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Two new Australian peacock spiders that display inflated and extended spinnerets (Araneae: Salticidae: Euophryinae: *Maratus* Karsch 1878)

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Abstract. Two new, closely related species within the Australian genus *Maratus* Karsch 1878 are described, *M. calcitrans* and *M. digitatus*. Males of both species inflate the posterior opisthosoma and extend their four posterior spinnerets as they display to females. Although closely related, only male *M. digitatus* have prominent lateral opisthosomal flaps. The display behaviour and known distribution of these species is compared to that of a third, related species of *Maratus* (*Maratus* species B) that has not yet been named. The three species represent a distinct clade (*calcitrans* group) within the genus *Maratus*. Evolutionary convergence of *Maratus* with North American salticids of the genus *Habronattus* is also discussed.

Introduction

Previously we published photographs of a species of *Maratus* (*Maratus* species B) that had been recently discovered by one of us (J. Otto) near Sydney, Australia (Hill 2009, Otto & Hill 2011). This spider is very unusual with respect to the assymetry of male display. When displaying to a female, a male *Maratus* species B rotates its elevated opisthosoma to each side in turn, but extends only the lateral flaps of the opposite (contralateral) side of the opisthosoma.

Here we describe two closely related species that are similar to *Maratus* species B, but even more closely related to each other. Males of these species have the ability to inflate and to extend the posterior segments of their opisthosoma, including spinnerets, toward the rear. Although at least one other species of *Maratus* (*M. spicatus* Otto & Hill 2012b) is known to include extended spinnerets in its courtship display, the degree of anatomical specialization and the prominent role of the spinnerets in the two species that we describe here is unique. The spinnerets of unrelated tropical Afro-Asian salticids of the genus *Orsima* Simon 1901 (Heliophaninae) are elongated and are thought to mimic insect mouthparts and antennae (Reiskind 1976, Żabka 1992), but these spiders are not known to inflate their posterior opisthosoma as part of their display.

Maratus calcitrans, new species

Type specimens. All specimens were collected in the Black Mountain Nature Park, Canberra, ACT (35° 15' 56.7" S, 149° 05' 43.1" E). The male holotype, one male paratype and one female paratype were found on 13 OCT (S. Harris coll.), and a further 11 male and 5 female paratypes were found on 20 OCT (S. Harris & J. Otto coll.). All specimens will be deposited in the Australian Museum, Sydney.

Etymology. The species name (*calcitrans*) is derived from the Latin word *calcitrare* ('to kick'), referring to the very rapid movement of legs III during display by males of this species.

Diagnosis. The distinctive figure of the dorsal opisthosoma readily identifies males of this species. Males resemble *M. digitatus* in the presence of inflatable spinnerets, but do not have lateral opisthosomal flaps.

Description of male. Body length including retracted spinnerets 4.5-5.6 mm (n=12). Carapace black and mostly glabrous, eye region with four longitudinal brown to orange bands, one behind each anterior eye, separated by grey bands, narrowly separated at the median (Figures 1-2). Carapace with thick white marginal band, a wider lateral band of white scales and setae extending to the rear beneath each PLE, and a median band of white scales behind the eye region. PME slightly closer to PLE than to ALE.

Figure 1. Holotype (1-6) and paratype (7-9) male *Maratus calcitrans*. **1,** Spinnerets retracted. **2,** Opisthosoma slightly elevated and posterior opisthosoma including spinnerets extended. **3,** Posterior partly extended. **4,** Displaying to female by waving extended, ipsilateral (relative to rotation of opisthosoma) leg III behind the extended spinnerets. **5,** Lateral view with retracted spinnerets. **6,** Posterior view of displaying male. **7,** Dorsal view of expanded opisthosoma, showing dark black rear segments and spinnerets, and central figure. **8,** Lateral view with partly elevated opisthosoma, showing edge of opisthosomal plate and lack of lateral flaps. **9,** Face view, showing long pedipalps covered with white setae.

Figure 2. Nine different paratype male *Maratus calcitrans*, all with retracted spinnerets. The central figure of the dorsal opisthosoma is fairly consistent in shape, comprised of either orange to red-orange (7), or tan to orange (8) pigmented scales on a background of iridescent blue-green scales. The colour of the posterior part of this figure, just in front of the black spinnerets, is most intense or saturated.

Dorsal plate of opisthosoma without lateral flaps, with a distinctive central figure comprised of tan to orange, or orange to bright red-orange, pigmented scales on a background of iridescent blue-green scales. This figure includes 4-5 fused transverse bands, 3-4 toward the front and one of more intense colour near the rear. At each anterior corner of the dorsal plate is a tuft of longer white setae. The underside of the opisthosoma is covered with uniform white to off-white setae. Spinnerets and posterior segments bearing the spinnerets black and mostly glabrous. The posterior segments are only visible when they are inflated during display (Figure 1:7). There is a variable fringe of black and white setae on the spinnerets,

less prominent than in *M. digitatus*. At each side of the spinnerets is a tuft of dark setae, visible from above even when the spinnerets are retracted.

Legs I and II shorter than III and IV, legs III by far the longest. Legs almost uniformly dark with dense cover of white scales and long white setae, with longer fringes dorsally on femora I-III, and ventrally beneath all tibiae. Metatarsi III dark with black setae, contrasting with the white setae that cover tarsi III.

Pedipalps relatively long, covered with uniform long white setae. Underside of pedipalp with a medial sclerotized area (Figure 3:4), and a distinctive thick cusp at beginning of the outer ring of the embolus (Figure 3:5). The serrated distal margin of the RTA is like that of other euophryines.

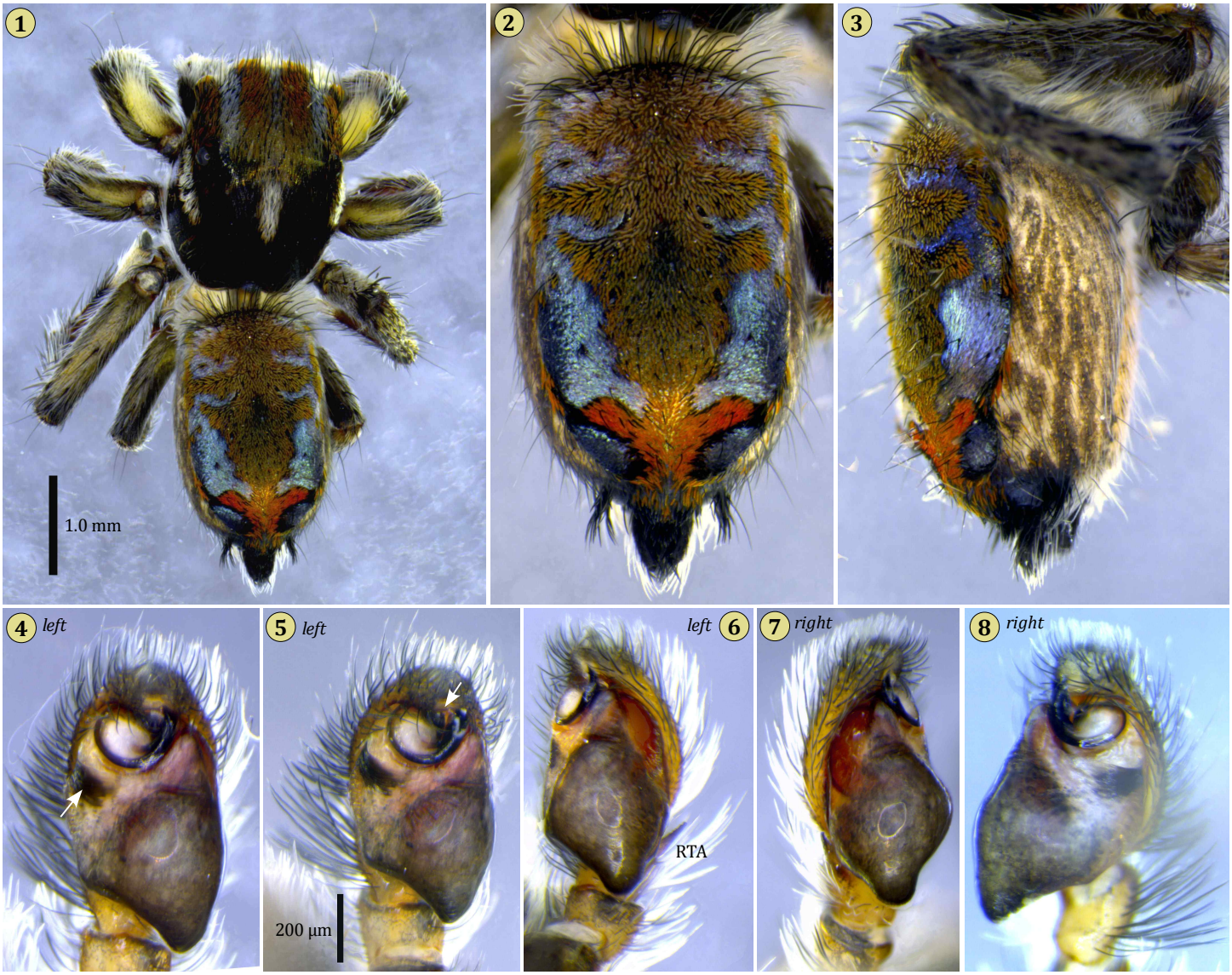

Figure 3. Paratype male (♂#2) *Maratus calcitrans*. **1,** Dorsal view of specimen, with spinnerets and posterior opisthosoma retracted. **2,** Detail of dorsal opisthosoma. **3,** Lateral view of opisthosoma, showing edge of dorsal opisthosomal plate with no lateral flap. **4-6,** Ventral (4) to ventro-lateral (6) views of left pedipalp. There is a dark, medial sclerotized area proximal to the embolus (4, arrow). The outer (superior) ring of the embolus begins with a thick cusp (5, arrow), and fuses with the inner ring to form a thick, pointed apex laterally. As is the case with many related euophryines where this has been examined, the distal margin of the RTA (6) is rough or serrated. **7-8,** Lateral (7) to ventral (8) views of right pedipalp.

Description of female. Body length 5.0-6.1 mm (n=6). As with other *Maratus*, females have cryptic colouration, without the bold patterns that facilitate identification of males (Figure 4). The integument of the female is lighter than that of the male, the sides of the carapace glabrous and translucent, with no

marginal band. The carapace, opisthosoma, and legs are covered mostly with off-white scales or setae, with thicker scale cover along the dorso-lateral margins of the carapace, and around the PLE, where scattered orange-brown scales may be present. PME slightly but distinctly closer to PLE than to AME. Legs I and II shorter and about the same length, legs III longest but otherwise not remarkable.

Figure 4. Six different adult female *Maratus calcitrans*. In some individuals (1-3, ♀#1) there is no distinct opisthosomal pattern. In others (8-12, ♀#4-6) a dark lateral band separates a darker dorsal opisthosoma from lighter scales of the venter.

Fossa of epigynum circular and about 4/5 the diameter of the large, semi-ovate posterior spermatheca. Sclerotized structures, including ducts and smaller anterior spermathecae, are readily visible through clear, translucent cuticle (Figure 5).

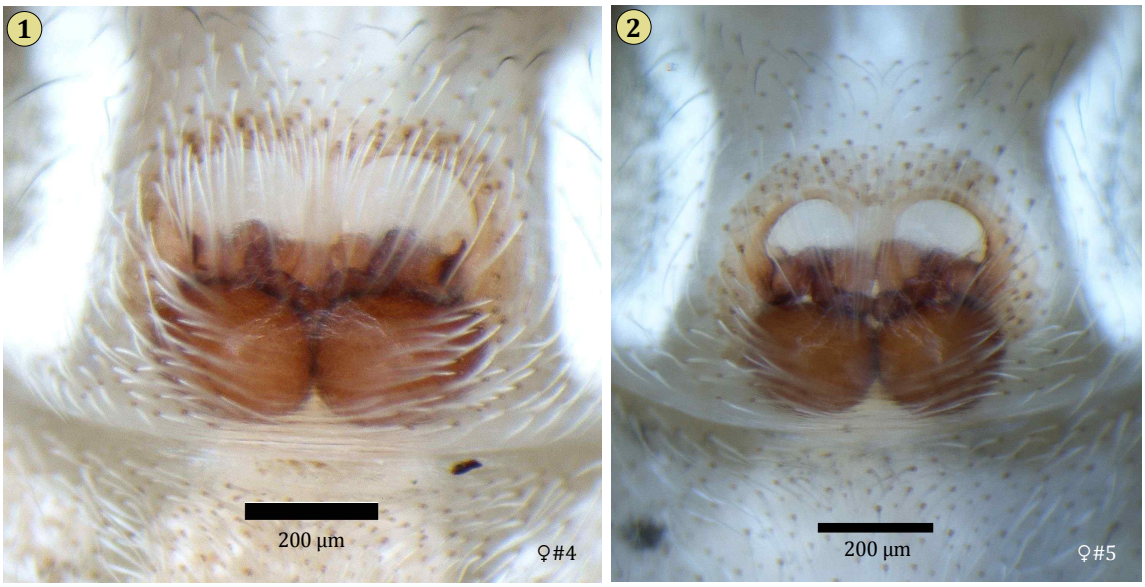

Figure 5. Ventral view of the epigyna of two different female *Maratus calcitrans*. Internal structures are relatively easy to observe through the clear cuticle.

Courtship display and mating. Examples of the courtship display of male *Maratus calcitrans* are shown in Figures 6-10. This display includes elevation and rotation of the opisthosoma to one side and then the other, with fully inflated and extended spinnerets. When turned to one side, the ipsilateral leg III is elevated and extended (usually behind the opisthosoma), lowered, then suddenly kicked back up to its original elevated position. This pattern is repeated at about 2 cycles/s. Each time that the ipsilateral leg III is kicked back to its elevated position, the contralateral leg III is rapidly extended and then flexed at the femuro-patellar joint, returning to its original flexed position by the the time that the ipsilateral leg III is fully extended. This movement of the contralateral leg III is so fast that it cannot be seen at normal speed and requires slow motion playback to detect it. Even then the entire cycle of extension and flexion appears only as a faint blur within a single frame (1/60 s exposure) of a 50 FPS video clip. Thus we have not been able to determine the actual speed of the moving leg. We also have not recorded any audio components that must be associated with this rapid oscillatory movement. Display also included rapid stepping forward and to the side as the male displayed alternately to the left and to the right.

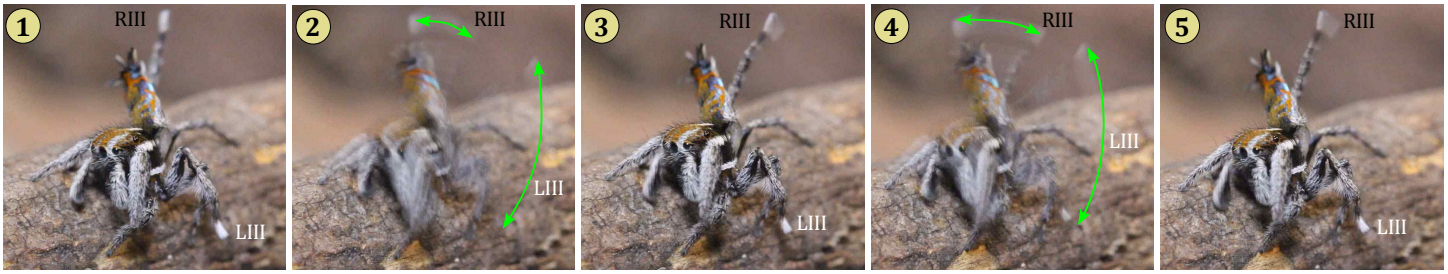

Figure 6. Sequential (not consecutive) frames from a 50 FPS (1/60 s exposure) video clip of display by a male *Maratus calcitrans*, from an antero-lateral perspective. Frames are separated by about 0.25s, and each cycle (1-3, 3-5) took about 0.5s. **1,** At the start of this sequence the ipsilateral leg RIII was extended behind the elevated opisthosoma. The contralateral leg LIII was slightly elevated and flexed at the femuro-patellar joint. **2,** In this blurred frame the spider rapidly kicked contralateral LIII, returning it to its original flexed position. A faint blur at the end of the arc indicates the fully extended position of this leg. A second arc indicates the lesser amplitude of the simultaneous kick of the ipsilateral leg III (RIII). **3,** Blurring of the ipsilateral leg III (RIII) in this frame indicates its waving movement as LIII was held in position. **4,** Repeat of the fast kicking movement shown in (2). **5,** Repeat of the wave of the extended ipsilateral leg III shown in (3).

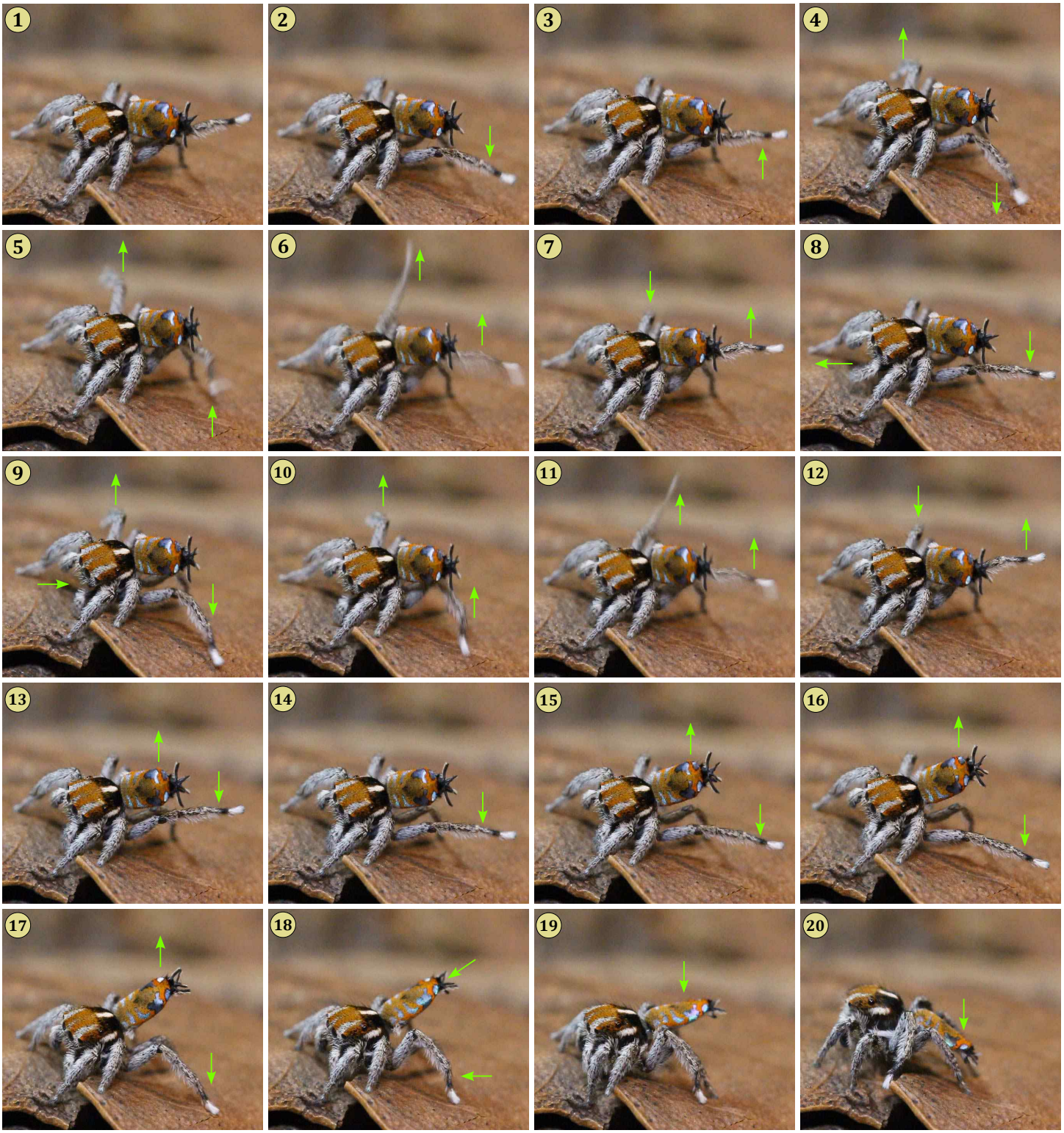

Figure 7. Sequential (not consecutive) frames from a 50 FPS (1/60 s exposure) video clip of display by a male *Maratus calcitrans*, from a dorso-lateral perspective. This entire sequence took place in about 4s. Each 'wave and kick' cycle (3-7, 7-12) lasted about 0.5s. Arrows indicate the direction of movement of appendages or body parts that moved relative to their position in the preceding frame. **1,** Start with ipsilateral leg III behind elevated opisthosoma. **2-3,** Ipsilateral leg III waved down and up. **4-5,** Legs III moved relatively slowly in a partly extended position. **6,** Fast kick of legs III. **7-8,** Ipsilateral leg III waved up and down. In (8) pedipalps were extended to the front. **9-10,** Slower movement of partly extended legs III. **11,** Fast kick of legs III, as in frame (6). **12-16,** Wave of ipsilateral leg III, accompanied by side to side rotation of the opisthosoma. **17-20,** Ipsilateral leg III flexed and returned to contact with the surface as opisthosoma was lowered. Note that the black posterior opisthosoma and spinnerets were held in a fairly rigid, fully extended position during this display (1-16). During the 'fast kick' portion of each cycle (6, 11), the ipsilateral leg III was extended as the contralateral leg III was raised and extended and then immediately lowered and flexed at the femuro-patellar joint.

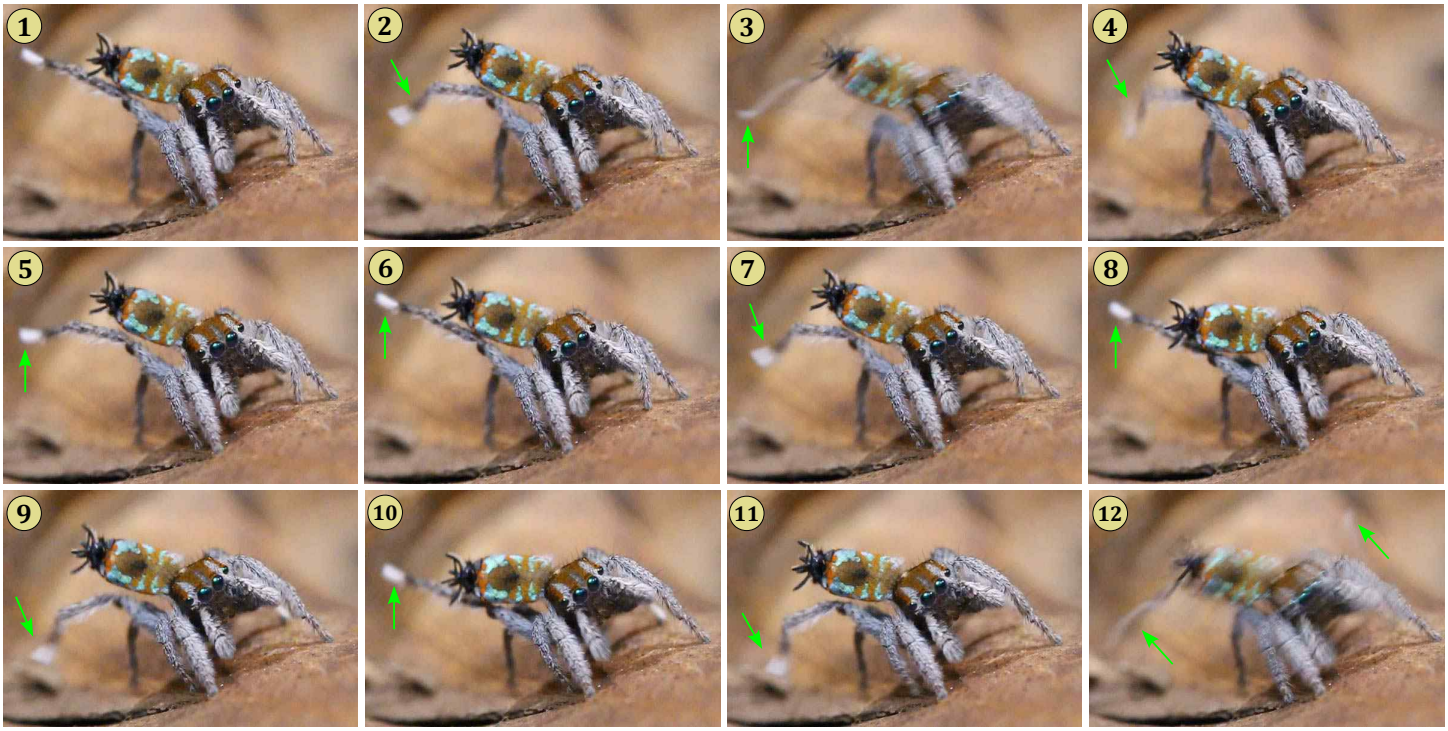

Figure 8. Sequential frames (~0.25s interval) from a 50 FPS video clip of display by a male *Maratus calcitrans*, from a frontal perspective representing the view of a watching female. **1,** Start with extended ipsilateral leg III. **2,** Flexion of ipsilateral leg III. **3,** Rapid kicking movement of ipsilateral leg III. **4-11,** Slower waving movement of ipsilateral leg III as it was alternately extended and then flexed. **12,** Very fast simultaneous kick of both legs III, accompanied by much vibration.

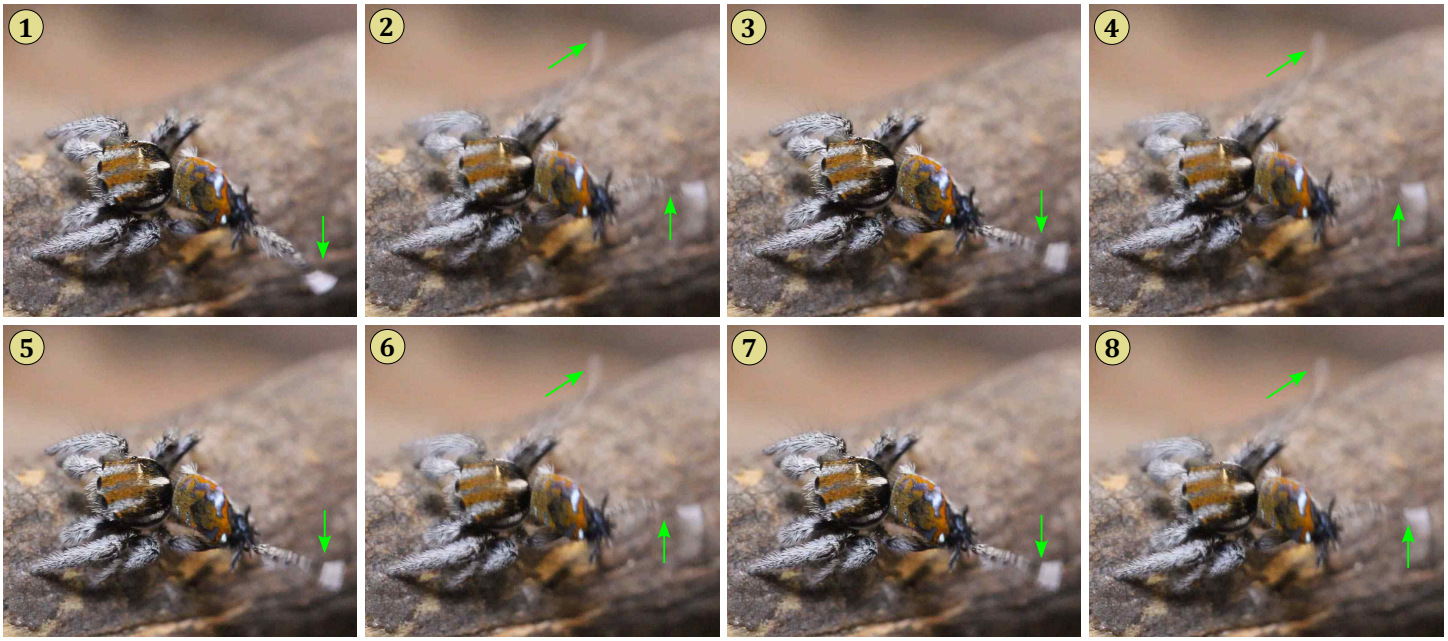

Figure 9. Sequential frames (~0.25s interval) from a 25 FPS video clip of display by a male *Maratus calcitrans*, from a dorsal perspective. **1,** Blurring indicated lowering of extended ipsilateral leg III behind the elevated opisthosoma. **2,** Fast kick of both legs III. **3-4, 5-6, 7-8,** Repeat of sequence described in (1) and (2). Each kick cycle (1-3, 3-5, 5-7) lasted about 0.5s, beginning with the lowering of ipsilateral leg III (1, 3, 5, 7), followed by very rapid elevation of ipsilateral leg III and the simultaneous extension and flexion of contralateral leg III (2, 4, 6, 8).

Figure 10. Still photographs of four sequences of display (1-3, 4-6, 7-9, 10-12) by two different male *Maratus calcitrans*. **1-3,** Holotype male. Image (1) is a composite to improve depth of field. **4, 6,** These pictures show the pre-kick elevation and flexion of the contralateral leg LIII (upper right). **10-12,** Note changes in the angle of rotation of the opisthosoma to the spider's left. Photograph (10) may have captured leg RIII during a rapid contralateral kick.

The final approach of a male to a female is shown in Figure 11. Beginning with bilaterally extended legs III, the male lowered these legs laterally as it approached and raised legs I to initiate contact with the dorsal carapace of the female.

Figure 11. Final approach of a male (♂#2) *Maratus calcitrans* to a female. **1,** Approaching with both legs III elevated and extended, and inflated opisthosoma elevated. **2,** Opisthosoma lowered and legs III extended laterally. **3,** Legs I extended to contact the dorsal carapace of the female, legs III flexed toward the surface of the branch prior to contact, and posterior opisthosoma including spinnerets deflated.

***Maratus digitatus*, new species**

Type specimens. The holotype (♂#4), with 10 male and 4 female paratypes, will be deposited in the Australian Museum, Sydney. All are from Mount Kaputar near Narrabri in northern New South Wales (30° 15' 50.8" S, 150° 03' 21.7" E, 30 SEP 2012, J. Otto coll.). This species has also been reported from Dunmore State Forest in southeastern Queensland (27° 37' 39" S, 151° 01' 12" E, D. Knowles).

Etymology. The species name (*digitatus*) is derived from the Latin word for finger, *digitus*, a reference to the finger-like extension and display of the four long posterior spinnerets by the male.

Diagnosis. Like the related *M. calcitrans*, males inflate and extend their black posterior opisthosomal segments, including the two pairs of posterior spinnerets, as they display to females. The pattern of the dorsal opisthosoma is similar in the two species, but with separate lateral bands of red scales and the central figure absent in *M. digitatus*. In addition, a prominent, extensible flap is present on each side of the opisthosoma. The legs of *M. digitatus* are not as heavily fringed, and legs III are darker. Instead of four longitudinal bands of red scales across the eye region, there are six bands across only the front 1/2 of the eye region in *M. digitatus*. Male pedipalps are similar, but *M. digitatus* lacks the thick cusp found at the beginning of the outer ring of the embolus of *M. calcitrans*.

Description of male. Body length including retracted spinnerets 4.34-5.14 mm (n=8). Carapace black and mostly glabrous (Figures 12-13). Front half of eye region with 6 longitudinal bands of pigmented red scales, separated by bands of white to grey scales. Carapace with white marginal band, and a white lateral band extending to the rear from beneath the PLE, on either side. Between the PLE is a median patch of white scales, and behind this a narrower, median white stripe extends to the rear, but only to the beginning of the posterior slope of the carapace. Lateral eyes and top of AME surrounded by red to orange scales, the PME distinctly closer to the PLE than to the ALE. Clypeus and basal segments of pedipalps may have some bright red and iridescent blue scales

Dorsal plate of opisthosoma with a distinctive pattern that lacks a central figure, but is comprised of transverse lateral bands of pigmented red to red-orange scales separated by spots of iridescent blue scales, with four prominent blue spots in front of a single, median red-orange spot at the rear, just in front of the dark posterior segments associated with the spinnerets. On either side of the dorsal plate, there is

a prominent inflatible flap covered with iridescent olive-green to blue-green scales, normally wrapped around the lateral sides of the opisthosoma (Figure 13:3). A continuous band of white scales may extend across the anterior margin, in front of these flaps. At the rear, there is a tuft of black setae extending to the rear on either side of the spinnerets. The inflatible posterior opisthosoma and spinnerets are black, with prominent fringes of ivory-coloured setae on the posterior medial and posterior lateral spinnerets.

Figure 12. Two male *Maratus digitatus* (1-5, holotype ♂#4; 6-8, paratype ♂#1). **1,** Lateral view. **2,** Detail of pigmented red to orange and iridescent light blue scales of opisthosomal plate. **3-5,** Views of living holotype. Note the coloured scales associated with the clypeus and basal segments of the pedipalps in (5). **6-7,** Submerged (6) and dry views of a paratype. **8,** detail of (7).

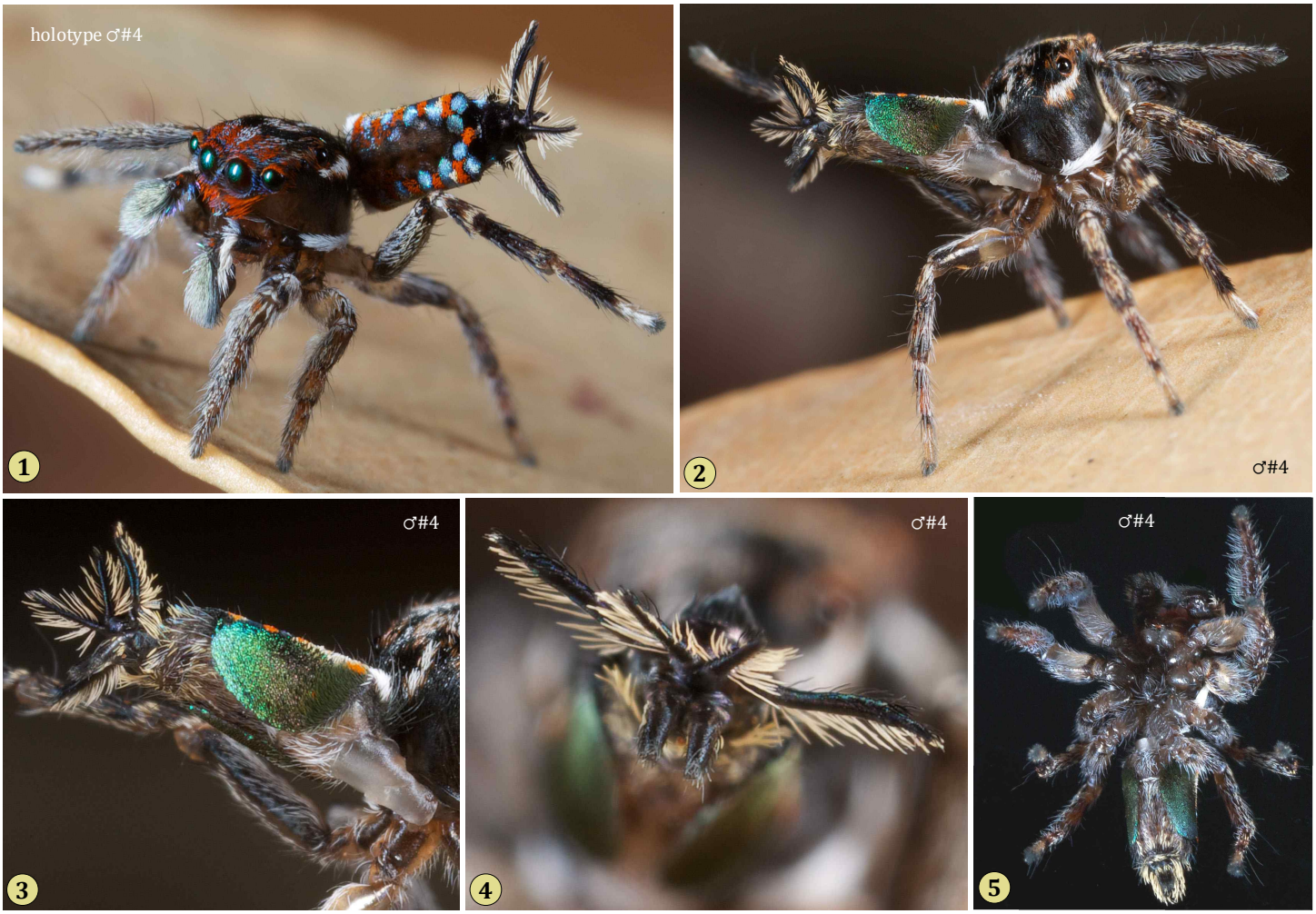

Figure 13. Living male *Maratus digitatus* holotype (♂#4). **1,** Courtship display with spinnerets extended, opisthosoma turned to one side, and waving ipsilateral leg LIII. Note the bright red and scattered iridescent scales of the clypeus and basal pedipalps. **2,** Rear view of display, showing dull to bright green iridescence of the lateral opisthosomal flaps, behind the hyperextended pedicel. **3,** Detail of opisthosoma during display. **4,** Rear view of spinnerets, showing 'normal' appearance of anterior spinnerets, and heavy setal fringing of posterior medial and longer posterior lateral spinnerets. **5,** Ventral view.

Legs I and II nearly equal in length, shorter than legs III and IV, legs III by far the longest. Legs banded light and dark with cover of white setae, but without the heavy fringes observed in *M. calcitrans*. Coxae, trochanters, proximal femora lighter brown and translucent. White setae on the front of femora III. Patella to metatarsus III mostly dark, without prominent fringes and with fewer setae than the other legs. Tarsus III covered with white setae. Legs I, II and IV more uniform in colouration. Pedipalps (Figure 14) covered with long grey-white setae in front, medially with dark setae, and laterally with bright white setae. Scattered red or iridescent blue scales may also be present on the basal segments of the pedipalps. The underside of the pedipalp is similar to that of *M. calcitrans*, with a heavy, pointed apex of the embolus, but there is no thick cusp at the beginning of the outer ring of the embolus in *M. digitatus*. Like *M. calcitrans* and some related euophryines, there is a dark sclerotized area proximal and medial to the embolus, and the distal margin of the RTA is irregular or serrated. Laterally, there is a heavily sclerotized proximal margin of the cymbium where it meets the tegulum (Figure 14:6). This has not been observed in *M. calcitrans*.

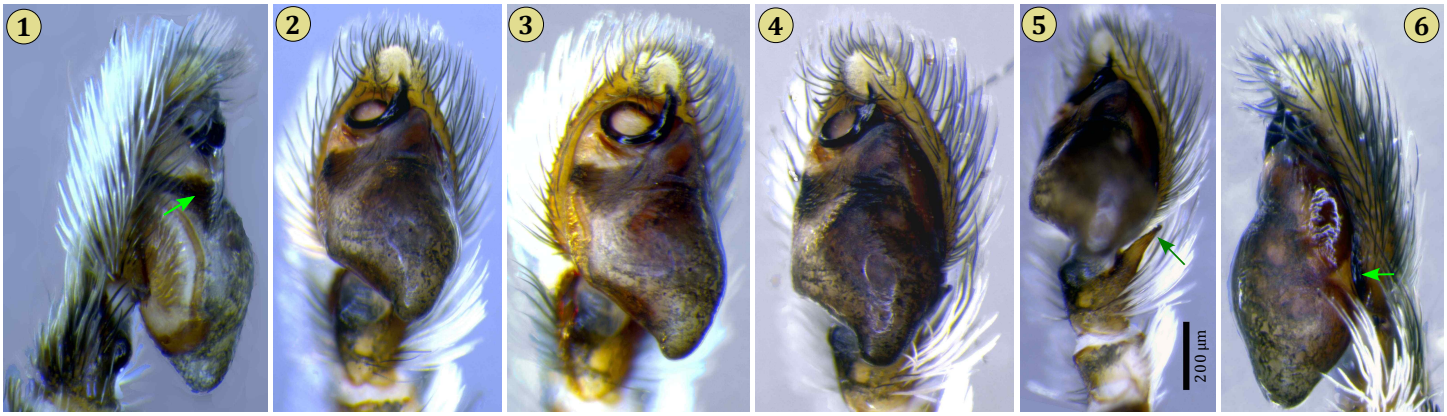

Figure 14. Medial (1) to lateral (6) views of the left pedipalp of a paratype male (♂#1) *Maratus digitatus*. The apex of the embolus is thick and pointed. Unlike *M. calcitrans*, there is no thick cusp at the beginning of the outer ring of the embolus, but there is a region of heavily sclerotized cuticle at the lateral, proximal border of the cymbium with the tegulum (6, arrow) in this species. As in *M. calcitrans*, there is also a heavily sclerotized medio-distal area of the tegulum (1, arrow), and the distal margin of the RTA is serrated or irregular (5, arrow).

Description of female. Body length including spinnerets 4.93-5.2 mm (n=3). Prosoma and opisthosoma dark brown-black dorsally, elsewhere, including legs, integument is light-brown, almost translucent (Figures 15-16). Band of off-white or ivory scales below lateral eyes on each side, below this the carapace is glabrous and there is no marginal band. Scattered dull orange-brown scales around PLE. PME closer to PLE than to ALE. Clypeus with scattered white setae, chelicerae glabrous.

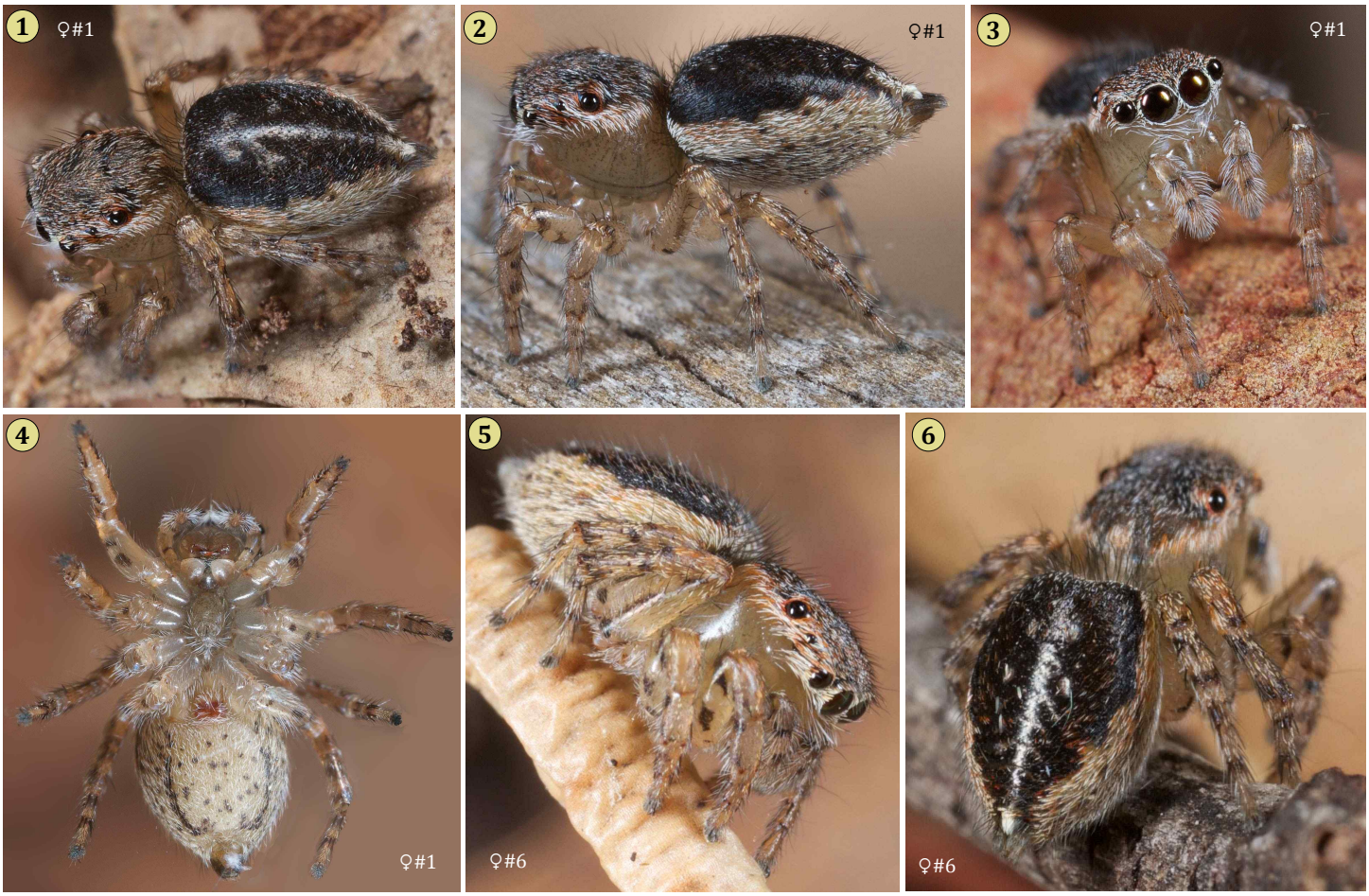

Figure 15. Two adult female *Maratus digitatus* (1-4, 5-6). Except for the dark dorsal prosoma and opisthosoma, the integument is uniformly light brown, almost translucent. Note the small patch of white setae above the anal tubercle (1-2, 6), a feature commonly seen in male *Maratus*.

Figure 16. Views of a third adult female *Maratus digitatus*.

Dorsal opisthosoma dark and shiny, almost glabrous, bounded by dark setae antero-laterally, and beneath these setae with broad lateral bands of dense off-white to ivory setae. Ventral opisthosoma with a narrow dark arc on either side, and scattered, small dark spots, but mostly covered with shorter off-white to ivory setae. Spinnerets dark brown but unremarkable.

Legs I and II nearly equal in length, shorter than legs III and IV, legs III the longest. Legs uniformly light in colour, except for darker segmental bands or mottling, with a cover of mostly off-white to ivory setae. Trochanters and femora light brown, mostly glabrous and translucent. Pedipalps coloured as legs. Sternum and coxae colourless, translucent, and glabrous. Labium somewhat darker but glabrous, endites light brown.

Epigynum (Figure 17) similar to that of *M. calcitrans*, but fossae of some individuals are relatively smaller, only about 3/5 of the width of the large posterior spermathecae. Anterior spermathecae or ducts are similar in general appearance.

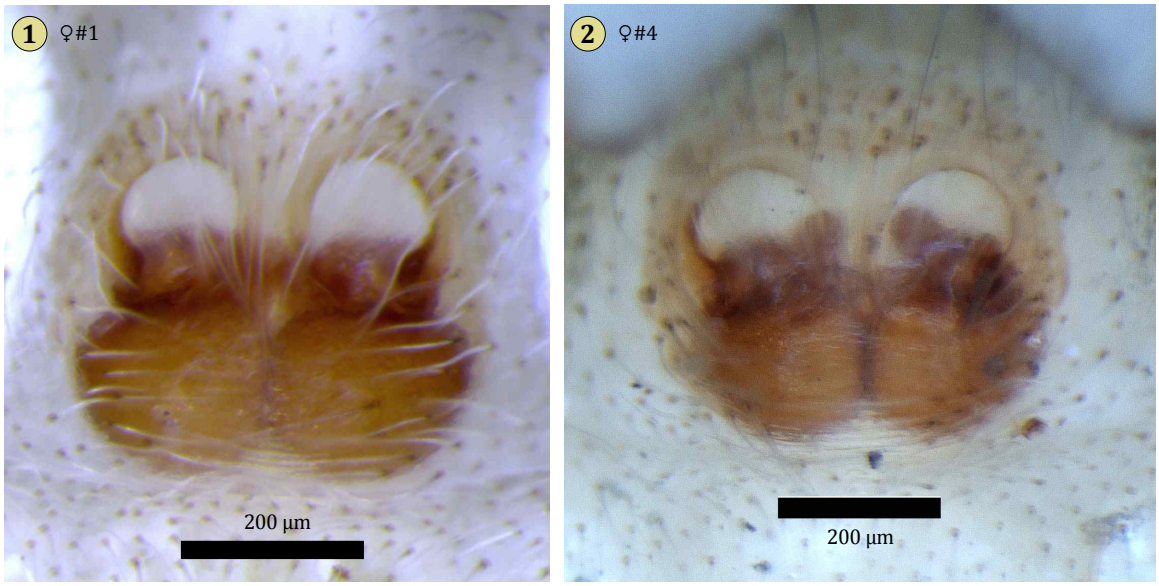

Figure 17. Ventral view of the epigyna of two different female *Maratus digitatus*. As with the related *M. calcitrans*, the relatively colourless cuticle facilitates viewing of internal structures in an intact specimen. When compared to *M. calcitrans*, the fossae of *M. digitatus* are smaller and the septum between them is larger. As shown by these two examples, the relative size of the large posterior spermathecae, and the appearance of anterior ducts that are visible beneath the fossae, varies.

Courtship behaviour. Examples of the visual courtship display of male *Maratus digitatus* are shown in Figures 18-24. This display resembles that of *M. calcitrans* with respect to 1) inflation of the posterior opisthosoma and posterior spinnerets, 2) elevation and lateral rotation of the opisthosoma, 3) waving the ipsilateral leg III, and 4) display on one side alternating with movement and display to the opposite side. The contralateral leg III may be waved with the ipsilateral leg III, but its movement is not so fast as the contralateral leg III kicks of *M. calcitrans*. Male *M. digitatus* are the only *Maratus* known to elevate four legs during this display (Figures 22-23). Usually with much heavier fringes on their posterior spinnerets than *M. calcitrans* males, they often vibrate and twitch individual spinnerets as they display. After a waving display on one side (about 3 'wave' cycles/s), a male may elevate its opisthosoma and then vigorously vibrate its extended and elevated spinnerets before it moves to display on the other side (Figure 21:10-20). Although male *M. digitatus* have lateral opisthosomal flaps, these do not appear to play a significant role in the 'fan dance' that they present to females. The lateral flaps may however be extended by a wary male when it first sights a female (Figures 18, 21), and thus may provide a kind of warning or alert in advance of courtship. We have not studied the possible use of these flaps in male-male interactions, something that we have observed in *M. vespertilio* (Otto & Hill 2012a).

Figure 18. Frames from a video clip of a male *M. digitatus* expanding the lateral flaps of its opisthosoma as it watched a female from a low-profile or 'wary' position. During this display only the spinnerets were moved. In this and in subsequent figures frames are sequential but not consecutive. This position was held for about 12s, then the male moved forward toward the female and began its courtship display.

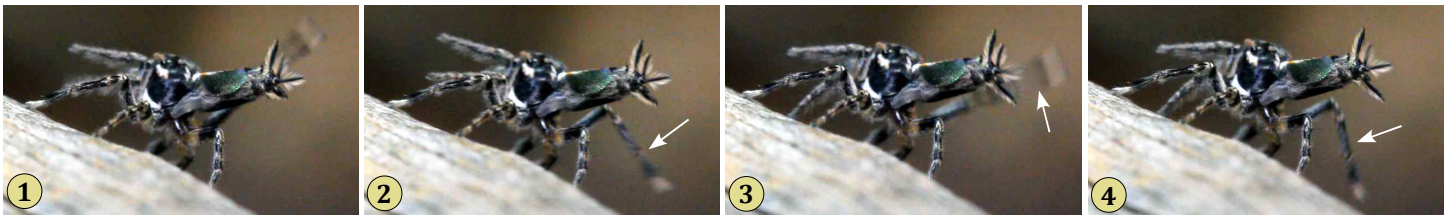

Figure 19. Sequential frames from a 25 FPS video clip of a male *M. digitatus* displaying to a female (postero-lateral view). The ipsilateral leg III (arrows) was alternately extended and waved (1, 3), then flexed at the femuro-patellar joint (2, 4). Each cycle of movement (1-3) took about 0.3s. By comparing frames, movement of one of the spinnerets can also be seen.

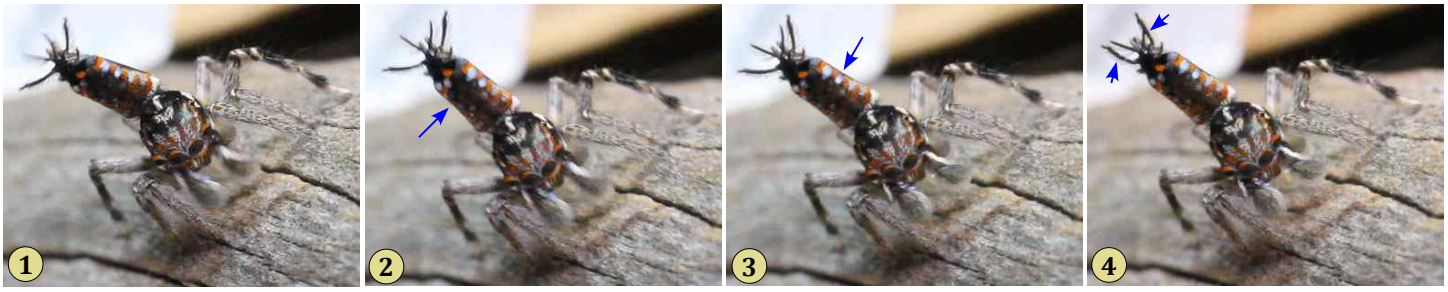

Figure 20. Sequential frames from a 25 FPS video clip of a male *M. digitatus* displaying to a female (antero-dorsal view). In this sequence, the male moved its opisthosoma from side to side (2-3, arrows), and also moved its posterior lateral spinnerets (4, arrows), but did not extend or wave its legs. The sequence shown here spanned about 2s.

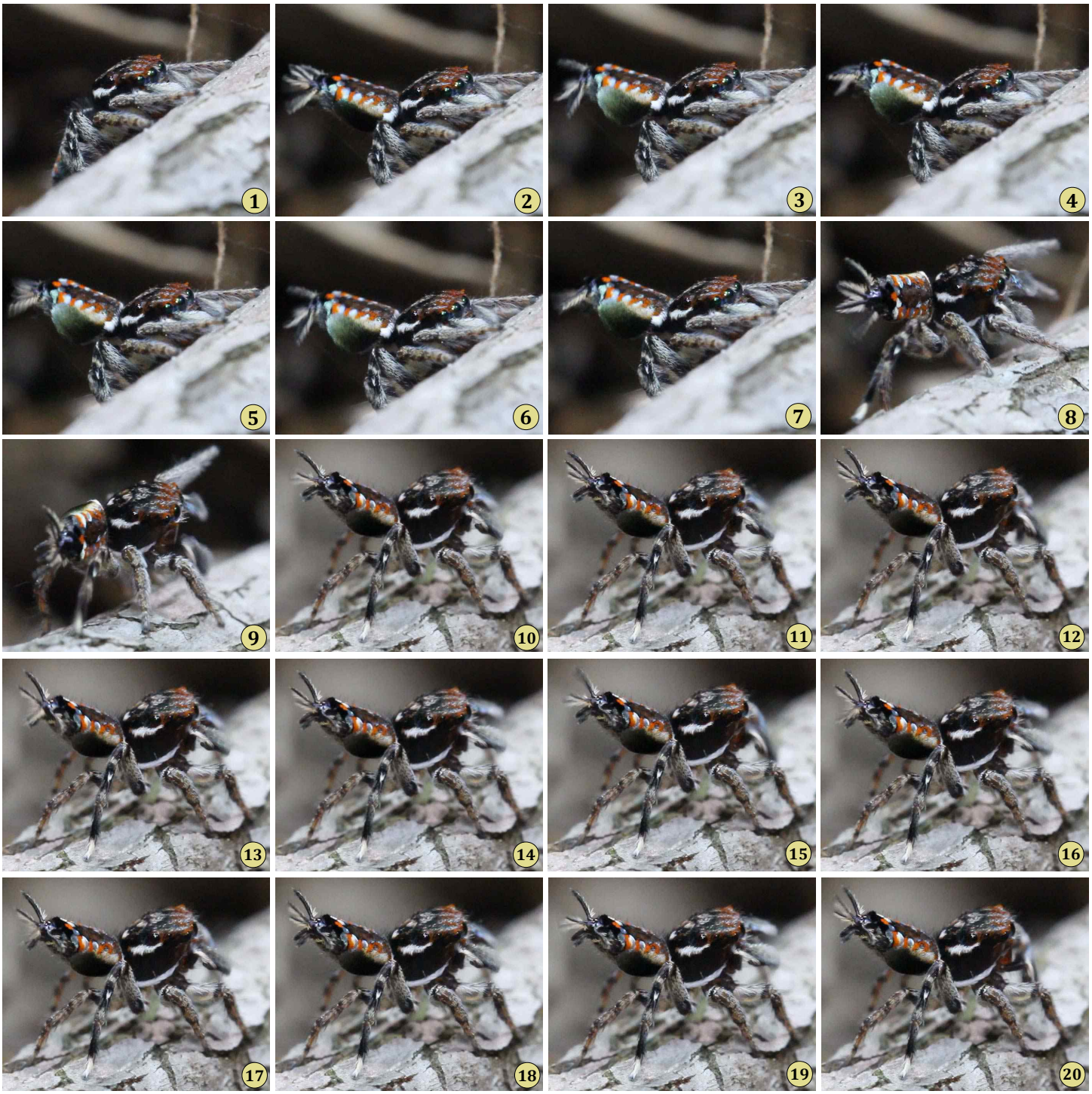

Figure 21. Sequential (not consecutive) frames from a 45s sequence of a male *M. digitatus* encountering a female of the same species (lateral view). **1,** Watching the female from a 'safe' or less visible low-profile position. **2-7,** With elevated opisthosoma, extending the lateral flaps and rapidly twitching or vibrating the extended spinnerets. **8-9**, Two frames from a sequence of the fan dance, waving ipsilateral leg RIII with the opisthosoma turned to one side, also with elevated and extended contralateral legs LI and LII. **10-20,** Twitching or vibrating the extended posterior spinnerets with the opisthosoma elevated; all legs were in contact with the substrate and no leg waving took place, but pedipalps were moved up and down in synchrony.

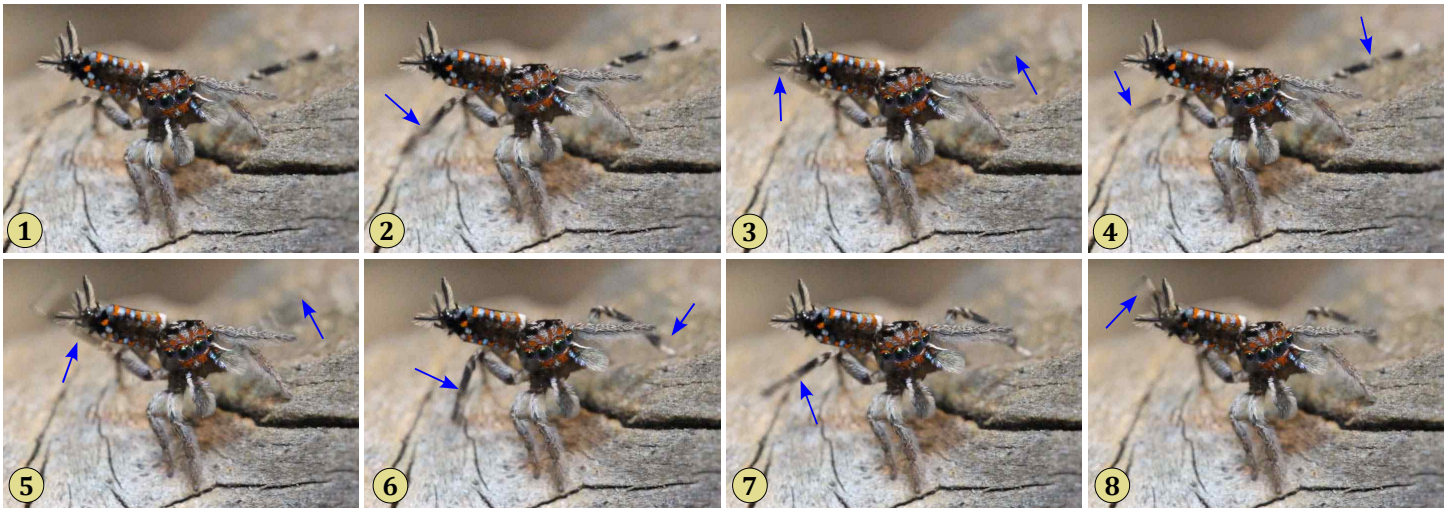

Figure 22. Sequential frames spanning about 1s from a 25 FPS video clip showing courtship by a male *M. digitatus* encountering a female of the same species. Movement of legs III or spinnerets prior to the image shown in each frame is highlighted with arrows. This assymetrical position of the pedipalps, with the ipsiplateral pedipalp pointed down and the contralateral pedipalp, along with contralateral legs I and II, elevated and extended to the side, is quite typical for this species. Each 'wave' cycle (*e. g.*, 3-5) lasted about 0.3s.

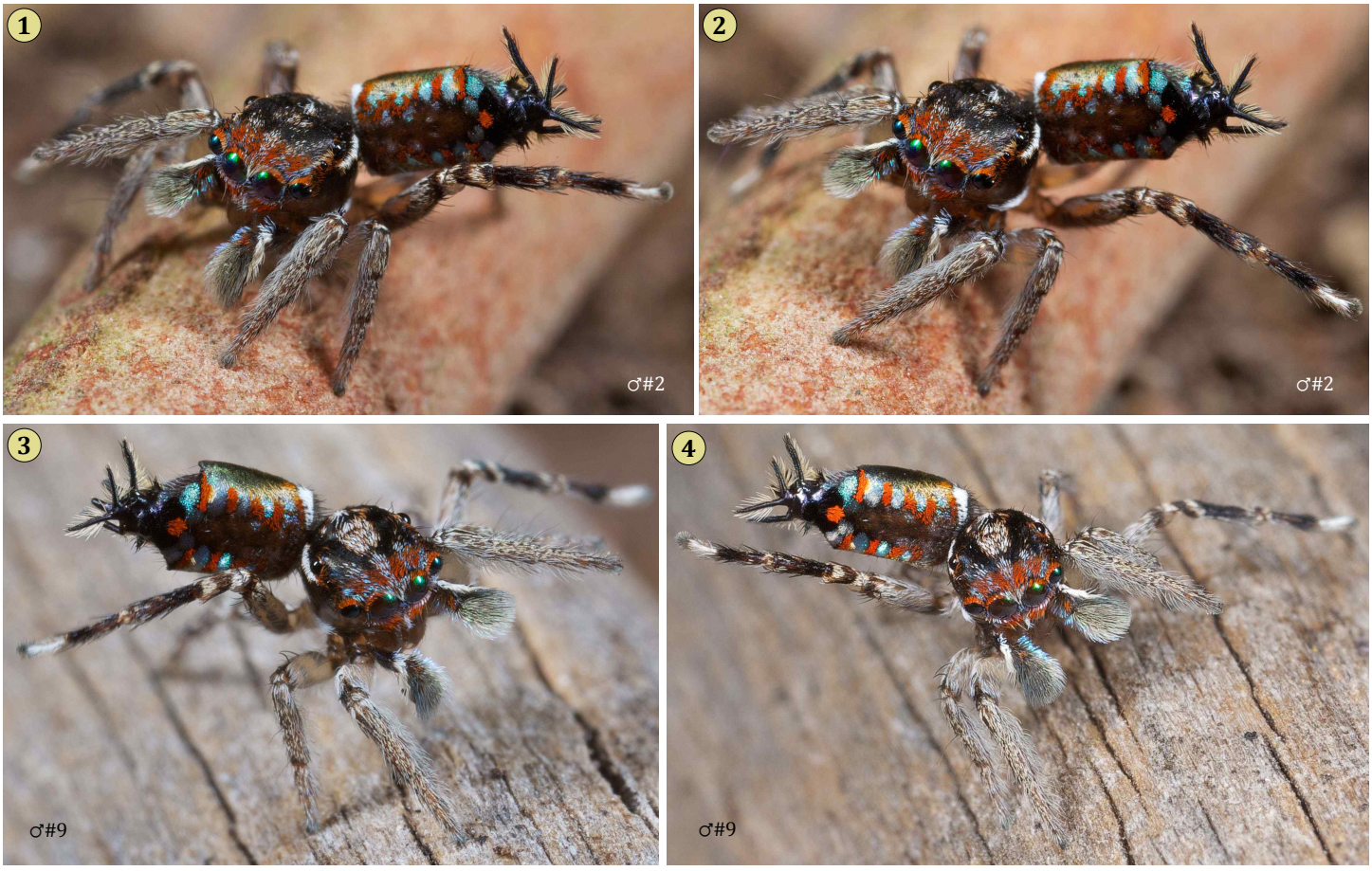

Figure 23. Still photographs of display by two different male *M. digitatus* (1-2, 3-4). In (2), the first male held contralateral legs RI and RII in an elevated position as it waved LIII. Photos (3) and (4) show the elevation of three contralateral legs (LI, LII, LIII) as the second male waved R3. This is the only species of *Maratus* known to display with four legs elevated in this manner. In (3), the lateral flaps of the opisthosoma, bounded on the rear by a transverse red stripe, were slightly extended. Distinctive red pigmented and iridescent blue scales of the chelicerae and basal segments of the pedipalps can also be seen in these views.

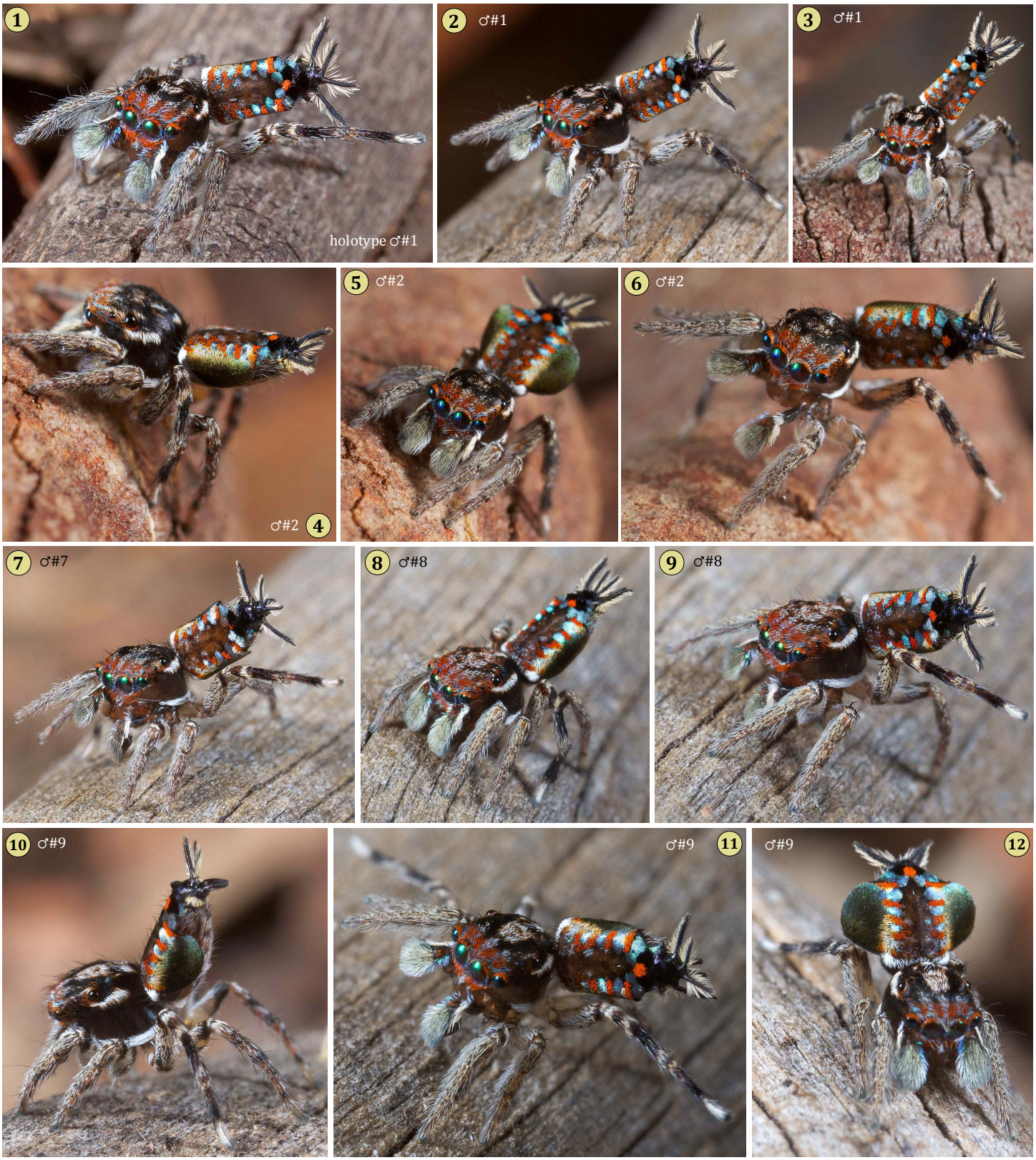

Figure 24. Still photographs of display by five different male *M. digitatus*. **1-2, 6-7, 9, 11,** Ipsilateral leg LIII wave with elevated contralateral legs RI and/or RII. **3, 10,** With prominent, heavily fringed posterior spinnerets held high. **4-5, 8, 12,** In lower body position displaying fan and/or spinnerets.

Display by the female. We have observed female *M. digitatus* engaged in a display that includes elevation of the body and opisthosoma, and waving the opisthosoma from side to side (Figure 25). This display takes place after a female has sighted a male, and appears to signal that the female is not willing to mate. This display is never associated with mating. A similar display has been observed in other female *Maratus* (Otto & Hill 2012b).

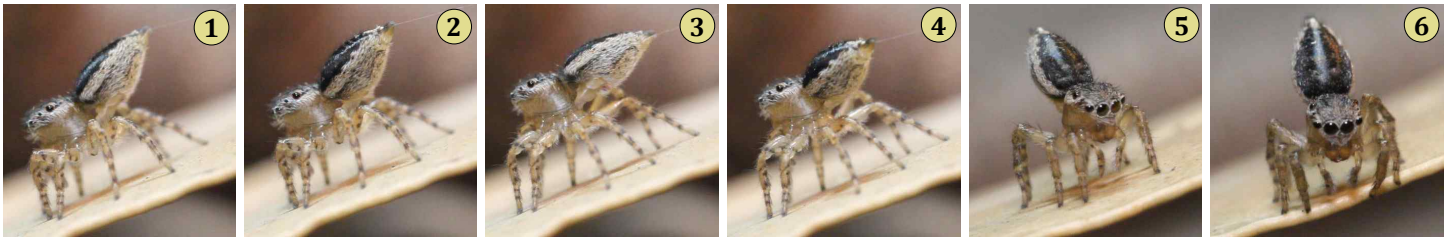

Figure 25. Video frames of a female *M. digitatus* displaying in the vicinity of a male. This female walked and turned slowly on extended legs and rotated its elevated opisthosoma from side to side.

Mating (Figures 26-27). A male *M. digitatus* approached a female with both legs III extended to the front, then lowered legs III laterally as he extended legs I to touch the top of the female's carapace. Through some combination of stimulation by the advancing male with legs I and II, and female cooperation, the opisthosoma of the female was rotated by 180° before the male inserted a pedipalp into the epigynum. This rotation is undoubtedly facilitated by the remarkable flexibility of the pedicel, the same flexibility that allows males to perform their varied courtship rituals. This extreme (180°) rotation of the female opisthosoma has been observed in all *Maratus* species for which mating has been observed, and may represent a useful character to distinguish members of this genus from related euophryines of the *Saitis* group (Otto & Hill 2012b).

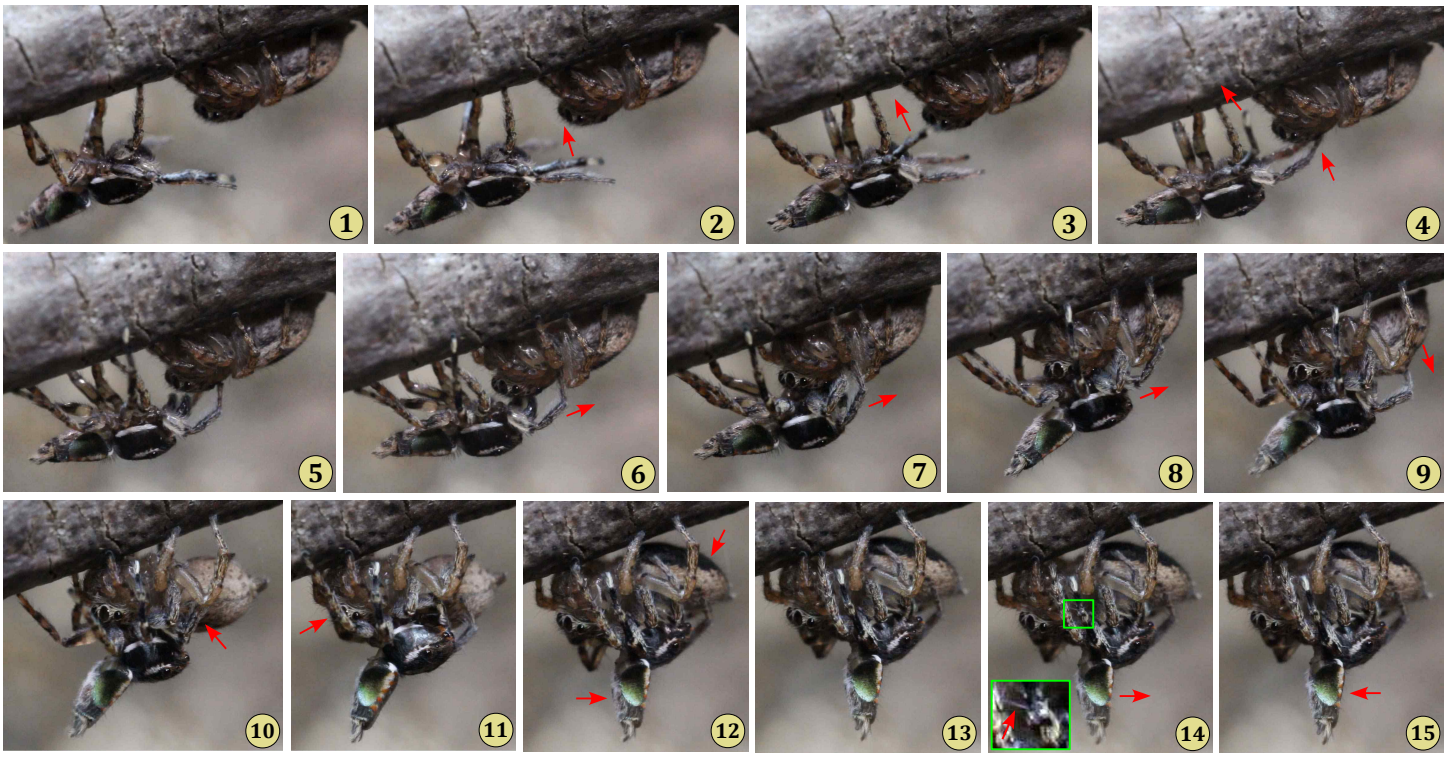

Figure 26. Initiation of mating by an advancing male and female *Maratus digitatus*. **1,** Male approach with both legs III extended. **2-4,** Legs III lowered laterally as legs I were brought into contact with the female carapace. Between (1) and (4) about 16s elapsed. **5-8,** Beginning with pedipalp contact, the male continued to advance over the female. **9-12,** Rotation of the female opisthosoma by 180°. Between (4) and (10) about 40s elapsed. **12-15,** Mating, accompaned by some movement of the male opisthosoma. As is generally observed in salticids, cyclic increases in internal fluid pressure associated with pedipalp inflation also led to pulsatile erection of spines (14, inset). In this example each pressure cycle lasted about 1s.

Figure 27. Still images of mating *M. digitatus*. This pair was originally upside-down (Figure 26), and their mating continued unabated after the twig to which they were clinging was rotated to facilitate these photographs. Note the partial expansion of the lateral opisthosomal flaps of the male.

In this instance, the female moved under a branch prior to mating, a behaviour that has also been observed in other species of *Maratus*. This behaviour may facilitate the rotation of the suspended opisthosoma, but it may also contribute to the concealment and safety of a mating pair.

Maratus species B

The assignment of a species name for this distinctive spider is expected in 2013.

A comparison of *Maratus* species B (Hill 2009, Otto & Hill 2011) with *M. calcitrans* and *M. digitatus* reveals many similarities, but also some intriguing differences. Males have a similar pattern of scales on the dorsal opisthosoma, including mostly transverse bands of pigmented orange to red scales on a light-blue iridescent background (Figure 28). *M.* sp. B, however, does not inflate or extend its spinnerets, but instead has a prominent pair of spinneret-like setal tufts on each postero-lateral opisthosomal flap (Figure 28:3). These tufts, most curiously, appear to mimic the extended spinnerets of the two related species. In addition, the flat anterior surface of femora III of *M.* sp. B is bright iridescent blue when viewed from the front, and the tarsi III have dark rather than white setae.

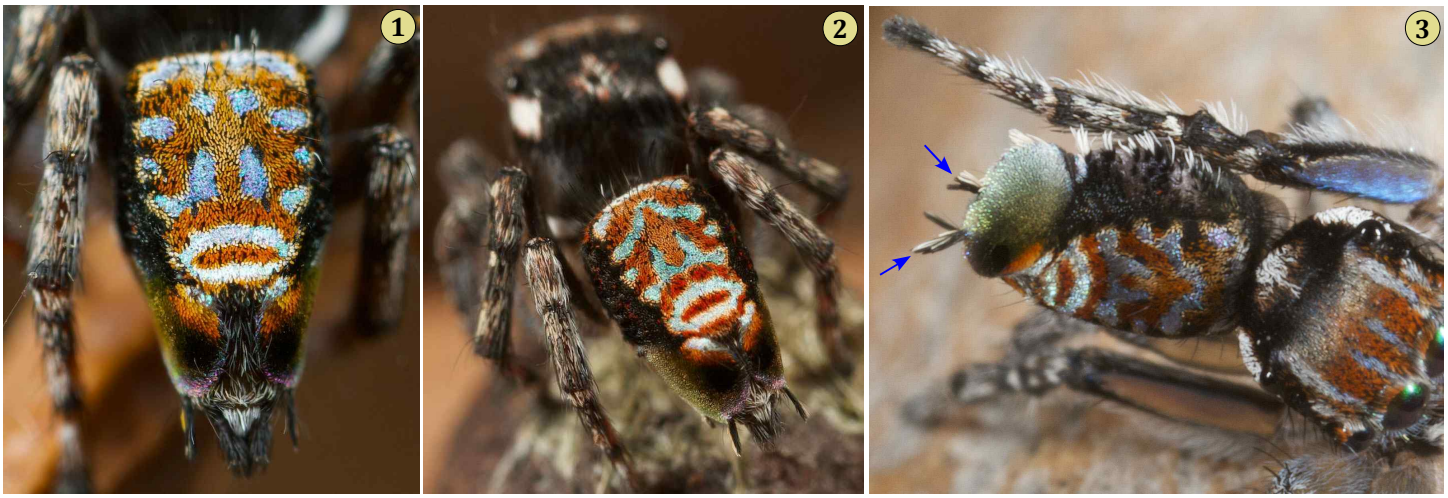

Figure 28. Three different adult male *Maratus* species B from the Wildflower Garden Reserve near Sydney, Australia (J. Otto). Each posterior lateral flap of the opisthosoma bears two tufts of thick black and white setae (3, arrows). The anterior surface of each femur III is also bright iridescent blue (3).

Similar to *Maratus digitatus*, male *M.* sp. B have a lateral border of bright white scales on their pedipalps They also raise and rotate their opisthosoma to one side and then to the other as they display to females. This display ('fan dance') differs from that of *M. calcitrans* and *M. digitatus*, however, in that males 1) extend opisthosomal flaps on the side opposite to the direction of opisthosomal rotation (contralateral side), and 2) they wave the contralateral rather than the ipsilateral leg III (Figure 30). As the contralateral leg III is waved, the femur is held in a relatively fixed, erect position, displaying its bright, iridescent blue anterior surface. Most of the movement of this waving leg is distal to the femur, at either the femuro-patellar or the tibio-metatarsal joint.

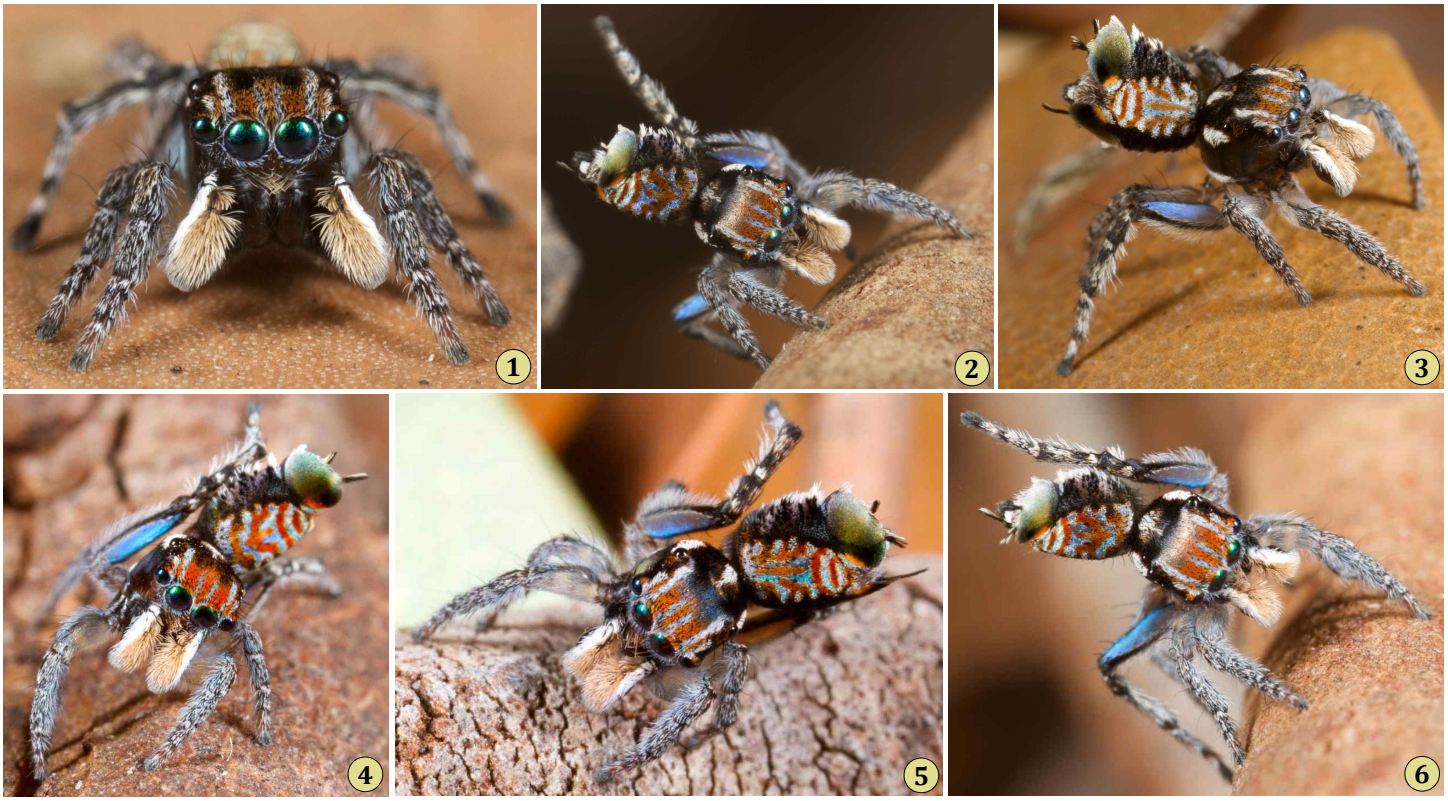

Figure 29. Display by male *Maratus* species B from the Wildflower Garden Reserve. **1,** Prominent pedipalps spread apart to reveal dark chelicerae. **2-6,** Fan dance. Tufts on each posterior lateral opisthosomal flap resemble a pair of spinnerets when the flap is extended as shown here (4-5).

This species has now been found at four new localities in southeastern Australia. The Sydney form shown in Figures 28-29 has also been reported from southern Queensland (Applegrove Farm, 139 Booth Lane, Fletcher, 28° 46' 50.1" S, 151° 50' 22.19" E, 28 SEP 2012, R. Whyte) (Whyte 2012), and from two locations in southeastern New South Wales (north of Mayfield, 35° 09' 55.2" S, 149° 47' 55.1" E, S. Harris; 1 km ENE of Wee Jasper, 35° 06' 43.1" S, 148° 41' 19.3" E, A. Cruz & S. Harris). A second male form was also reported recently from Melbourne (SEP 2012, N. Quittner, pers. comm.; Figure 30).

Figure 30. Adult male *Maratus* species B from Melbourne ('Melbourne form'). The most distinctive characteristic of this form is the presence of dark, orange-bordered (instead of bright orange to red) transverse scale fields on the dorsal opisthosoma, and brown, rather than bright orange to red, bands on the carapace. **2,** Display with flaps on one side of opisthosoma extended. **6,** A pair of thick, black tufts extend to the rear from each posterior flap of the opisthosoma. **7,** Two silk strands of the drag line (arrow) can be followed back to small grey, conical spigots of the anterior spinnerets. Photographs by Elan Lewinsohn, used with permission of Elan Lewinsohn and Nicole Quittner, who found this spider.

Female *Maratus* species B (Figure 31) are very similar to those of *M. calcitrans* and *M. digitatus*.

Figure 31. Female *Maratus* species B from the Wildflower Garden Reserve near Sydney.

Phylogeny and evolution of the *calcitrans* group

The hypothetical relationship of *Maratus calcitrans*, *M. digitatus* and *M.* species B, as members of the '*calcitrans* group' within the genus *Maratus*, is shown with defining characters in Figure 32.

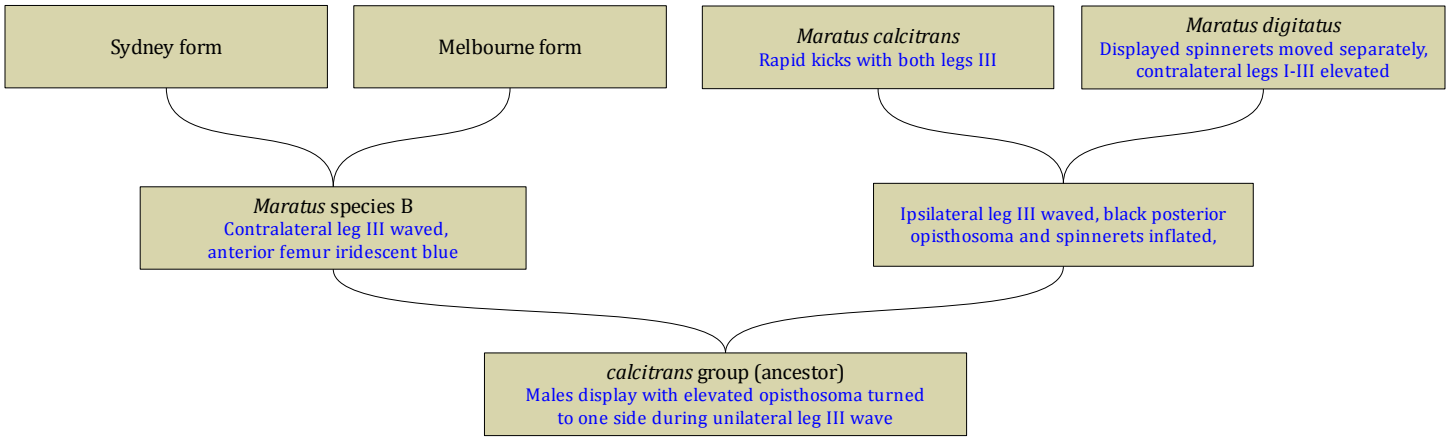

Figure 32. Hypothetical relationship of the three known species of the *calcitrans* group, a sub-clade of the genus *Maratus*.

The close relationship between *M. calcitrans*, with no lateral opisthosomal flaps, and *M. digitatus*, with flaps, supports our earlier conclusion (Otto & Hill 2012b) that the presence or absence of flaps at the lateral margins of the dorsal opisthosomal plate cannot be used to define the scope of the genus *Maratus* Karsch 1878. The ancestor of the *calcitrans* group may have had lateral opisthosomal flaps, retained by *M.* sp. B and *M. digitatus* but lost by *M. calcitrans*. However, these flaps (or lateral extensions of the dorsal plate) are quite different in *M.* sp. B and *M. digitatus* and it is possible that they evolved separately in the two species.

The pair of conspicuous tufts associated with each posterior flap of *Maratus* species B closely resembles a pair of extended spinnerets. This suggests that the ancestor of the *calcitrans* group also extended and displayed its spinnerets above its elevated opisthosoma. Subsequent sexual selection driven by a hypernormal female response to exaggeration of this feature (Andersson 1994, Emlen & Nijhout 2000) could account for the evolution of prominent posterior tufts in one group (*M.* sp. B), and parallel evolution of an ability to inflate the posterior opisthosoma in another group (*M. calcitrans* and *M. digitatus*).

Distribution and ecology

The three species that comprise the *calcitrans* group have all been found in dry sclerophyll forest areas of southeastern Australia (Figures 33-34).

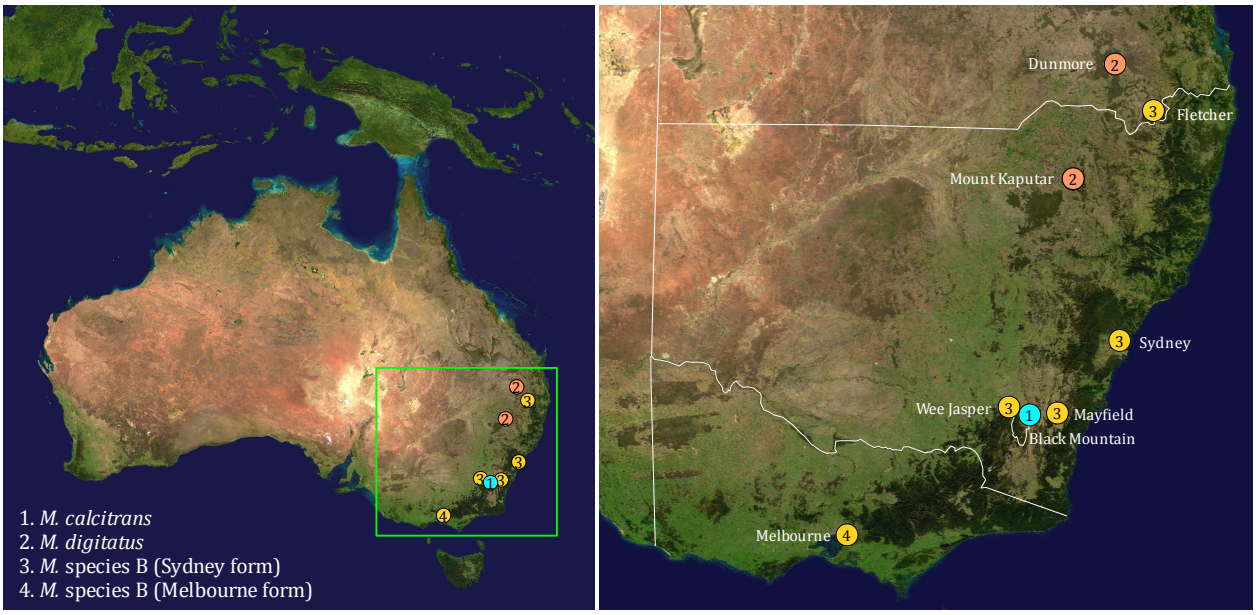

Figure 33. Australian localities where members of the *calcitrans* group of the genus *Maratus* have been found. See the text under each species account for details. Background map courtesy of *NASA Blue Marble*.

Figure 34. Dry sclerophyll forest in three localities mapped in Figure 33. **1,** Black Mountain (*M. calcitrans*). *Eucalyptus rossii* (Scribbly Gum) may be dominant in this area (S. Harris, pers. comm.). **2,** Mount Kaputar (*M. digitatus*). Tree species in this area include *Eucalyptus crebra* (Narrow-leaf Ironbark), *E. dealbata*, *E. sideroxylon* (Mugga) and *E. chloroclada* (Dirty Red Gum). **3-4,** Wildflower Garden Reserve near Sydney (*M.* sp. B).

Convergent evolution of salticids that power their jump with legs III

Most jumping spiders begin a jump with legs I and II elevated and extended to the front, and legs III and IV in contact with the substrate. In these spiders, legs IV are usually flexed in a parasagittal plane in preparation for a jump, and their simple extension produces the rearward ground force required to propel the spider forward (Hill 2010). Australian *Maratus* Karsch 1878 (Euophryinae) and North American *Habronattus* F. O. Pickard-Cambridge 1901 (Plexippoida: Pellininae) represent two diverse groups that appear to have independently evolved the ability to power their jump primarily by extension and rotation of relatively long, flexed legs III rather than by simple extension of legs IV (Hill 2009). Some jumping positions of *Maratus* species in the *calcitrans* group are shown in Figures 35-36.

Figure 35. Consecutive frames from a video clip (25 FPS) showing a male *Maratus digitatus* preparing to jump. **1,** Starting position. **2,** Legs III in a 'cocked' position (arrow points to white tarsus RIII) prior to their extension. In this example legs III were flexed to a greater extent than depicted in Figure 36. **3,** Legs I (arrow) elevated in the last frame of this video clip before the spider jumped.

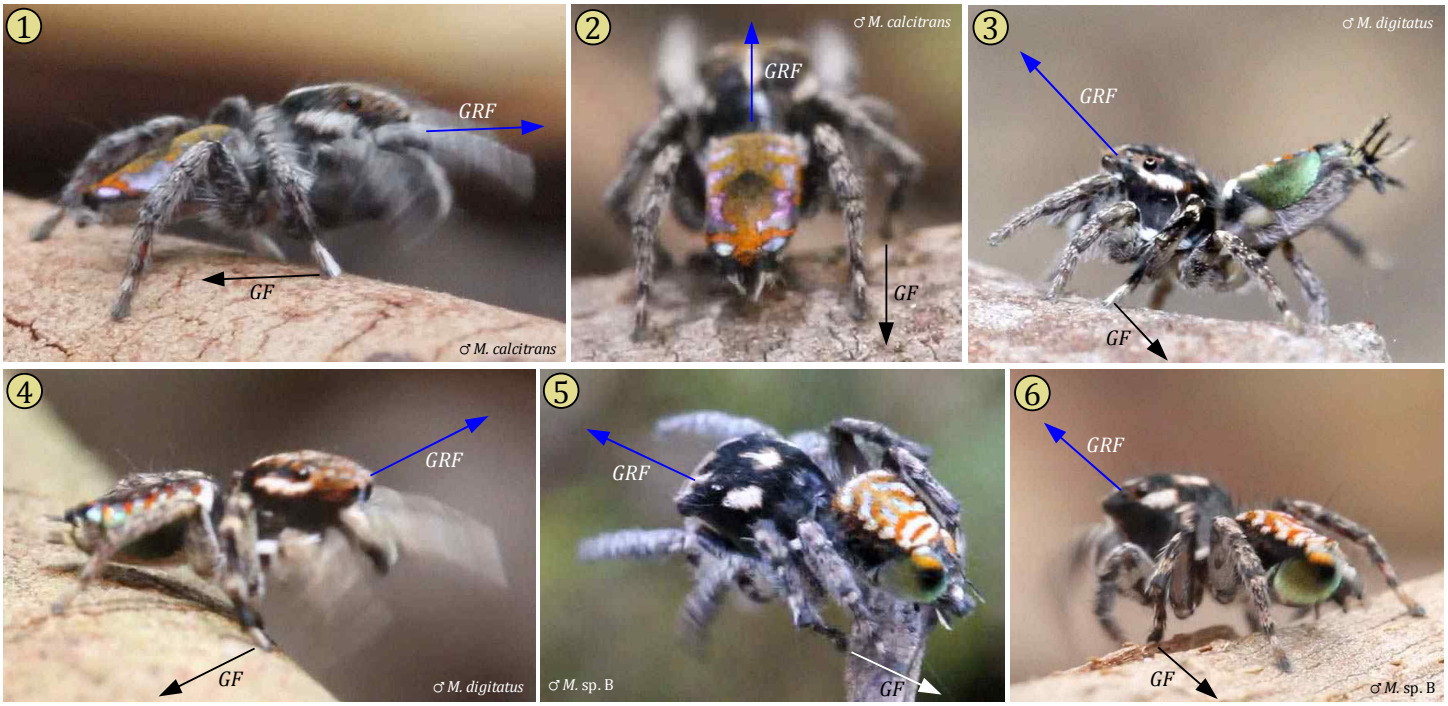

Figure 36. Final pre-jump frames from 25 FPS video clips of jumping male *Maratus* of the *calcitrans* group. In each example, the direction of the net ground reaction force vector (GRF) was traced from parallel blurred lines in the subsequent video frame. The direction of the equal and opposite ground force (GF) required to produce this GRF is indicated with respect to the contact position of each flexed leg III. Note that most of the flexion of legs III in each example was in a transverse rather than parasagittal plane. For a vertical jump (2) simple extension of legs III can explain the trajectory of the spider, but in order to power a forward jump these legs must be able to rotate forward at the coxae during their initial rearward push, before they can extend completely. Torque associated with this forward rotation may provide additional force to the jump. Extension of legs IV may also contribute to early acceleration, but these are never flexed as they are in most other salticids prior to a jump.

Jumping with legs III usually (but not always; see Figure 35) begins with flexion of these legs in a transverse rather than parasagittal plane. With the coxae of legs III perhaps closer to the center of gravity, this may facilitate vertical jumps (Figure 36:2), but it also requires forward rotation of each leg III at the coxa before its extension can be completed to power a forward jump. In these spiders, legs IV are also partly flexed and then extended during take-off, and may thus contribute some ground force at the beginning of a jump.

There are many known species of *Habronattus* distributed across North America (Griswold 1987, Richman *et al.* 2012). Most males have elaborate ornamentation, and use legs III as they display to females (Figure 37). However, they are not known to extend these legs when they display, as do *Maratus* species, but rather raise and display their ornamented legs III in a flexed position. Like *Maratus*, they use only partly flexed legs IV and rely primarily on legs III, flexed in a transverse plane, to power their jumps (Figures 37:2, 38). The evolutionary convergence of these two genera is documented in Table 1.

Figure 37. *Habronattus coecatus* (Hentz 1846), also known as *H. coronatus* (Hentz 1846) after Peckham & Peckham (1909, first revision of species name), from southern Greenville County, South Carolina, USA (near Reedy River, 34° 42' 49.4" N, 82° 18' 54.7" W, JUL 2011, D. E. Hill). **1,** Front view of male feeding on nematoceran (composite image). Ornamentation includes large setae on the underside of legs I, long setae on pedipalps, bright red setae of the clypeus, and the 'upper' parts of legs III, including sculptured distal femora and patellae, and green tibiae. As males approach females, they rotate each leg III in turn to display the distal femur at the midline, above the carapace, but they do not extend legs III as they do this. **2,** Adult female prepared to jump, with flexed legs III. **3-4,** Two sequential photographs of a male (at left) courting a female. At this distance (3) the male rotated each leg III in turn to display these above the carapace. Females often turned away from courting males (4), but could often be brought back to an attentive position if the male rapidly moved and flexed the tarsi of legs I. Males of this species are quite wary of females, often approaching them from a concealed position until they are close enough to initiate this display. Related and very similar species within the *coecatus* group of the genus *Habronattus* are found across temperate North America (Griswold 1987).

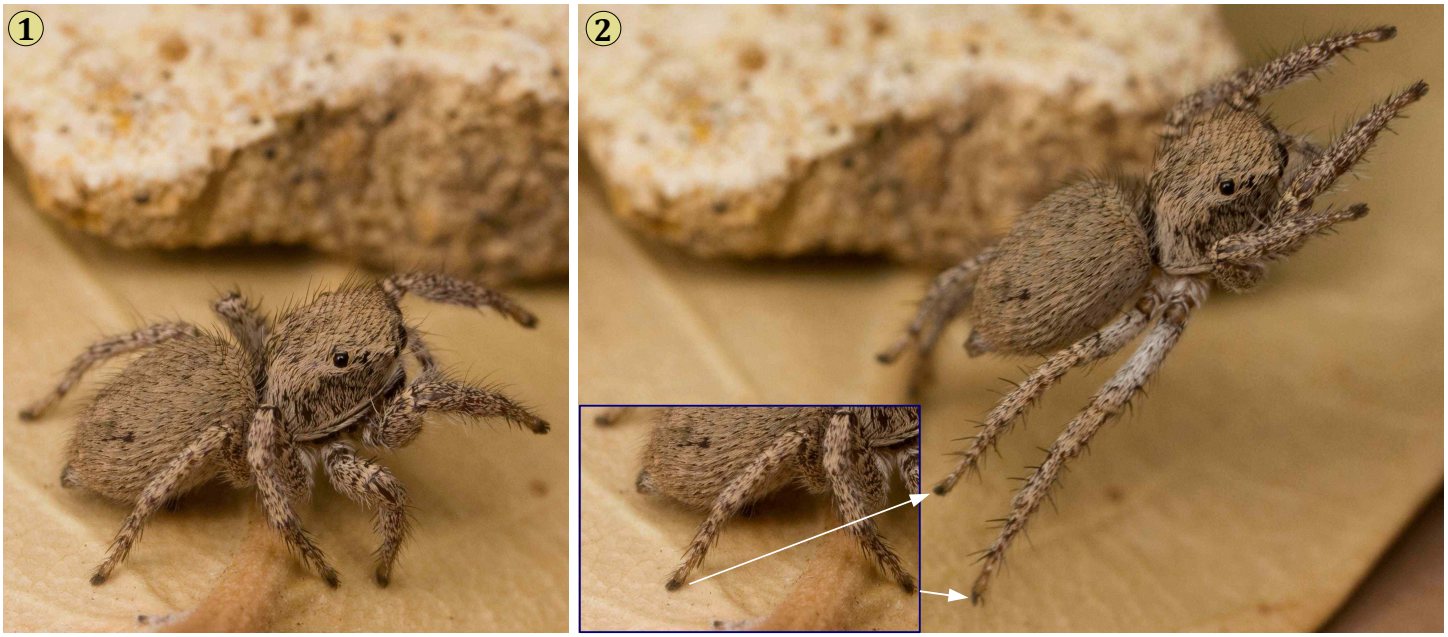

Figure 38. Sequential photographs (f/11, 1/160 s) of a jump by an adult female *Habronattus* [either *H. clypeatus* (Banks 1895) or *H. dossenus* Griswold 1987]. **1,** In preparation for this jump, legs IV were partly flexed in a nearly parasagittal plane, and the longer legs III were flexed to a much greater extent in a nearly transverse plane, at the trochanto-femoral and femuro-patellar joints. **2,** The same spider, about 0.001s after take-off (based on an estimated velocity of 90 cm/s). The inset at lower left shows the relative position of legs RIII and RIV from (1). Note the much greater translation of pretarsus RIV (upper arrow) compared to that of RIII (lower arrow). This difference indicates that leg RIV left the substrate earlier (by about 0.0035s) than leg RIII. Although legs III and IV can both provide ground force for the jump, the distance through which the longer leg III can apply this force and thus deliver energy to the jump is much greater, and it can also provide vertical lift. Note the clockwise rotation of leg RIII, but not leg RIV, as it was extended. This rotation is best seen by comparing the orientation of respective tibiae in the two photographs. In (2) the spines of all legs are erect as a result of the transient increase in internal fluid pressure that powers these jumps (Anderson & Prestwich 1975). In the case of predatory jumps, this erection of the spines on all four extended legs produces a wide 'catching basket' that facilitates the capture of prey (Hill 2010).

Table 1. Evolutionary convergence of North American pellenines of the genus *Habronattus* with Australian euophryines of the genus *Maratus*. The use of legs III to power jumps may be of advantage to spiders that live on or near the ground, as it may facilitate vertical jumps (Hill 2009).

	Habronattus	***Maratus***
Distribution	Many species and local varieties across temperate North America	Many species and local varieties across temperate Australia
Habitat	Found in areas of varying aridity on or near the ground	
Size	Mostly small to medium (3-6 mm body length)	
Legs III	Legs III longer than other legs, used to power jumps through both extension and rotation, and usually used in male courtship display	
Legs IV	Legs IV shorter than legs III, only partly flexed at the beginning of a jump	
Pattern of male ornamentation	Many colourful ornaments, including distal femur, patella and tibia of leg III, elevated and moved from side to side above the carapace	Many colourful ornaments, including dorsal opisthosomal plate, elevated and moved from side to side above the carapace
Diversity of male ornamentation	High variation between species and within some species	
Colouration of females	Little variation between species, mostly cryptic light to dark brown colours	
Diversity of genitalia	Relatively little variation between most species	

Acknowledgments

We thank Stuart Harris for sharing his discovery of *Maratus calcitrans*, and Stuart Harris, David Knowles, Nicole Quittner, and Robert Whyte for sharing their records of related *Maratus*. We thank Ryan Kaldari, Elan Lewinsohn, and the NASA Blue Marble project for allowing us to include their photographs. We would also like to acknowledge the cooperation of the Land Management and Planning Division of the Australian Capital Territory, the National Parks and Wildlife Service of New South Wales, and the Wildflower Garden Reserve, St. Ives for granting permission to collect spiders on lands that they manage. We are grateful to Bruce Cutler, Ryan Kaldari, and David B. Richman for their review of the manuscript.

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