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Do jumping spiders (Araneae: Salticidae) draw their own portraits?

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Abstract. Many different insects appear to mimic the appearance of the salticid spiders as viewed from the front. Examples of this mimicry are reviewed with respect to the hypothesis that these are examples of *predator mimicry*, whereby salticid spiders are less likely to attack prey that present images of other salticid spiders.

Key words. *Anastrepha*, Batesian mimicry, Blattodea, *Brenthia*, *Brixia*, *Ceratitis*, *Choreutis*, *Chrysops*, Cixiidae, Derbidae, Fulgoroidea, Glyphipterigidae, *Glyphipterix*, *Goniurella*, *Graphopsocus*, Leptoceridae, metalmark moths, *Mimarachne*, mimicry, *Nectopsyche*, *Olethreutes*, *Phidippus*, *Platensina*, *Plexippus*, predator mimicry, *Procecidochares*, Psocoptera, *Rhagoletis*, *Rhotana*, Rhotanini, *Saltissus*, Stenopsocidae, Tabanidae, Tephritidae, Tortricidae, Trichoptera, *Tritoxa*, *Trupanea*, *Zonosemata*

Many insects display an image that suggests the appearance of a salticid spider as viewed from the front. In some cases this display also includes movement suggestive of the aggressive or agonistic displays of these spiders (e.g., Lim & Li 2004; Hill 2018). Here we review a series of examples that may represent *predator mimicry*, or the mimicry of predators, in this case salticid spiders, by their prey. Our working hypothesis is that, because salticid spiders are less successful at preying on insects that resemble other salticid spiders, they have "drawn" their own portraits on these insects by selectively preying on individuals with less effective mimicry. Salticid spiders may be less successful in preying on these mimics because their predatory responses are interrupted or delayed, or because these images elicit a different kind of reaction. This hypothesis is not new. Rota & Wagner (2006) noted that many different kinds of insects display groups of spots and leg-like patterns that resemble, respectively, the eyes and crouched legs of salticid spiders. They saw this as evidence for advanced visual discrimination by these spiders, a capability that allows them to recognize these patterns and related behavior.

The high resolution of the anterior medial eyes (AME) of salticids is unrivaled with respect to its support for the detailed examination of prey (Eakin & Brandenburger 1971; Williams & McIntyre 1980; Jackson & Blest 1982; Blest & Price 1984; Harland et al. 2012). It is well-known that salticid spiders can interpret two dimensional images, including simple stick images, as either prey or as conspecific spiders (e.g., Clark & Uetz 1990; Dolev & Nelson 2014). Bednarski et al. (2012), in a study of *Phidippus audax*, found that movement but not details of the prey image could elicit an attack. However more recently De Agrò et al. (2017) reported that *P. regius* could learn to associate geometric shapes with an objective, and they also noted that the preference for realistic targets varied considerably between salticid species, often requiring prolonged visual inspection by the spider. Many other observers (e.g., Gardner 1966; Edwards & Jackson 1993) have also found that salticids approach different kinds of prey differently based on characteristics of that prey.

The insects most often described as mimics of the jumping spiders are flies, particularly fruit flies of the family Tephritidae (Figures 1-2).

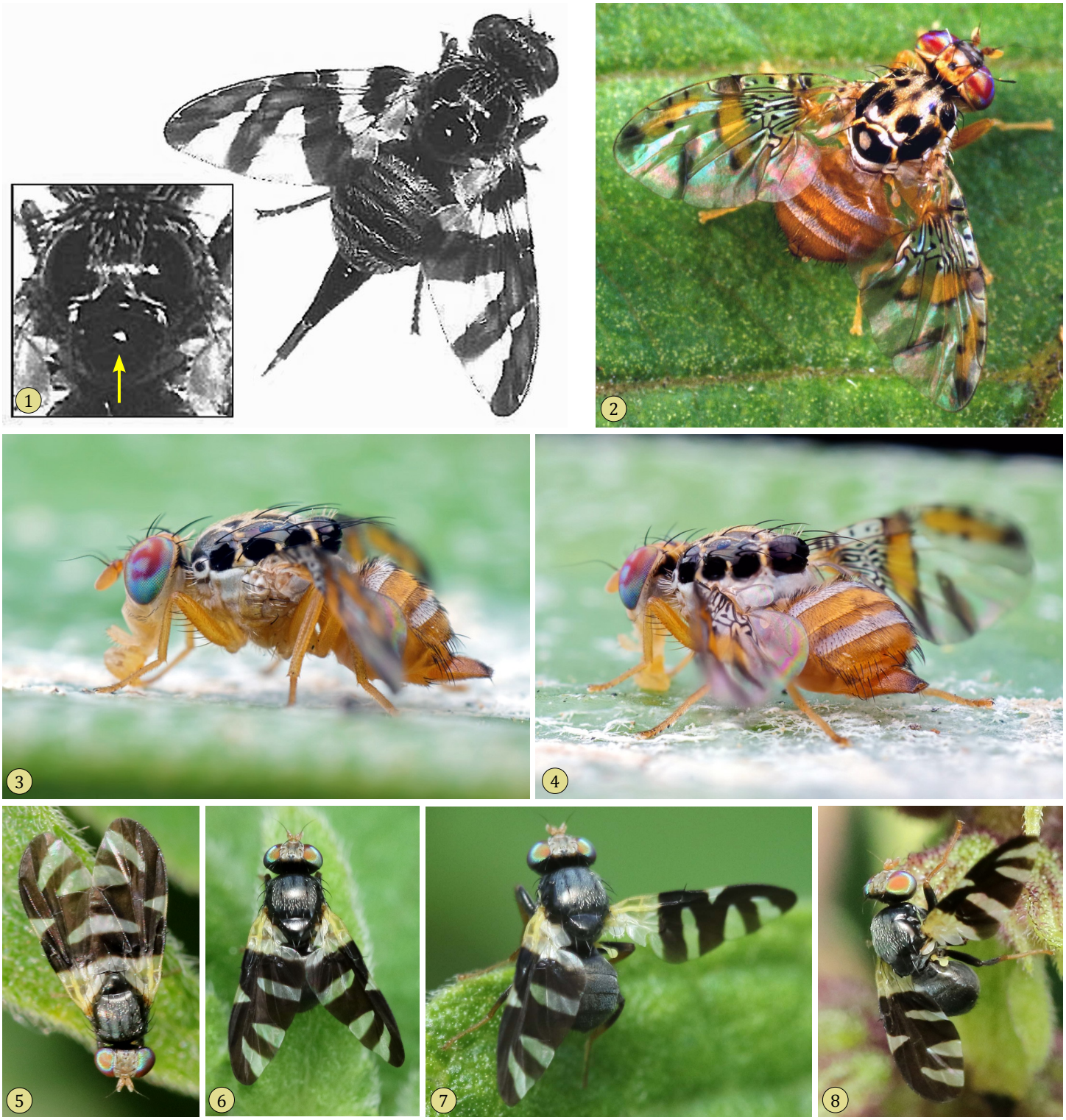

Figure 1. Tephritid flies (Diptera) that may mimic salticid spiders. **1,** *Procecidochares atra* from Ithaca, New York (photo by David E. Hill). When viewed in a rear-oblique direction the middorsal bump on the thorax (inset, arrow) resembles one of the principle eyes (AME) of a salticid. **2,** Mediterranean Fruit Fly, *Ceratitis capitata*. Photo by Scott Bauer, USDA. **3-4,** *Ceratitis alba* from Sorocaba, São Paulo, Brazil. Photos by João P. Burini, 7 NOV 2014. **5-8,** Views of tephritid fly from Karnataka. Photos by Abhijith APC. In many tephritid flies the appearance of 2 or 4 dark "jumping spider eyes" on the thorax may complement bold markings on the wings that resemble the legs of a crouching spider when viewed in certain directions.

Figure 2. Flies (Diptera) that may mimic salticid spiders. **1,** Peacock Fly, *Goniurellia* sp. (Tephritidae), Swaziland. Photo by Kate Braun, used with permission (Braun 2019). **2,** *Goniurellia tridens* (Tephritidae), Dubai. Photo by Peter Roosenschoon, used with permission. **3,** *Trupanea* sp. (Tephritidae) from Ban Nang Lae, Chang Rai, Thailand. This fly rested on a leaf and extended/rotated one wing at a time as it was approached. Photo and information by Ian Jacobs, 22 MAR 2013, used under a Creative Commons Attribution-Noncommercial 2.0 Generic (CC BY-NC 2.0) license. 4**-5,** *Platensina* sp. (Tephritidae) dancing on a leaf in Karnataka. Photo by Abhijith APC, 8 OCT 2018. **6-7,** Picture-winged Fly (Ulidiidae: *Tritoxa incurva*), Greenville County, South Carolina. Scale bar 1.0 mm. Photos by David E. Hill. **8,** *Chrysops* sp. (Tabanidae) in Karnataka. Photo by Abhijith APC, 15 JUL 2018.

Many flies, including the Tephritidae (fruit flies) and Ulidiidae (picture-winged flies) in particular, have markings on their wings that resemble the legs of a crouching spiders, and they often move their wings in a manner that exaggerates this effect. Movement of the wings (including alternating extension and rotation) observed when these flies encounter or display in front of salticid spiders appears to be part of their normal repertoire for intraspecific aggression or agonistic behavior (Goeden et al. 1994; Hasson 1995; Briceño et al. 1999; Benelli 2013, 2015; Aguilar-Argüello et al. 2015a, 2015b). The role of this display in intraspecific communication does not, however, preclude an additional role with respect to predator mimicry.

One of the authors (DEH) first observed the interactions of the tephritid *Procecidochares atra* with jumping spiders in Ithaca, New York in 1978 (Figure 1:1). *P. atra* is a common and widely distributed species in eastern North America, with larvae that produce stem galls in goldenrod (*Solidago*) (Philips & Smith 1998). Like the well-known Mediterranean Fruit Fly (*Ceratitis capitata*; Figure 1:2-4), a shiny black middorsal hump aligns with other black areas of the thorax when viewed obliquely from either side and to the rear, to produce the image of a set of anterior eyes of a salticid spider. We take this combination of a crouching spider leg pattern with a salticid anterior eye pattern to represent strong evidence that salticid mimicry is at work here. We see essentially the same pattern in many different insects.

Later a colleague in Ithaca (Eisner 1985) described a similar display by the tephritid *Zonosemata vittigera*, but considered this movement to mimic the evasive behavior of jumping spiders as an example of Batesian mimicry, thought to cause avoidance by predators that would tend to avoid spiders that were either poisonous or difficult to capture. It may be, however, that the predators most affected by this display, to avoid these flies, are actually the salticid spiders that are mimicked by them. The latter represents the more favored hypothesis in recent studies of the phenomenon. Greene et al. (1987), motivated by Eisner's photographs, reported that the agonistic display of a number of different salticids (*Colonus*, *Eris*, *Metaphidippus*, *Phidippus*, *Sassacus*) was elicited by the display of *Z. vittigera*. According to Greene et al. these spiders waved the leg-like pattern on their wings to mimic agonistic displays by salticid spiders, thereby reducing the chance that a salticid would prey on it. They also suggested that this represented specialized mimicry of salticids in particular since this display had no deterrent effect on predation by the oxyopid spider *Oxyopes* sp., the assassin bug *Pselliopus*, the mantid *Mantis*, or the race-runner lizard *Cnemidophorus*. Sivinski et al. (2004) restated the hypothesis that the display of these flies mimics the agonistic display of salticids.

In their study of the Mexican Fruit Fly *Anastrepha ludens*, Rao & Díaz-Fleischer (2012) did not measure a significant deterrent effect of the wing bands of these flies on predation by the large jumping spiders *Paraphidippus aurantius* and *Phidippus bidentatus*. In a study of the Caribbean Fruit Fly *A. suspensa* Sivinski & Pereira (2005) likewise could not measure any impact of these wing patterns on mating success. However a significant deterrent effect on salticid predation, associated with wing pattern in controlled laboratory trials, was reported by Mather & Roitberg (1987) in studies of the Snowberry Fly (*Rhagoletic zephyria*), Whitman et al. (1988) in studies of the tephritid *Zonosemata vittigera* and Rao et al. (2014) in studies of *A. ludens*. Whitman et al. (1988) found that *Z. vittigera* with intact wing markings elicited courtship or agonistic display by salticids, but this effect was not observed for *Z. vittigera* with obscured markings. In a study of the Mediterranean Fruit Fly (*Ceratitis capitata*) Hasson (1995) found that display by these flies had significantly more deterrent impact on younger, rather than older, jumping spiders (mostly *Plexippus paykulli*).

Some tephritid flies in the genera *Goniurellia* and *Trupanea* (Figure 2:1-3) have an unusual pattern on each wing that in some species resembles a small salticid spider, but might also mimic a small insect. Given the position of these images on the distal part of the wing these may play a role in the misdirection of an attacking predator. Many other flies (Figure 2:4-5, 8) also display patterned wings that might also distract predators, but their resemblance to salticid spiders is not obvious.

Picture-winged flies of the family Ulidiidae, closely related to tephritids (Kameneva & Korneyev 2010), represent another world-wide family with many representatives bearing prominent wing bands that resemble spider legs. *Tritoxa incurva* (Figure 2:6-7) is a common ulidiid in the eastern United States, seldom flying but frequently walking about on the upper surfaces of herbaceous plants. Larval *T. incurva* feed on bulbs of the Wild Garlic *Allium canadense* (Allen & Foote 1975). These flies engage in an almost constant display, presumably a courtship display, involving wing elevation and waving. One of the authors (DEH) has observed a series of interactions between *T. incurva* and jumping spiders of the genus *Phidippus* in the laboratory. In these interactions *T. incurva* continuously oriented toward and actively displayed in the direction of these spiders and they were often, but not always, avoided as prey. In a natural setting even a brief delay in the attack of a salticid could allow these flies to escape.

Salticid spiders may also be mimicked by moths with either a symmetrical pattern on both wings (Figure 3), or an even more convincing image visible when viewed on either side (Figures 4, 5).

Figure 3. Metalmark moths (Choreutidae). **1-2,** Two views of *Choreutis* sp. resting on a leaf in Karnataka. This moth lifts its wings but remains motionless during the day. Although the resemblance to a spider is not definitive, the image that is presented may be confusing to a visual predator. Photos by Abhijith APC, 27 NOV 2018. **3,** *Choreutis orthogona* from Karnataka. Photo by Abhijith APC, 5 SEP 2016. 4**-5,** Front (4) and rear (5) views of an actively displaying choreutid moth on a leaf in Karnataka. Photos by Pavitra Kumar, 10 SEP 2018, used with permission.

Figure 4. Tortricid moths of the genus *Olethreutes*. **1-2,** Arched Marble *Olethreutes arcuella* from Dolná Súča, Slovakia, 16 MAY 2015 **3-5,** *O. arcuella* from Melčice-Lieskové, Slovakia, 16 MAY 2010. Photos 1-5 by František Šaržík, used under a Creative Commons Attribution 3.0 Unported (CC BY 3.0) license. **6,** Silver-spotted *Olethreutes*, *O.* cf. *astrologana* from Rock Creek Park in Washington, D. C. Photo by Katja Schultz, used under a Creative Commons Attribution 2.0 Generic (CC BY 2.0) license. This moth has bright, reflective spots that might confuse a salticid, but lacks the arrangement of salticid-like features (row of eyes, legs) seen in *O. arcuella*.

Figure 5. Moths that appear to mimic salticid spiders when viewed from the side. **1-2,** Two views of an iridescent Sedge Moth *Glyphipterix* sp. (Glyphipterigidae) with a remarkable salticid image on either side, photographed by João Burini in the Southeast Atlantic Forest of Tapirai, São Paulo, Brazil, 10 JAN 2016. This species has also been photographed in Ecuador (Kay 2012), and closely related *Glyphipterix* species including *G. circumscriptella* (Chambers 1881) can also be found in North America (Heppner 1985). A very similar form that might represent the same species has also be found in Wayanad, North Kerala, India (Shyamal 2014). **3,** *Aeolocosma cycloxantha* (Lepidoptera: Oecophoridae) on *Boronia ovata*, at Kalamunda near Perth in Western Australia. Photo by Jean and Fred Hort, 12 NOV 2016, used under a Creative Commons Attribution 2.0 Generic (CC BY 2.0) license. **4,** Tortricid moth from Singapore. Photo by Melvyn Yeo, 27 NOV 2015, used with permission.

Rota & Wagner (2006) considered some metalmark moths of the genus *Brenthia* to be salticid mimics, and found that these had a significantly higher survival rate after encounters with salticids (*Phiale formosa*) than did moths of similar size that did not display in the same manner. They found that *Brenthia* were attacked as often as the other moths, but appeared to survive by misdirecting their predator. Displaying *Brethia* (see Figure 3:4-5) elicited "territorial" displays that included the waving of elevated legs I by these salticids. Rota & Wagner also listed a number of other moths that appeared to mimic jumping spiders, to include diurnal tortricids (Figures 4, 5:4), glyphipterigids (Figure 5:1-2), and oecophorids (Figure 5:3), all of which include a number of representatives that bear a more definitive and remarkably convergent image of a salticid face and legs as viewed from the front on either side.

In a subsequent study Wang et al. (2017), based on staged encounters between moths and several different salticids (*Hasarius*, *Menemerus*, *Plexippus*, *Ptocasius*), observed significantly less predation on *Brenthia coronigera* that included both spider-like visual imagery and movement in their display, and more predation on *Choreutis hyligenes* of similar size that lacked the visual imagery but otherwise moved in a similar manner.

Many caddisflies of the genus *Nectopsyche* (Trichoptera: Leptoceridae) resemble tortricid moths (Figure 4:4) and also have patterns on each forewing that resemble the face (including anterior eye row) and legs of salticids as viewed from the front (Figure 6; Holzenthal 1995, pp. 79-80, figs. 14-22).

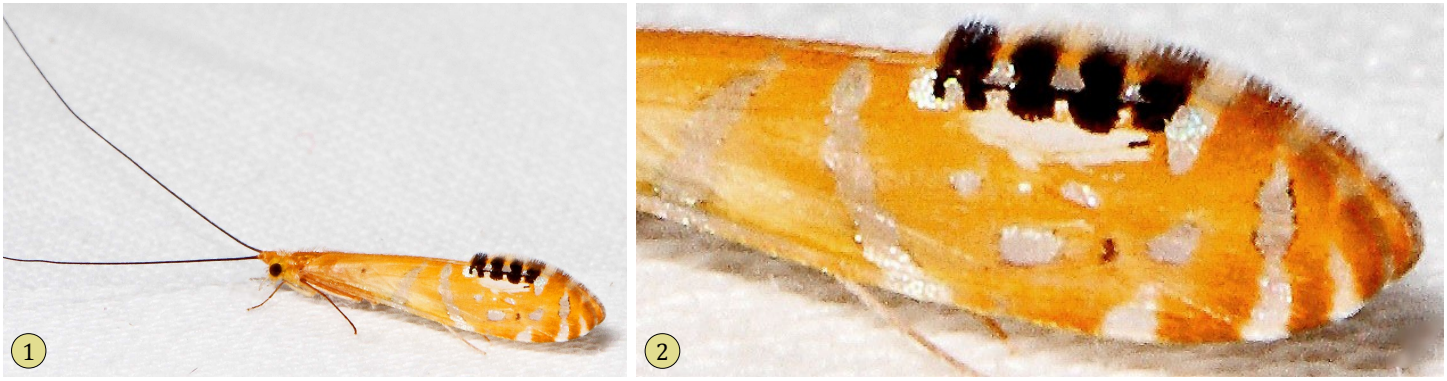

Figure 6. *Nectopsyche* sp. from Caves Branch Jungle Lodge, Belmopan, Belize. Photos by Judy Gallagher, 22 JAN 2013, used under Creative Commons Attribution 2.0 Generic (CC BY 2.0) license. Many related leptocerid Tricoptera have similar patterns that appear to mimic a salticid spider as viewed from the front.

The barklice (Psocodea: Psocoptera), a polyphyletic group of about 5500 species related to the Hemiptera and Thysanura (Yoshizawa 2005), also includes a number of species that resemble salticid spiders when viewed from the side (Figure 7). One recently photographed species from Singapore (Figure 7:1-2), has white scales that resemble the reflection of light from salticid eyes. This species is also remarkably similar to some quite unrelated neotropical Sedge Moths of the genus *Glyphipterix* (Figure 5:1-2). This similarity extends to the elevation of the "salticid anterior eye row" above each forewing, and the transversely striped pattern of scales over the "chelicerae." *Graphopsocus cruciatus* (Stenopsocidae; Figure 7:3-5) has boldly striped wings that resemble a crouching salticid, but a less-distinct row of "salticid" eyes that are not elevated above the wing margin. Nonetheless the resemblance of *G. cruciatus* to a salticid is unmistakable. *G. cruciatus* is widely distributed in the Americas and Afroeurasia, and the genus *Graphopsocus* is particularly diverse in China and southeast Asia (Lienhard & Smithers 2002; Liang et al. 2013).

Similar patterns that include detailed representation of "salticid eyes, legs and chelicerae" on the side of each wing can be found in a number of cixiid planthoppers (Hemiptera: Fulguroidea: Cixiidae; Figure 8:1-5). Floren & Otto (2001) described a similar pattern on each wing of a 6-7 mm derbid planthopper (Hemiptera: Fulguroidea: Derbidae), and attributed the remarkable accuracy of this pattern to the "defense mimicry" of jumping spiders by these insects. Small derbid planthoppers of the genus *Rhotana* (Derbidae: Rhotanini) from Australia and the Orient often have elaborate patterns on their wings (Zelazny 1981). In some species these resemble salticids when viewed from either side (Figure 9:1). Other *Rhotana* species raise and extend their wings to reveal a very realistic image of a salticid across all four wings (Figure 9:2-3). In addition to the black "anterior eye row and crouching spider legs," this display may include an accurate image of clypeal scales and chelicerae, and in some cases closely resembles the female salticid *Telamonia dimidiata* (Figure 9:4), found in the same localities and microhabitat.

Figure 7. Barklice (Psocoptera). **1,** Barklouse from Singapore. Photo by David Ball, used with permission. **2,** A second barklouse of the species shown in (1), also photographed in Singapore. Photo by Melvyn Yeo, used with permission. **3-5,** *Graphopsocus cruciatus*, Rock Creek Park, Washington D.C., and Meadowside Nature Center, Rockville, Maryland. Photos by Katja Schultz, used under a Creative Commons Attribution 2.0 Generic (CC BY 2.0) license. This species is widely distributed from the Americas to Afroeurasia. **6-7,** Two views of a boldly-marked barklouse (Pscocodea: Psocidae: *Clematoscenea* sp.) from Karnataka. Photos by Abhijith APC, 9 JAN 2019. From the front (6) a row of four black spots is visible at the rear of the thorax. Although the markings of this barklouse might confuse a salticid predator, they have little resemblance to a salticid.

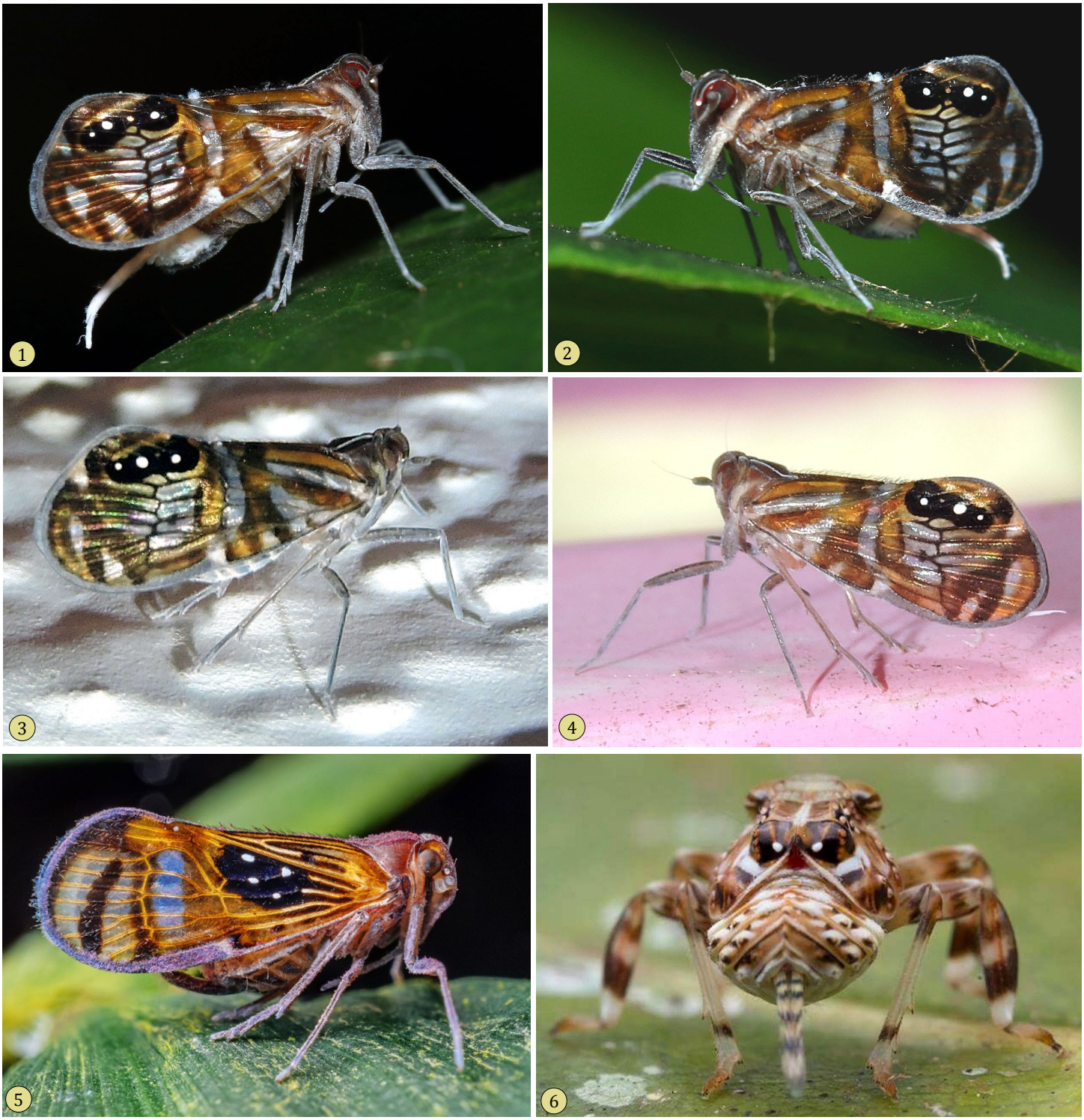

Figure 8. Fulgoroid Hemiptera that appear to mimic salticid spiders. **1-4,** *Brixia albomaculata* (Cixiidae) from Puttur, Karnataka. Photos by Abhijith APC and Sanath Ramesh. **5,** Cixiid planthopper from Tapiraí, São Paulo Brazil. Photo by João P. Burini. **6,** Rear view of fulgoroid nymph from the Philippines. Photo by Aloke Sahu.

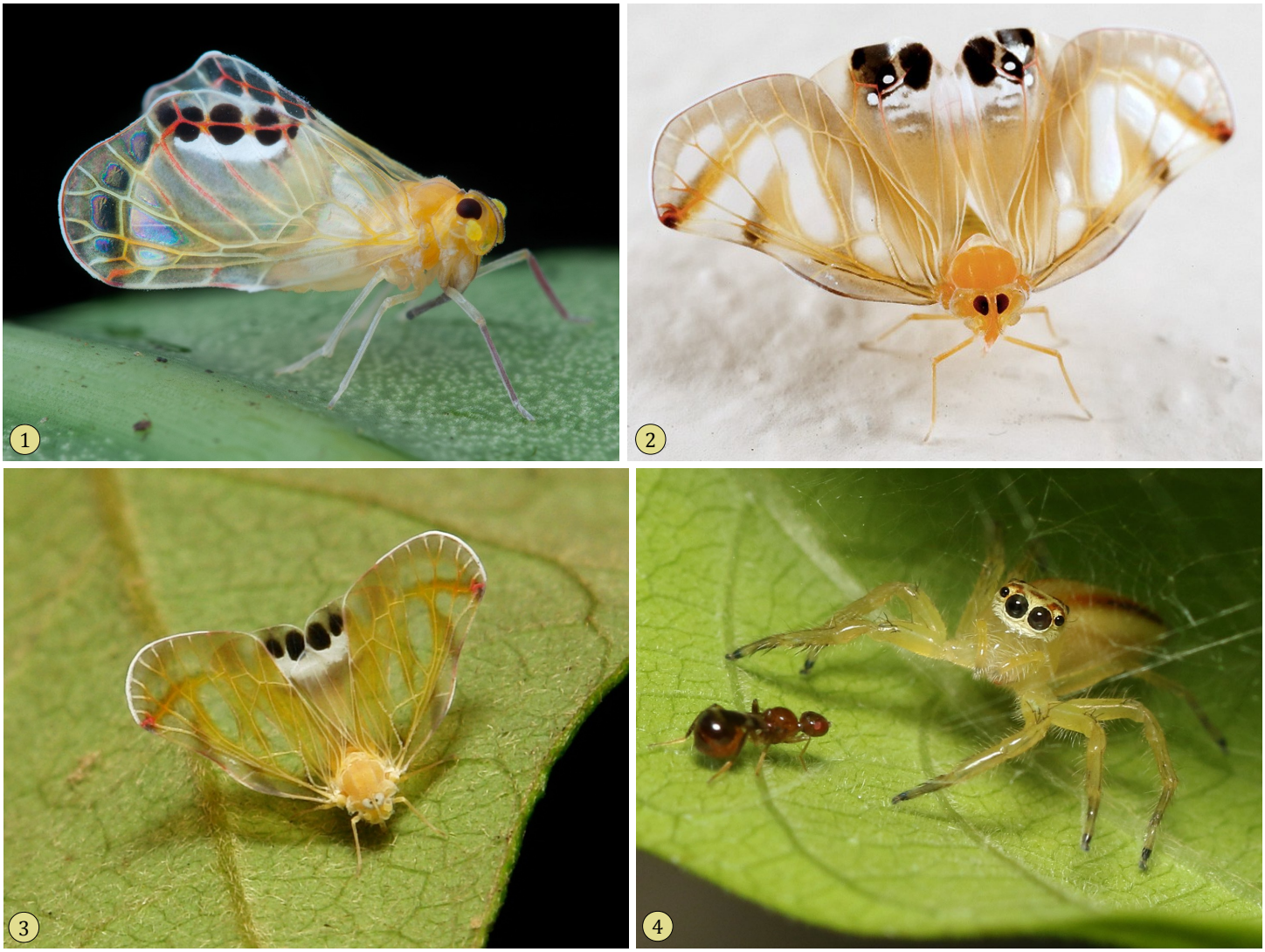

Figure 9. Derbid (Homoptera: Fulgoroidea: Derbidae: Otiocerinae: Rhotanini: *Rhotana*) planthoppers that appear to mimic salticid spiders. **1,** *Rhotana* sp. that appears to mimic a salticid when viewed from either side, Singapore. Photo by Melvyn Yeo, used with permission. **2,** A different *Rhotana* sp. that extends and rears its wings to look like a salticid from the front, from the Danum Valley, Sabah, Malaysia. Photographed on a wall at night by Marcus Ng, 24 JUL 2013, used with permission. **3,** A third *Rhotana* sp. from Simao, Yunnan, China. Photo by John Horstman/itchydogimages, used with permission. When this photo was posted it was compared to *Telamonia dimidiata*. **4,** Adult female *Telamonia dimidiata* from Karnataka for comparison. Photo by Abhijith APC, 1 OCT 2018. When this photo was taken a sepsid fly (left, center) was entering the nest of this spider. *T. dimidiata* is widely distributed throughout the range of these derbid planthoppers in south and southeast Asia.

Shcherbakov (2007) described a new family and two new genera of pre-cixioid planthoppers, including new species (†*Mimarachne mikhailovi* and †*Saltissus eskovi*) with dark "eye" spots and bands on the forewings (tegmen) that suggested that these were spider mimics. These fossils are from the Early Cretaceous of Baissa, Transbalaika (ca. 130-140Ma; Vršanský et al. 2002). Shcherbakov suggested that spider mimicry might date back to 200Ma. Presently we know nothing of Cretaceous salticids (Hill & Richman 2009; Penney 2010), but the possibility remains that pre-salticid spiders with acute vision occupied a similar niche at a much earlier time.

In addition to insects that carry what appears to be a two-dimensional drawing of a salticid, there are a number of insects that may deter salticid predators by appearing to be salticids when viewed from the rear (Figures 8:6, 10). Zolnerowich (1992) also described a fulgoroid nymph from Mexico with four shiny areas that look like anterior salticid eyes when viewed from the rear.

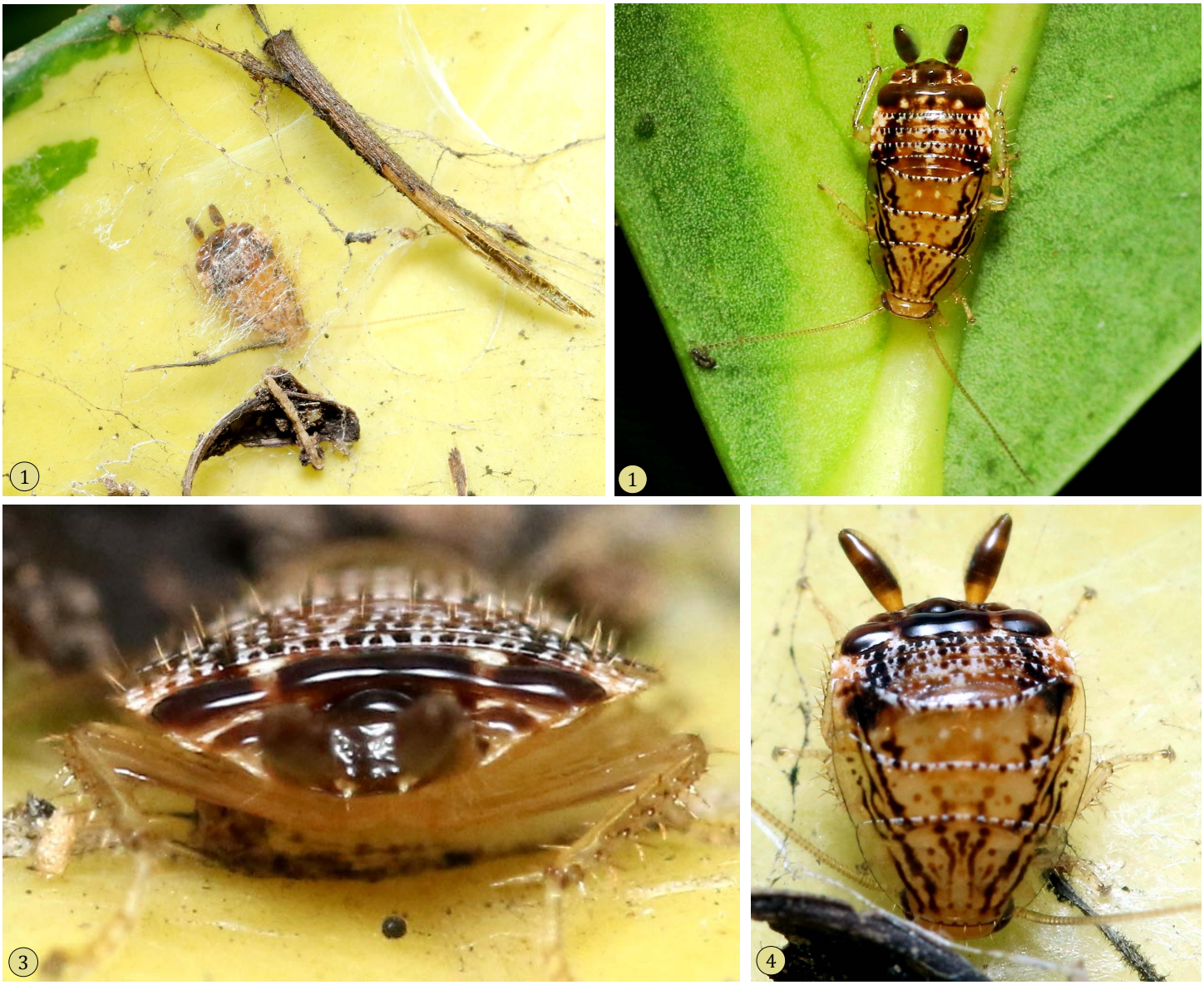

Figure 10. Cockroach nymph (Blattodea) from Karnataka. Photos (1-4) by Abhijith APC. **1,** Two of these cockroaches were observed inside of silken retreats like this one (25 NOV 2018). **2,** Dorsal view of cockroach outside of retreat. **3,** Rear view showing four dark, reflective areas acoss the rear of the abdomen. When viewed obliquely from above (4) these may resemble the anterior eye row of a salticid. **4,** The cerci of this cockroach (at top) may also resemble the chelicerae of a male *Myrmarachne*, particularly when it is resting in a silk shelter (1).

The evidence that many of these insects are mimicking the salticids that prey on them can be summarized as follows:

[1] Salticids are active and often abundant visual predators that live in the same microhabitats, relying on their acute vision to evaluate potential prey and to differentiate prey from conspecifics or other creatures to be avoided.

[2] Unrelated insects from many different groups show similar patterns that appear to mimic the anterior eyes and crouched legs of salticid spiders. In some cases (e.g., derbids of the genus *Rhotana*) this mimicry is quite realistic.

[3] Experimental studies conducted in the laboratory have shown that the appearance and display of these insects (hypothetical *predator mimicry*) can reduce predation by salticids, and that this effect is not extended to a number of other predators that they may encounter.

Demonstrations that the appearance or behavior of an insect can delay or prevent a salticid attack can provide *support* to the hypothesis of predator selection, but do not by themselves demonstrate that this selection has been a significant factor in the evolution of these insects. We are not presently aware of non-salticid arthropods, or other relevant predators, for which images of salticid spiders elicit avoidance or misdirection. Indeed these images might attract a number of predators to an insect that would otherwise be avoided. More studies are needed to examine the interaction of salticids with these insects and the importance of salticid predation with respect to populations of the insect species that appear to mimic them.

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