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Notes on the jumping spider *Myrmarachne exasperans* (Araneae: Salticidae: Astioida: Myrmarachnini) in Bali, a possible mimic of parasitoid wasps (Hymenoptera: Ichneumonidae: Cryptini: *Goryphus*)

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Summary. Male, female and immature *Myrmarachne exasperans* from Bali, their concealment of nests under detritus, and their likely mimicry of ectoparasitoid ichneumonid wasps of the genus *Goryphus* are documented in a series of photographs.

Key words. agonistic behaviour, Borneo, ectoparasitoid, *Emertonius exasperans*, *Emertonius koomeni*, *Goryphus basilaris*, Java, nesting, *Polistes*, Sabah, Sahul, Sarawak, Sunda, Vespidae, Wallacea

Myrmarachne MacLeay 1839 is a large genus of salticid spiders that are thought to closely mimic the ant species with which they associate (Nelson et al. 2005; Ceccarelli & Crozier 2007; Ceccarelli 2008, 2009, 2010, 2013; Yamasaki & Ahmad 2013; Shamble et al. 2017; Pekár et al. 2017; Ramachandra & Hill 2018). *Myrmarachne* is a member of the tribe Myrmarachnini, part of a large Australasian clade, the Astioda (Maddison et al. 2008). Myrmarachnines probably migrated from Australasia (Sahul) over the islands of Wallacea to tropical southeast Asia (Sunda) as the respective continents converged during the last half of the Cenozoic era (Hill 2010). *Myrmarachne* are not known to feed on ants but consume a variety of other insects including moths, and may also feed on the eggs of other spiders (Jackson & Willey 1994). One member of the genus, the African *M. melanotarsa* Wesołowska & Salm 2002, lives in communal nests that may be shared with other salticids (Wesołowska & Salm 2002; Jackson et al. 2008). It has recently been reported that females of the Formosan species *M. magna* Saito 1933 feed their young in the nest and cohabit with female offspring to their maturity (Chen et al. 2018).

Myrmarachne exasperans (Peckham & Peckham 1892) was originally described as the sole member of a new genus, *Emertonius*. Several recent papers have proposed the reinstatement of *Emertonius* based on division of *Myrmarachne* into a number of separate genera (Prószyński & Deeleman-Reinhold 2010; Prószyński 2016, 2017, 2018).

The original description of *M. exasperans* was based on a female specimen for which the epigynum is missing. Perhaps based on the large, clavate black pedipalps of the female, the Peckhams erroneously described this as a male. Wanless (1978) subsequently designated a female lectotype of questionable identity for *M. exasperans* and associated this with a male *Myrmarachne* from the Philippines of a different species (Yamasaki 2010; Hill & Otto 2015; renamed *E. palawensis* by Prószyński 2018); this male had transverse fringes on the dorsal opisthosoma and limited violet colouration of the chelicerae. Although published illustrations of the genitalia that claim to represent this species are not reliable, *M. exasperans* is nonetheless quite easy to identify from field marks, to include the pattern of scales on the female opisthosoma and the fringed middorsal crest behind the eye region figured by the Peckhams. Yamasaki

(2015, p. 50, figs. 2-3) has recently published diagnostic photographs of an adult male and an adult female from Bali, for the first time illustrating the similarity of males and females collected at a single locality. Although *M. exasperans* may be found throughout tropical southeast Asia, including Sundan (Western) Indonesia, it has most often been found in Bali, representing easternmost Sunda (Hill 2010; Hill & Otto 2015; Yamasaki 2015). Based on recent observations of this species in Bali (Figure 1) by one of the authors (THC), we provide new illustrations of males, females and immatures (Figures 2-10), and document key features of the biology of this species to include nesting and its likely mimicry of ectoparasitoid ichneumonid wasps of the genus *Goryphus*.

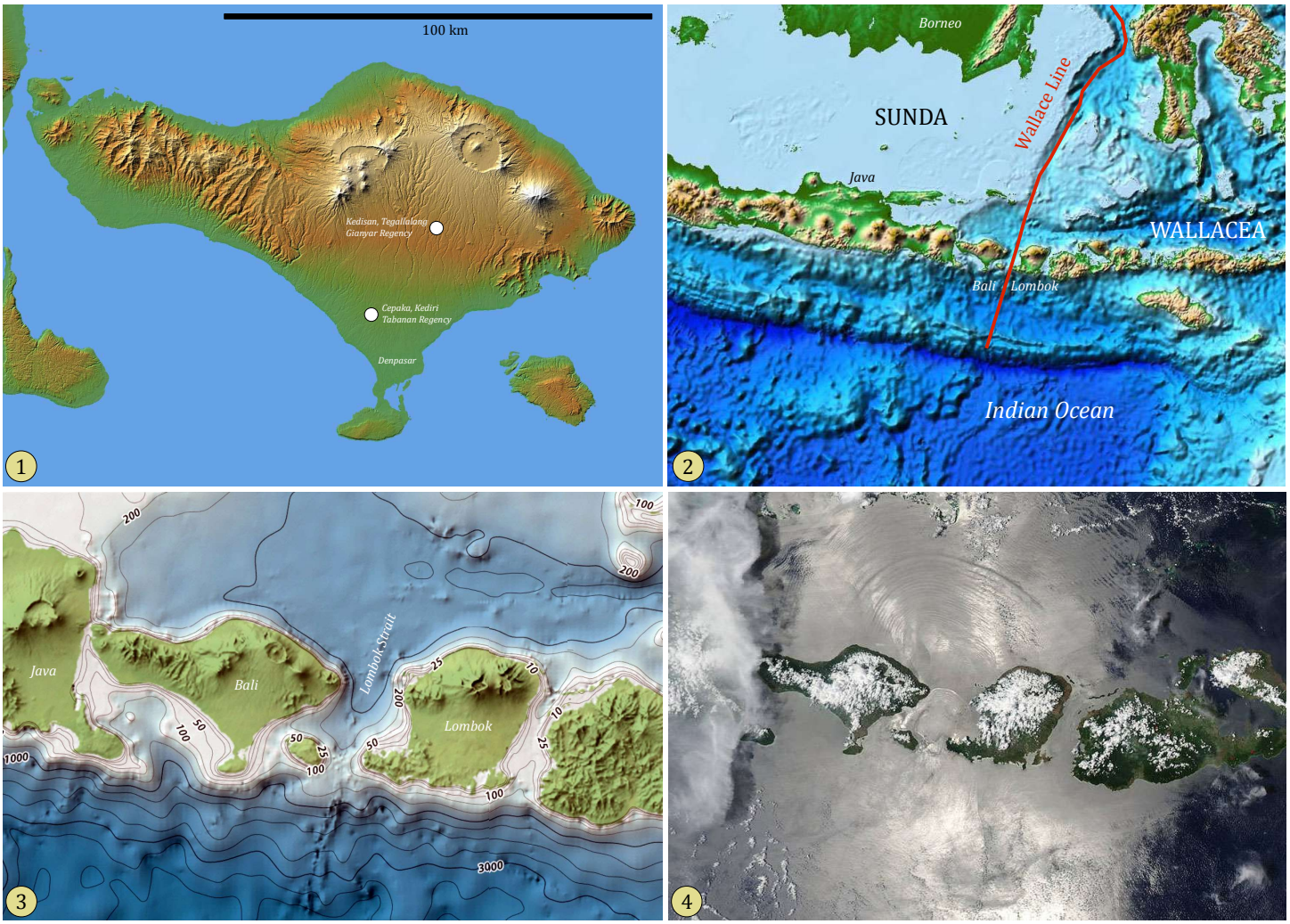

Figure 1. Bali and neighboring islands. **1,** Localities where *Myrmarachne exasperans* was observed in Bali. Most were found in the garden of one of the authors (THC) at Cepaka, others in a garden at Kedisan. This background map is a shaded relief image of color-coded elevations generated from data collected by the NASA Shuttle Radar Topography Mission, image courtesy of the SRTM Team at NASA/JPL/NIMA. **2,** Bali represents the southeastern margin of Sunda and the tropical Afroeurasian biogeographic province. It is separated from Australasia by the transitional archipelago of Wallacea, demarcated by the Wallace Line running through the Lombok Strait that separates Bali from Lombok to the east. During the glacial epochs of the Pleistocene Bali, as part of Sunda, was part of the Asian mainland. This background map is adapted from the ETOPO1 Global Relif Model, courtesy of NOAA/NCEI. **3,** Ocean bathymetry (depth in meters) surrounding Bali and Lombok, showing the deeper waters of the Lombok Strait that separates the two islands. This background map was adapted from an NOAA/NCEI visualization based on the GEBCO World Map 2014 with regional bathymetric contours (www.gebco.net). **4,** True-color image of nonlinear internal solitary waves (revealed by sunglint) in the current moving north through the Lombok Strait from the Indian to the Pacific Ocean. This image was produced by the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the NASA Aqua satellite (1 NOV 2016). Image courtesy of Jeff Schmalz, MODIS Land Rapid Response Team, NASA GSFC.

Figure 2. Living adult male *Myrmarachne exasperans*. Length is ~5-6 mm, not including the chelicerae.

Figure 3. Living adult male *Myrmarachne exasperans*.

Figure 4. Detailed views of living adult male *Myrmarachne exasperans*.

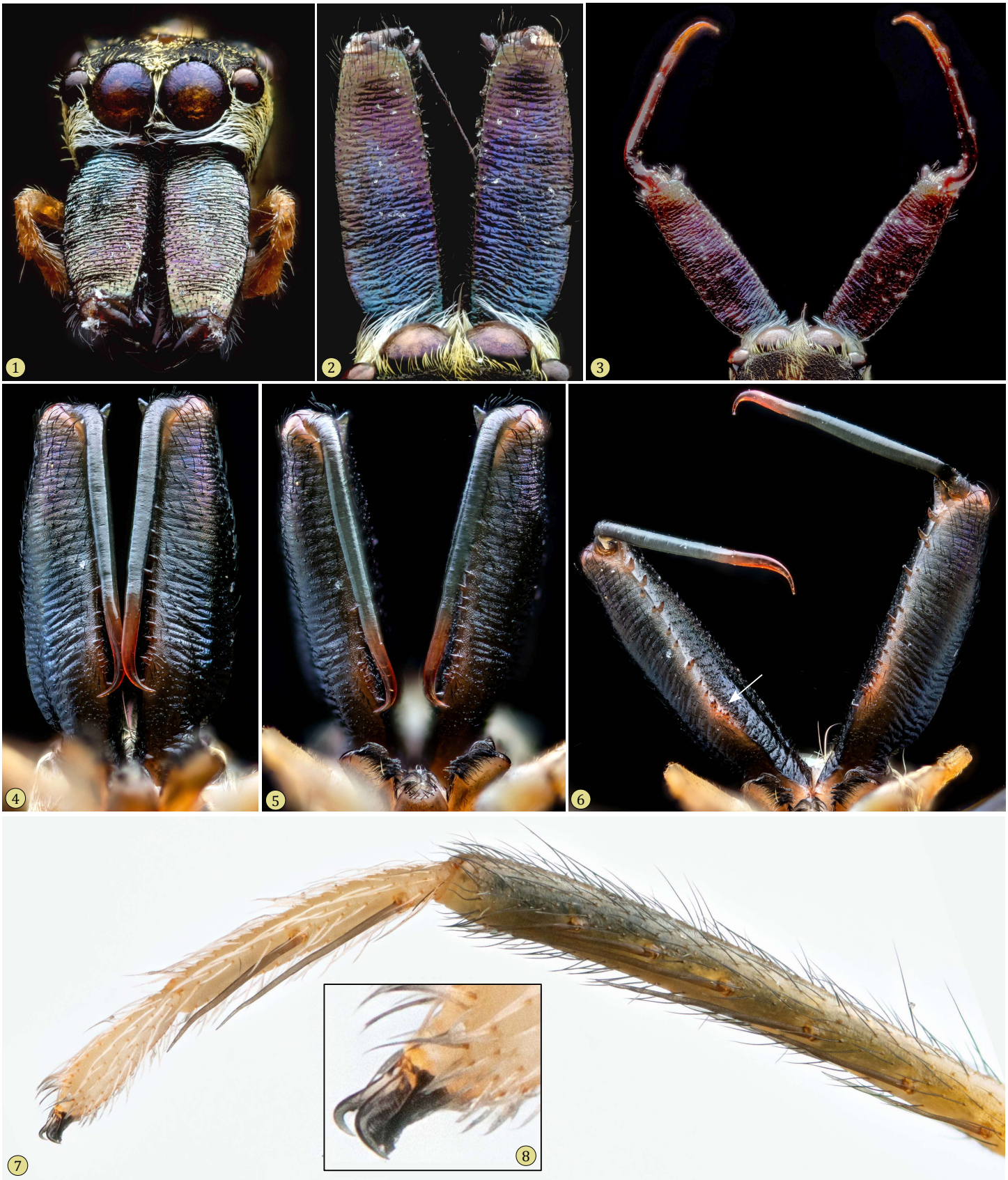

Figure 5. Detailed views of a dried adult male *Myrmarachne exasperans* (not living). **2-3,** Dorsal view of chelicerae with fangs retracted (2) and extended (3). **4-6,** Ventral views of chelicerae in different positions. Note the posterior (ventral) position of the fang groove (6, arrow), lined with short spines along the rear margin. **7,** Prolateral or anterior view of right leg I showing six long spines of each tibia and two long spines of each metatarsus. These spines are very thin and sharp. **8,** Detail of distal tarsus and pretarsus from (7).

Figure 6. Living adult female *Myrmarachne exasperans*. Length is ~5-6 mm, not including the chelicerae.

Figure 7. Living adult female *Myrmarachne exasperans*.

Figure 8. Detailed views of the prosoma of an adult female *Myrmarachne exasperans*. Note the array of short, papillate setae between the posterior eyes (5), and the rugose texture of the sides of the posterior middorsal crest of the carapace (6).

Figure 9. Detailed views of an adult female *Myrmarachne exasperans*. **1,** The anterodorsal carapace of the female has the same iridescent violet color as the male chelicerae. **4**, Detail of inset from (3), showing the elongated, fringed scales that comprise the distinctive markings of the dorsal opisthosoma.

Figure 10. Early immature *Myrmarachne exasperans*. These small spiders (several mm in length) lack the distinctive features of the adults and are decidedly not ant-like. Later immatures (Figure 12) resemble adult females but are not as brightly colored.

Habitat. These spiders were found with their nests under the broad leaves of *Ficus, Asplenium nidus* and *Hibiscus* (Figure 11).

Figure 11. Plants occupied by *Myrmarachne* and the wasps that they may mimic in a Cepaka garden. Nests were found on the underside of broad leaves. **1,** *Ficus*. **3,** Bird's Nest Fern (*Asplenium nitens*). **4,** Many wasps (*Goryphus*) were found hunting on these poolside bromeliads.

Nesting. Like other species in the genus *Myrmarachne*, *M. exasperans* nests on the underside of medium to large leaves. Nests were found under the leaves of the Bird's Nest Fern *Asplenium nidus*, a *Ficus* tree and *Hibiscus* plants, usually near banana trees (*Musa*) and *Heliconia* (where *M. plataleoides* or a related species are easily found). The majority of the nests were found under the leaves of a *Ficus* tree. Unlike nests of other *Myrmarachne* species, *M. exasperans* nests observed in Bali were covered with bits of debris, making them easy to identify. The debris incorporated into a nest is quite variable but includes leaves and bits of bark as well as dead insects and insect exuviae (Figures 12-15). Nests of adult males tended to be small, loose and simple, using less silk. Subadult and female nests without an egg sac were silk sheets with debris stuck to the exterior and smooth silk lining the interior. Nests with eggs had a thicker layer of fluffy silk underneath this sheet. The debris and thick cover of silk most likely made it more difficult for the eggs to be located or accessed by either parasitoids or egg predators.

Figure 12. Activity of a subadult *Myrmarachne exasperans* near its nest. Note the cover of plant material and the wings of a moth, as well as the distinctive tufts of cottony silk within the nest. **1,** Spider concealed beneath the dead moth at one entrance of the nest. **2,** detail from (3) to show similarity of this subadult (most likely a penultimate female) to the adult. **3,** Spider approaching the nest from one side. **4,** Spider entering the nest.

Figure 13. Nesting by *Myrmarachne exasperans*. **1,** Adult female with sporangia on the underside of an *Asplenium* leaf. **2,** Adult female at entrance of nest built beneath an *Asplenium* leaf, covered largely with *Asplenium* spores. **3-4,** Adult female at entrance of nest. See also Figure 14. **5,** Nest of adult female with a variety of detritis above cottony silk tufts but no egg sac (6-7, detail). **8,** Adult female nest containing egg sac. **9,** Nest of adult male.

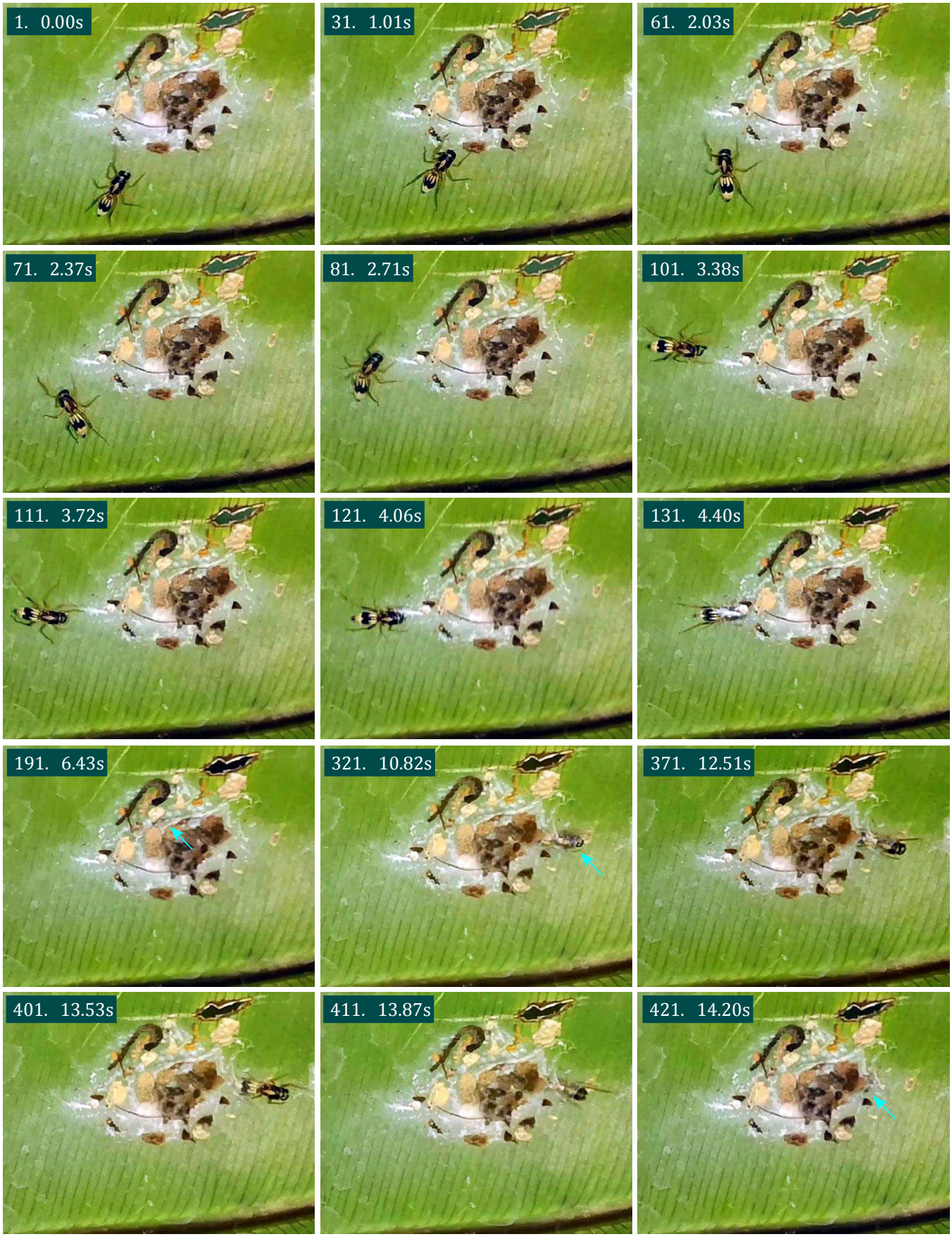

Figure 14. Sequential frames from a 29.57fps video showing a female *M. exasperans* entering her nest at one end (frame 131) and emerging from the other end (frame 401). Arrows (191, 321, 421) indicate position of female in nest.

Figure 15. Nest containing egg sac before (1) and after (2) removal of the covering silk sheet and debris. **1,** Most debris covering the nest was removed before this photograph was taken. **2,** Note eggs in egg sac (arrow).

The nests of *Myrmarachne* species are generally flattened tubes of silk, but these may be constructed either on detritis suspended in the webs of other spiders or within the nests of other spiders, including other salticid spiders and colonial spiders. One adult female listed as *M. exasperans* was found occupying the nest of an eresid (*Stegodyphus sarasinorum* Karsch 1892) colony in Sri Lanka (Jackson & Willey 1994). Given the fact that small groups of ants collect debris either to conceal or to protect their nests in Bali (Figure 16), it is possible that *M. exasperans* occupy the nests of other arthropods and do not collect debris for themselves. Collection of debris by *M. exasperans* has not been observed directly. However the manner in which debris is attached to the outer silk sheet of nests and the presence of many of the cottony silk tufts that have been associated with the nests of other *Myrmarachne* species, also known to manipulate and secure detritis (Jackson & Willey 1994), suggest that at least some of these nests are built with debris collected by the spiders themselves.

Figure 16. Small ant nest covered with collected debris (Bali). **2-3,** Two close-up views of the nest shown in (1).

Mimicry of ichneumonid wasps. *Myrmarachne* species usually closely resemble the species of ant they mimic and are often found close to the nests of those ants (e.g., Ceccarelli 2008, 2009, 2010, 2013). *M. exasperans* does not resemble any known species of ant and the role of the distinct colouration of both males and females has been a mystery (Hill & Otto 2015). One possibility is that *M. exasperans* is a mimic of the parasitoid wasps that frequent its habitat in Bali (Hymenoptera: Ichneumonidae: Cryptinae: Cryptini: Goryphina: *Goryphus* cf. *basilaris* Holmgren 1868) (Figure 17).

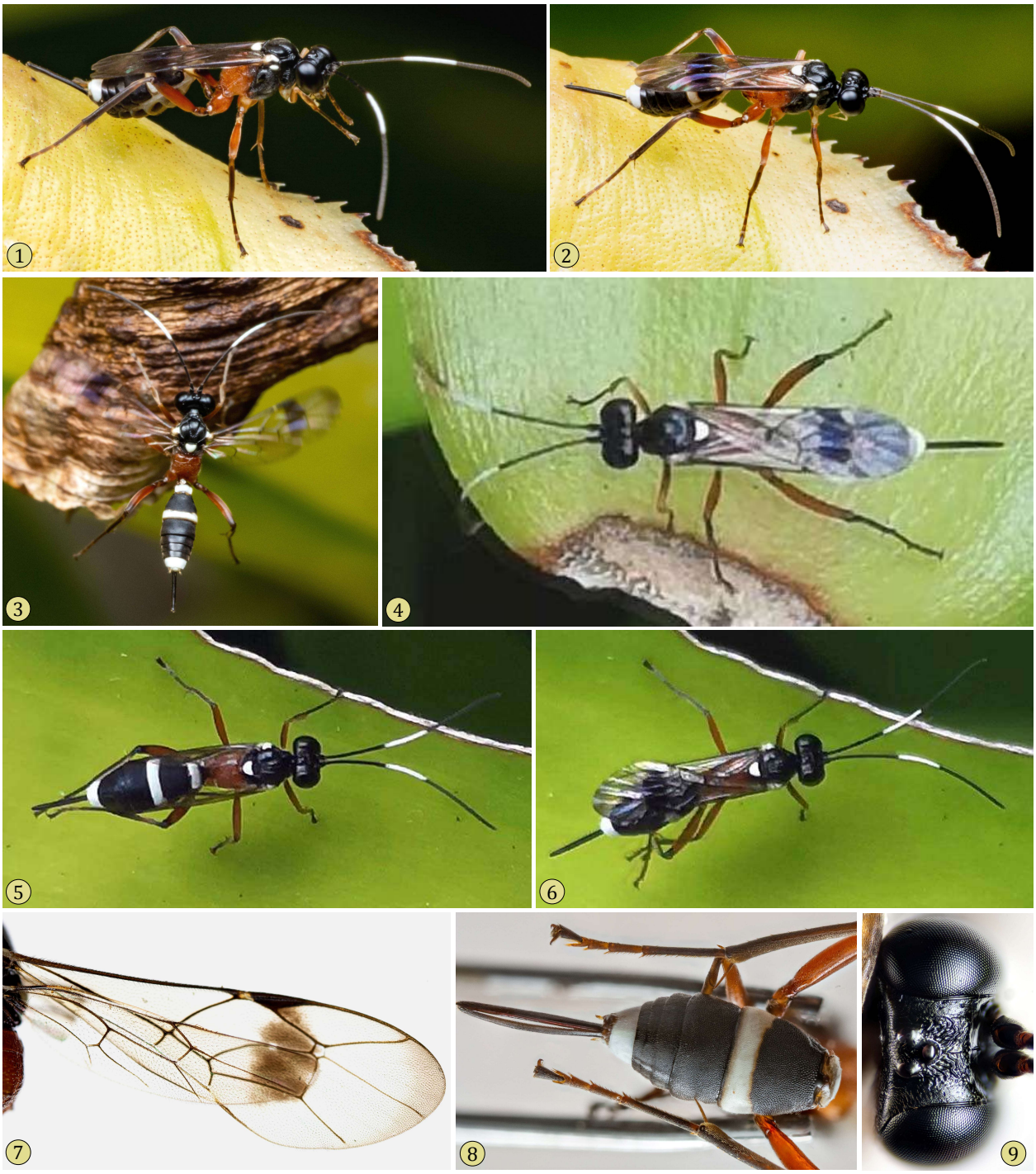

Figure 17. Ichneumonid wasp (female *Goryphus* cf. *basilaris* Holmgren 1868) that frequents the leaves occupied by *M. exasperans* in Bali. **5,** Grooming with rear legs raised above the wings. Note the presence of bold white transverse bands on the abdomen, and a bright white segment on each antenna. **7-9,** Detailed views of right wing (7), abdomen and ovipositor (8), and top of head (9).

The hypothesis that *M. exasperans* is a mimic of these wasps is supported not only by the similarity of their appearance, but also in their similar pattern of movement (Figures 18-22). As it moves a male or female *M. exasperans* raises and lowers legs I, marked with light-coloured tarsal segments, as it bobs its brightly banded opisthosoma. Corresponding movements of the local *Goryphus* cf. *basilaris* include movement of the banded antennae and wings up and down, also at a maximum but intermittent rate of ~15 cycles/s. Even up close, these spiders and wasps can be difficult to distinguish.

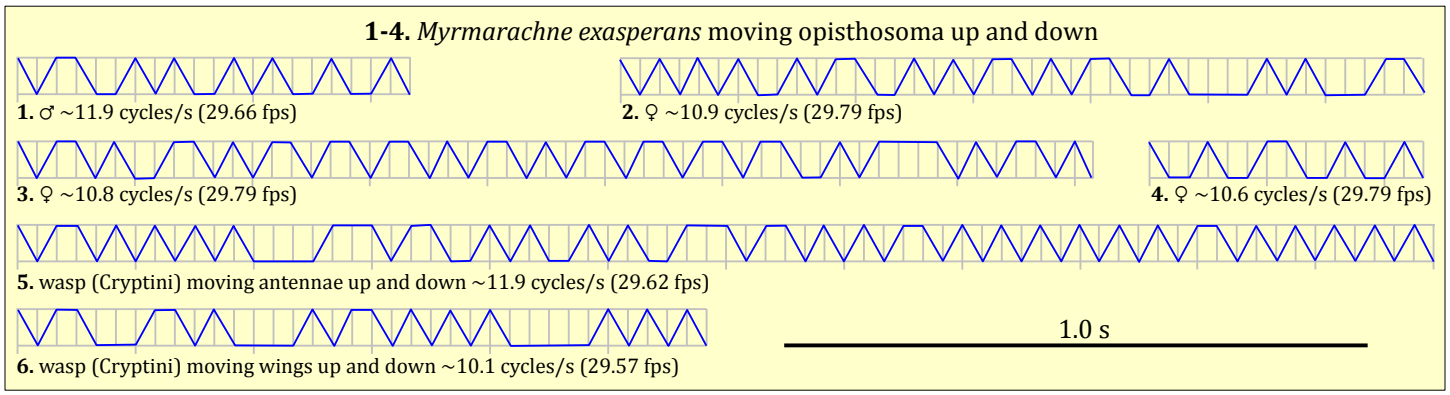

Figure 18. Timing of rapid up and down movements by *M. exasperans* (1-4) and *Goryphus* cf. *basilaris* (5-6) based on comparison of sequential video frames (~30 fps). Maximum rates of movement for both were ~15 (up+down) cycles/s, or ~11 cycles/s over several seconds due to frequent interruption. Thus not only the rate of this movement, but the irregularity or interrupted aspect of this movement, was essentially the same in the two species.

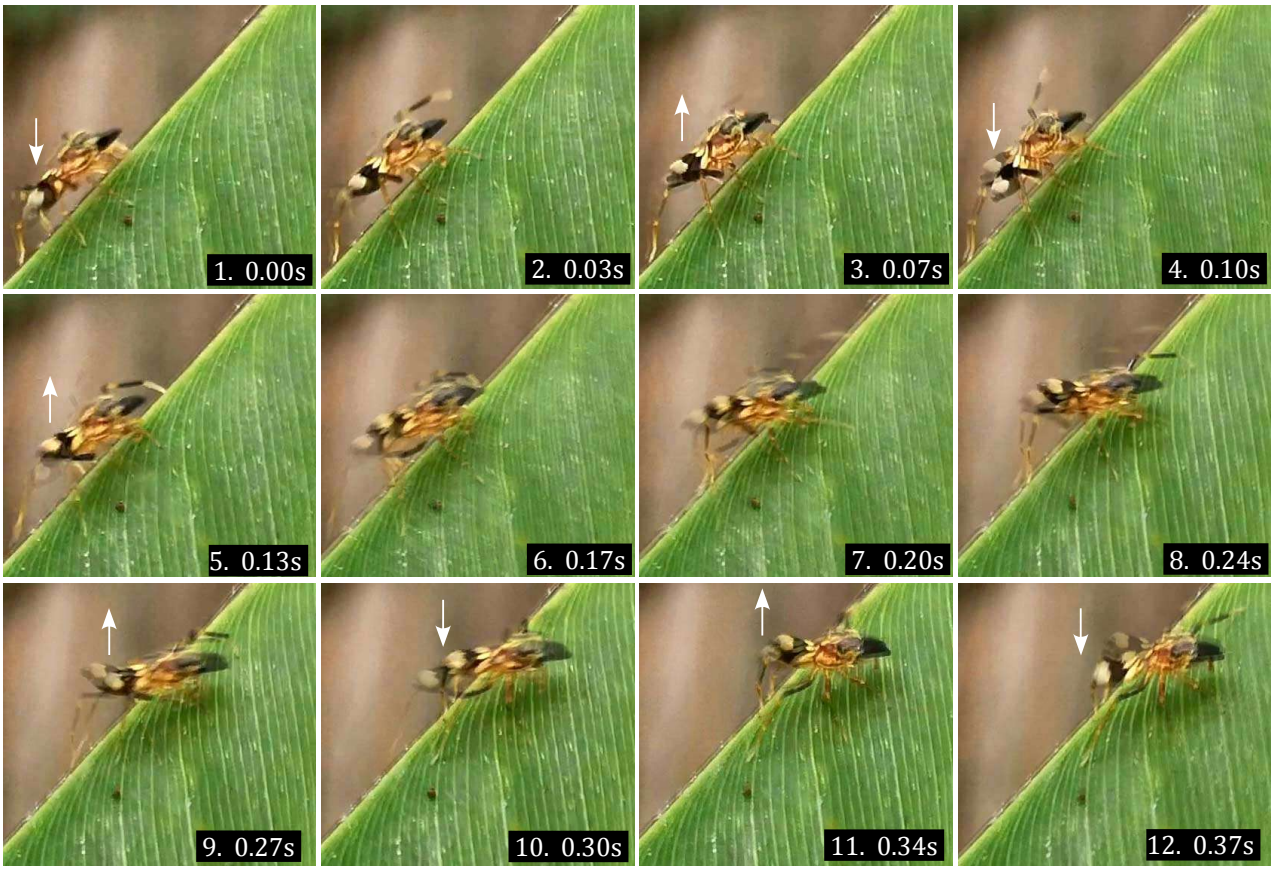

Figure 19. Sequential frames from a video (29.63 fps) of a moving adult male *Myrmarachne exasperans*. Up and down (bobbing) movement of the opisthosoma relative to each preceding frame is indicated with arrows. Between frames [8] and [12] the opisthosoma was bobbed at ~15 cycles/s. With interruptions the average was ~11 cycles/s for this entire sequence.

Figure 20. Sequential frames from a video (29.79 fps) of a moving adult female *Myrmarachne exasperans*. Up and down (bobbing) movement of the opisthosoma relative to each preceding frame is indicated with arrows. Maximum recorded rates of movement were ~15 cycles/s (e.g., between frames [1] and [4]), with 10 cycles completed in this 0.97s sequence for an average, including interruptions, of 10.3 cycles/s.

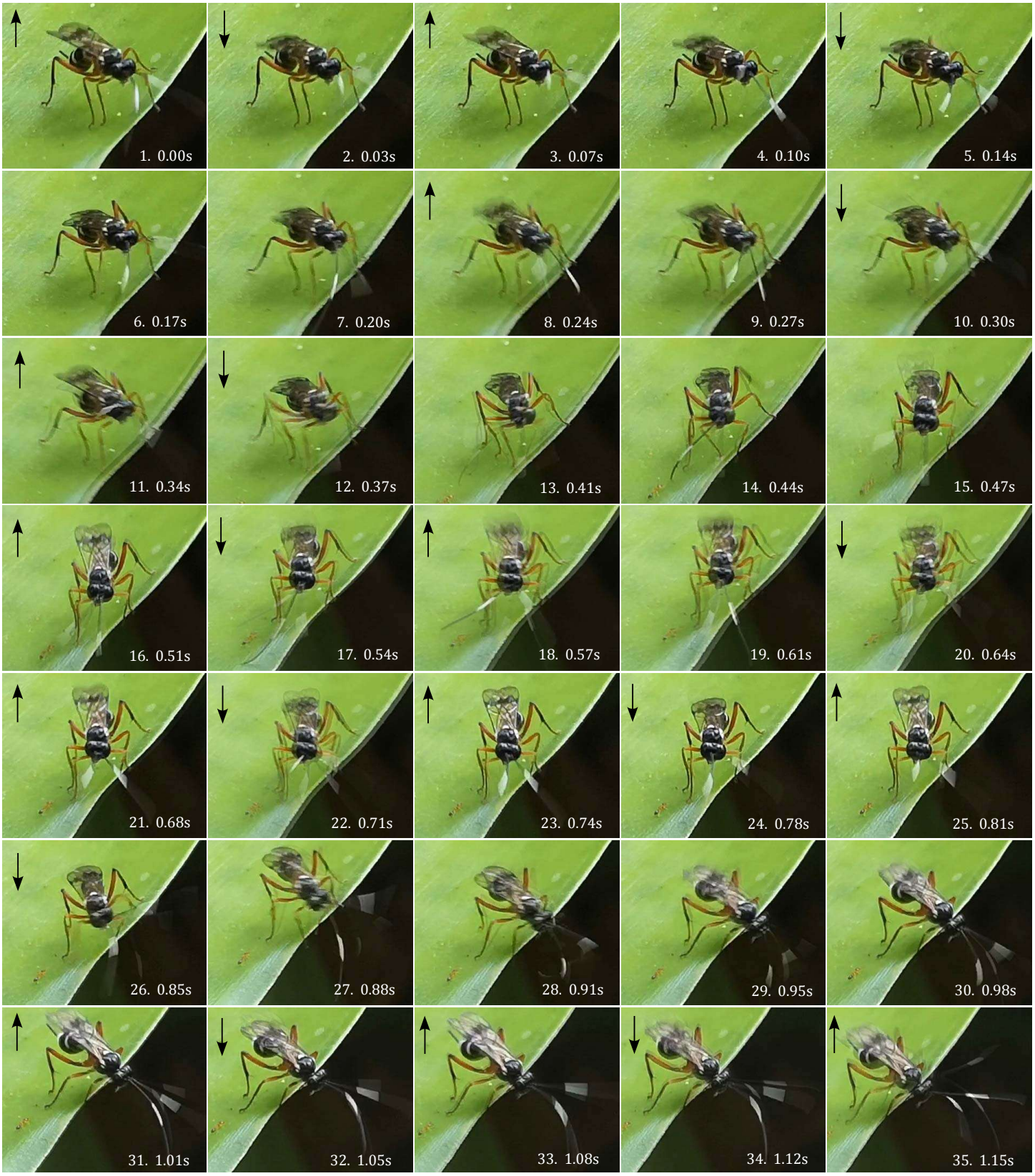

Figure 21. Sequential frames from a video (29.57 fps) of a moving ichneumonid wasp (female *Goryphus* cf. *basilaris*). Up and down movement of the wings relative to each preceding frame is indicated with arrows. A chart of this movement, peaking at ~15 cycles/s and averaging 10.1 cycles/s with interruptions, is shown in Figure 18:6.

Figure 22. Sequential but not consecutive frames from a video (29.71 fps) of a moving ichneumonid wasp (female *Goryphus* cf. *basilaris*). Up and down movement of the wings relative to each preceding frame is indicated with arrows. This movement peaked at ~15 cycles/s (frames [4] to [8] and frames [21] to [25]).

The rapid but intermittent stepping movements, including lagging positions of the long hind legs of *M. exasperans* and *Goryphus* cf. *basilaris*, could not be measured directly with video at the relatively low rate of 30 fps, but to the naked eye these appear much the same. This mimicry hypothesis is also supported by the fact that both male and female *M. exasperans* display the same colour pattern. The series of separate tracts of yellow scales around the anterodorsal opisthosoma of *M. exasperans* may even mimic the broken appearance of the white bands of the abdomen as these appear through the folded wings of this wasp. The only ant of comparable size that has been observed near these spiders in Bali is the weaver ant *Oecophylla smaragdina* Fabricius 1775, which they do not resemble (see Ramachandra & Hill 2018).

No interactions between *Myrmarachne exasperans* and *Goryphus* cf. *basilaris* were observed, but these wasps were often seen hunting near other wasps of the same kind. When another wasp approached on the same leaf, one would flee almost immediately. Some parasitoid cocoons were observed in the nests of other *Myrmarachne* species in the area, but not in the nests of *M. exasperans*. Although some ichneumonid wasps are parasitoids that prey on spider egg masses (e.g. *Tromotobia* sp., Sobczak et al. 2012 and *Gelis festinans*, van Baarlen et al. 1996), *Goryphus* species are ectoparasitoids that deposit their eggs on the surface of the pupae or cocoons of a variety of insects. *G. basilaris*, the type species for the genus, has been found from Japan, China and India southeast to Malaysia and Java in Indonesia (Momoi 1970; Jonathan 2006; Kandibane et al. 2006; Yu 2012; Nhi & Long 2016, Viet 2017). Hosts for *G. basilaris* include many different moths or butterflies (Lepidoptera: Crambidae, Erebidae, Hesperiidae, Lasiocampidae, Noctuidae, Nolidae, Pieridae, Zygaenidae) as well as leaf beetles (Coleoptera: Chrysomelidae: *Oulema*) (Jonathan 2006; Gurr et al. 2012). The great diversity of ichneumonid parasitoids in tropical forests is a recent and unexpected discovery (Laurenne 2008; Veijalainen et al. 2012; Quicke 2012). The large tribe Crypini contains many colourful species in the tropics, including those assigned to the large genus *Goryphus* (Santos 2017).

Our working hypothesis is that *M. exasperans* benefits from its mimicry of *Goryphus* to the extent that the many wasps that hunt for insects or spiders rely on their vision for detection of prey and avoid these parasitoid wasps based on their distinct markings and pattern of movement. This avoidance might be innate or learned. The relative abundance of *Goryphus* in areas frequented by *M. exasperans* would ensure the effectiveness of this disguise. The role of vision in the identification of prey by hunting wasps has received relatively little study, although this has been expected to play a role in short-range prey recognition (e.g. Koedam et. al. 2009). Recently it has been demonstrated that some polistine wasps (*Polistes fuscatus*) can recognize their nestmates by their unique facial patterns (Figure 23), or by a combination of facial and abdominal markings (Tibbetts 2002; Sheehan & Tibbetts 2011; Sheehan 2012; A. Avarguès-Weber 2012). Even more remarkably, it has been possible to train both honey bees (*Apis mellifera*) and vespid wasps (*Vespula vulgaris*) in flight to associate the image of a specific human face with either a reward (learned attraction) or a distasteful substance (learned avoidance) (Avarguès-Weber et al. 2017, 2018). These observations suggest that even relatively minor details of the appearance of a spider could impact the decisions of a hunting wasp in flight, even if these must be learned.

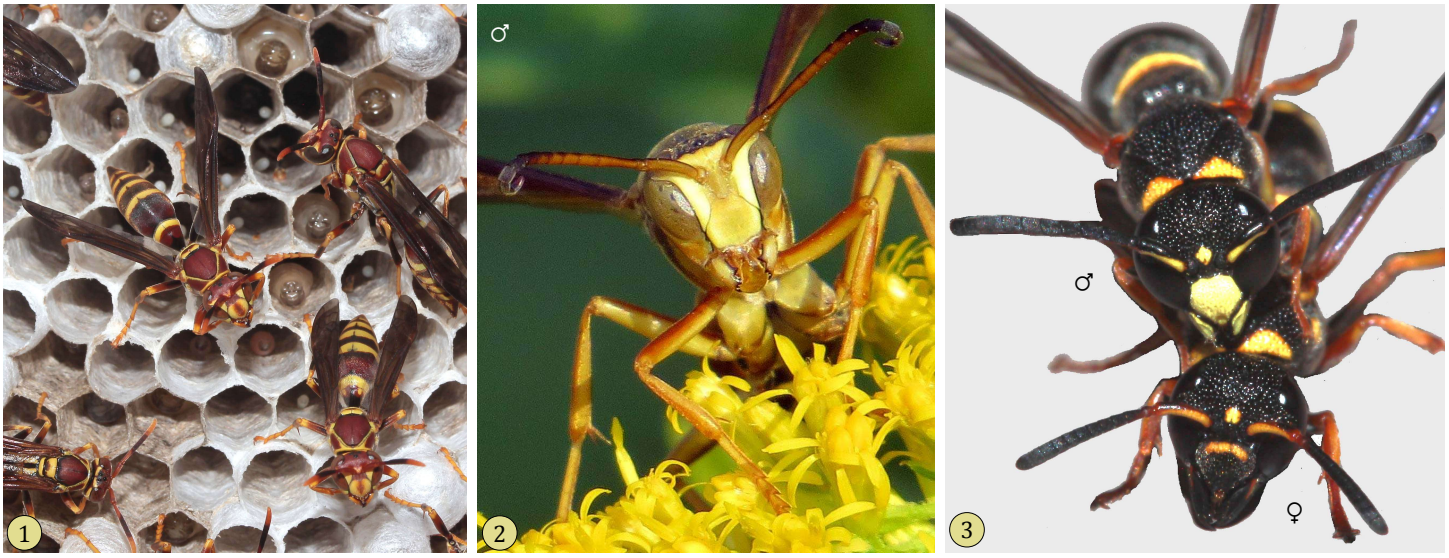

Figure 23. Faces of some vespid wasps. **1,** *Polistes exclamans* colony. Two workers turned to face the photographer. **2,** Distinctive yellow face of a male *P. fuscatus*. **3,** Different facial patterns of mating male and female potter wasp (*Parancistrocerus* sp.). All were from Greenville County, South Carolina.

Agonistic behaviour. Adult male *Myrmarachne exasperans* placed near other males moved their outstretched legs I back and forth at a rate of ~8-10 cycles/s through an angle of ~8° (Figures 24-25). Invariably one male ran away as the other advanced. This movement was clearly not wasp-like. More extensive studies are needed to determine the full repertoire of intraspecific communication in this species.

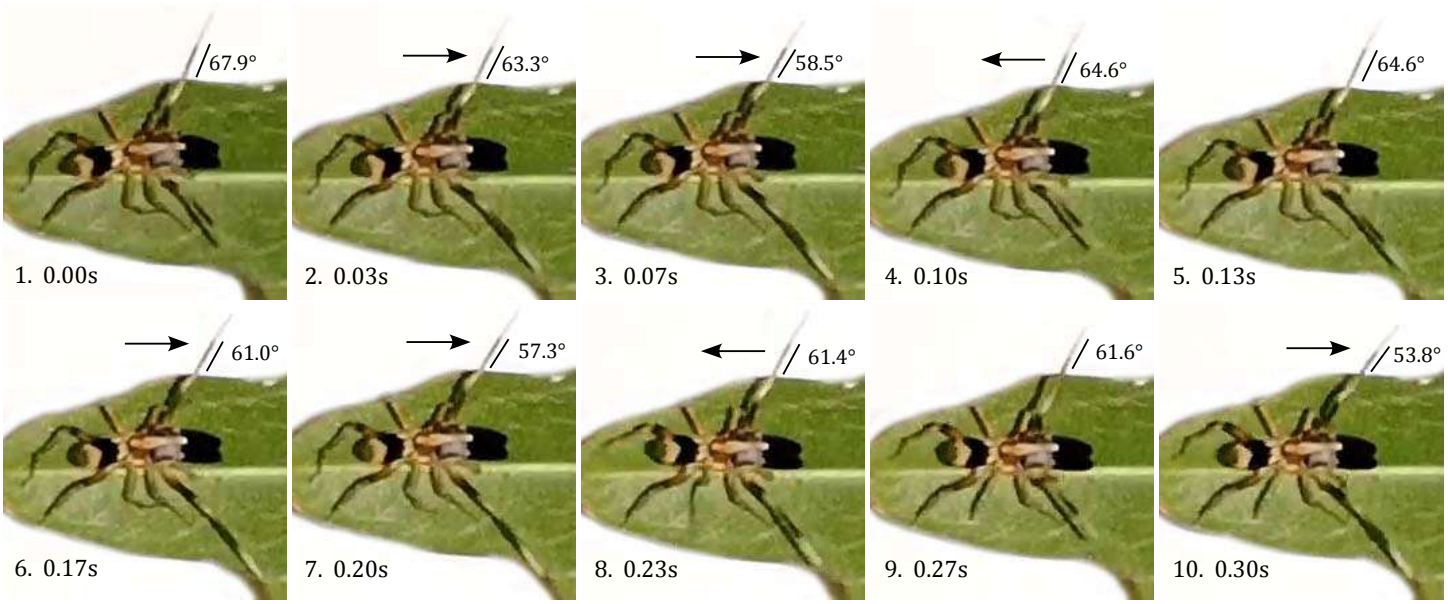

Figure 24. Consecutive frames from a video (29.80 fps) of a male *M. exasperans* displaying to a nearby male of the same species. In 0.30s 2.5 cycles of back and forth movement of legs I (~8° amplitude, ~8.3 cycles/s) was observed.

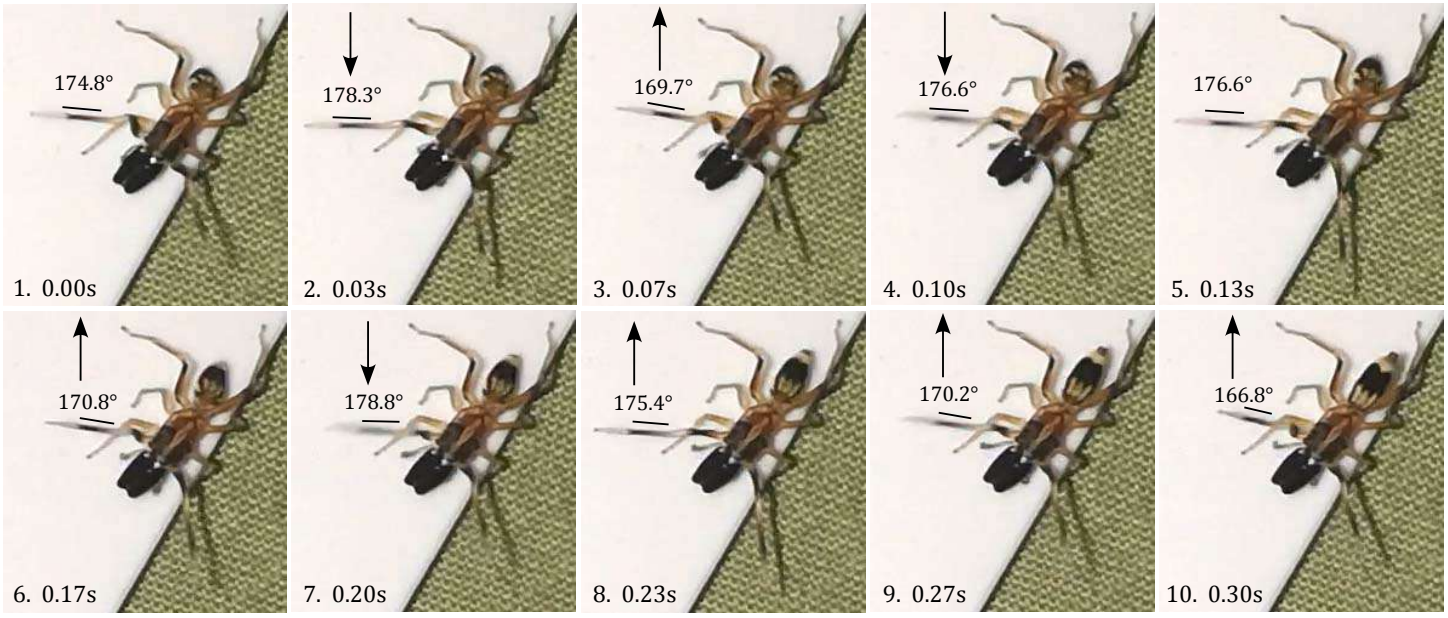

Figure 25. Consecutive frames from a video (29.81 fps) of a male *M. exasperans* displaying to a nearby male of the same species. In 0.30s 3.0 cycles of back and forth movement of legs I (~8° amplitude, ~10.0 cycles/s) was observed.

Distribution. To our records of *Myrmarachne exasperans* from Bali we can add one more record of this species from Puncak, West Java (Figure 26). Although the type for this species was collected in Java, the locality associated with that type is not known with certainty but is shown here as Banten in West Java. This new record clearly establishes that *M. exasperans* can be found from West Java to Bali. Published records outside of this area (see Hill & Otto 2015) are not reliable and may pertain to different but closely related species.

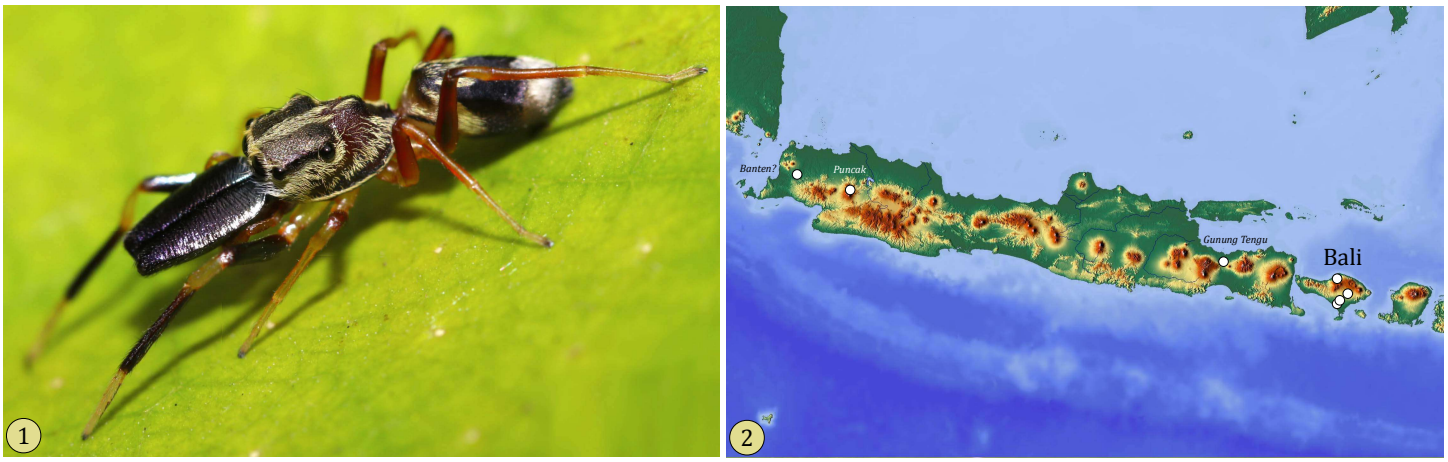

Figure 26. Distribution of *Myrmarachne exasperans* in Indonesia. **1,** Adult male photographed 23 June 2017 in Puncak, West Java, by Janus Olajuan Boediman. Photograph used with permission. **2,** Reported distribution of *M. exasperans* in Java and Bali (white circles). This background relief map is in the public domain (CC0), courtesy of maps-for-free (https://maps-for-free.com).

A close relative of the *Myrmarachne exasperans* of Bali and Java has been described recently from Borneo. Prószyński (2018) named this spider *Emertonius koomeni* after a single female specimen from the Rafflesia Garden of the Perkasa Hotel in Ranau, Sabah, Malaysia (also listed as "Sarawak") kept and photographed by P. Koomen (Leeuwarden, Netherlands). Overall colouration and scale patterns of *koomeni* are very close to *exasperans*, but there is a white triangle on the dorsal carapace of *koomeni* and the central yellow "petal" of the dorsal anterior opisthosoma is missing. W. P. Maddison has photographed a similar female from Mulu National Park in nearby Sarawak (Figure 27). This typological (morphological) species is quite possibly the same biological species as *M. exasperans*, but further study is needed to determine this. The same consideration applies to a female photographed in Vietnam (Otto & Hill 2015, fig. 1:3), lacking the carapace stripe of *exasperans* and the carapace triangle of *koomeni*.

We have not yet been able to confirm the locality, but a photograph of an adult male from "Madagascar" with scale patterns similar to those of *koomeni* has been posted on the internet (Bertner 2018). The chelicerae of this male are longer than those of male *exasperans* from Bali or Java. Although a Madagascar locality seems far afield for these spiders, Madagascar was in fact settled from the Malaysian Archipelago by seafaring "Austronesians" accompanied by a number of different agricultural plants (Dewar & Wright 1993; Beaujard 2011).

Figure 27. Adult female *Myrmarachne* cf. *exasperans*, specimen SWK12-3132, collection WPM#12-095, from Sarawak, Malaysia, Headquarters Area, tree foliage, Mulu National Park (4.042°N, 114.814°E). **6,** Note series of six long spines on the tibia and two long spines on the metatarsus of this preserved female, as seen in *M. exasperans*. **7,** Ventral view of epigynum. Scale patterns and locality suggest that this is *Emertonius koomeni* Prószyński 2018. Photographs © W. Maddison 2015, used under a Creative Commons Attribution (CC BY) 3.0 license.

Acknowledgments

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