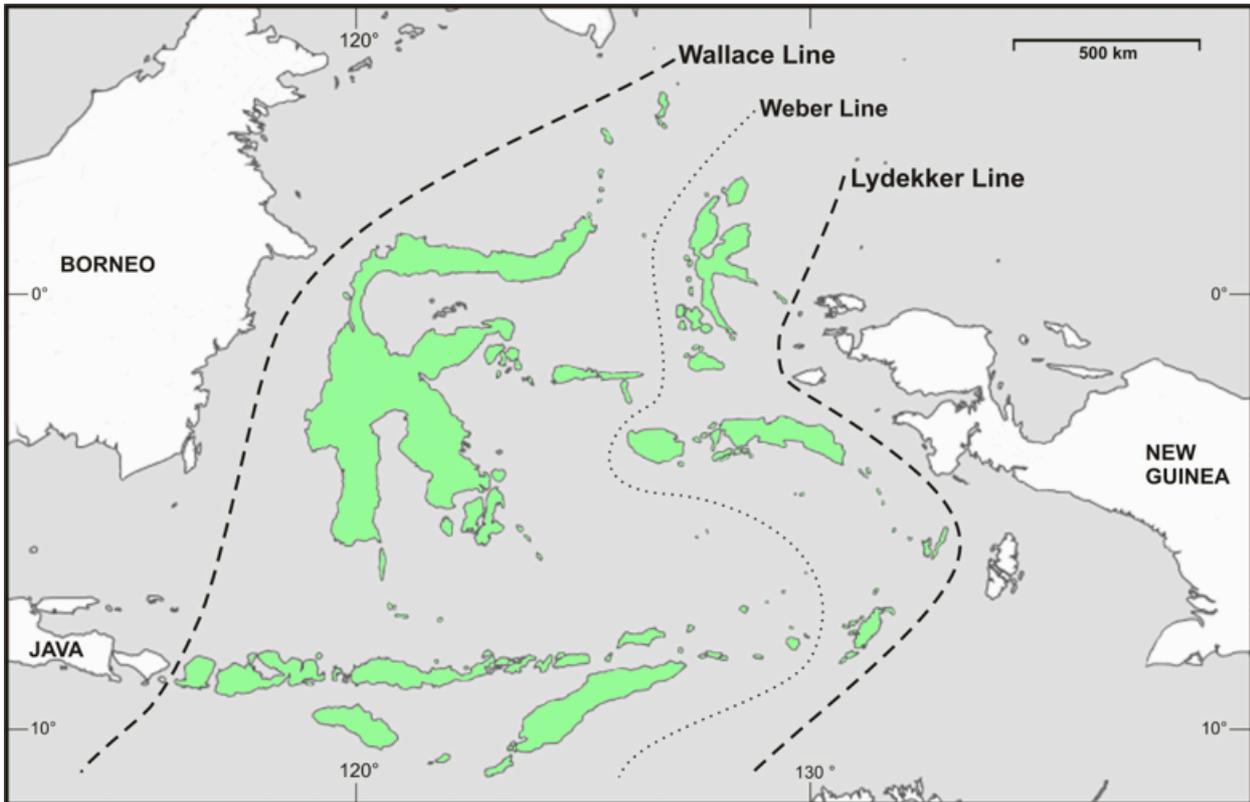


Fig. 1. Area defined as Wallacea (in green), bordered to the northwest by Wallace's line and to the southeast by Lydekker's line.

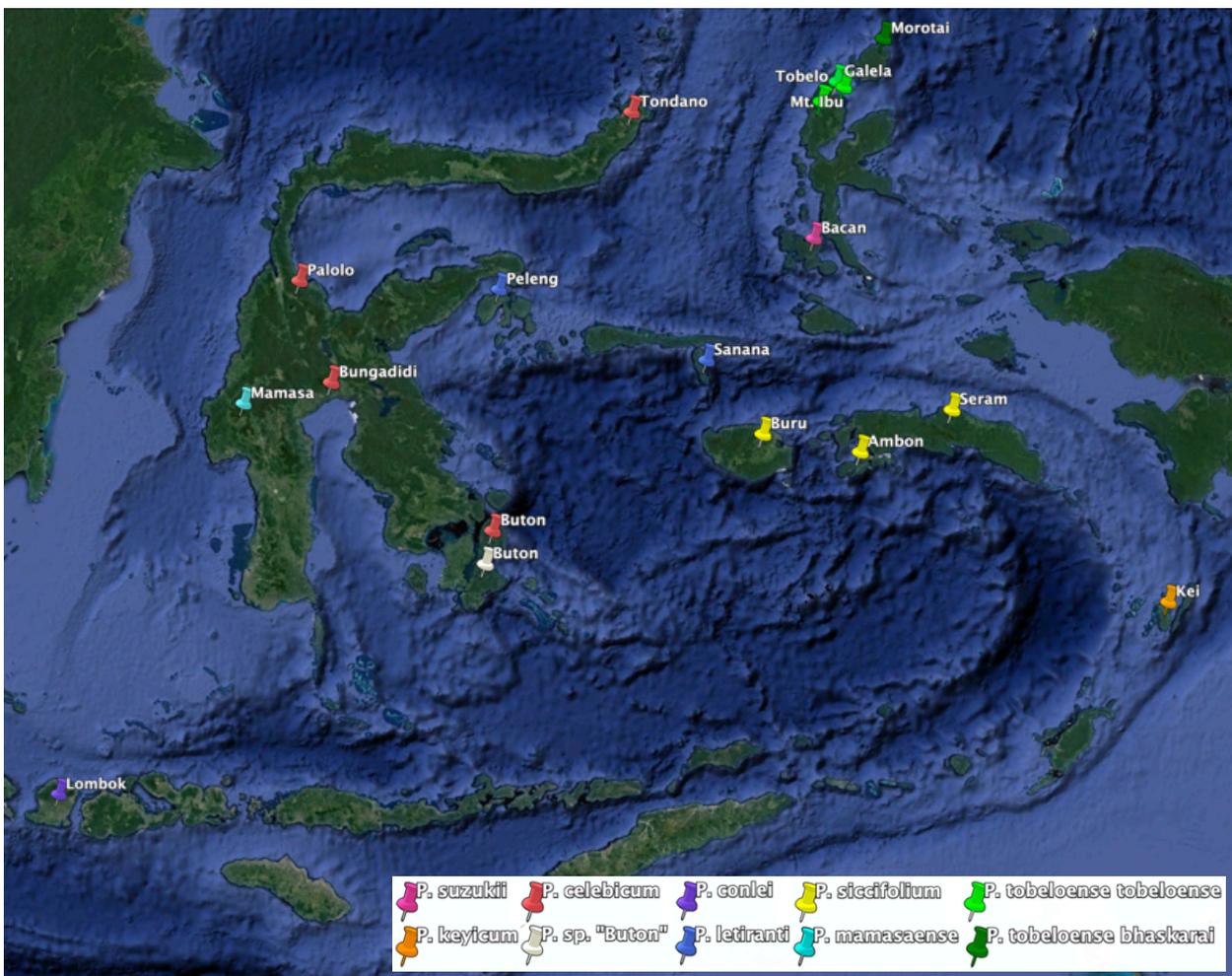


Fig. 2. Distribution map of the *Phyllium* species currently known within the boundaries of Wallacea. (Google Earth: Image Landsat/ Copernicus: Data SIO, NOAA, U.S. Navy, NGA, GEBCO: Accessed December 13th, 2018.

Hennemann *et al.* (2009) are known from Wallacea at present. One is only known from a unique specimen collected on the island of Bacan west of Halmahera in the northern Maluku Islands and the other species is not uncommon on the Kai Islands in the very southeastern portion of Wallacea. Additionally, both species are the only ones of the *frondosum* species group that are found outside of mainland New Guinea, and currently only known from female specimens.

***Phyllium (Pulchriphyllium) suzukii* Gröber, 2008**

(Fig. 5, 7, 9 & 61)

*Phyllium (Pulchriphyllium) suzukii* Gröber, 2008: 137, fig. 171-172.

Holotype, ♀: *Phyllium (Pu.) suzukii* det. Gröber, Molukken, Ins. Bacan, 9.2006; *Phyllium (Pu.) suzukii* Gröber sp. nov. Holotypus, det. D. Gröber 9.2006; DEI Hemimetabola #100121 [SDEI].

**Distribution.**

– INDONESIA: North Maluku Province, South Halmahera Regency, Bacan Island [SDEI].

**Discussion.** – *Phyllium suzukii* is one of only two species from the *frondosum* species group found outside of mainland New Guinea (the other being *Phyllium keyicum* Karney, 1914 discussed below) and is currently the only known species of *Phyllium* recorded from Bacan Island. This species is currently only known from the single holotype female held within the SDEI. This species is most characterized by the unique mesopraescutum which is 3.7 times wider than long (Fig. 9, the most extreme width to length ratio of known *Phyllium* females) as well as an abdomen with prominent, posteriorly directed projections on segments VI-VIII giving the abdomen a unique overall shape (Fig. 5); the outer margins of segments VII and VIII posteriorly project beyond the apex of the anal segment. With a body length of only 57.6 mm it is the smallest of all known representatives of the Phylliidae within the boundaries of Wallacea. The egg was illustrated by Gröber (2008: 137, fig. 171) and is easily recognized by the unusually ovoid overall shape and large roughly circular impressions of the capsule.

***Phyllium (Pulchriphyllium) keyicum* Karny, 1914**

(Fig. 3, 4, 6 & 8)

*Phyllium keyicum* Karny, 1914: 7, fig. 5. Holotype, ♀: Kei Islands, Toeal Island [depository unknown].

= *Phyllium insulanicum* Werner, 1922: 126. Holotype, ♀: Toeal, Kei-eilanden, J.H. Jurriaanse 1920 [RMNH]. (Synonymised by Hennemann *et al.*, 2009: 65)

= *Phyllium indicum* Günther, 1929: 614 (Misspelling of *insulanicum*).

**Distribution.**

– INDONESIA: Maluku Province, Southeast Maluku Regency, Kai Islands [NHMUK, NHMW, NMR, RMNH, SMNS, FH].

**Discussion.** – A detailed description of the females of this species and the synonymous *Ph. insulanicum* was presented by Willemse (1947). Since the holotype female of *Ph. keyicum* is not traced and presumed lost (Otte & Brock, 2005: 274), it may become necessary to designate a neotype. The egg was illustrated by Gröber (2008: 123, fig. 146).

Despite the Kai islands being rather remote, there have been a number of female specimens collected over the years. Unfortunately despite the female being not uncommon, the male *Ph. keyicum* is still unknown. This species is most notable for its profemoral exterior lobe with a posterior margin that is straight or very nearly so (Fig. 6, black line), this is the only

species within the *frondosum* species group with this feature. *Ph. keyicum* also has the unique morphology of a single posteromedial tubercle on the head capsule versus other members of the *frondosum* species group which have the tubercle split into two. Their most variable morphological feature is the terminal abdominal segments which can range from nearly straight across (Fig. 4) to more pronounced lobes (Fig. 3) and the full range between these two extremes. This intraspecific variability led to the description of *Phyllium insulanicum* Werner, 1922, based on the more strongly lobed females. Willemse (1947) extensively described and compared a series of specimens from the Kai Islands and from his thorough review it appears as though the variation in the abdominal lobes is the only notable feature between the two taxa. It was not until Hennemann *et al.* (2009: 65) correctly synonymized the *Ph. insulanicum* with *Ph. keyicum*, leaving there only a single species of *Phyllium* known from the Kai Islands. Variation in abdominal shape is now well known as a common occurrence in many species of *Phyllium* and not a feature that should singularly be relied upon for differentiation. With a body length of 70-79 mm females of this species are considerably larger than the related *Ph. suzukii* from Bacan Island.

**Subgenus *Phyllium (Phyllium)* Illiger, 1798**

**Type species:** *Gryllis (Mantis) siccifolius* Linnaeus, 1758: 425, by monotypy.

**Remarks.** – The seven species known to occur throughout Wallacea belong to two species groups defined by Hennemann *et al.* (2009). While only the Sulwesian *Ph. celebicum* de Haan, 1842 belongs to the *celebicum* species group all other known species fall within the *siccifolium* species group.

***Phyllium (Phyllium) celebicum* de Haan, 1842**

(Fig. 10–16, 81 & 82)

*Phasma (Phyllium) celebicum* de Haan, 1842: 111. Holotype, ♀: Celebes, Tondano [RMNH - not traced].

**Distribution.**

– INDONESIA: North Sulawesi Province, Minahasa Regency, Tondano [RMNH - type locality].

– Central Sulawesi Province, Sigi Regency, Palolo [RC].

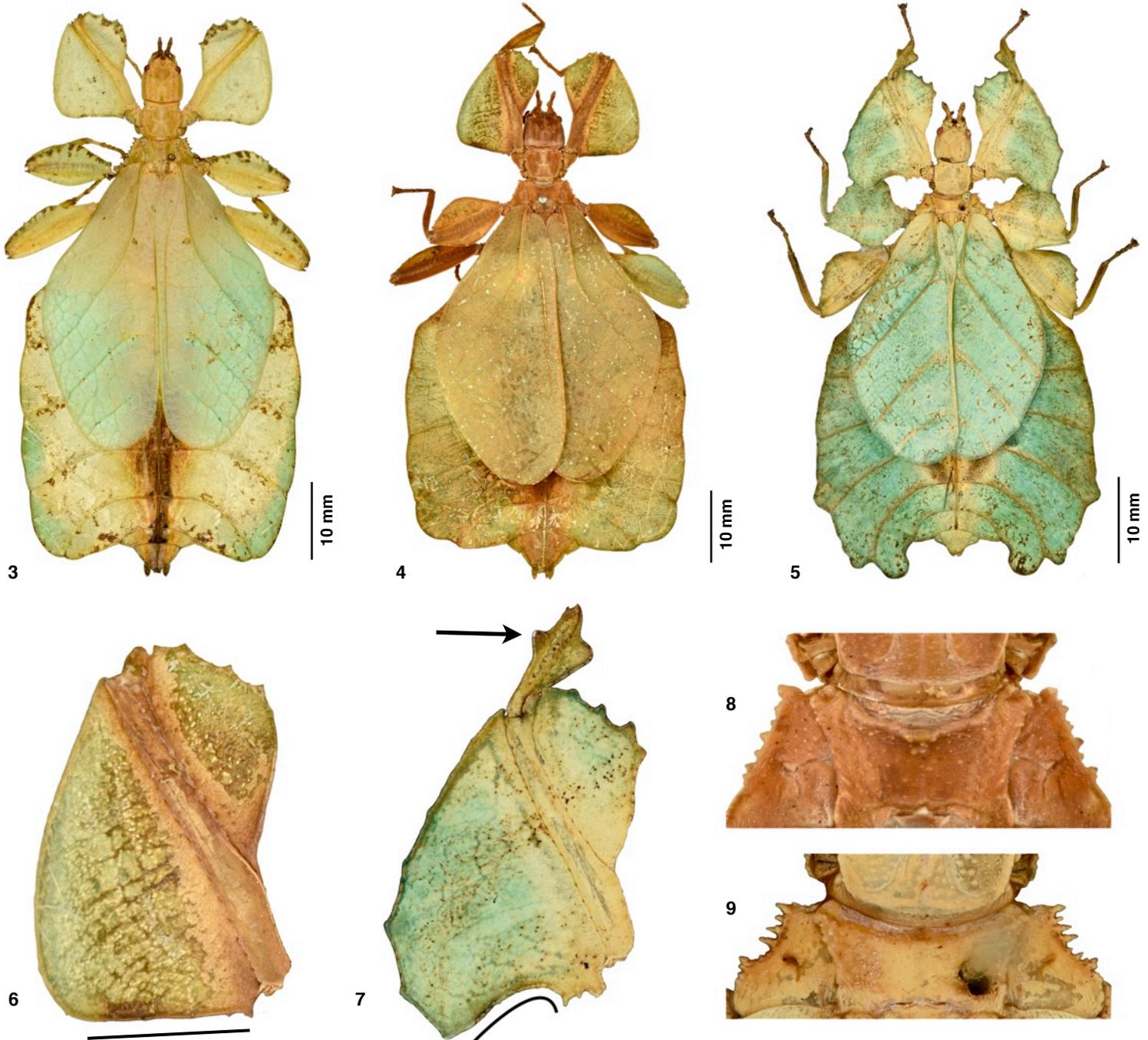
– South Sulawesi Province, North Luwu Regency, Bungadidi [FH, OC, SLT].

– South Sulawesi Province, North Luwu Regency, Tiulapolu [FH, RC].

– Southeast Sulawesi Province, Buton Regency, Buton Island [OC].

**Discussion.** – The female holotype was first reported lost in Hennemann *et al.* (2009: 15) after their extensive search within the RMNH collection in April 2006. Examination of the presumed holotype in the same collection (Bragg, 1996: 110) has revealed a female clearly not *celebicum* as originally described by de Haan (1842: 111) or illustrated by Willemse (1947: 319, fig. 3). The concerned specimen has features much more agreeing with *Ph. tobeloense* based on the thorax and profemoral lobes and does not represent the lost *Ph. celebicum* holotype.

True *Ph. celebicum* is discussed in depth in Hennemann *et al.* (2009: 11) where the authors provided illustrations, a detailed redescription of the female, descriptions of the previously unknown males and eggs, summarized the intraspecific variability, and discussed the numerous misidentifications over



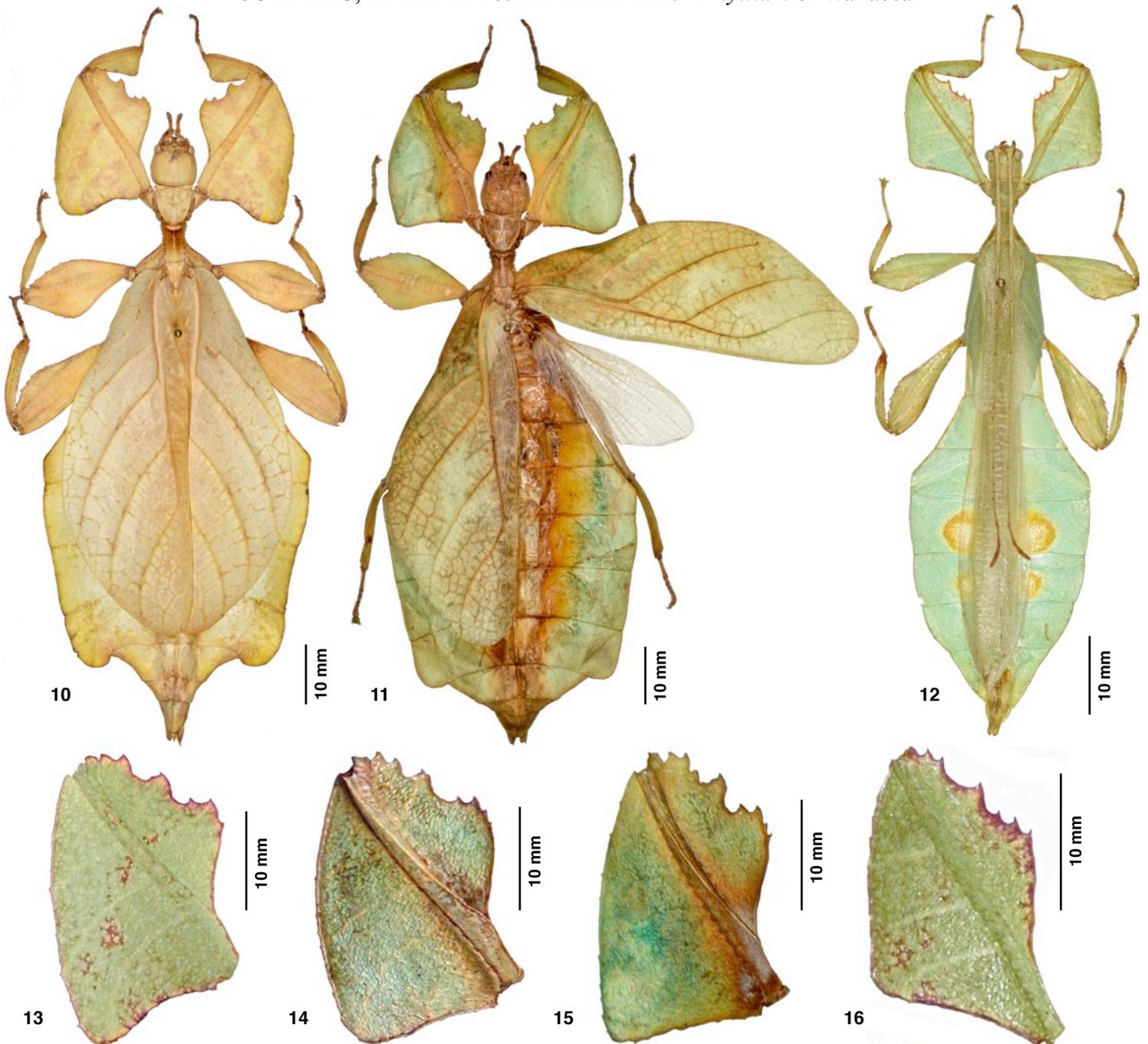
**Fig. 3–9.** Females, *frondosum* species group, dorsal view. - 3: *Phyllium keyicum* [FH 0083-1]. - 4: *Phyllium keyicum* [NHMUK 012496951 (Kei Is., 1923)]. - 5: *Phyllium suzukii* Gröber, 2008 holotype [SDEI]. - 6: Left profemur *Phyllium keyicum*; line illustrating the straight profemoral exterior lobe proximal edge, a unique feature to this species [NHMUK 012496951 (Kei Is., 1923)]. - 7: *Phyllium suzukii* holotype; line illustrating the curved profemoral exterior lobe proximal edge, and the arrow pointing out the protibial exterior spur, both features clearly contrasting *Ph. suzukii* from *Ph. keyicum* [SDEI]. - 8: Mesopraescutum and mesopleurae *Phyllium keyicum* [NHMUK 012496951 (Kei Is., 1923)]. - 9: Mesopraescutum and mesopleurae *Phyllium suzukii* holotype [SDEI].

the years. *Phyllium celebicum* is currently the only known member of the *celebicum* species group from Wallacea. This species group is characterized by males with profemoral lobes which are broader than the interior lobes (Fig. 16), and females which have developed alae (length 26.0–32.0 mm, fig. 11), both features which easily separate them from any other *Phyllium* of Wallacea.

*Phyllium celebicum* is currently only known from throughout Sulawesi and from nearby Buton Island. The single female specimen from the island of Ambon in the MNHU listed in Hennemann, *et al.*, (2009: 11) has been reexamined and found to not represent *Ph. celebicum*. Although very similar, this female specimen has several features which differentiate it from *Ph. celebicum* such as: a subgenital plate that is long and slender almost reaching the apex of the abdomen (in *Ph.*

*celebicum* the subgenital plate is short and stout, only just reaching to terminal segment X); mesopleurae which reach nearly to the anterior of the mesopraescutum (in *Ph. celebicum* the mesopleurae are distinctly shorter reaching only half way through the mesopraescutum); and alae which are notably longer than any examined *Ph. celebicum* females (49.0 mm in the MNHU specimen versus 26.0–32.0 mm in *Ph. celebicum*, see Hennemann, *et al.*, 2009: 16). The vague historic collection data of “Amboina” unfortunately cannot be trusted as truly coming from the island of Ambon and must be taken with little confidence. Realistically this *celebicum* species group member likely represents one of the many poorly described species from mainland Asia.

Body lengths: ♀♀ 75.5–92.0 mm, ♂♂ 62.0–66.0 mm.



**Fig. 10–16.** *Phyllium celebicum* dorsal. - 10–11: Females; note the well developed alae which help to characterize the *celebicum* species group [FH 0634-5 (left) and 0634-1 (right)]. - 12: Male [FH 0634-4]. - 13–15: Female left profemora showing intraspecific variability [FH 0634-6, 0634-2, 0634-1]. - 16: Male left profemora; note the exterior lobe with its strong angle and notably larger than the interior lobe, a feature which defines the *celebicum* species group [FH 0634-4].

***Phyllium (Phyllium) conlei*** Cumming, Valero, & Teemsma, 2018  
(Fig. 23 & 44)

*Phyllium (Phyllium) conlei* Cumming, Valero, & Teemsma, 2018: 3, fig. 3a-i. Holotype, ♂: Indonesien, Lombok, XII.2012 [ZSMC].

**Distribution.**

– INDONESIA: West Nusa Tenggara Province, Lombok Island [ZSMC].

**Discussion.** – Currently only known from the unique holotype male deposited in the State Zoological Collection of Munich (ZSMC) originally from the collection of Oskar Conle (Germany). Cumming, Valero, & Teemsma (2018) discuss the lack of knowledge for the Phylliidae of the Lesser Sunda Islands

and described *Ph. conlei* as the first unique species to the island chain. With the unique male at only 47.5mm in length, *Ph. conlei* is one of the smaller species of *Phyllium*. Nearby species also with males of a similar size range are *Phyllium jacobsoni* Rehn & Rehn, 1934: 42.5-50.4 mm, Java (Hennemann *et al.*, 2009), *Phyllium hausleithneri* Brock, 1999: 51.4-57.8 mm, West Malaysia and Sumatra (Cumming, Le Tirant, & Teemsma, 2018), and *Phyllium chenqiae* Seow-Choen, 2017 (53 mm, Borneo). From all species of a similar size, *Ph. conlei* can be differentiated by the slender abdomen with a width only about 30% of the total abdominal length versus the others with broad spade shaped abdomens 40-55%.

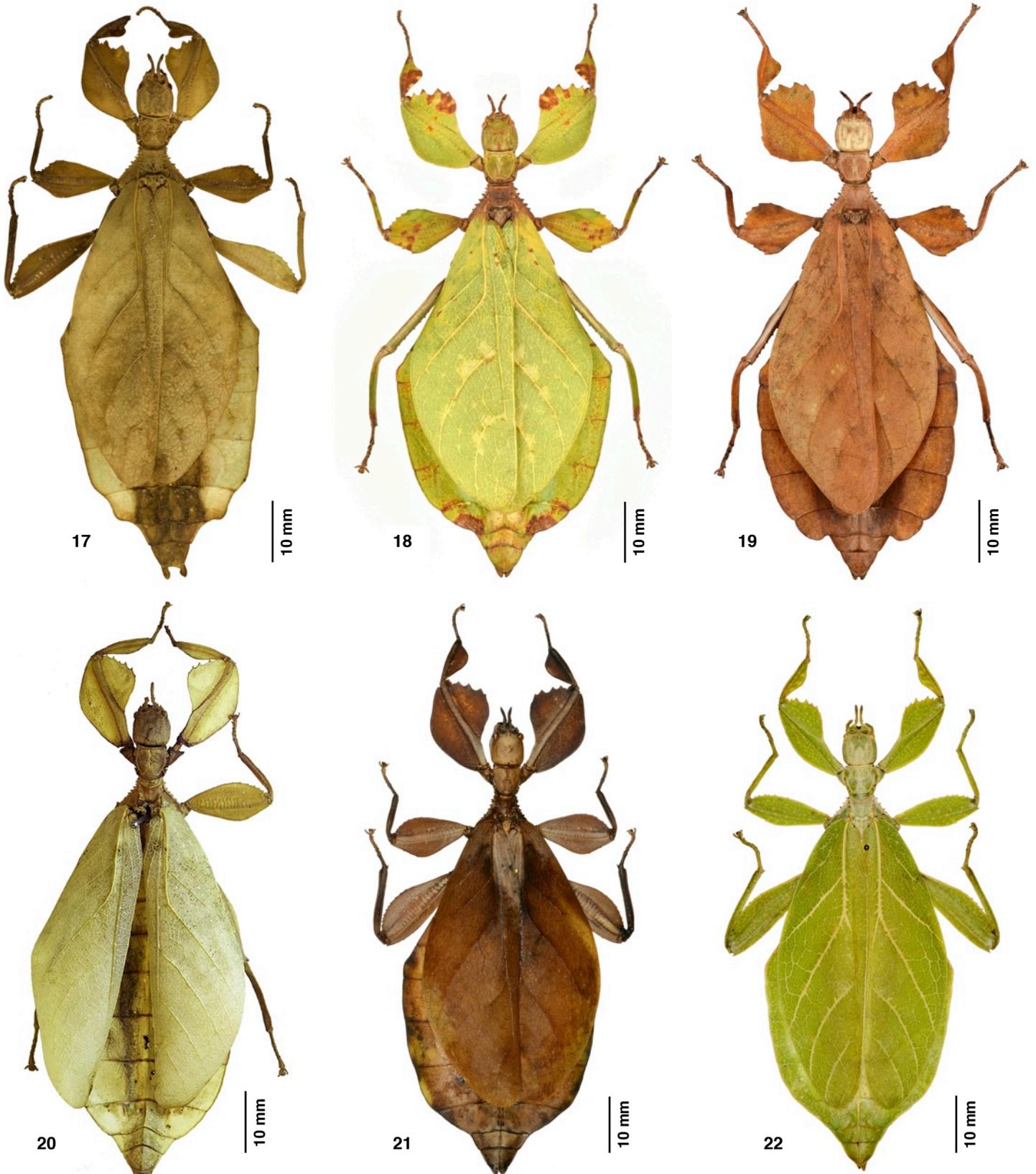


Fig. 17–22. Females, dorsal. - 17: *Phyllium mamasense* holotype [SDEI]. 18–19: *Phyllium letiranti* green and brown colorforms [SLT coll.]. - 20: *Phyllium siccifolium* holotype [UUZM]. - 21: *Phyllium siccifolium* from Seram Island [FH 1042-1]. - 22: *Phyllium tobeloense tobeloense* from Halmahera Island, Mount Ibu [FH 0657-7].

***Phyllium (Phyllium) sp. “Buton”***

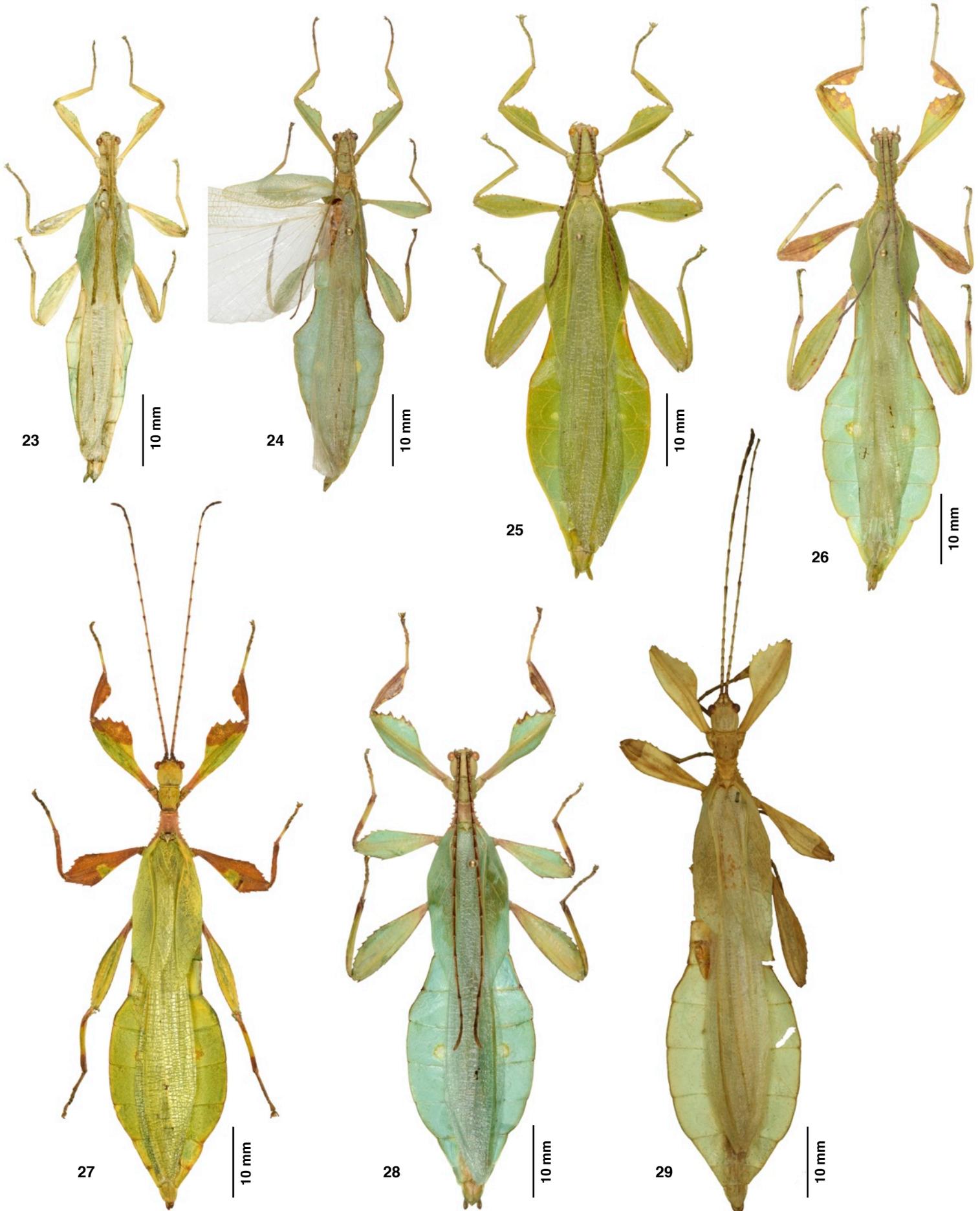
(Fig. 24 & 45)

***Distribution.***

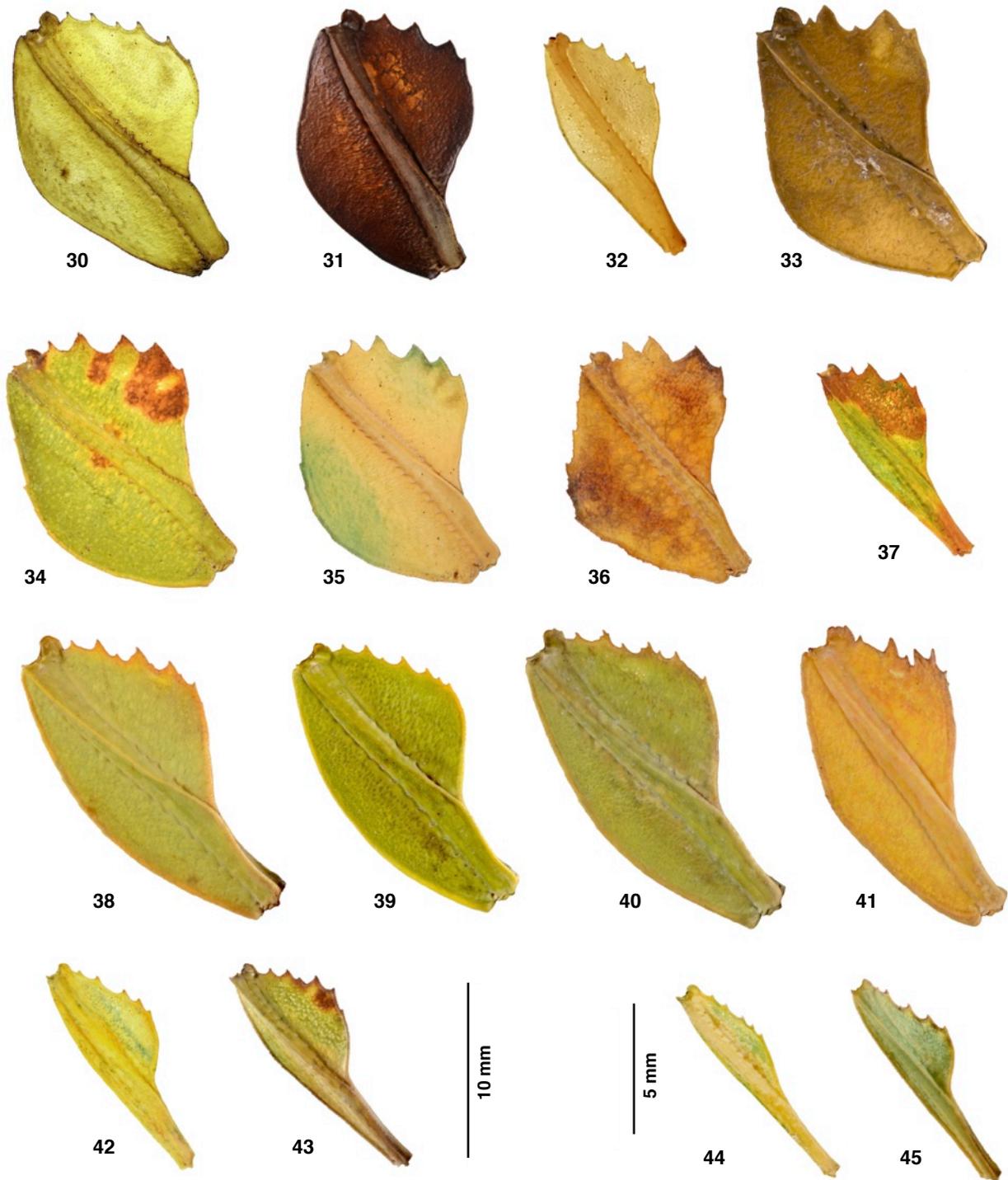
– INDONESIA: Southeast Sulawesi Province, Buton Regency, Buton Island [FH].

***Discussion.*** – Known only from a single male within the Hennemann private collection (FH 0673-1) this specimen was

the most difficult to place, with a near perfect match within the intraspecies morphological range of *Ph. hausleithneri* Brock, 1999 and *Ph. jacobsoni* Rehn and Rehn, 1934, both species found outside of Wallacea. Finding either species on Buton (far from their known distributions outside of Wallacea) would be very surprising and would challenge the well-defined biogeographic boundary lines of Wallacea. The authors are confident in the collection data, but, mistakes by collectors or specimen dealers are a possibility and we cannot ignore the fact that this could simply be a clerical error. Additionally, the



**Fig. 23–29.** Males, dorsal. - **23:** *Phyllium conlei* holotype [ZSMC]. - **24:** *Phyllium* sp. “Buton” [FH 0673-1]. - **25:** *Phyllium toboloense toboloense* from Halmahera Island, Mount Ibu [FH 0657-9], note the antennae not reaching the apex of the resting tegmina. - **26:** *Phyllium toboloense toboloense* captive reared from Halmahera Island, Galela [FH 0657-13]. - **27:** *Phyllium letiranti* from Peleng Island [SLT coll.]. - **28:** *Phyllium letiranti* from Sanana Island, Waifara [FH 1008-10] note the antennae exceeding the apex of the resting tegmina. - **29:** *Phyllium siccifolium* from Ambon Island [NHMUK].



**Fig. 30–45.** Profemora, dorsal. - **30:** Female *Phyllium siccifolium* holotype [UUZM]. - **31:** Female *Phyllium siccifolium* [FH 1042-1]. - **32:** Male *Phyllium siccifolium* [NHMUK]. - **33:** Female *Phyllium mamasaense* holotype [SDEI]. - **34–36:** Female *Phyllium letiranti* showing intraspecies variation in color and lobe serration. - **37:** Male *Phyllium letiranti* [SLT coll.]. - **38–41:** Females *Phyllium toboloense bhaskarai* **ssp. nov.** paratypes, showing remarkable intraspecies variation in color and lobe serration [FH 1077-3, 1077-1, 1077-2, 1077-6]. - **42:** Male *Phyllium toboloense bhaskarai* **ssp. nov.** allotype [IMQC]. - **43:** Male *Phyllium toboloense bhaskarai* **ssp. nov.** paratype [FH 1077-21]. - **44:** Male *Phyllium conlei* holotype [ZSMC]. - **45:** Male *Phyllium* sp. “Buton” [FH 0673-1].

female and egg from this “Buton” species are not yet known, leaving the possibility that clear morphological features identifying it as a new taxon might simply only be visible in the female or egg morphology. With *Ph. toboloense bhaskarai* **ssp. nov.** only easily separated from the nominate subspecies by the unique egg morphology, it is very possible that this male could represent a new species or subspecies, only recognizable by female or egg morphology. Therefore, with a lack of significant morphological features to base a new taxon on, we simply refer to this species as *Phyllium (Phyllium)* sp. “Buton” throughout this work. Body length 48.5 mm.

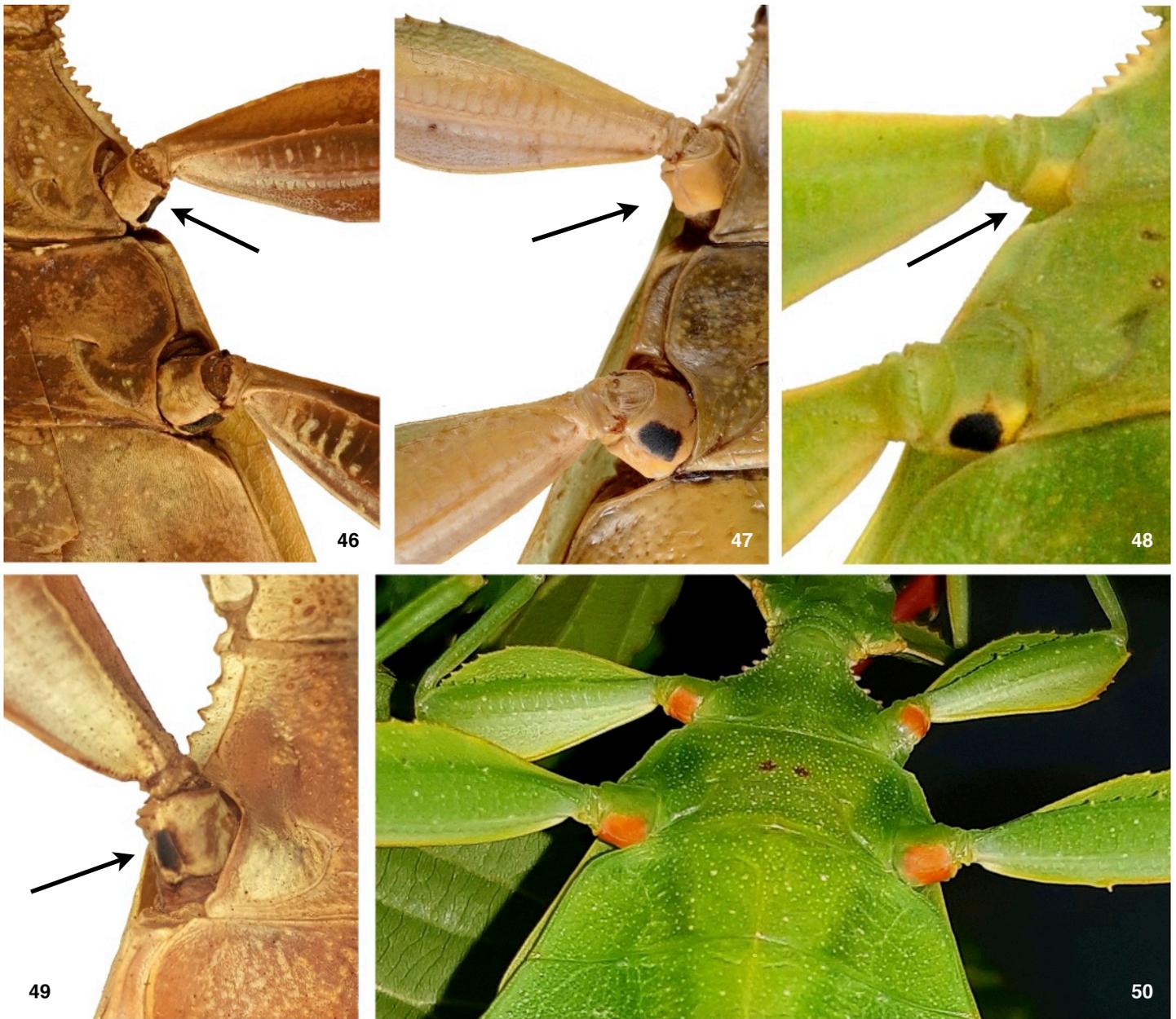
***Phyllium (Phyllium) letiranti* Cumming & Teemsma, 2018**

(Fig. 18, 19, 27, 28, 34–37, 50, 51, 54, 87, 88, 91 & 96–98)

*Phyllium (Phyllium) letiranti* Cumming & Teemsma, 2018: 2, fig. 1A–D, 2B–D, F–G, 3A–E, 4A–D, 5A–D, 6A–C. Holotype, ♀: Indonesia, Peleng Island, Tinagkung Utara, near Luksagu Village: December, 2016: ~60 m. elv. 1°17' S 123°25.4' E [IMQC]; Paratypes [IMQC, SDNHM, CASC, SDEI, RC, ST, SLT, and FH].

*Phyllium (Phyllium) siccifolium*, Klante, 1976: 65, 76, fig. 10, (in part).

*Phyllium (Phyllium) siccifolium*, Hennemann *et al.*, 2009: 58 (in part).



**Fig. 46–50.** Females, ventral view of coxae. - **46:** *Phyllium mamasense* holotype, showing black interior mark on meso- and metacoxae [SDEI]. - **47:** *Phyllium toboloense toboloense*, showing metacoxae only with a black interior marking, mesocoxae lacking colored mark [FH 0657-3]. - **48:** *Phyllium toboloense bhaskarai* ssp. nov. paratype, showing metacoxae only with a black interior marking, mesocoxae lacking colored mark [FH 1077-2]. - **49:** *Phyllium siccifolium*, mesocoxae with black interior marking [NHMUK]. - **50:** *Phyllium letiranti* live female bred by Maxime Ortiz (France) showing lack of black coxae markings and the vibrant orange coxae color (© Maxime Ortiz).

#### **Distribution.**

– INDONESIA: Central Sulawesi Province, Banggai Regency, Peleng Island [RC, FH, ST, SLT, CASC, IMQC, SDNHM]; Banggai Islands [MNHU].

– INDONESIA: North Maluku Province, Sula Islands Regency, Sanana Island [FH - distribution expansion].

**Discussion.** – Only recently collected (2016) and described (2018), this species has become widely available for sale as dried specimens and has entered the phasmid breeding community. In captivity it has been described as a relatively easy species to raise with a trend to produce a wide variety of female colorforms (Fig. 96–98). Originally described from Peleng Island, the authors have received photos of *Phyllium* from the nearby coast of Sulawesi (Central Sulawesi Province, East Peninsula) which appear very similar in morphology to *Ph. letiranti*, but without high resolution photos or specimens to review, a confident identification is not possible at this time. It would not be surprising to find *Ph. letiranti* on the Sulawesi coast near Peleng Island but with the similar species *Ph.*

*mamasense* also found on Sulawesi, from photos alone an identification cannot be confirmed. Hopefully future collecting on Sulawesi can bring to light the distribution of *Ph. letiranti* with more clarity.

A range expansion can however be made for Sanana Island (Sula Islands) as represented by a male specimen from the Hennemann private collection (Fig. 28, FH 1008-10). With the island of Sanana known to have *Ph. letiranti*, the female from “Taliaboe” (Taliabu) in the RMNH illustrated in Klante (1976) and the female from the MNHU from “Bangkei” (Banggai) discussed in Hennemann, *et al.*, (2009) likely also represents *Ph. letiranti*. Examination of the specimen within the MNHU does reveal a female which matches well with slender *Ph. letiranti* females from Peleng Island.

The two easiest diagnostic features to differentiate female *Ph. letiranti* from *Ph. siccifolium* are the ventral color of the coxae (*Ph. siccifolium* having distinct black markings and *Ph. letiranti* without) and the number of antennal segments (nine in *Ph. siccifolium* and ten in *Ph. letiranti*). Unfortunately, in Klante (1976) neither feature was illustrated clearly and

therefore a thorough examination of the specimen in question must eventually be done to confirm this identification.

With the Sula Islands situated just to the east of the Banggai Islands, this distribution expansion is not surprising and opens the possibility that this species can also be found on the other Banggai or other Sula Islands.

Body lengths: ♀♀ 86.6-91.2 mm, ♂♂ 57.6-62.2 mm.

***Phyllium (Phyllium) mamasaense* Gröber, 2008**

(Fig. 17, 33, 46, 68, 89 & 90)

*Phyllium (Phyllium) mamasaense* Gröber, 2008: 124, fig. 147-148. Holotype, ♀: *Phyllium (Ph.) mamasaense* det. Gröber, Sulawesi, Mamasa, 9.2006; *Phyllium (Ph.) mamasaense* Gröber sp. nov. Holotypus, det. D. Gröber 9.2006; DEI Hemimetabola #100116 [SDEI].

**Distribution.**

– INDONESIA: West Sulawesi Province, Mamasa Regency, Mamasa District [SDEI].

**Discussion.** – Only known from very few female specimens collected over the last ten years from the type locality of Mamasa, Sulawesi (Fig. 2). This species has the unique characteristic of having meso- and metacoxae with black interior markings on the ventral surface (Fig. 46) a feature within Wallacea currently only known from *Ph. siccifolium* (Fig. 49), or only partially seen in *Ph. tobeloense* (Fig. 47, only metacoxae with black marking). Interestingly, all females observed (although not a wide sample size) have had a very steady morphology with abdominal segments VII and VIII consistently roundly angular (Fig. 68) and the profemoral interior lobe with two large prominent teeth (as well as several small minor teeth) (Fig. 33). These features are variable among certain other *Phyllium* females and we look forward to hopefully reviewing more material in the future as well as describing the currently unknown male once it is identified. The large eggs are very distinctive (Fig. 89 & 90) and differ from those of all other Wallacean Phylliidae by the feather-like fringes of the capsule forming several parallel longitudinal ridges and the very large cup-shaped operculum. Body length 93.5-105.0 mm.

***Phyllium (Phyllium) siccifolium* (Linnaeus, 1758)**

(Fig. 20, 21, 29, 30–32, 49, 52, 55, 63 & 69)

*Gryllus (Mantis) siccifolium* Linné, 1758: 425, No. 3. Holotype, ♀: Indes, Gustav IV Adolph; *Gryllus (Mantis) siccifolius* type; Coll. n° 1818 [UZZM].

= *Phyllium brevicorne* Latreille, 1806: 272. (Synonymised by Gray, 1835: 30).  
 = *Phasma chlorophylla* Stoll, 1813, 69, pl. 23: 89. (Synonymised by Redtenbacher, 1906: 176).  
 = *Phasma citrifolium* Lichtenstein, 1796: 78. (Synonymised by Gray, 1835: 30).  
 = *Phasma donovani* Gray, 1835: 31. (Synonymised by Redtenbacher, 1906: 176).  
 = *Phasma foliatus* Perry, 1810: plate 24. (Synonymised by Westwood, 1859: 172).  
 = *Phasma gorgon* Gray, 1835: 31. (Synonymised by Westwood, 1859: 172).  
 = *Phyllium stollii* Le Peletier de Saint Fargeau & Serville, 1827: 115. (Unnecessary replacement name for *Phasma chlorophylla* Stoll, 1813).  
 [Not: *Phyllium (Phyllium) tobeloense* Gröber, 2007: 15. Erroneous synonym of Hennemann *et al.*, 2009: 53].

**Distribution.**

– INDONESIA: Maluku Province, Ambon [MNHU, NHMUK, RMNH, UZZM], Seram [NHMUK, FH] and Buru Islands [NHMW].

**Discussion.** – As the type species for the family, this species is one of great importance but unfortunately it is also one of the many poorly known species because of the lack of available material in modern times. The holotype female (Fig. 20) was redescribed in Hennemann *et al.* (2009: 55) as well as a male specimen from the island of Ambon from NHMUK (Fig. 29). These authors also discussed the numerous synonyms and provided information of the intraspecific variability. The exact type-locality of *Ph. siccifolium* originally stated to be “Habitat in Indiis” by Linnaeus (1758: 425) was discussed in detail in Hennemann *et al.* (2009: 57). These authors stated the holotype female in the UZZM collection to be most likely from the island of Ambon.

In addition to the island of Ambon, various collections examined over the years have revealed numerous females from the islands of Seram and Buru which match well with the morphology of the holotype. The likely misidentification by Klante (1976) discussed above from Taliabu Island is probably the morphologically similar *Ph. letiranti* known from the Banggai and Sula Islands, leaving true *Ph. siccifolium* restricted to east of Weber’s Line (Fig. 1) and only known from Ambon, Seram, and Buru. Unfortunately, the male of this species is little known and the eggs are still unknown for *Ph. siccifolium*. With egg morphology so drastically different between *Ph. letiranti* and *Ph. tobeloense* hopefully future fresh material will reveal the eggs of *Ph. siccifolium* and their morphology should shed light on the relationship to the other similar species.

Body lengths: ♀ 89.0-94.0 mm, ♂♂ 67.0-73.0 mm.

Feature	<i>Phyllium tobeloense</i>	<i>Phyllium siccifolium</i>
Ventral coxae color ♀	Metacoxae with distinct black interior marking, mesocoxae slightly orange or light green, no black interior mark (Fig. 47 & 48)	Mesocoxae and metacoxae and with distinct black interior marking (Fig. 49)
Profemoral exterior lobe* ♀	Thin and smoothly arcing, greatest width only 1.5 to 2 times the width of the profemora shaft (Fig. 38–41)	Broad and slightly angular, greatest width 2.5 to 3 times the width of the profemora shaft (Fig. 30 & 31)
Antennae Length ♂**	Short, not projecting beyond the apex of the resting tegmina (Fig. 25)	Long, reaching or projecting beyond the apex of the resting tegmina (Fig. 29)

**Table 1.** Summary of comparison between *Phyllium tobeloense* and *Phyllium siccifolium* females and males.

\* Measured at the proximal edge of the profemoral interior lobe. \*\* When antennae are held at rest back along the body.

Feature	Holotype ♀	Allotype ♂	Paratypes ♀♀	Paratypes ♂♂
Length of body*	94.2	60.6	89.0 - 102.0	60.5 - 66.0
Length/greatest width of head	8.9 / 7.0	4.1 / 3.5	8.1-9.0 / 5.5-7.1	3.8-4.2 / 3.5-3.7
Pronotum	7.1	3.9	5.9 - 7.2	3.8 - 4.1
Mesonotum	9.2	4.3	8.8 - 9.5	4.3 - 4.6
Length of tegmina	61.6	23.5	58.5 - 64.0	21.6 - 24.0
Length of alae	-	42.8	6.1**	42.5 - 48.0
Greatest width of abdomen	35.0	13.2	35.0 - 43.5	13.5 - 17.2
Profemora	18.7	11.6	18.2 - 21.5	11.6 - 12.8
Mesofemora	16.5	12.5	15.9 - 18.8	11.1 - 12.9
Metafemora	20.8	14.7	20.5 - 23.6	13.9 - 16.0
Protibiae	11.3	7.8	10.9 - 14.8	7.8 - 8.2
Mesotibiae	11.5	7.5	10.8 - 14.0	7.2 - 8.3
Metatibiae	17.1	12.0	16.9 - 20.5	11.0 - 12.3
Antennae	5.7	24.8	5.1 - 6.0	24.0 - 25.3

**Table 2.** Measurements of *Phyllium (Phyllium) toboloense bhaskarai* ssp. nov., holotype female and allotype male. For the paratype material only the smallest and largest in the series were measured to give a range. All measurements made to the nearest 0.1mm.

\* Including cerci and head, excluding antennae.

\*\* Only measured on paratype specimen RC 18-421 which measures 101.2 mm in length.

***Phyllium (Phyllium) toboloense toboloense* Gröber, 2007**

(Fig. 22, 25, 26, 47, 64, 66, 83, 84, 92, 99 & 100)

*Phyllium (Phyllium) toboloense* Gröber, 2007: 15, fig. 1-4. Holotype, ♀: *Phyllium (Ph.) toboloense* det. Gröber, Molukken, Halmahera, Tobelo, 8.1998 [SDEI].

**Distribution.**

– INDONESIA: North Maluku Province, North Halmahera Regency, Tobelo [SDEI, FH, OC - type locality], Mount Ibu [FH, RC, SLT] and Galela [FH].

**Discussion.** – Originally collected in Tobelo, Halmahera, this species has been widely bred by enthusiasts and like *Ph. letiranti* has yielded a number of beautiful female colorforms (Fig. 99 & 100). This species was briefly disputed in Hennemann *et al.* (2009) where it was presented as a junior synonym for *Ph. siccifolium* until Gröber (2011) where it was reestablished. Here we agree with the reestablishment of *Ph. toboloense* as a valid species and discuss the morphological reasoning for our decision.

Although very similar in morphology, when a review of a significant series is examined these two species can be separated by the following characteristics. The first feature for differentiating females is the ventral color of the coxae, with *Ph. toboloense* having a black marking only on the metacoxae, not on the mesocoxae (Fig. 47 & 48) versus *Ph. siccifolium* with both meso- and metacoxae with black markings. Also for females, the width of the profemoral exterior lobe is consistently different with *Ph. toboloense* having a more slender lobe, no more than two times the width of the profemoral shaft (Fig. 38–41), as compared to *Ph. siccifolium*

which always has a profemoral exterior lobe that is notably wider (2.5 to 3 times) than the width of the profemoral shaft (Fig. 30 & 31). For males, the antennae immediately separate the two species, with *Ph. toboloense* with shorter antennae, not longer than tegmina length when at rest (Fig. 25), versus *Ph. siccifolium* males which have longer antennae which reach to or past the apex of the folder tegmina. These distinguishing features are presented in summary in table 1. These features have proven to be consistent across all specimens examined of both populations, including extreme variations within each population.

Body lengths: ♀♀ 89.0-101.0 mm, ♂♂ 59.0-62.0 mm.

***Phyllium (Phyllium) toboloense bhaskarai* Cumming, Le Tirant, and Hennemann, ssp. nov.**

(Fig. 38-41, 48, 53, 56-58, 65, 67, 70-77, 79, 80, 85, 86, 101-103)

ZooBank : <http://zoobank.org/4ED84870-BA6D-4546-B518-278B66EEAF4D>

**Holotype:** ♀: INDONESIA, Morotai island, North Maluku, Pulau Morotai Regency, Dao village, XI-XII.2018 [IMQC].

**Allotype:** ♂: INDONESIA, Morotai island, North Maluku, Pulau Morotai Regency, Dao village, XI-XII.2018 [IMQC].

**Paratypes:** [103 ♂♂, 90 ♀♀, 46 eggs], INDONESIA, Morotai island, North Maluku, Pulau Morotai Regency, Dao Majiko village, XI-XII.2018.

**Depositions.**

– 1 ♂, 2 ♀♀, 1 egg [AMSA]

– 1 ♂, 1 ♀ [BPBM]

– 1 ♂, 2 ♀♀, 1 egg [BYU]

- 2 ♂♂, 2 ♀♀, 1 egg [CASC]
- 5 ♂♂, 18 ♀♀, 10 eggs [IMQC]
- 1 ♂, 3 ♀♀ [IRSN]
- 1 ♂, 1 ♀ [LEMQ]
- 2 ♂♂, 2 ♀♀, 2 eggs [MNHN]
- 1 ♂, 3 ♀♀ [MNHU]
- 1 ♂, 1 ♀ [MZSF]
- 2 ♂♂, 2 ♀♀, 2 eggs [NHMUK]
- 2 ♂♂, 3 ♀♀ [NHMW]
- 1 ♂, 3 ♀♀ [RMNH]
- 2 ♂♂, 2 ♀♀ [SDEI]
- 2 ♂♂, 2 ♀♀, 1 egg [SDNHM]
- 1 ♂, 3 ♀♀ [SMFM]
- 1 ♂, 2 ♀♀, 1 egg [UCRC]
- 2 ♂♂, 3 ♀♀, 1 ♀ (penultimate instar) [ZSMC]
- 1 ♂, 1 ♀ [coll. AB]
- 1 ♂, 2 ♀♀ [coll. EB]
- 15 ♂♂, 20 ♀♀, 12 eggs [coll. FH, No's 1077-1 to 35, E]
- 1 ♂, 1 ♀ [coll. MO]
- 5 ♂♂, 5 ♀♀ [coll. OC]
- 6 ♂♂, 7 ♀♀, 5 eggs [coll. RTC 18-421, 18-422, & 19-087 to 19-102]
- 20 ♂♂, 20 ♀♀, 5 eggs [coll. SLT]
- 1 ♂, 1 ♀, 1 egg [coll. ST]
- 1 ♂, 1 ♀ [coll. TM].

#### **Distribution.**

– INDONESIA: North Maluku Province, Morotai Island Regency.

**Remarks.** – Currently only known from Morotai Island, Indonesia. Morotai is separated from northern Halmahera by the Morotai Strait, a stretch of water only about 10 kilometres (6.2 mi) wide. The only other island near Morotai is Bau Island, a small island on the west coast. It is possible that *Phyllium (Phyllium) tobeloense bhaskarai* **ssp. nov.** may also be found on Bau Island, due to its close proximity but currently no specimen records exist.

**Discussion.** – This new population has only recently been discovered (November, 2018 by Alim Yasin) on Morotai and the first impression was that this was likely a range expansion for *Phyllium tobeloense* until photos of the eggs were received. Immediately it became apparent that this Morotai population was not identical to the Halmaheran population. The decision to classify this Morotai population a subspecies of *Phyllium tobeloense* and not full species status is tentative but was based on a number of observations. Upcoming genetic analysis will help reveal the extent of the variability between the populations, but our present morphological review suggests a very close relationship. First is the incredible similarity of the adult morphology between the two populations. With the Halmaheran population rather popular in both phasmid breeding communities and commonly bred for commercial export as dried specimens, a wide review of the intraspecific variation has been possible. This has revealed that the females of this species have moderate variability in the profemoral interior lobe, and slight variability in abdominal segment VIII. Captive bred specimens have also resulted in a significant variety of color forms (Fig. 99 & 100) and a variety of major and minor profemoral interior lobes, similar to those seen in exported dried specimens. With this significant view into the intraspecific variation of males, females, and eggs, the egg morphology differences between the Morotai and Halmahera populations can easily be identified as not simply intraspecific variation and is discussed in detail below. With egg

morphology one of the only concrete features to allow differentiation between the populations, and the obvious similarity between the population's eggs, we consider this Morotai population an offshoot of the mainland Halmahera population and classify it as a subspecies.

An additional reason for our decision to classify the Morotai population as a subspecies is the significant number of other insect species which follow this trend. Frequently, the Morotai populations are subspecies with sibling subspecies from the other northern Maluku Islands. For example, Wallace's golden birdwing butterfly *Ornithoptera croesus* Wallace, 1859 is endemic to the northern Maluku islands, with five total subspecies distributed throughout these islands. In particular, from Halmahera there is *Ornithoptera croesus lydius* (Felder & Felder, 1865) and from Morotai *Ornithoptera croesus toeantei* Parrot & Schmid, 1984. Interesting, these butterfly subspecies parallel our own *Phyllium tobeloense* subspecies as the females are more easily morphologically separated than males are, with males of these two-island populations near impossible to differentiate (pers. comm. Gilles Delisle, birdwing butterfly expert). As discussed in more detail below, we were able to find consistent morphological differences between the females and eggs of these two populations of *Phyllium tobeloense* but between males no reliable features could be found.

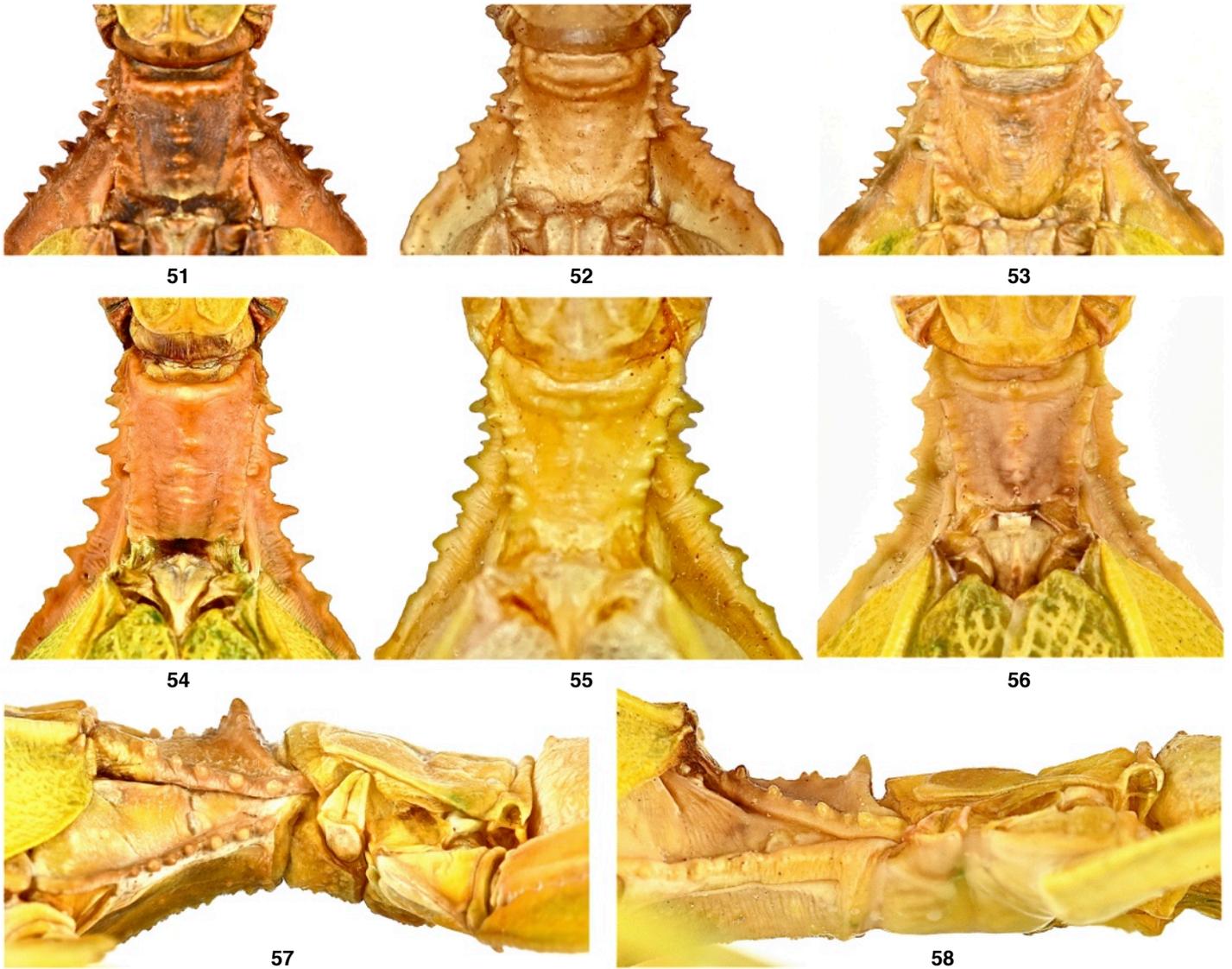
**Differentiation.** – *Phyllium tobeloense bhaskarai* **ssp. nov.** may be separated from the nominate subspecies from Halmahera by only a few subtle morphological features. This Morotai population is the first subspecies described for *Phyllium tobeloense* Gröber, 2007 and is only easily separated from the nominate by the egg morphology.

The most easily seen morphological feature separating the eggs of the two subspecies is the overall shape when viewed laterally. The nominate subspecies has eggs that are asymmetrical with a reniform (kidney shaped) (Fig. 83) whereas the new subspecies has eggs which are ovoid in shape and almost symmetrical (Fig. 85). Also, in the nominate subspecies the long pinnae along the margins are not fully formed around the entire capsule with the area opposite the micropylar plate and below the operculum bald (Fig. 83). In the new subspecies the long pinnae along the margins are fully formed around the entire capsule, with no bald portion opposite of the micropylar plate below the operculum (Fig. 85).

Adults of the two subspecies are much more difficult to differentiate morphologically with only subtle differences found when examining a large series of both populations. The only consistent feature observed on the females were the length of the subgenital plate. In the nominate subspecies the subgenital plate was stouter, protruding only about half the length of sternite X, leaving a significant amount of the gonapophyses exposed (Fig. 64), and for the new subspecies the subgenital plate was longer, about three-quarter the length of sternite X, leaving only the tips of the gonapophyses exposed (Fig. 65).

After an extensive search for a consistent feature to differentiate males of these two populations, none was found that was reliable enough to be useful in a morphological key. With this species so common thus allowing the intraspecific variation to be well known, our conclusion is that it is likely that only molecular comparison can confidently differentiate these two populations males.

**Habitat and Host Plant.** – The local collectors were kind enough to share a number of photos of live specimens in the wild on their host plant (Fig. 78–80). The photos of this host plant were shared with Binjie Ge of the Shanghai Chenshan



**Fig. 51–58.** Mesothorax - **51:** Female *Phyllium letiranti*, dorsal view [SLT coll.]. - **52:** Female *Phyllium siccifolium*, dorsal view [NHMUK]. - **53:** Holotype female *Phyllium toboloense bhaskarai* ssp. nov. dorsal view [IMQC]. - **54:** Male *Phyllium letiranti*, dorsal view [SLT coll.]. - **55:** Male *Phyllium siccifolium*, dorsal view [NHMUK]. - **56:** Allotype male *Phyllium toboloense bhaskarai* ssp. nov., dorsal view. - **57:** Holotype female *Phyllium toboloense bhaskarai* ssp. nov. lateral view of thorax [IMQC]. - **58:** Allotype male *Phyllium toboloense bhaskarai* ssp. nov. lateral view of thorax [IMQC].

Plant Research Center who identified them as likely a species of *Macaranga* (Euphorbiaceae) but without a specimen to examine a definitive identification is not possible at this time. *Macaranga* would not be surprising as this has been recorded as a phasmid host plant in the past for several other phasmids (Seow-Choen, 1997). The native people of Morotai call the tree by the common name “Liwiwi”.

Also accepted as a host plant was *Psidium guajava* (Myrtaceae) by individuals collected in the wild and kept in captivity by Edy Bhaskara (Fig. 101).

#### **Morphological description of the female.**

**Coloration.** – Coloration descriptions are largely based on photographs of live material sent to the authors from collectors on Morotai. Preserved specimens with color that was decently retained were also examined to help describe the spectrum of observed colors.

Two main color forms have been observed, a green form (Fig. 103) and a yellow/orange form (Fig. 102). In both color forms the antennae are of a slightly darker color than the rest of the body and with the terminal three segments with more dense setae and a general darker color than the other antennae segments. Compound eyes of both forms are generally of a similar color to that on the head capsule or slightly lighter in color (in some dried specimens the eyes were a reddish brown but that is possibly from the drying of the specimen). In the green form, the

serration of the femoral lobes, the margins of the mesothorax, and the venation of the tegmina are lighter in color than the remaining surfaces, generally a pale green/yellow or cream color.

In the yellow/orange form, the wing venation is a darker orange than the tegmina ground color which can be more yellow than orange. In both color forms the ventral surface of the metacoxae have a clear black marking, mesocoxae without, cream, yellow, or pale green only.

#### **Morphology**

**Head.** – *Capsule* longer than wide (1.1-1.2 times). – *Vertex* nearly smooth, with only slight texture and no notable granules except the prominent posteriomedial tubercle. Frontal convexity stout, only slightly shorter than the length of the first antennomere, and with a moderate number of clear setae throughout. – *Antennae* consisting of nine segments, with the terminal two segments (VIII and IX) approximately the same length, and segments IV through VII shorter than the terminal two, and IV through VII of a uniform length (Fig. 76). – *Antennomeres* 1-VII sparsely marked with transparent setae (segments I through III with longer setae than the following segments), and the terminal two antennomeres are more densely covered in brown setae with fewer transparent setae. – *Compound eyes* snug to the head capsule, not strongly protruding from the head capsule. – *Ocelli* absent. Antennal fields wider than the first antennomere but not protruding back farther than the frontal suture.

**Thorax.** – *Pronotum* with anterior and lateral margins that are nearly straight, lateral margins converging to a straight posterior margin that is about 60 percent the width of the anterior rim. The pronotum surface lacks nodes but has prominent furrows giving it a lumpy surface. The surface has a prominent pit in the center and one along the sagittal plane near the anterior rim, the remaining furrows are prominent and clearly visible. The pronotum has a moderate anterior rim, lateral rims are weak, and the posterior lacks a rim. – *Prosternum* and the anterior quarter of the *mesosternum* with slight granulation. – *Metasternum* rather smooth, without prominent granulation. – *Mesopraescutum* approximately as long as wide, with lateral rims with five prominent tubercles rather uniform in size, with occasionally one to two small nodes between the anterior most tubercles. – *Mesopraescutum anterior rim* prominent with a large tubercle in the center with the remainder of the rim without clear nodes but slightly lumpy, not perfectly smooth (Fig. 53). – *Mesopraescutum crest* (excluding the tubercle of the anterior rim) nearly flat, not prominent, with four small nodes unevenly spaced along the sagittal plane (Fig. 53). – *Mesopraescutum surface* lumpy, but lacking clear nodes. – *Mesopleurae* straight and evenly diverging; lateral margin with five to seven major tubercles which are almost always even in size; occasionally those with five tubercles have one to two smaller tubercles present (Fig. 53). Face of the mesopleurae smooth, with two divots, one more prominent divot on the anterior third and one closer to the center that is faint. – *Tegmina* slightly variation in length, at the shortest only reaching the anterior margin of segment VIII and at the longest reaching just over three quarters the way through VIII.

**Alae.** – Rudimentary, only about 6mm in length.

**Abdomen.** – *Abdominal segments II* through the anterior two thirds of IV diverging, posterior third of IV through VII gently converging. – *Segments VIII-X* converge more acutely than the previous segments, converging uniformly to a terminal segment that is about as wide as it is long with a broad rounded apex. – *Subgenital plate* starts at the anterior margin of segment VIII and extends three quarters of the way into segment X ending in a fine point, leaving only the tips of the gonapophyses exposed. – *Gonapophyses* long, reaching the posterior margin of segment X (Fig. 65). – *Cerci* relatively flat not strongly cupped, with a prominently granular surface and very few short setae near the apex only.

**Legs.** – *Profemoral exterior lobe* smoothly arcing from end to end without an angle, exterior lobe approximately the same width as the interior lobe, or slightly thinner and with a granular surface. – *Profemoral interior lobe* obtuse angled and marked with five to seven serrate teeth with generally four to five of these teeth larger than the other smaller teeth and not perfectly evenly spaced. – *Mesofemoral interior lobe* smoothly arcs from end to end and has five to seven serrate teeth distributed on the distal half. – *Interior and exterior lobes* are of a similar width, but the exterior lobe is clearly angled, not smoothly arcing like the interior. – *Mesofemoral exterior lobe* with generally only a single small tooth on the distal half of the arc, rarely an additional smaller tooth is present. – *Metafemoral interior lobe* wider than exterior lobe, and arcs end to end and has nine to eleven serrate teeth pointing distally. – *Metafemoral exterior lobe* is thin and smooth, hugging the metafemoral shaft, lacks teeth. – *Protibiae* lacking an exterior lobe. – *Protibial interior lobe* spans the entire length in an evenly weighted triangle and is about twice the width of the protibiae shaft itself. – *Mesotibiae* and *metatibiae* lacking exterior and interior lobes.

### Morphological description of the male.

**Coloration.** – Most of the body is of a lime green color with little variation throughout. Ventral of coxae a cream color, without black markings. The antennae are of a slightly darker green/brown than that found throughout the body. Protibial interior lobe occasionally with slight brown markings.

### Morphology

**Head.** – *Capsule* slightly longer than wide, with a weakly granular vertex. Frontal convexity stout with a dull point and sparsely marked with transparent setae. – *Antennae* consisting of 25 segments (including the scapus and pedicellus which are marked with few transparent setae), all other antennal segments with a dense short covering of darker setae relatively uniform in length throughout all segments. – *Compound eyes* large and notably protruding away from the head capsule. – *Ocelli* developed clearly between compound eyes.

**Thorax.** – *Pronotum* with anterior margin slightly concave and lateral margins that are straight and gently converging to the posterior margin that is about 60 percent the width of the anterior rim. Anterior and lateral margins with moderate rims, posterior margin without a rim and smooth. Face of the pronotum with moderate furrow on the anterior half and the surrounding surface without granulation and smooth. – *Prosternum* with slight granulation throughout, not highly noticeable. – *Mesosternum surface* with more noticeable granules on the anterior. – *Metasternum surface* mostly smooth. – *Mesopraescutum* about as wide as long, with lateral rims with six to seven tubercles of varying sizes spread nearly evenly throughout. – *Mesopraescutum anterior rim* prominent with a large tubercle in the center with the remainder of the rim smooth (Fig. 56). – *Mesopraescutum crest* (excluding the tubercle of the anterior rim) with three to four small nodes unevenly spaced along the sagittal plane (Fig. 56). – *Mesopleura* diverging weakly on the anterior but more prominently on the posterior half; lateral margin with six to seven major tubercles throughout, with clear gaps between each tubercle with at most two small nodes in the gaps. – *Mesopleural face* with two faint divots, one on the anterior third and one on the posterior third, anterior and posterior of the face smooth, center of mesopleural face with a wrinkled texture. – *Tegmina* reaching half way through abdominal segment IV or to the posterior margin on IV.

**Alae.** – Well developed, reaching segment IX or partly into the anal abdominal segment.

**Abdomen.** – *Ovular*, with segments II through IV diverging, V and VI parallel or slightly convex, VII through X steadily converging to a blunt rounded apex. – *Anal abdominal segment* longer than wide with lateral margins that converge slowly throughout the majority of the length and then converge prominently at the terminal third. – *Poculum* starts in abdominal segment VIII, with parallel lateral margins, ending in a broad apex that slightly reaches under segment X. – *Cerci* are slightly cupped and exceed the length of segment X, lateral margins are straight and the surface of the cerci are covered in nodes and short brown setae throughout. – *Vomer* broad with nearly straight margins converging to the apical hook which points upwards into the paraproct.

**Legs.** – *Profemoral exterior lobe* lightly granular and slightly thinner than the profemoral shaft, lobe gently arcing along the entire profemoral length. – *Profemoral interior lobe* about as wide as the shaft and the exterior lobe combined, situated on the distal two thirds and obtuse, not sharply angled. Profemoral interior lobe with four to five serrate teeth of similar sizes or with those in the center only slightly larger. The spacing is uniform except for the middle space which is slightly greater than the spacing on the sides. – *Mesofemoral exterior lobe* about as wide as the shaft, arcing from end to end with the widest portion weighted slightly off center on the distal end and with two to four small serrate teeth. – *Mesofemoral interior lobe* slightly thinner than the exterior lobe and with less of a bend, and six to eight serrate teeth on the distal half of the lobe. – *Metafemoral exterior lobe* thin and lacking distinct dentition but with a slight rough texture, hugging femoral shaft. – *Metafemoral interior lobe* slightly wider than exterior lobe with ten to twelve serrate teeth throughout the distal two-thirds of the length. No exterior protibial lobe, interior lobe extends the entire length in a rounded triangle, with the widest portion in the center or slightly off center on the distal end and slightly wider than the shaft width. – *Meso-* and *metatibia* simple, lacking lobes.

### Description of Egg (Fig. 85 & 86).

The lateral surfaces are flattened and the dorsal and posterior surfaces are slightly convex, which gives the egg a slightly rounded ovular appearance. When viewed from the lateral aspect, the anterior and posterior widths of the capsule are similar, with the center of the capsule the widest point. When viewed from the lateral aspect, the anterior, posterior, and lateral margins are set with numerous rope-like pinnae, each with a split, slightly hooked apex giving them a barbed appearance (Fig. 92). Lateral surfaces with textured surface of circular markings, with 16 to 25 of those circular markings developed into deeper pits. These pits are in no detectable pattern and vary from egg to egg. Area around all pits lacking

### Keys to known species of *Phyllium* from Wallacea

Keys are broken into female, male, and egg morphology due to the marked sexual dimorphism. Female and egg *Ph. (Ph.) conlei* and *Ph. (Ph.)* sp. “Buton” unknown. Egg of *Ph. (Ph.) siccifolium* unknown. Male of *Ph. (Ph.) mamasaense*, *Ph. (Pu.) keyicum* and *Ph. (Pu.) suzukii* unknown. Males of *Ph. (Ph.) tobeloense tobeloense* and *Ph. (Ph.) tobeloense bhaskarai* **ssp. nov.** cannot be morphologically separated and are simply listed together as *Ph. (Ph.) tobeloense* in the below key.

#### Female

1. Mesopraescutum distinctly wider than long (>1.7 times) (Fig. 8 & 9) ..... 2  
— Mesopraescutum about as long as wide, or longer than wide (Fig. 51-53) ..... 3
2. Protibia with an exterior spur near the center (Fig. 7 arrow); profemoral posterior margin distinctly recurved (Fig. 7 line); length to width ratio of the mesopraescutum approximately 1 : 3.4 (Fig. 9) ..... *Ph. (Pu.) suzukii*  
— Protibiae lacking exterior lobe; profemoral posterior margin straight (Fig. 6 line); length to width ratio of the mesopraescutum approximately 1 : 1.8 (Fig. 8) ..... *Ph. (Pu.) keyicum*
3. Alae developed (Fig. 11) ..... *Ph. (Ph.) celebicum*  
— Alae rudimentary ..... 4
4. Mesocoxae or metacoxae with distinct black interior marking (Fig. 46-49); antennae with nine segments ..... 5  
— Mesocoxae and metacoxae without distinct black interior marking (Fig. 50); antennae with ten segments ..... *Ph. (Ph.) letiranti*
5. Mesocoxae and metacoxae with distinct black interior marking; exterior lobe of the profemora wide and gently angled with the greatest width 2.5 to 3 times the width of the profemora shaft (measured at the proximal edge of the interior lobe of the profemora) (Fig. 30-31) ..... 6  
— Metacoxae with distinct black interior marking, mesocoxae slightly orange or light green, no black interior mark; exterior lobe of profemora thin and smoothly arcing with the greatest width only 1.5 to 2 times the width of the profemora shaft (measured at the proximal edge of the interior lobe of the profemora) (Fig. 38-41) ..... 7
6. Three to five teeth of approximately even size on the interior lobe of the profemora (Fig. 30-31); abdominal segment VIII margin always almost perfectly straight (Fig. 69 line) ..... *Ph. (Ph.) siccifolium*  
— Two large teeth and smaller minor teeth between on the interior lobe of the profemora (Fig. 33); abdominal segment VIII margin always with a smooth bend giving a slight lobe to the segment (Fig. 68 line) ..... *Ph. (Ph.) mamasaense*
7. Subgenital plate stout, protruding about half the length of sternite X, leaving a significant amount of the gonapophyses exposed (Fig. 64) ..... *Ph. (Ph.) tobeloense tobeloense*  
— Subgenital plate long, about three-quarter the length of sternite X, leaving only the tips of the gonapophyses exposed (Fig. 65) ..... *Ph. (Ph.) tobeloense bhaskarai* **ssp. nov.**

#### Male

1. Profemoral exterior lobe wider than the interior lobe, strongly angled (Fig. 16) ..... *Ph. (Ph.) celebicum*  
— Profemoral exterior lobe thinner than the interior lobe, arcing end to end, not strongly angled (Fig. 42-45) ..... 2
2. Interior lobe of the protibia thin and arcing from end to end without a distinct triangular shape and slender, only about as wide as the protibial shaft; abdomen long and slender, at its greatest width only about 30% of the total abdomen length (Fig. 23) ..... *Ph. (Ph.) conlei*  
— Interior lobe of the protibia with a distinct triangular shape and wider than the protibial shaft; abdomen broad, with a greatest width of about 37–50% of the length of the total abdomen ..... 3
3. Abdomen spade shaped with abdominal segments V through the apex distinctly converging (Fig. 24) ..... *Ph. (Ph.)* sp. “Buton”  
— Abdomen ovoid, with abdominal segments V and VI with parallel margins or only slightly subparallel, only segments VII through the apex distinctly converging (Fig. 25) ..... 4
4. Antennae when resting back along the dorsal surface are similar in length or longer than the folded tegmina (Fig. 28) ..... 5  
— Antennae when resting back along the dorsal surface are shorter than the folded tegmina (Fig. 25) ..... *Ph. (Ph.) tobeloense*
5. Large species 67.0-73.0 mm; antennae apex when resting back along the dorsal surface reaching apex of tegmina or only exceeding length by one to two segments; mesopraescutum stout (length to maximum width ratio of about 0.8-0.9) and with an anterior that is distinctly broader than the posterior (Fig. 55) ..... *Ph. (Ph.) siccifolium*  
— Medium species 57.6-62.2 mm; antennae apex when resting back along the dorsal surface exceeding apex of tegmina by four to five segments; mesopraescutum long and thin (length to maximum width ratio about 1.0-1.2) and with anterior and posterior margins approximately the same width (Fig. 54) ..... *Ph. (Ph.) letiranti*

**Egg**

- |   |  |
|---|--|
| 1. Capsule entirely lacking distinct pinnae .....   | 2  |
| — Capsule with distinct pinnae (most prominent along the operculum rim, if not prominent along the rim, then with short distinct pinnae along the longitudinal margins of the capsule itself) .....                     | 3  |
| 2. Lateral margins of the micropylar plate with four to five large pits throughout the length .....   | <i>Ph. (Pu.) suzukii</i>                               |
| — Lateral margins of the micropylar plate with eight to nine small pits throughout the length .....   | <i>Ph. (Pu.) keyicum</i>                               |
| 3. Operculum raised, not flat, lacking long pinnae along the rim (Fig. 81) .....  | <i>Ph. (Ph.) celebicum</i>                             |
| — Operculum flat, with long straight pinnae along the rim (Fig. 83-90) .....  | 4  |
| 4. Opercular rim with pinnae that are broad and featherlike (Fig. 91), broadest throughout their length .....   | 5  |
| — Opercular rim with pinnae that are thin, ropelike, broadest at the apex (Fig. 92) .....   | 6  |
| 5. Lateral surface with short pinnae, notably shorter than the pinnae of the posterior and anterior ends (Fig. 88) .....  | <i>Ph. (Ph.) letiranti</i>                             |
| — Lateral surface with rows of long pinnae, of a similar length to the pinnae of the posterior and anterior ends (Fig. 90) .....  | <i>Ph. (Ph.) mamasaense</i>                            |
| 6. Overall shape somewhat reniform (kidney shaped) (Fig. 83); long pinnae along the margins not fully formed around the entire capsule, area opposite the micropylar plate and below the operculum bald (Fig. 83) ..... | <i>Ph. (Ph.) toboloense toboloense</i>                 |
| — Overall shape more symmetrical, ovoid in shape (Fig. 85); long pinnae along the margins fully formed around the entire capsule, no bald portion opposite of the micropylar plate below the operculum (Fig. 85) .....  | <i>Ph. (Ph.) toboloense bhaskarai</i> <i>ssp. nov.</i> |

long pinnae, leaving the lateral surfaces without significant projections. Micropylar plate covering approximately half of the overall length, situated near the center, not weighted towards either end of the capsule. Micropylar plate in a thin teardrop shape, with most of the width thinner than the micropylar cup. Micropylar cup of moderate size and placed on the posterior third of the capsule. Operculum nearly circular, with around ten round impressions encircling the center, and the outer margin of the operculum has a row of pinnae similar in length to those found along the other edges of the capsule. Overall color yellow, tan, or light brown.

**Measurements** [mm].

- length (including operculum) : 3.8
- length (excluding operculum) : 3.5
- height : 2.1
- width : 2.4
- length of micropylar plate : 2.2

**Etymology.** – This new subspecies is dedicated to Edy Bhaskara from Malang, Indonesia who was the first to send us specimens for this description. May he be thanked for his numerous collaborations to discover new taxa.

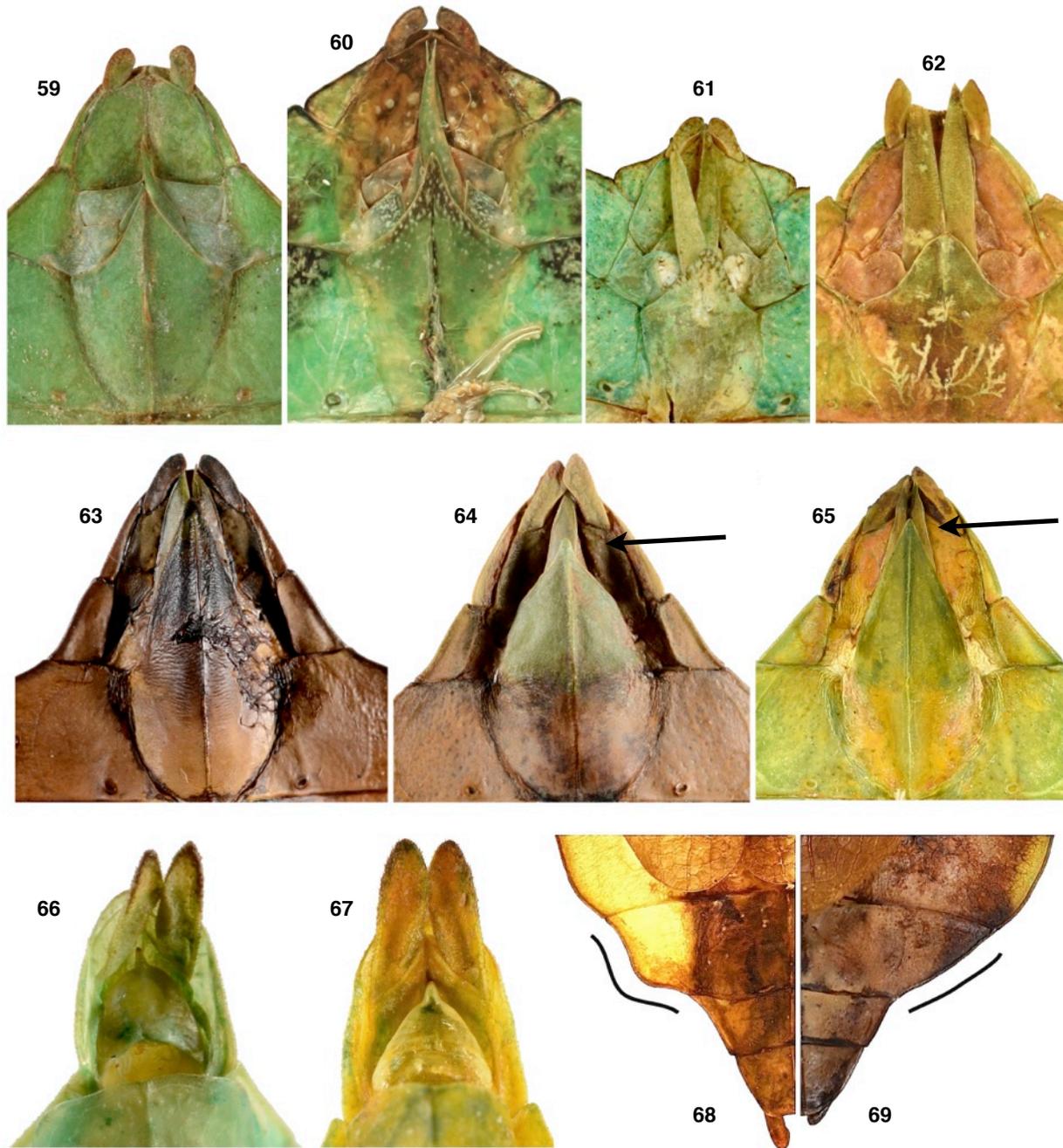
**Note on *Phyllium* female genitalia in relation to egg morphology**

As discussed in depth above, the only easily observed distinguishing features between the two subspecies of *Phyllium toboloense* are egg morphology and the female subgenital plate length. This difference in subgenital plate length is likely linked to the morphological variation observed between the eggs of the two populations, with subgenital plate length reflecting the ideal arrangement to hold the egg before it is flung away. Within the Phylliidae in general, the ratio of subgenital plate and gonapophyses lengths help to reveal general features of egg morphology. Members of the *bioculatum* species group with eggs characterized by five distinct ribs along the egg (with the exception of *Phyllium giganteum* Hausleithner, 1984 which has 3 rounded ribs) have females with shorter subgenital plates and

shorter gonapophyses, likely because the eggs can easily be held with this arrangement or the shorter features aid in the action of flinging the egg away from the female (Fig. 59). In contrast, the *frondosum* species group have short subgenital plates and longer gonapophyses (Fig. 61 & 62), with eggs which lack these distinct ribs. In this case the longer gonapophyses are likely needed to help hold the egg in place before flinging it. This arrangement of a short subgenital plate and long gonapophyses is also seen in *Phyllium giganteum* (Fig. 60) likely for the same reason, as *Ph. giganteum* eggs have stout rounded ribs much like the rounded ribs of the *frondosum* species group. Members of the *Phyllium* (*Phyllium*) subgenus generally all have longer gonapophyses and a range of subgenital plate lengths (presumed to be according to the ideal length for their specific egg shapes). With eggs of varying morphologies, the subgenital plate appears to be the feature most variable among females with differing egg morphologies, as observed by the two *Ph. toboloense* subspecies and their eggs.

**Biogeography and discussion**

With nine species of *Phyllium* currently known from throughout Wallacea (Fig. 2), several biogeographical trends can clearly be seen. Particularly the Weber Line which separates the Papuan subregion species (*Ph. suzukii* and *Ph. keyicum* within the *frondosum* species group, which is only found additionally in the Papuan subregion) from the Oriental elements, particularly illustrative *Ph. celebicum*, the only member of the *celebicum* species group found this far south, with the others either further north in the Philippines, Micronesia, or on mainland Asia. The Weber line also illustrates the likely delineation between *Ph. letiranti* (west of the line: Banggai and Sula Islands) from *Ph. siccifolium* (east of the line: Buru, Ambon, and Seram Islands). Of the Lesser Sunda Islands within Wallacea, currently only *Phyllium conlei* from Lombok Island is known, with all other islands devoid of literature and specimen records (Cumming, Valero & Teemsmas, 2018). To date *Phyllium mamasaense* has only been recorded from the type locality of Mamasa, Sulawesi, but with the other



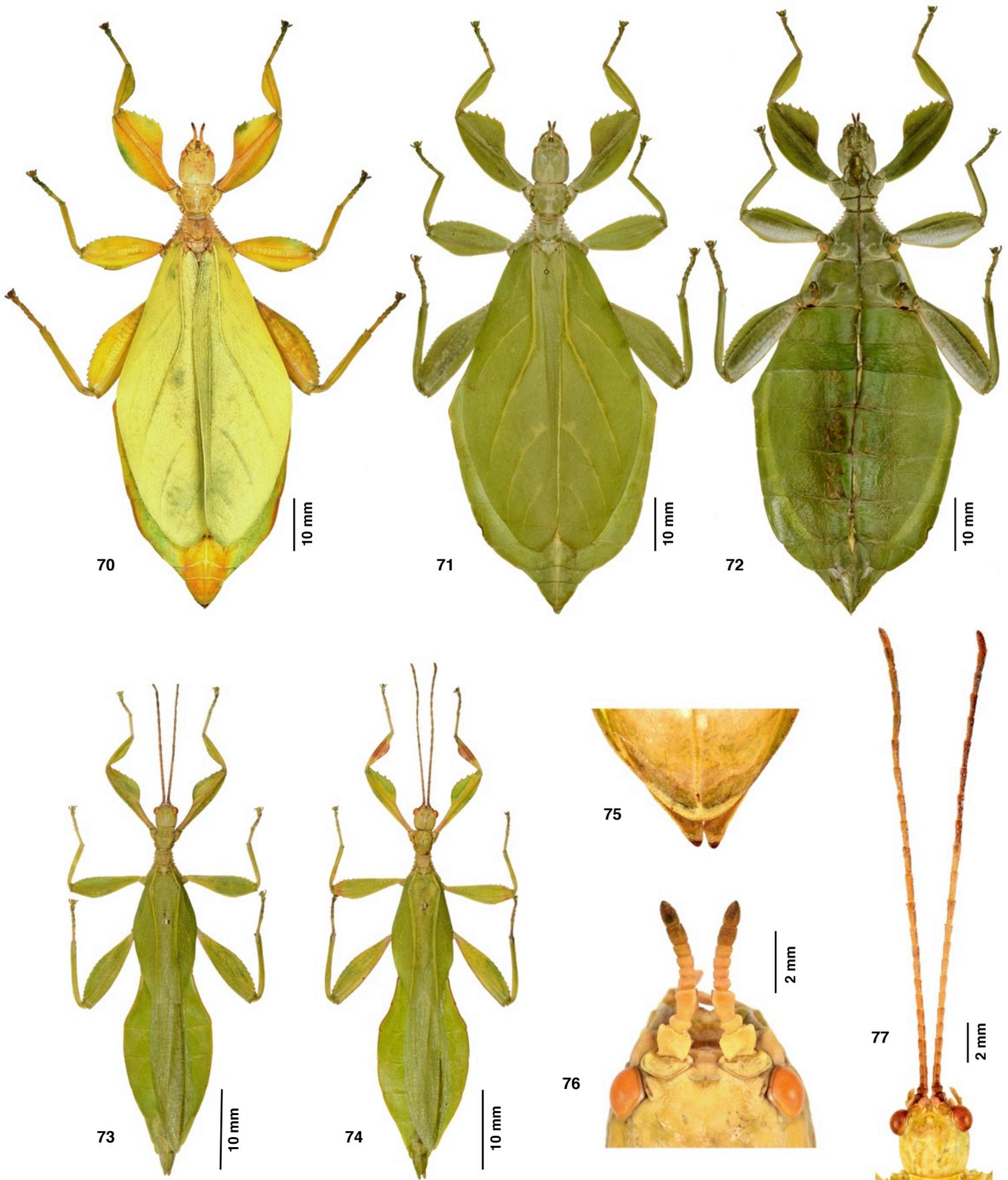
**Fig. 59–69.** Fig. 59–67. Genitalia ventral view. - 59: *Phyllium abdulfatahi* Seow-Choen, 2017 [RC16-039], short subgenital plate and short gonapophyses. - 60: *Phyllium giganteum* [RC16-044], short subgenital plate and long gonapophyses. - 61: *Phyllium suzukii* holotype [SDEI] female short subgenital plate and long gonapophyses. - 62: *Phyllium keyicum* [NHMUK 012496951 (Kei Is., 1923)]. - 63: *Phyllium siccifolium* [FH 1042-1] Seram Island. - 64: *Phyllium tobeloense tobeloense* [FH 0657-4] Halmahera Island, Tobelo. - 65: *Phyllium tobeloense bhaskarai* ssp. nov. holotype female [IMQC]. - 66: *Phyllium tobeloense tobeloense* [FH 0657-6] Halmahera Island, Tobelo. - 67: *Phyllium tobeloense bhaskarai* ssp. nov. allotype male [IMQC]. **Fig. 68–69.** Dorsal view of female terminal abdominal segments; lines show the curve of segment VIII, illustrating a consistent feature found between *Ph. mamasense* and *Ph. siccifolium*. - 68: Holotype *Phyllium mamasense* [SDEI]. - 69: *Phyllium siccifolium* [FH 1042-1].

Sulawesian species *Ph. celebicum* found throughout the island it would not be surprising if *Ph. mamasense* were also more widely distributed on the island.

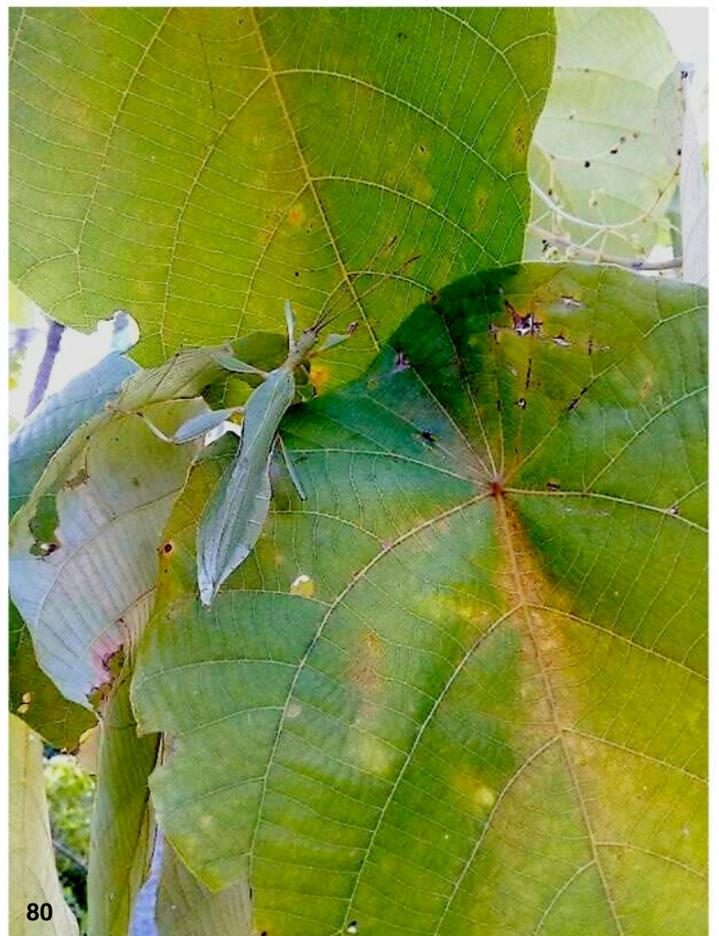
Within Wallacea there are a number of islands currently devoid of Phylliidae records, some of the largest being from the eastern Lesser Sunda Islands: Sumbawa, Sumba, Flores, and Timor. With the island of Timor a rather large island situated just south of the Phylliidae rich island of Sulawesi, the authors expected there to be records from Timor as well. However, after speaking with Chris Reid, Principal Research Scientist at the Australian Museum in Sydney he is skeptical Phylliidae can be found on the island. The Australian Museum has been conducting field work on Timor since 2012 and his observations were as follows, “Most of Timor is dry woodland on limestone dominated by either *Eucalyptus*, *Casuarina*, or

*Acacia* (now mostly introduced spp), with a bit of sandalwood etc. Plus a lot of pasture and a lot of weedy arable. The remaining rainforest is almost entirely dry vine thicket – the wetter stuff is either converted to coffee or too remote for easy access or we just didn’t get into it. So in general I’d say *Phyllium* is unlikely” (pers. comm. Chris Reid).

Undoubtedly, our current knowledge of Wallacean Phylliidae is still fractional. Of the nine species that have so far become known from throughout Wallacea, five are only known from a single sex: *Ph. conlei* and *Ph. sp. ‘Buton’* are both only known from unique males, and *Ph. mamasense*, *Ph. keyicum* and *Ph. suzukii* are only known from females. There is another questionable *celebicum*-like species only known from an old female specimen labelled “Amboina” in the collection of MNHU, whose identity deserves clarification by additional



**Fig. 70–77.** *Phyllium tobeloense bhaskarai* **ssp. nov.** - 70: Holotype female dorsal [IMQC]. - 71: Paratype female dorsal [FH 1077-1]. - 72: Paratype female ventral [FH 1077-1]. - 73: Paratype male [FH 1077-22]. - 74: Paratype male [FH 1077-23]. - 75: Dorsal view of terminal abdominal segment (= tergum X) and cerci, holotype [IMQC]. - 76: Dorsal view of antennae, holotype female [IMQC]. - 77: Dorsal view of antennae, allotype male [IMQC].



**Fig. 78–80.** *Macaranga* sp. (Euphorbiaceae) with wild *Phyllium* (*Phyllium*) *tobeloense bhaskarai* **ssp. nov.** on Morotai Island (© Alim Yasin).  
 - 78: *Macaranga* sp., host plant. - 79: Subadult female on *Macaranga* sp. - 80: Adult male on *Macaranga* sp.

material (see discussion on *Ph. celebicum*). Also, the authors are aware of at least one further still undescribed *Phyllium* species which is only known from a photograph. It is very much hoped that the present paper will encourage collectors to look out for Phylliidae throughout Wallacea to obtain fresh specimens that can help broaden our knowledge of these fascinating insects from this particular region so well known for its high biodiversity and high degree of endemism.

### Acknowledgments

The authors thank René Limoges, entomological technician at the Montreal Insectarium for taking many photos for this work, as well as for many professional courtesies. Thank to Vadim Voitsekhovskii (Bali, Indonesia) for sending a series of specimens for this study. A special thanks to Alim Yasin (Morotai, Indonesia) who sent to us an extra 50 males and 50

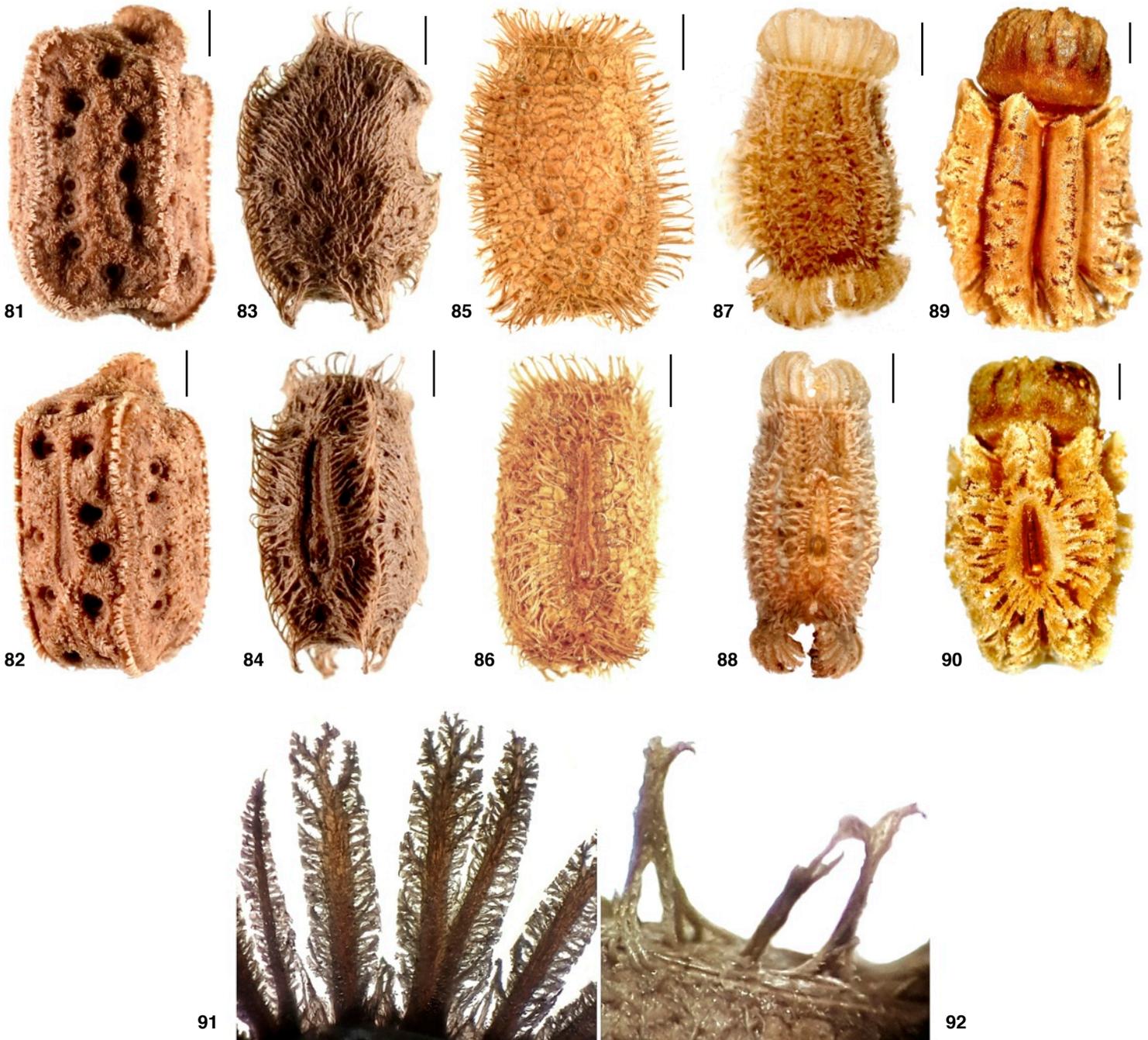


Fig. 81–92. *Phyllium* eggs. Fig. 81, 83, 85, 87, 89 lateral view, micropylar plate to the left. Fig. 82, 84, 86, 88, 90 dorsal view showing micropylar plate. - 81 & 82: *Phyllium celebicum*. - 83 & 84: *Phyllium tobeloense tobeloense*. - 85 & 86: *Phyllium tobeloense bhaskarai* ssp. nov. paratype. - 87 & 88: *Phyllium letiranti* paratype. - 89 & 90: *Phyllium mamasense* (© Größer D.). Fig. 91–92. Pinnae from the opercular rim. - 91: Featherlike pinnae, frills throughout length, wide throughout length, apex not widest portion, *Phyllium letiranti*. - 92: Ropelike pinnae, stalk without frills, broadest portion the apex, *Phyllium tobeloense tobeloense*. Scale bar = 2 mm.

females that allowed us to deposit many paratypes in various museums and who also sent us photos of wild specimens and the habitat. Thanks to Maxime Ortiz (France) who sent us eggs that have been used in this work. Thanks also to Binjie Ge (Shanghai Chenshan Plant Research Center and Gilles Vincent, Special advisor of the Executive President of the Chenshan Botanical Garden-Shanghai, China) for the identification of the host plant. Thank you to Jim Berrian (SDNHM, San Diego) for years of support and access to the museum's camera. Thank you to Tim Van molle (Rupelmonde, Belgium) for allowing us to use photos of his beautiful *Phyllium tobeloense* color forms and Detlef Größer (Berlin, Germany) for allowing us to use his photos of *Phyllium mamasense* eggs in this work. Sigetake Suzuki (Hokkaido, Japan) kindly provided various specimens from Sulawesi and helpful information. We thank Edy Bhaskara (Malang, Java, Indonesia) for providing the specimens of *Phyllium tobeloense bhaskarai* ssp. nov. and *Ph. tobeloense tobeloense* for description as well as pictures of live

specimens of the new subspecies. Thanks are also due to the curators of various museums for access to the corresponding collections that contain material listed in the present paper and/or providing photographs of specimens: Dr. Michael Ohl and Ulrike Dorandt (MNHU, Berlin), Dr. Susanne Randolf and Prof. Ulrike Aspöck (NHMW, Vienna), Dr. Caroline Pepermans (RMNH, Leiden) and Hans Mejlom (UZM, Uppsala). Mandy Schröter and Stephan Blanke (SDEI, Senckenberg German Entomological Institute Müncheberg) for photographs of specimens used in this work. Judith Marshall and Benjamin Price (NHMUK, London) for processing the loan of the *Phyllium keyicum* specimen despite the lack of an Orthopteroid collection curator. To conclude we of course thank our two peer reviewers who gave us valuable feedback and suggestions on how to improve this text, thank you Philip E. Bragg (Nottinghamshire, United Kingdom) and Dr Allan Taylor (Quebec, Canada).



Fig. 93–95. Live *Phyllium celebicum* captive reared F1-generation. - 93: Male/female pair. - 94: Male. - 95: Female.



**Fig. 96–98.** Live *Phyllium letiranti* captive reared (© Maxime Ortiz). - 96: Yellow form female. - 97: Yellow form female, detail of head, thorax, and profemoral lobes. - 98: *Phyllium letiranti* Males.



99



100

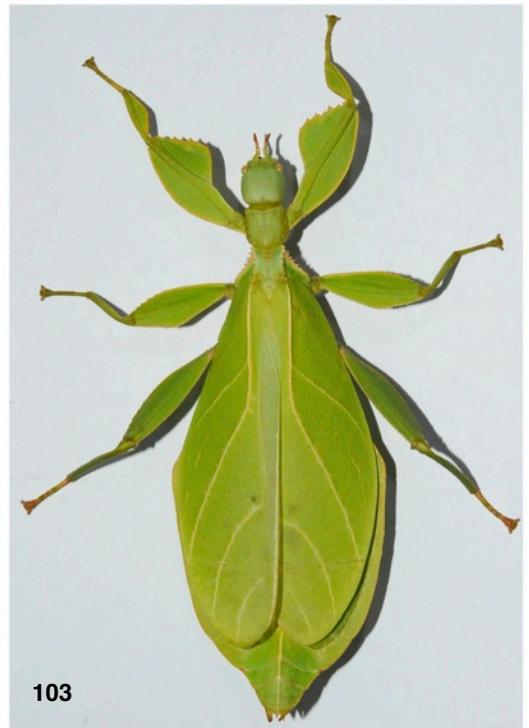
Fig. 99–100. Live *Phyllium tobeloense tobeloense* captive reared female (© Tim Van molle). - 99: Red color form. - 100: Yellow and green color forms.



101



102



103

Fig. 101–103. Live *Phyllium tobeloense bhaskarai* ssp. nov. - 101: Captive adult pair feeding on *Psidium guajava* (Myrtaceae) (© Alim Yasin). - 102: Orange form female, paratype (© Alim Yasin). - 103: Green form female, paratype (© Edy Bhaskara).

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## Résumé

Cumming R. T., Le Tirant S. & Hennemann F. H., 2019. – Révision des *Phyllium* Illiger, 1798 de Wallacea (Indonésie), avec la description d’une nouvelle sous-espèce de l’île Morotai (Phasmatodea: Phylliidae: Phylliinae). *Faunitaxys*, 7(4) : 1 – 25.

Les Phylliidae de Wallacea sont révisés. La répartition des espèces est précisée. Une nouvelle sous-espèce de *Phyllium (Phyllium) tobeloense* Größer, 2007 est décrite de l’île de Morotai, *Phyllium (Phyllium) tobeloense bhaskarai* Cumming, Le Tirant et Hennemann **ssp. nov.** dont l’identification est basée principalement sur la morphologie distincte des œufs. Enfin une clé de tous les *Phyllium* connus de Wallacea est présentée permettant une identification rapide.

Mots-clés. – Phasmatodea, Phasmida, Phylliinae, Phylliini, *Phyllium*, Wallacea, Indonesia, Morotai, *tobeloense*, *bhaskarai*, description, espèce nouvelle, distribution, biogéographie.

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**Illustration de la couverture:** Forêt tropicale de Morotai.

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