PECKHAMIA 176.2, 20 April 2019, 1—28
urn:lsid:zoobank.org:pub:7828FB77-C4F0-49E6-968F-0A712017BBF9 (registered 4 APR 2019)
ISSN 2161—8526 (print)
ISSN 1944—8120 (online)

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

Tiziano Hurni-Cranston [1] and David E. Hill [2]

[1] 450 Rue Saint Louis, H2Y1A9, Montreal, Quebec, Canada, *email* tiziano@jumpingspiders.ca
[2] 213 Wild Horse Creek Drive, Simpsonville, SC 29680-6513, USA, *email* platycryptus@yahoo.com

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. Their relationship to other *Myrmarachne* species from Sunda is also discussed.

Key words. agonistic behaviour, Borneo, ectoparasitoid, *Emertonius exasperans*, *Emertonius koomeni*, *exasperans* group, *Goryphus basilaris*, Java, *Myrmarachne malayensis*, 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; Maddison 2015). 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 the ants that they mimic but may consume smaller ants (Holmes 2019) and many other insects including moths, or 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). Females of the Formosan species *M. magna* Saito 1933 may 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 2-11), 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*.

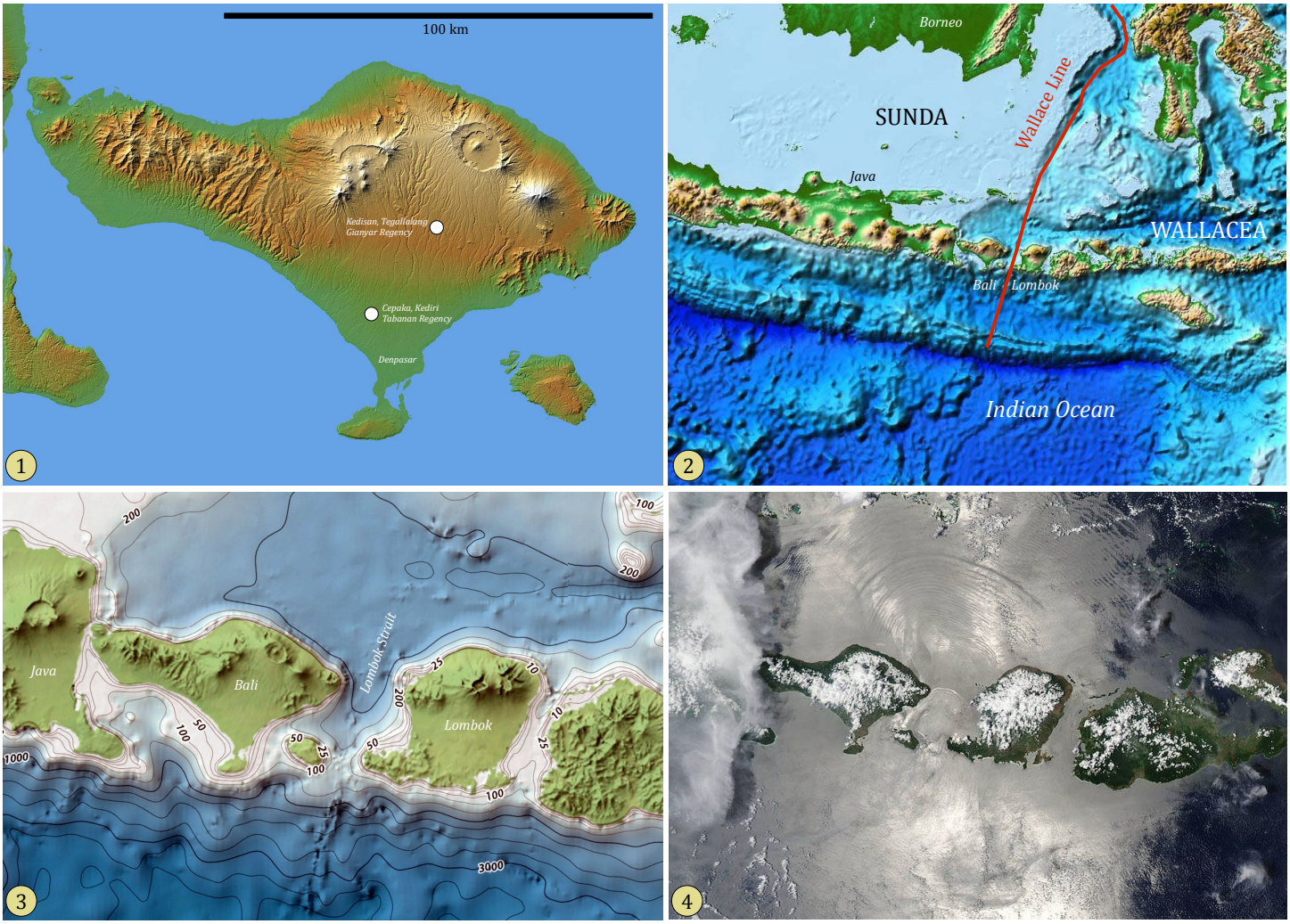

Figure 1. Bali and neighboring islands. **1,** Localities where *Myrmarachne exasperans* was observed in Bali. Most were found in the garden of one of the authors (THC) at Cepaka, others in a garden at Kedisan. This background map is a shaded relief image of color-coded elevations generated from data 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*.

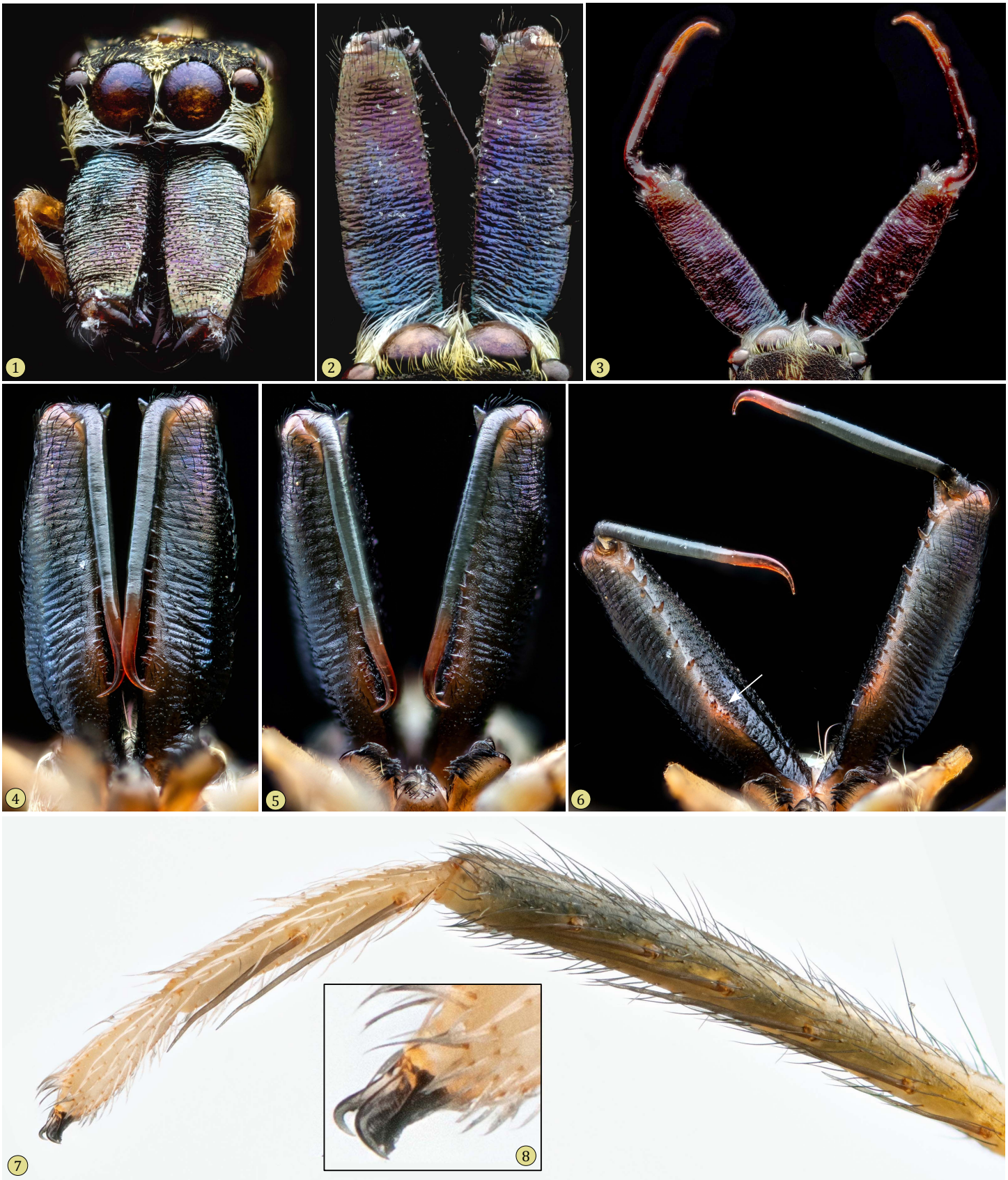

Figure 5. Detailed views of a dried adult male *Myrmarachne exasperans* (not living). **2-3,** Dorsal view of chelicerae with fangs retracted (2) and extended (3). **4-6,** Ventral views of chelicerae in different positions. Note the posterior (ventral) position of the fang groove (6, arrow), lined with 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), showing closely spaced teeth of the anterior claw.

Figure 6. Pedipalps of adult male *Myrmarachne exasperans*. **1-5,** Ventral to ventrolateral views of left pedipalp. **6-7,** Detail of (3). Note the two (proximal and distal) processes of the retrolateral tibial apophysis (RTA) at lower right. **5, 8,** Tips of the distal setae of the pedipalp are aligned in a plane (arrows). **9,** Extended right pedipalp. **10,** Flexed left pedipalp.

Figure 7. Living adult female *Myrmarachne exasperans*. Length is ~5-6 mm, not including the chelicerae.

Figure 8. Living adult female *Myrmarachne exasperans*.

Figure 9. 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).

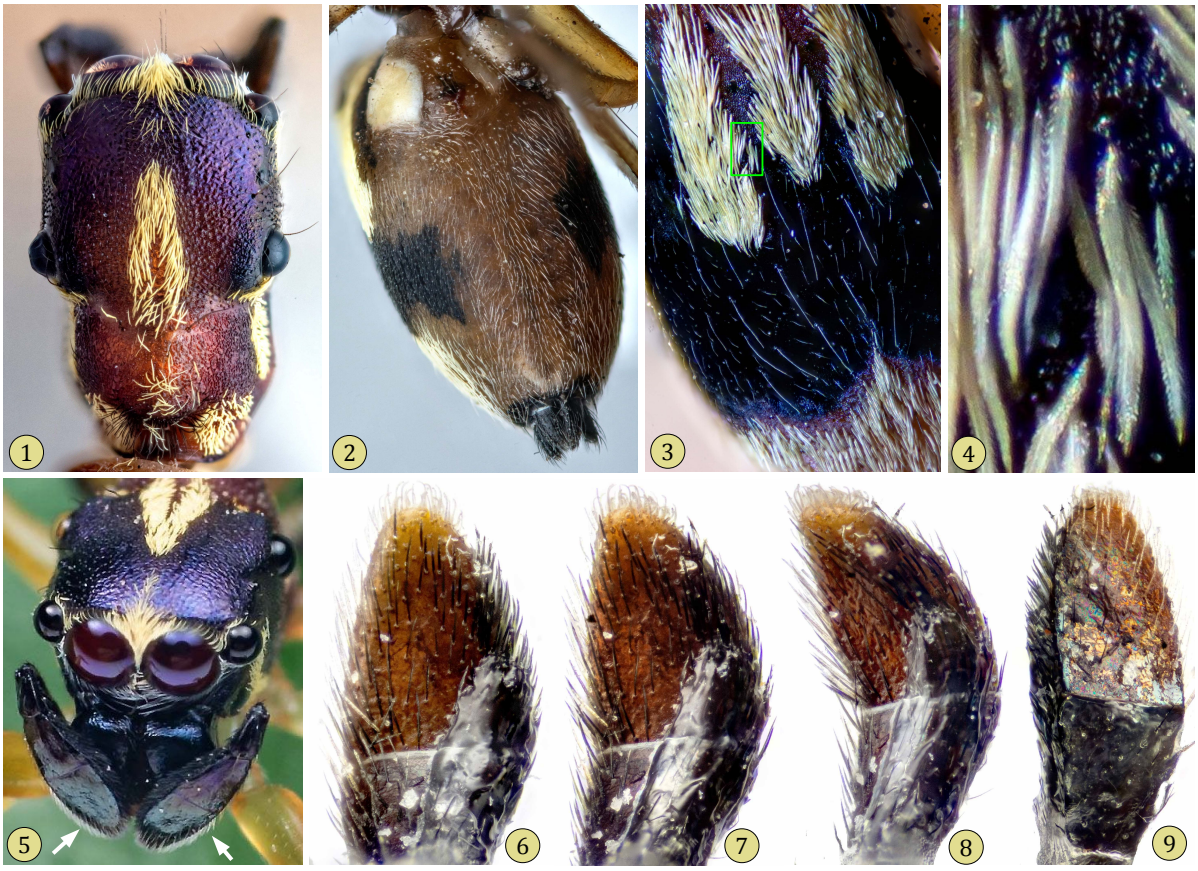

Figure 10. Detailed views of an adult female *Myrmarachne exasperans*. **1,** The anterodorsal carapace of the female has the same iridescent violet color as the male chelicerae. **4**, Detail of inset from (3), showing the elongated, fringed scales that comprise the distinctive markings of the dorsal opisthosoma. **5,** The flattened pedipalps of the female are mostly glabrous dorsally, fringed with stout, sharply pointed setae (arrows). **6-9,** Ventral (6) to dorsal (9) composite images of dried left pedipalp of female, showing stout ventral and marginal setae and relatively smooth dorsal plate (9). Distally (toward the top of the page) there appears to be a small tuft of more flexible, light-colored spondylae (whorled or chemosensory setae).

Figure 11. 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 13) 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 12).

Figure 12. 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 many other *Myrmarachne* species, *M. exasperans* nests observed in Bali were covered with bits of debris, making them easy to identify. As observed in captivity, these spiders collect and decorate their own nests with this debris. The debris incorporated into a nest by *M. exasperans* is quite variable but includes leaves and bits of bark as well as dead insects and insect exuviae (Figures 13-16). 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 attached 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 13. 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,** Spider approaching the nest from one side. **3,** Detail from (2) to show similarity of this subadult (most likely a penultimate female) to the adult. **4,** Spider entering the nest.

Figure 14. 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 15. **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.

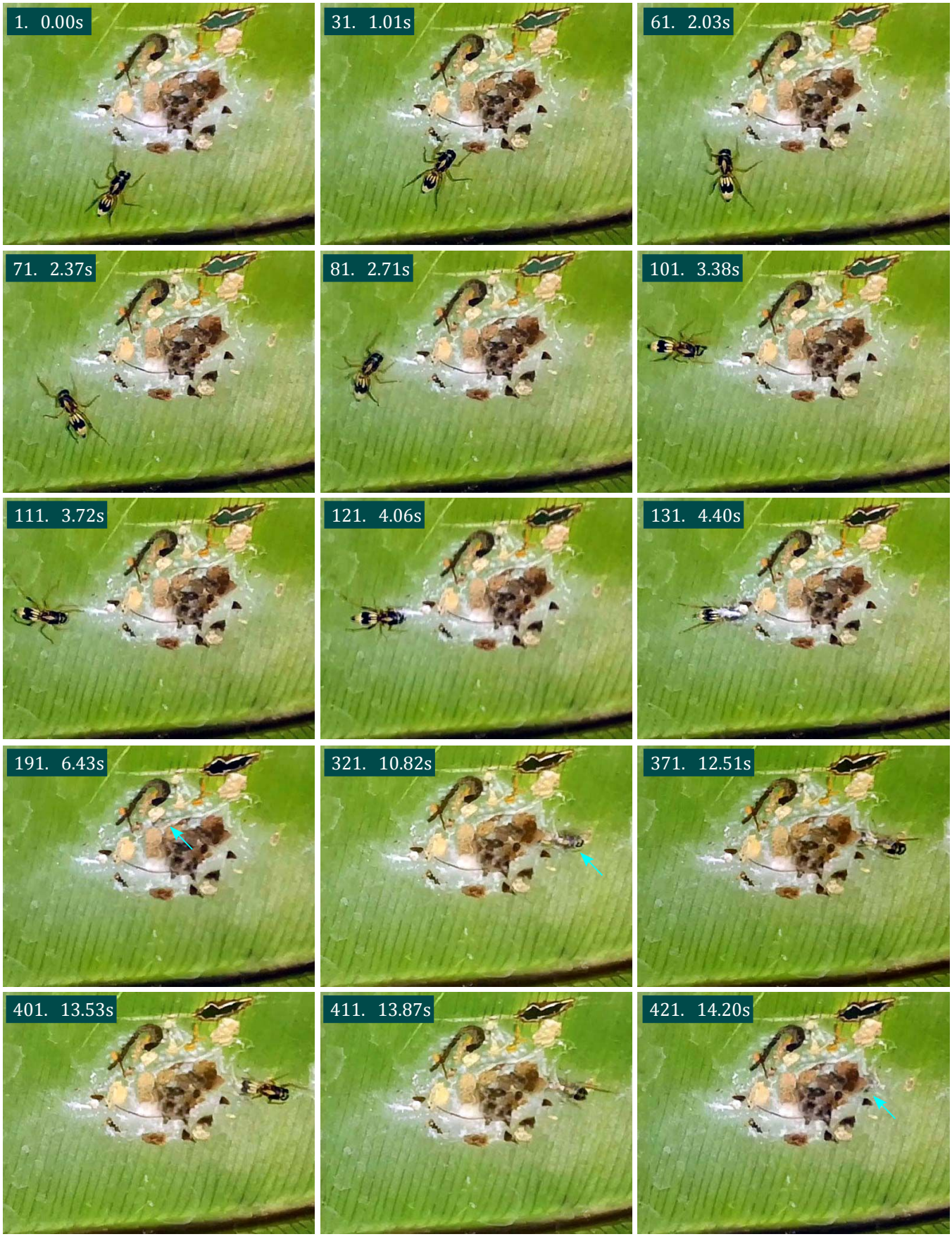

Figure 15. Sequential frames from a 29.57fps video showing a female *M. exasperans* entering her nest at one end (frame 131) and emerging from the other end (frame 401). Arrows (191, 321, 421) indicate position of female in nest.

Figure 16. 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). Small groups of ants may collect debris either to conceal or to protect their nests in Bali (Figure 17), and it is possible that *M. exasperans* sometimes occupy or modify the nests of other arthropods. However the manner in which debris is attached to the outer silk sheet of nests and the presence of the same kind of cottony silk tufts associated with the nests of other *Myrmarachne* species, also known to manipulate and secure detritis (Jackson & Willey 1994), indicate that *M. exasperans* usually construct and decorate their own nests with local debris that they have collected. As noted previously, this behaviour has now been observed in captivity.

Figure 17. 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 18).

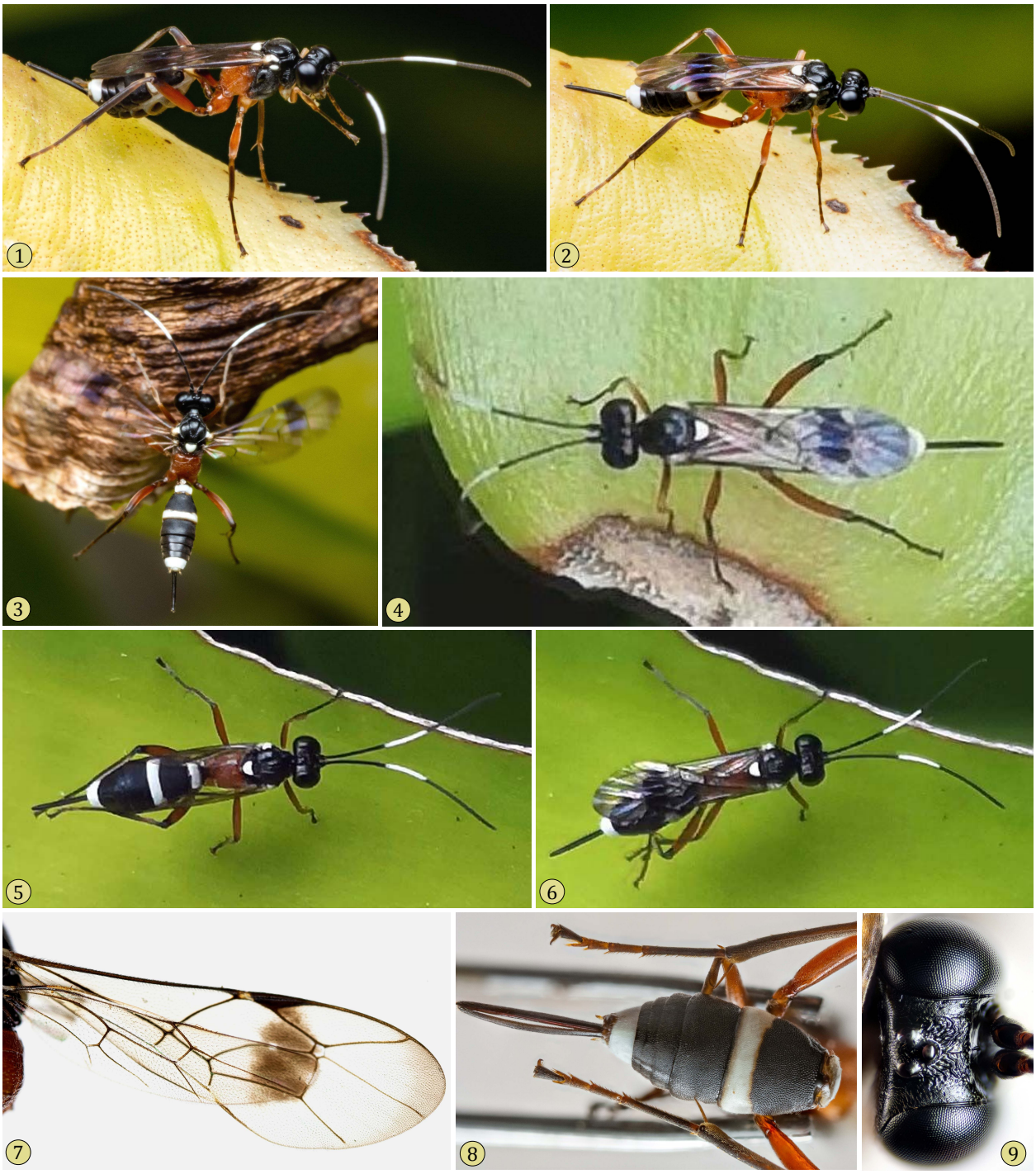

Figure 18. Ichneumonid wasp (female *Goryphus* cf. *basilaris* Holmgren 1868) that frequents the leaves occupied by *M. exasperans* in Bali. **5,** Grooming with rear legs raised above the wings. Note the presence of bold white transverse bands on the abdomen, and a bright white segment on each antenna. **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 19-23). 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.

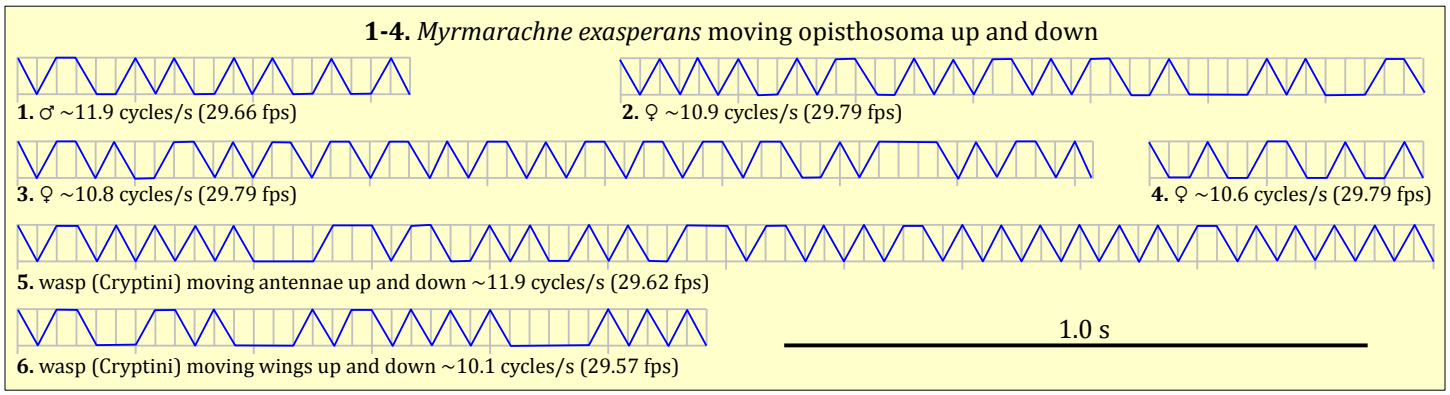

Figure 19. Timing of rapid up and down movements by *M. exasperans* (1-4) and *Goryphus* cf. *basilaris* (5-6) based on comparison of sequential video frames (~30 fps). Maximum rates of movement for both were ~15 (up+down) cycles/s, or ~11 cycles/s over several seconds due to frequent interruption. Thus 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 20. 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 21. 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.

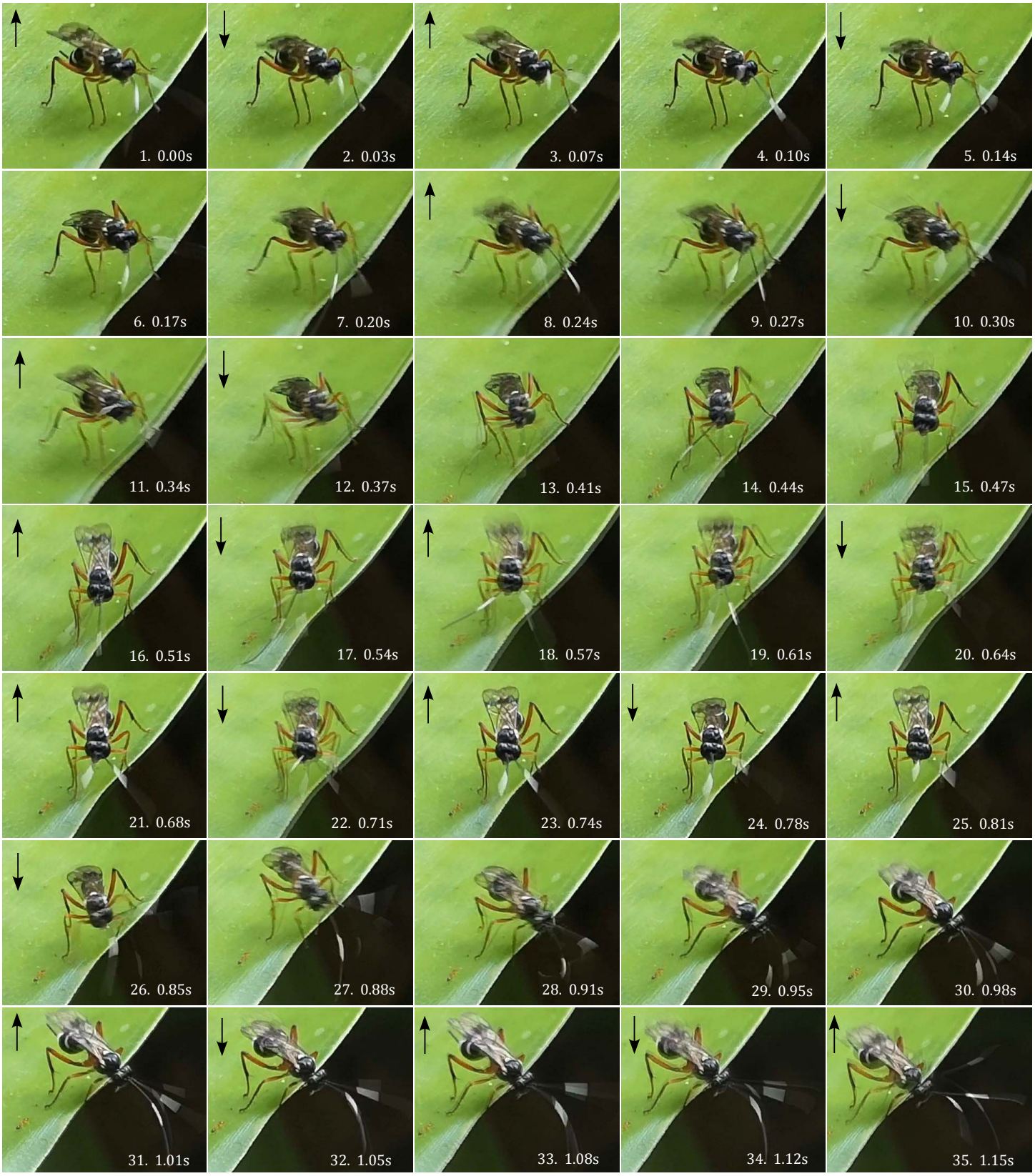

Figure 22. Sequential frames from a video (29.57 fps) of a moving ichneumonid wasp (female *Goryphus* cf. *basilaris*). Up and down movement of the wings relative to each preceding frame is indicated with arrows. A chart of this movement, peaking at ~15 cycles/s and averaging 10.1 cycles/s with interruptions, is shown in Figure 18:6.

Figure 23. 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 24), 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.

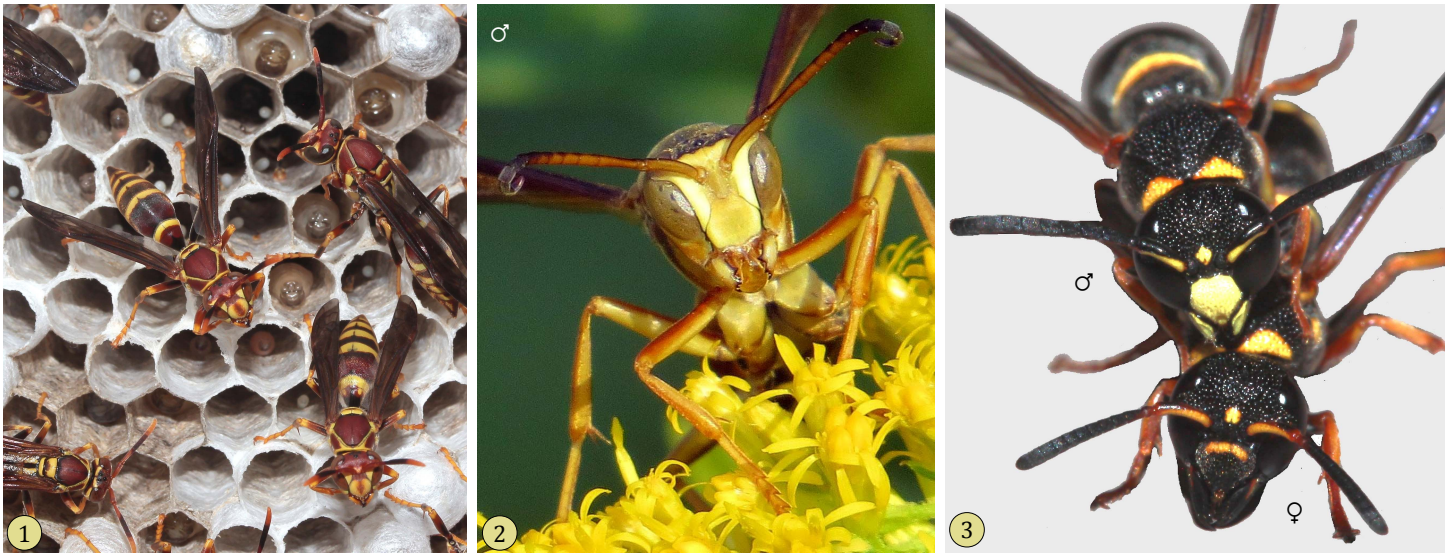

Figure 24. Faces of some vespid wasps. **1,** *Polistes exclamans* colony. Two workers turned to face the photographer. **2,** Distinctive yellow face of a male *P. fuscatus*. **3,** Different facial patterns of mating male and female potter wasp (*Parancistrocerus* sp.). All were from Greenville County, 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 25-26). 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.

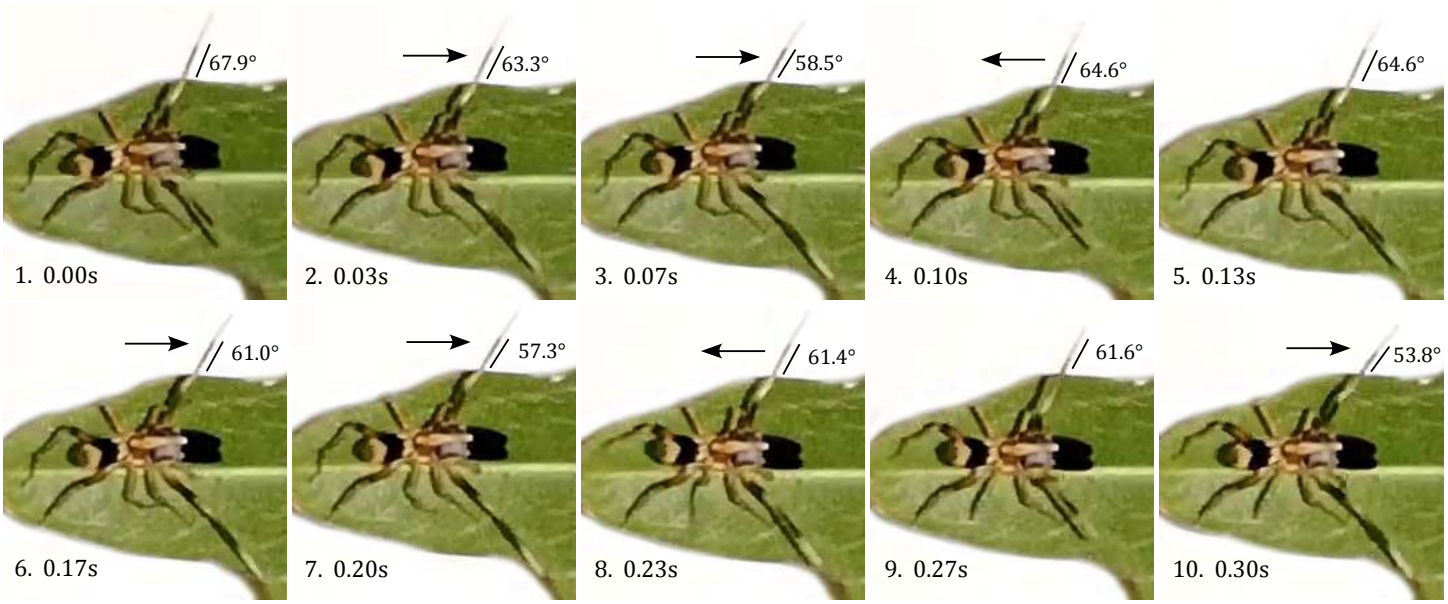

Figure 25. Consecutive frames from a video (29.80 fps) of a male *M. exasperans* displaying to a nearby male of the same species. In 0.30s 2.5 cycles of back and forth movement of legs I (~8° amplitude, ~8.3 cycles/s) was observed.

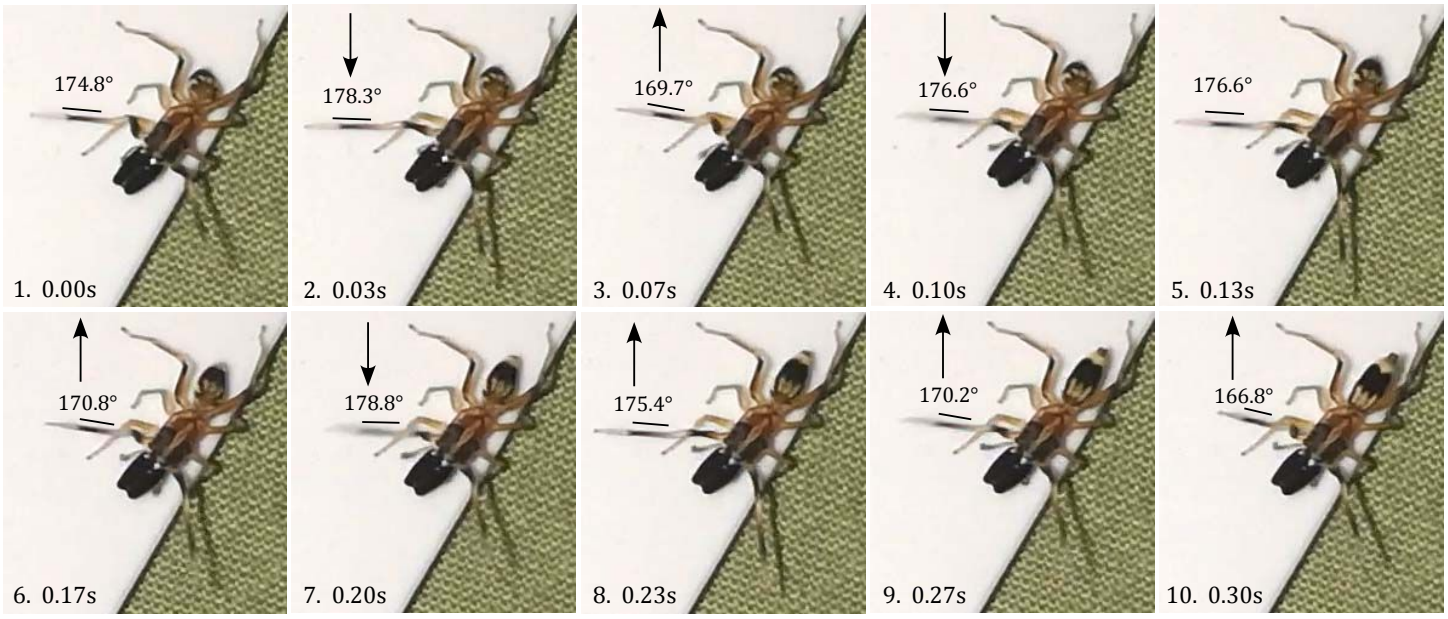

Figure 26. Consecutive frames from a video (29.81 fps) of a male *M. exasperans* displaying to a nearby male of the same species. In 0.30s 3.0 cycles of back and forth movement of legs I (~8° amplitude, ~10.0 cycles/s) was observed.

Distribution. To our records of *Myrmarachne exasperans* from Bali we can add one more record of this species from Puncak, West Java (Figure 27). 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 are not reliable and may pertain to different but closely related species (see Hill & Otto 2015).

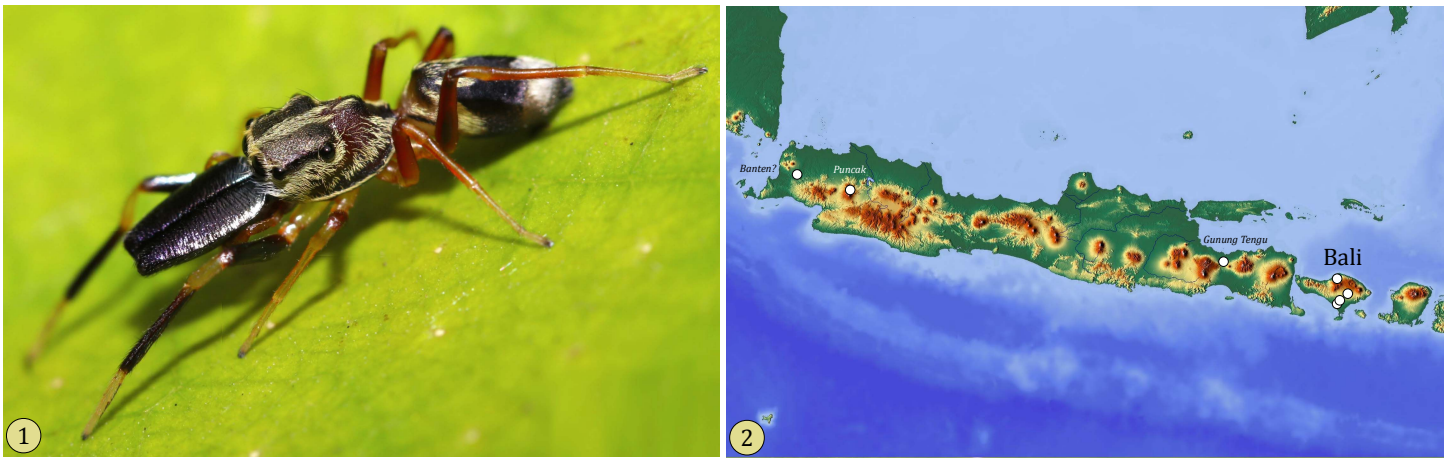

Figure 27. Distribution of *Myrmarachne exasperans* in Indonesia. **1,** Adult male photographed 23 June 2017 in Puncak, West Java, by Janus Olajuan Boediman. Photograph used with permission. **2,** Reported distribution of *M. exasperans* in Java and Bali (white circles). This background relief map 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 28). 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 28. 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.

The *exasperans* group in Sunda

Spiders that we group into the *exasperans* (or *Emertonius*) sub-clade of *Myrmarachne* are listed in Table 1. With the exception of *koomeni* (for which no data is available), these species construct nests covered with debris under leaves (Figure 29; Yamasaki, pers. comm.). Two projections of the RTA distinguish *M. exasperans* from other members of the group (Figure 6; Yamasaki 2016).

Table 1. Spiders associated with the *Myrmarachne exasperans* group (a Sundan subclade of *Myrmarachne*). Several authors have placed some of these species in the genus *Emertonius* Peckham & Peckham 1892 (Prószyński & Deeleman-Reinhold 2010; Prószyński 2016, 2017, 2018; WSC 2019).

**Emertonius exasperans* Peckham & Peckham 1892	Java east to Bali
Emertonius koomeni Prószyński 2018	Sabah, Borneo (one ♀ only), may be synonym of *M. exasperans*
**Myrmarachne malayana* Edmunds & Prószyński 2003	Sunda (Malay Peninsula to Borneo)
**Myrmarachne shelfordi* Peckham & Peckham 1907	Borneo
**Myrmarachne thaii* Żabka 1985	Vietnam

*Associated with this clade by Yamasaki (2016).

Figure 29. Adult male *Myrmarachne malayana* in nest, Danum Valley, Borneo (20 JUL 2017). **1,** Two nests on the underside of a large leaf. **2,** Detail of male emerging from one of these nests. Note the presence of cottony silk tufts and the covering of debris in the construction of each nest. Photographs © Nicky Bay, used with permission.

Acknowledgments

We thank Takeshi Yamasaki for translating relevant portions of his 2015 paper on *Myrmarachne* in Southeast Asia and for providing important information about *M. exasperans* and its relatives, Robert R. Jackson and Rui-Chang Quan for sharing their papers on *Myrmarachne*, and both Nicky Bay and Janus Olajuan Boediman for allowing us to use their photographs of these spiders. We also thank Wayne P. Maddison, Jeff Schmalz, NASA and NOAA for allowing us to use their photographs and maps.

References

Avarguès-Weber, A. 2012. Face recognition: lessons from a wasp. Current Biology 22 (3): R92.

Avarguès-Weber, A., D. d'Amaro, M. Metzler, J. E. Garcia and A. G. Dyer. 2017. Recognition of human face images by the free flying wasp *Vespula vulgaris*. Animal Behavior and Cognition 4 (3): 314-323.

Avarguès-Weber, A., D. d'Amaro, M. Metzler, V. Finke, D. Baracchi and A. G. Dyer. 2018. Does holistic processing require a large brain? Insights from honeybees and wasps in fine visual recognition tasks. Frontiers in Psychology 9 (1313): 1-9.

Beaujard, P. 2011. The first migrants to Madagascar and their introduction of plants: linguistic and ethnological evidence. Azania, The Journal of the British Institute of History and Archaeology in East Africa, Routledge (imprimé)/Taylor Francis Online (en ligne) 46 (2): 169-189.

Bertner, P. 2018 (accessed). Ant-mimicking jumping spider (*Myrmarachne* sp), Madagascar. *Online at* https://www.gettyimages.com/detail/photo/ant-mimicking-jumping-spider-madagascar-high-res-stock-photography/901744732

Ceccarelli, F. S. 2008. Behavioral mimicry in *Myrmarachne* species (Araneae, Salticidae) from North Queensland, Australia. The Journal of Arachnology 36: 344-351.

Ceccarelli, F. S. 2009. Ant-mimicking spider, *Myrmarachne* species (Araneae : Salticidae), distinguishes its model, the green ant, *Oecophylla smaragdina*, from a sympatric Batesian *O. smaragdina* mimic, *Riptortus serripes* (Hemiptera : Alydidae). Australian Journal of Zoology 57: 305-309.

Ceccarelli, F. S. 2010. New species of ant-mimicking jumping spiders of the genus *Myrmarachne* MacLeay, 1839 (Araneae: Salticidae) from north Queensland, Australia. Australian Journal of Entomology 49: 245-255.

Ceccarelli, F. S. 2013. Ant-mimicking spiders: strategies for living with social insects. Psyche 839181: 1-6.

Ceccarelli, F. S. and R. H. Crozier. 2007. Dynamics of the evolution of Batesian mimicry: molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. Journal of Evolutionary Biology 20 (1): 286-295.

Chen, Z., R. T. Corlett, X. Jiao, S. Liu, T. Charles-Dominique, S. Zhang, H. Li, R. Lai, C. Long, R. Quan. 2018. Prolonged milk provisioning in a jumping spider. Science 362 (6418): 1052-1055.

Dewar, R. E. and H. T. Wright. 1993. The culture history of Madagascar. Journal of World Prehistory 7 (4): 417-466.

Gurr, G. M., D. M. Y. Read, J. L. A. Catindig, J. Cheng, J. Liu, L. P. Lan and K. L. Heong. 2012. Parasitoids of the rice leaffolder *Cnaphalocrocis medinalis* and prospects for enhancing biological control with nectar plants. Agricultural and Forest Entomology 14: 1-12.

Hill, D. E. 2010. Sunda to Sahul: Trans-Wallacean distribution of recent salticid genera (Araneae: Salticidae). Peckhamia 80.1: 1-60.

Hill, D. E. and J. C. Otto. 2015. Exasperating taxonomy of the colourful ant-mimic *Myrmarachne exasperans* (Araneae: Salticidae: Astioida: Myrmarachninae). Peckhamia 131.1: 1-5.

Holmes, A. 2019. First observation of *Myrmarachne* species feeding on ants (Araneae: Salticidae: Myrmarachnini). Peckhamia 178.1: 1-4.

Holmgren, A. E. 1868. Hymenoptera. Species novas descripsit. Kongliga Svenska Fregatten Eugenies Resa omkring jorden. Zoologi. 6: 391-442.

Kandibane, M., S. Raguraman and N. R. Mahadevan. 2006. Species composition and taxonomic similarity of Hymenoptera in an irrigated rice ecosystem of Tamil Nadu, India. International Journal of Agricultural Science 2 (2): 474-477.

Jackson, R. R., X. J. Nelson and K. Salm. 2008. The natural history of *Myrmarachne melanotarsa*, a social ant-mimicking jumping spider. New Zealand Journal of Zoology 35 (3): 225-235.

Jackson, R. R. and M. B. Willey. 1994. The comparative study of the predatory behaviour of *Myrmarachne*, ant-like jumping spiders (Araneae: Salticidae). Zoological Journal of the Linnean Society 110: 77-102.

Jonathan, J. K. 2006. Ichneumonologia Indica, Part-I, Hymenoptera: Ichneumonidae. Published by the Director, Zoological Survey of India, Kolkata. 1-680.

Karsch, F. 1892. Arachniden von Ceylon und von Minikoy gesammelt von den Herren Doctoren P. und F. Sarasin. Berliner Entomologische Zeitschrift 36: 267-310.

Koedam, D., E. J. Slaa, J. C. Biesmeijer and P. Nogueira-Neto. 2009. Unsuccessful attacks dominate a drone-preying wasp's hunting performance near stingless bee nests. Genetics and Molecular Research 8 (2): 690-702.

Laurenne, N. 2008. Phylogeny of a taxonomically difficult group and evolution of host location mechanism. Dissertation, Department of Biological and Environmental Sciences, University of Helsinki: 1-17.

MacLeay, W. S. 1839. On some new forms of Arachnida . Annals of Natural History 2: 1-14.

Maddison, W. P. 2015. A phylogenetic classification of jumping spiders (Araneae: Salticidae). The Journal of Arachnology 43:231-292.

Maddison, W. P., M. R. Bodner and K. M. Needham. 2008. Salticid spider phylogeny revisited, with the discovery of a large Australasian clade (Araneae: Salticidae). Zootaxa 1893: 49-64.

Momoi, S. 1970. Ichneumonidae (Hymenoptera) of the Ryuku Archipelado. Pacific Insects 12 (2): 327-399.

Nelson, X. J., R. R. Jackson, G. B. Edwards and A. T. Barrion. 2005. Living with the enemy: jumping spiders that mimic weaver ants. The Journal of Arachnology 33: 813-819.

Nhi, P. T. and K. D. Long. 2016. A checklist of the family Ichneumonidae (Hymenoptera: Ichneumonoidea) from Vietnam. Tap Chi Sinh Hoc 38 (4): 411-441.

Peckham, G. W. and E. G. Peckham. 1892. Ant-like spiders of the family Attidae. Occasional Papers of the Natural History Society of Wisconsin 2(1): 1-84.

Peckham, G. W. and E. G. Peckham. 1907. The Attidae of Borneo. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 15: 603-653.

Pekár, S., L. Petrakova, G. Corcobado and R. Whyte. 2017. Revision of eastern Australian ant-mimicking spiders of the genus *Myrmarachne* (Araneae, Salticidae) reveals a complex of species and forms. Zoological Journal of the Linnean Society 179: 642-676.

Prószyński, J. 2016. Delimitation and description of 19 new genera, a subgenus and a species of Salticidae (Araneae) of the world. Ecologica Montenegrina 7: 4-32.

Prószyński, J. 2017. Pragmatic classification of the World's Salticidae (Araneae). Ecologica Montenegrina 12: 1-133.

Prószyński, J. 2018. Review of genera *Evarcha* and *Nigorella*, with comments on *Emertonius*, *Padilothorax* [sic], *Stagetillus*, and description of five new genera and two new species (Araneae: Salticidae). Ecologica Montenegrina 16: 130-179.

Prószyński, J. and C. L. Deeleman-Reinhold. 2010. Description of some Salticidae (Araneae) from the Malay Archipelago. I. Salticidae of the Lesser Sunda Islands, with comments on related species. Arthropoda Selecta 19: 153-188.

Quicke, D. L. J. 2012. We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology. PLoS ONE 7 (2): e32101: 1-9.

Ramachandra, P. and D. E. Hill. 2018. Predation by the weaver ant *Oecophylla smaragdina* (Hymenoptera: Formicidae: Formicinae) on its mimic jumping spider *Myrmarachne plataleoides* (Araneae: Salticidae: Astioida: Myrmarachnini). Peckhamia 174.1: 1-8.

Saito, S. 1933. Notes on the spiders from Formosa. Transactions of the Sapporo Natural History Society 13: 32-61.

Santos, B. F. 2017. Phylogeny and reclassification of Cryptini (Hymenoptera, Ichneumonidae, Cryptinae), with implications for ichneumonid higher-level classification. Systematic Entomology, DOI: 10.1111/syen.12238: 1- 27.

Shamble, P. S., R. R. Hoy, I. Cohen and T. Beatus. 2017. Walking like an ant: a quantitative and experimental approach to understanding locomotor mimicry in the jumping spider *Myrmarachne formicaria*. Proceedings of the Royal Society B 284: 1-10.

Sheehan, M. J. 2012. Individual recognition in paper wasps: correlated evolution of sender phenotypes and receiver cognition. PhD Dissertation, The University of Michigan. i-x, 1-172.

Sheehan, M. J. and E. A. Tibbetts. 2011. Specialized face learning is associated with individual recognition in paper wasps. Science 334: 1272-1275.

Sobczak, J. F., A. P. S. Loffredo and J. C. M. S. M. Sobczak. 2012. First record of egg sac predation of the wasp *Tromatobia* sp. Foster, 1869 (Hymenoptera: Ichneumonidae) upon *Araneus omnicolor* (Keyserling, 1893)(Araneae: Araneidae). Revista Iberica de Aracnologia 20: 113-115.

Tibbetts, E. A. 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. Proceedings of the Royal Society of London B 269: 1423-1428.

van Baarlen, P., C. J. Topping and K. D. Sunderland. 1996. Host location by *Gelis festinans*, an eggsac parasitoid of the liniphiid spider *Erigone atra*. Entomologia Experimentalis et Applicata 81: 155-163.

Veijalainen, A., N. Wahlberg, G. R. Broad, T. L. Erwin, J. T. Longino and I. E. Sääksjärvi. 2012. Unprecedented ichneumonid parasitoid wasp diversity in tropical forests. Proceedings of the Royal Society B 279: 4694-4698.

Viet, B. T. 2017. Ichneumonid wasps (Hymenoptera, Ichneumonidae) parasitizee a pupae of the rice insect pests (Lepidoptera) in the Hanoi area. JSM Anatomy & Physiology 2(1): 1008: 1-8.

Wanless, F. R. 1978. On the identity of the spider *Emertonius exasperans* Peckham & Peckham (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 33: 235-238.

Wesołowska, W. and K. Salm. 2002. A new species of *Myrmarachne* from Kenya (Araneae: Salticidae). Genus, Wrocław 13 (3): 409-415.

WSC. 2019. World Spider Catalog. Version 20.0. Natural History Museum Bern, *online at* http://wsc.nmbe.ch, accessed on 27 MAR 2019, doi: 10.24436/2

Yamasaki, T. 2010. Redescription of two Bornean species of the genus *Myrmarachne* (Araneae: Salticidae). Acta Arachnologica 59 (2): 63-66.

Yamasaki, T. 2015. [Studies on taxonomy, biogeography and mimicry of the genus *Myrmarachne* in Southeast Asia]. Acta Arachnologica 64 (1): 49-56.

Yamasaki, T. 2016. Group C (*Myrmarachne*). International Congress of Arachnology (2016) presentation, Colorada (pdf supplied by author).

Yamasaki, T. and A. H. Ahmad. 2013. Taxonomic study of the genus *Myrmarachne* of Borneo. Zootaxa 3710 (6): 501-556.

Yu, D. S. K. 2012. *Goryphus basilaris* Holmgren 1868, *online at* http://www.taxapad.com/local.php?taxonidLC=90184788

Żabka, M. 1985. Systematic and zoogeographic study on the family Salticidae (Araneae) from Viet-Nam. Annales Zoologici, Warszawa 39: 197-485.