

## Peacock spiders of the *pavonis* group from southern Australia (Araneae: Salticidae: Euophryinae: *Maratus*)

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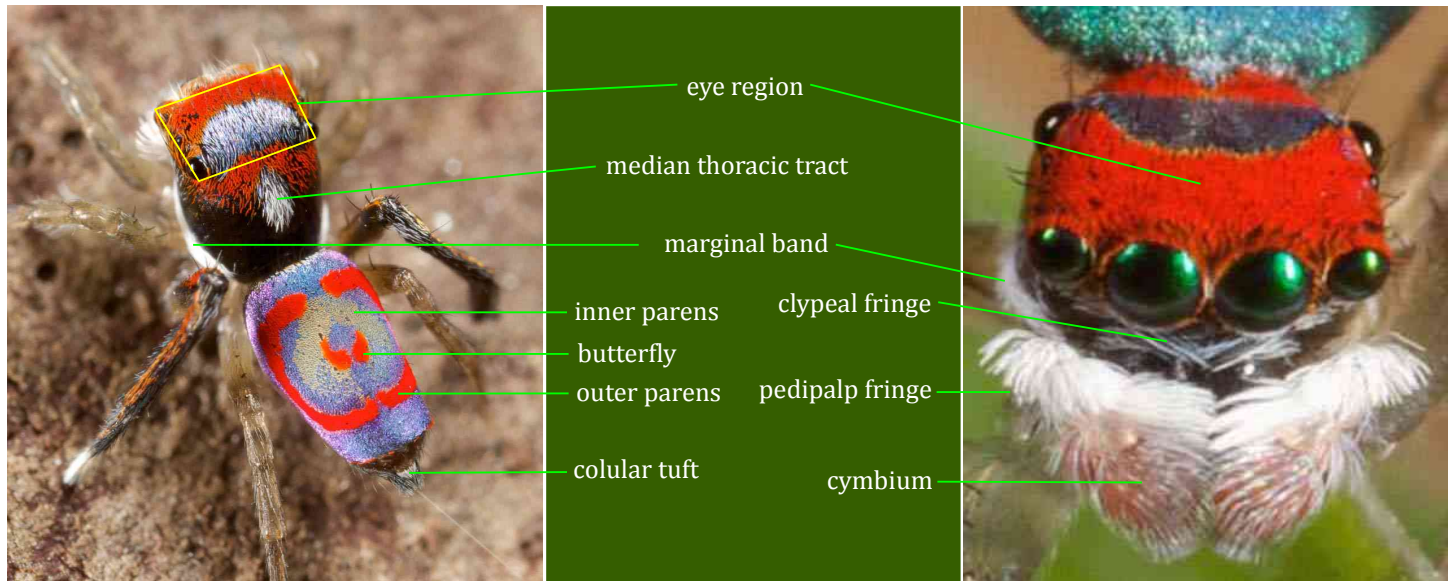
**Key words:** euophryine, jumping spider, salticid

**Abstract:** Four new species (*M. leo*, *M. literatus*, *M. maritimus*, *M. montanus*) are described and assigned to a clade (the *pavonis* group) contained within the genus *Maratus*. Three previously described members of that group (*M. pavonis*, *M. splendens*, and *M. watagansi*) are also reviewed, and the female *M. splendens* is described for the first time. Evolution and speciation within the *pavonis* group are discussed.

We have previously recognized three closely related but distinct species [*Maratus pavonis* (Dunn 1947), *M. splendens* (Rainbow 1896), and *M. watagansi* Otto & Hill 2013] as members of a *pavonis* group within the genus *Maratus* Karsch 1878 (Otto & Hill 2013, 2014). Characters that we presently associate with males of this group and consider potentially synapomorphic include the layout of scales on the dorsal opisthosomal plate (or fan) and the presence of a pedipalp fringe that appears as a bright line beneath the anterior eye row as the pedipalps are held in a horizontal position (Figure 1). We have also identified two distinctive forms of '*M. pavonis*' (brunneis, m-signitis; Otto & Hill 2012b, 2012c). Here we describe one of these forms (m-signitis) as a new species, and we also describe three additional species.

### The *pavonis* group of the genus *Maratus*

The *pavonis* group represents a hypothetical clade of peacock spiders (*Maratus*) from southern Australia including Tasmania. This group is characterized by the presence of a distinct 'target' pattern on the fan of males (Figure 1), or a pattern that appears to be derived from this pattern, generally comprised of a combination of bright to dark red or red-orange and grey to light brown pigmented scales, and a background of blue-green iridescent scales. The fan (dorsal opisthosomal plate) can be narrow (lanceolate) without lateral flaps, oval with or without lateral flaps, or circular (when expanded) with prominent lateral flaps. In some species the fan is not raised during courtship display. Males of this group also hold their pedipalps together in front of the chelicerae, so that long light-brown to white setae associated with both pedipalps form a continuous *pedipalp fringe* beneath the front eye row. The eye region is either uniform red to brown in colour, or it bears a more or less distinct 'm' pattern (as viewed from the rear) on a background of grey scales. Male *M. splendens* have a unique transverse crescent-shaped band of iridescent scales between the PLE. On the carapace, males of the *pavonis* group have a distinct white or ivory marginal band, and a white to light-brown median thoracic band of variable shape and length. Sides of the male carapace are dark brown to black and often glabrous, but may bear a cover of scattered scales. Legs I, II, and IV may be translucent with few markings, or ringed with alternate areas of dark pigment and light scales on each segment. Legs III of males are generally dark brown, often with dark red-brown setae, and fringed with longer black setae from the femur to the metatarsus; the tarsus is covered with bright white setae. The male pedipalp varies little between species in this group and both inner and outer rings of the embolus have heavy apices that may appear fused or separate.



**Figure 1.** Important characters of the adult male *Maratus splendens*. The general pattern of scales on the dorsal opisthosoma is fairly constant within the *pavonis* group, although certain features here (e.g., the 'butterfly') are missing in some species, and the inner and outer parens may be of different shape or intensity, or replaced by a single parens. Members of this group hold the pedipalps in the horizontal position shown at right, displaying a bright 'pedipalp fringe' beneath the anterior eye row. The pattern of scales in the eye region, and the shape and length of the median thoracic tract (behind the posterior eye row) are useful in the identification of species.

Females that have been described in this group are mostly dark brown in colouration, with a relatively glabrous opisthosoma, and a light-coloured median stripe (median thoracic tract) behind the posterior eye row. The sides of the carapace tend to be glabrous and translucent light-brown, and the marginal band is either less defined than in males or lacking altogether. Legs, also translucent light brown in life, may be strongly banded with black pigment.

Our key to the seven species associated with this group is based on readily observed characteristics of adult males:

*Key to adult males:*

- 1a. Dorsal opisthosomal plate (fan) oval or round, with or without lateral flaps, brightly coloured with a distinctive scale pattern comprised of a red-orange to red outer parens and central butterfly, and a light brown or tan to red-brown inner parens on a background of iridescent blue-green or blue-purple scales (Figures 1, 8-9, 52, 62) ..... 2
- 1b. Fan oval or lanceolate, without lateral flaps, background mostly light to dark brown with few if any iridescent scales; outer parens or butterfly if present either dark or indistinct (Figures 2, 6, 26-29, 39-41, 54, 64) ..... 4
- 2a. Small (~3-4 mm body length); prominent flaps and round fan when expanded, bright red outer parens and butterfly, fan margins bearing uniform iridescent, not tan or brown scales; bright red scales covering anterior eye region separated from bright red scales behind posterior eye row by a crescent-shaped band of light to dark blue, iridescent scales; small diamond-shaped median thoracic tract comprised of white scales; legs I, II, IV translucent with few markings (Figures 1, 62) ..... *M. splendens*
- 2b. Larger (~4-5 mm body length) with oval to round dorsal opisthosomal plate, with or without lateral flaps, red-orange outer parens and butterfly, fan margins bearing some mixed brown scales; eye region brown to red-brown or grey, longer median thoracic tract of variable shape, legs I, II, IV may be banded (Figures 8-9, 52) ..... 3
- 3a. Eye region bearing a distinct 'm' shape (as viewed from the rear) comprised of bright red scales on a background of grey scales; diamond-shaped median thoracic tract comprised of white scales; legs I, II, IV distinctly ringed or banded with dark pigment alternating with white scales (Figures 8-9, 20-22) ..... *M. literatus*
- 3b. Eye region covered with uniform brown to red-brown scales, long, narrow, rectangular median thoracic tract comprised of white to ivory scales, legs I, II, IV with relatively few markings (Figure 52) ..... *M. pavonis*

- 4a. Fan with relatively uniform light brown or tan scale cover and either no parens, or a less distinct outer parens comprised mostly of light brown or tan scales (Figures 26-29, 37, 39-41, 54) ..... 5
- 4b. Fan with dark red-brown or orange-brown parens (Figures 2, 64) ..... 7
- 5a. Opisthosoma lanceolate; fan mostly covered with uniform tan or light-brown scales and few iridescent scales and no parens; distal part of dorsal cymbium usually darker or brown (Figures 26-29, 37) ..... *M. maritimus*
- 5b. Opisthosoma oval; fan with outer and inner parens of tan or light brown to orange or red-orange scales and background iridescent scales confined to narrow median tract and two lateral tracts between the parens; dorsal cymbium white or ivory (Figures 39-41, 54) ..... 6
- 6a. Eye region covered with nearly uniform brown scales without distinctive markings; long, narrow, rectangular median thoracic tract comprised of white to tan scales; orange scales at either end of indistinct outer parens; bright white setae on dorsal segments of pedipalp (Figure 54) ..... *M. pavonis*, var. *brunneis*
- 6b. Eye region covered with grey scales mixed with dark red-brown scales that may form an indistinct 'm' shape (as viewed from the rear); grey to white median thoracic tract wide (more than 1/3 width of posterior eye row) at front and tapering toward the rear; may have patches of red-orange scales at anterior and posterior ends of outer parens; off-white (ivory to grey) scales on dorsal segments of pedipalp (Figures 39-41) ..... *M. montanus*
- 7a. Light grey setae above and below anterior eyes; eye region covered with background of grey scales and a distinct 'm' figure (as viewed from the rear) comprised of dark red-brown scales; median thoracic tract narrow and pointed at posterior eye row; scattered orange-brown to ivory scales on sides of carapace; opisthosoma oval; fan with grey background scale cover; dark red or red-brown parens and distinct x-shaped butterfly; legs I, II, IV ringed or banded with alternating dark pigment and white setae; white setae present on tibiae and tarsi; anterior femora of legs III dark with grey to ivory setae (Figures 2, 6) ..... *M. leo*
- 7b. Orange-brown setae above and white setae below anterior eyes; eye region mostly covered with tan or light brown scales, with an indistinct dark red-brown figure toward the rear; median thoracic tract wide at posterior eye row; sides of carapace dark and glabrous; opisthosoma lanceolate; fan with uniform tan background scale cover; dark orange-brown outer parens extends to lateral margin, no butterfly; legs I, II, IV translucent with scattered white setae and dark pigment on distal margin of segments; no white setae on tibiae and tarsi; anterior femora of legs III light-brown and translucent with black dorsal and ventral stripes (Figure 64) ..... *M. watagansi*

### *Maratus leo*, new species

*Type specimens.* The holotype (♂ #1) and three paratypes (♂ #2-4) were collected near Brookside Road, Darlington, Adelaide, South Australia (S 35.02458°, E 138.56275°, 24 SEP - 3 OCT 2013, A. Leo coll.) and will be deposited in the South Australian Museum, Adelaide.

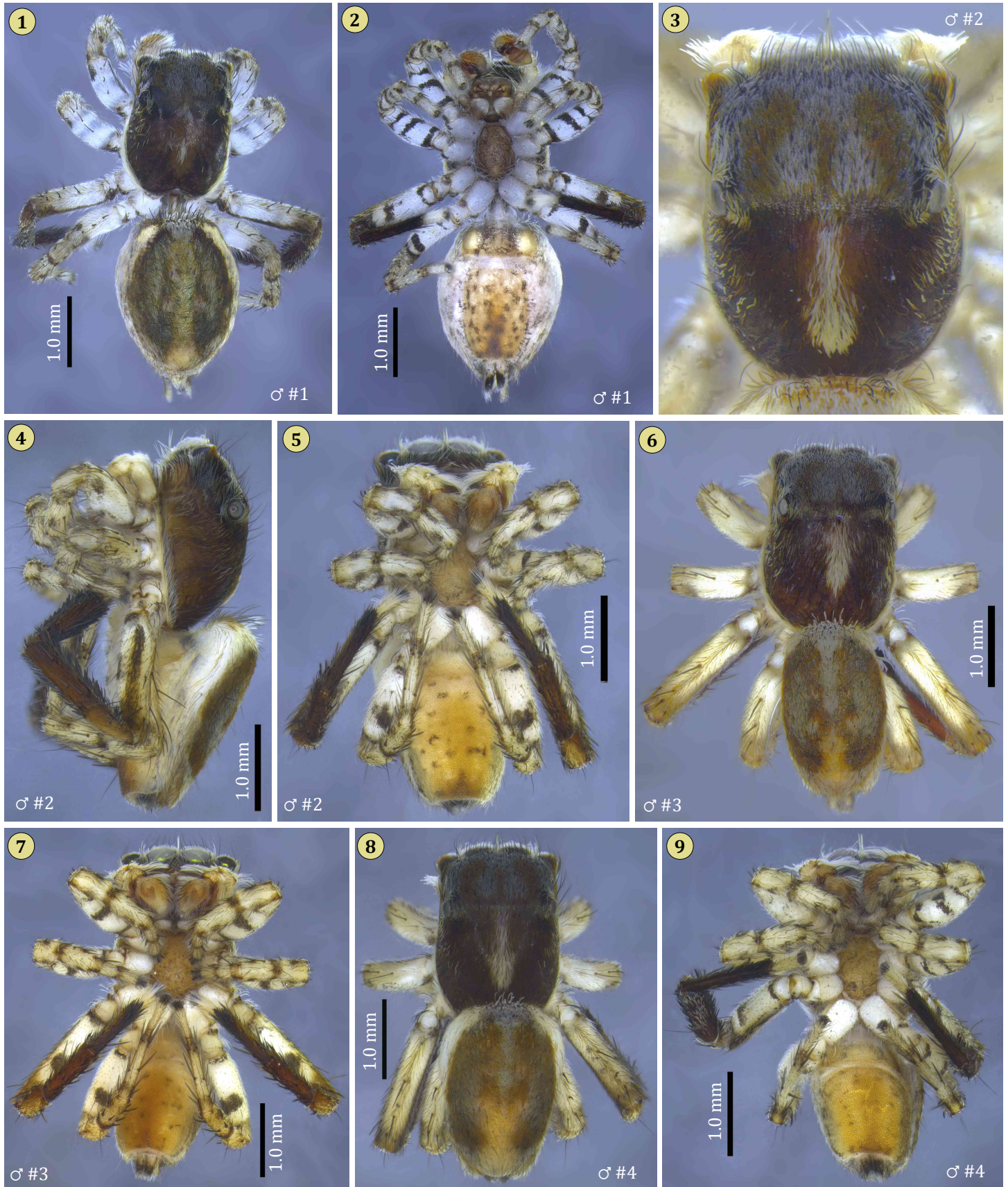
*Etymology.* The species group name (*leo*, nom., Latin) is a reference to the person who brought this spider to our attention and supplied the type specimens, Andrew Leo.

*Diagnosis.* *M. leo* is similar to *M. watagansi*, *M. maritimus*, *M. montanus* and *M. pavonis* var. *brunneis* in having a rather subdued colouration. *M. leo* can be distinguished from these by the presence of a distinct central butterfly figure on the opisthosoma and the relatively light colouration surrounding the dark parens, in particular posteriorly, and the complete absence of any iridescent scales. A central "butterfly" figure is also present in *M. splendens*, *M. pavonis* and *M. literatus*. However in these species the opisthosomal plate has many iridescent scales and the parens and butterfly figures are bright red instead of brown.

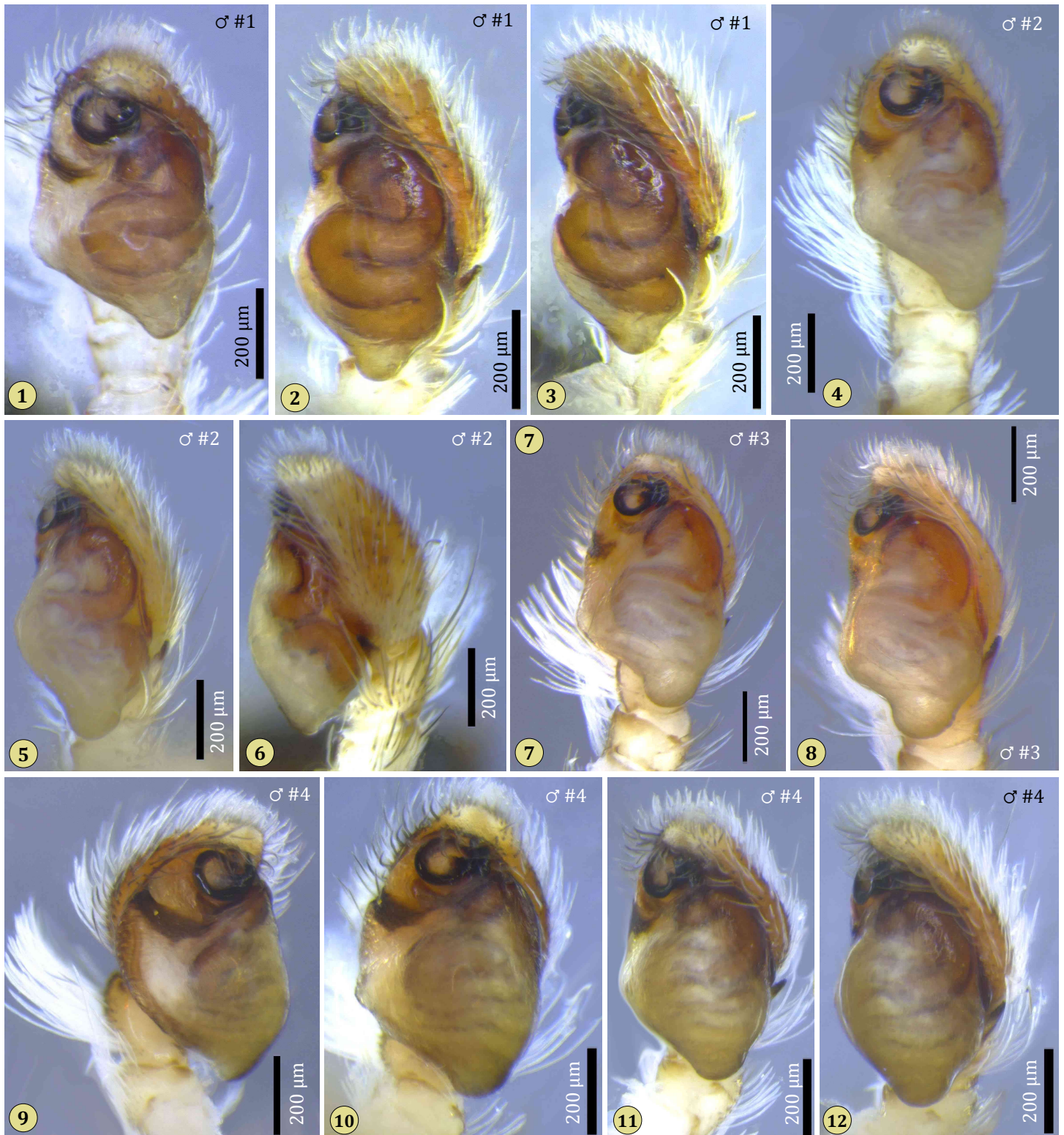
*Description of male* (Figures 2-5). The holotype and paratype males (N=4) range from 4.11 to 4.37 mm in body length, not including the spinnerets.



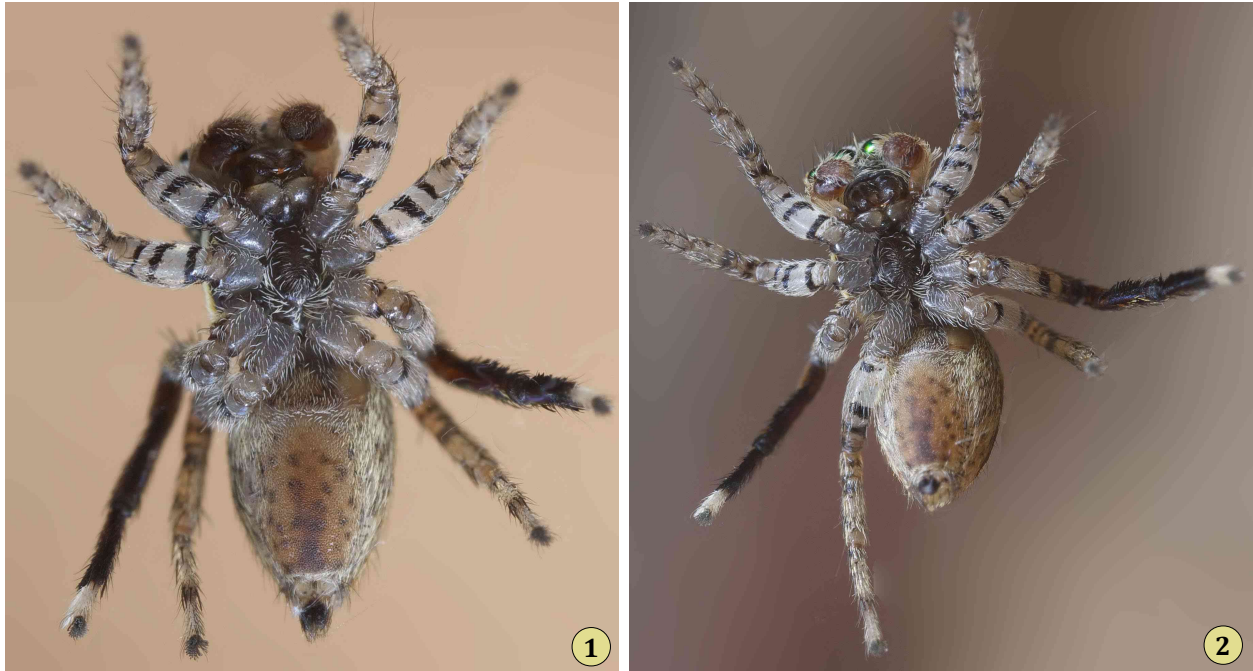
**Figure 2.** Living holotype ( $\sigma$  #1) and paratype ( $\sigma$  #2-4) *Maratus leo* from the type locality. At this locality, the 'm' figure of the eye region is discontinuous at the front. Each cymbium is distinctly darker than, and offset from, the pedipalp fringe, which appears as a bright line as the pedipalps are held in the horizontal position characteristic of the *pavonis* group. Background scales of the opisthosomal plate are predominately grey, with some mixing of dark red-orange scales in some individuals. Note the presence of both an outer parens and central butterfly, varying in colour from dark brown to dark red-orange. The contrast between these figures and the light background thus varies from high (2) to intermediate (6, 8) to low (5). The median thoracic tract is more diamond-shaped than rectangular. **9**, The sides of the carapace bear many dark orange-brown to ivory or grey scales, unlike the relatively glabrous carapace of *M. literatus*, *M. pavonis*, and *M. splendens*.



**Figure 3.** Holotype (♂ #1) and paratype (♂ #2-4) specimens of *Maratus leo* in ethanol.



**Figure 4.** Ventral views of left pedipalp of holotype (♂ #1) and paratype (♂ #2-4) specimens of *Maratus leo*. 7, Separation of the heavy apices of the inner and outer rings of the embolus is only visible when viewed from a certain direction.



**Figure 5.** Two views of the underside of the living holotype (♂ #1) *Maratus leo*. From below, each femur is translucent with scattered white setae and prominent bands of black pigment (three bands under legs I and II, two bands under legs III and IV).

The carapace and chelicerae are dark brown or black. The anterior eyes are bordered with grey scales above and below. Numerous but not dense grey setae are present on the dark clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with uniform grey scales, bounded laterally by dark orange-brown scales along each lateral eye row, and bearing toward the rear a distinct but often interrupted 'm' (as seen from the rear) comprised of dark orange-brown scales. Behind the PLE row, and to the sides, the carapace is mostly glabrous, with scattered grey or dark orange-brown scales. There is a median thoracic tract of ivory scales that tends to be pointed toward the front and rear (not rectangular), and extends at least half-way to the rear margin, and a prominent marginal band of bright white setae on either side. The PME are closer to the PLE than to the ALE.

The opisthosoma is oval to lanceolate in shape, with a distinct dorsal plate (fan) but without lateral flaps. Stout white setae project forward from this plate which is otherwise fringed with only scattered setae. The fan is mostly covered with light grey or light brown, but no iridescent, scales, and bears both an outer parens figure extending to the lateral margins and a central butterfly figure. These figures are dark red-orange to dark brown. Darker scales may also be mixed with the general background of light grey or light tan scales. The contrast between the dark figures and the light background of the fan varies (Figure 2). There is a small triangular tuft of grey setae just above the anal tubercle. Spinnerets are generally light in colour, but the distal end of each anterior spinneret is black. The ventral opisthosoma is brown with darker brown spots at the center, bordered laterally by tan setae of moderate length. The sternum and labium are dark brown, and the endites are light brown and translucent in living spiders. The coxae are grey, the trochanters light brown, and both are translucent. In preserved specimens the sternum, labium, coxae, and trochanters fade to white.

Legs I and II are about the same length, much shorter than legs III and IV. Legs III are by far the longest. Legs I, II and IV are similar in appearance. Femora of these legs are light in colour and translucent with three prominent black bands on the underside of femora I and II, and two black bands on the underside of femora III and IV. Distal to each femur alternating bands of white and brown setae in combination with darker pigmentation of the cuticle create a more or less distinct banding pattern on each segment. Femora of legs III are lighter proximally with many grey to ivory scales. Distal femora to patellae of legs

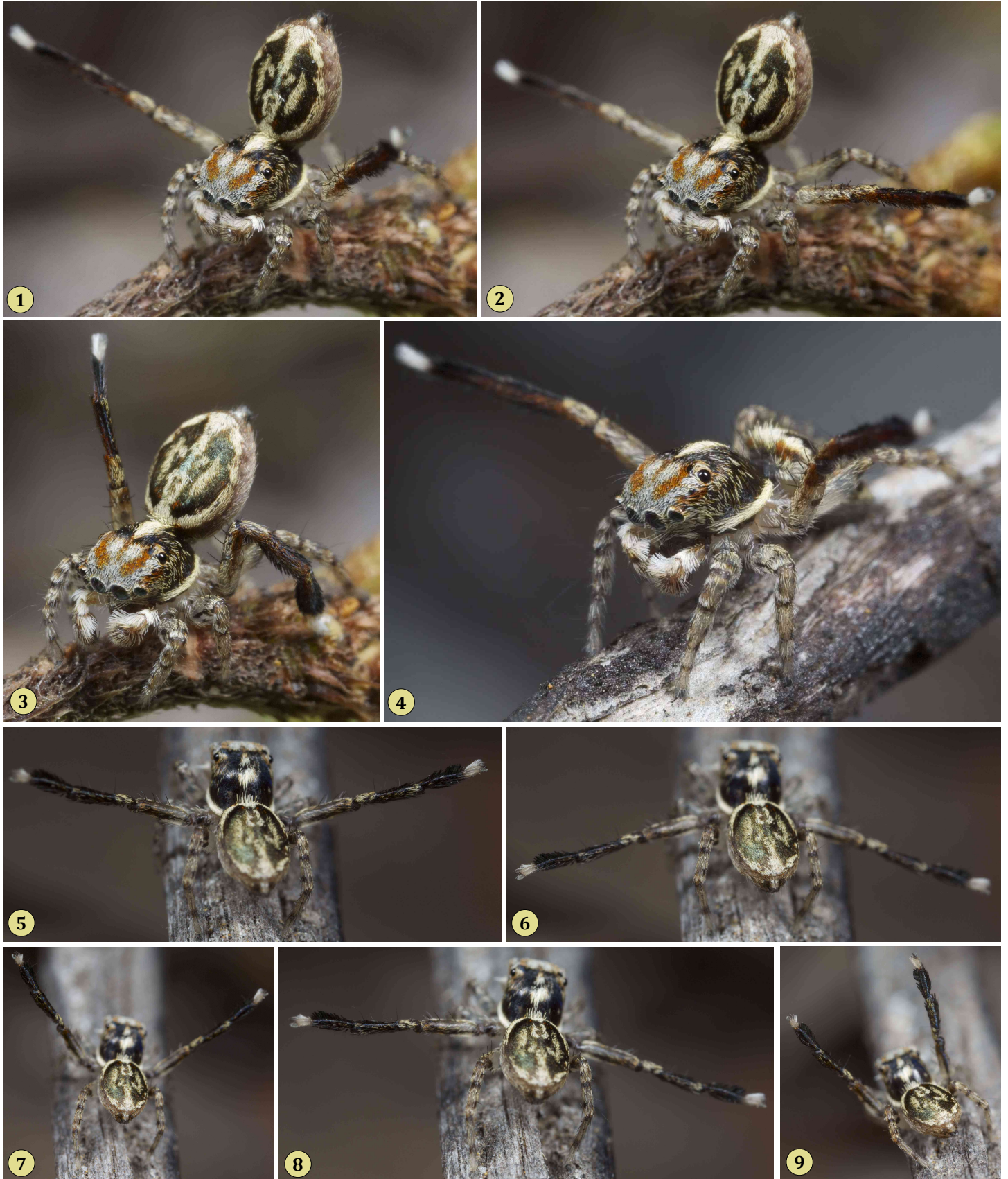
III are covered with lighter grey to tan scales dorsally, and dark orange-brown scales anteriorly. The tibia and metatarsus of these legs are dark orange-brown with brushes of long, stout black setae extending dorsally and ventrally. The cuticle of the tarsus III is light in colour and covered with dense, bright white setae that extend over the pretarsus. Tenent setae of the footpads are dark grey.

Proximal to the cymbium each pedipalp is fringed with many long ivory to white setae, and each cymbium is distinctly darker with more sparse setation, distinctly separated proximally from the rest of the pedipalp by darker cuticle. When viewed from below (Figure 4), each pedipalp is typical for members of the *pavonis* group, with apices of the inner and outer rings of the embolus in close contact or fused to form a single heavy apex, a medial sclerite of the tegulum, sclerotization of the lateral margin of the cymbium where it makes contact with the tegulum, and a retrolateral tibial apophysis (RTA) with a dark, pointed apex.

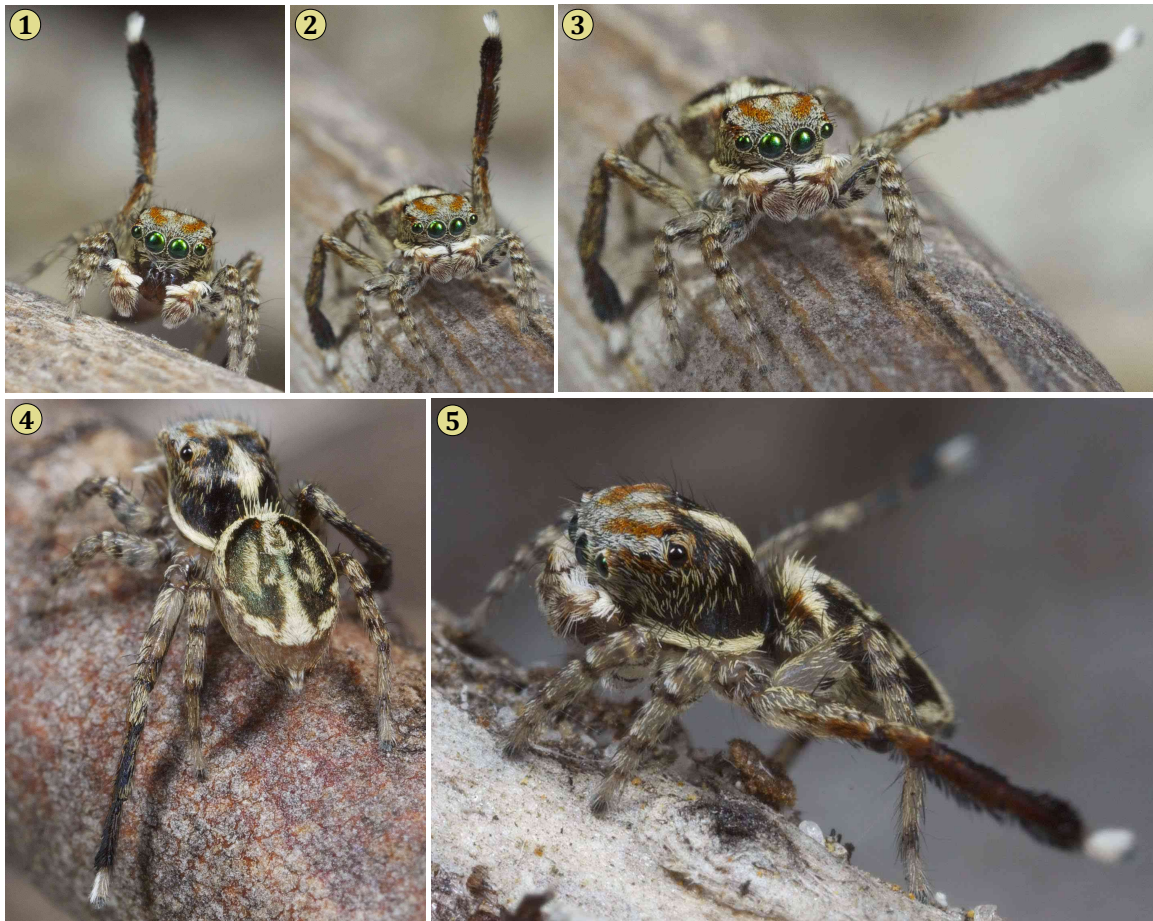
A population of spiders that we tentatively identify as *M. leo* has been reported from Bordertown, South Australia (Lance 2014a). Although the colouration and general appearance of this spider is much the same, the 'm' figure of the eye region is more continuous in front, and legs I, II, and IV are translucent light brown with relatively few setae and without prominent banding.

*Display by males* (Figures 6-7). Like *Maratus pavonis* (Hill & Otto 2011) and other species of *Maratus*, *M. leo* males appeared to advertise their presence by rapidly raising either a single leg or both legs III and then lowering them in a series of small steps (almost continuously) to the side over a 0.5-3.2s cycle, while at the same time keeping the opisthosoma still. After they were lowered, legs III were often kept in a lower position for extended periods, bobbing up and down over a short distance. Frequently the legs were held towards the rear. When encountering a female (of a different species) the opisthosoma started to vibrate with increasing frequency, followed by a sudden and extremely rapid bout of "tapping" during which legs III are raised and lowered at a rate of 20-22 cycles per second. Visible in high speed video, each time the legs III are raised the opisthosoma is lowered onto the substrate and seemingly scraped along it. This "tapping" behaviour is similar to what we have described for *M. pavonis* and *M. splendens* (Hill & Otto 2011) and now not only observed in all other species of the *pavonis* group but also in *M. amabilis* (Otto 2013) and *M. harrisi*. In *M. harrisi* the "tapping" produced an audible sound when the display was performed on a dry leaf. Such sounds were previously also noted by Waldock (2007) for *M. pavonis* and had been attributed to the legs hitting the surface. However, according to Girard and Endler (2014), although males appear to be drumming their third legs on the ground, the majority of percussive energy is produced through abdominal contact with the substrate. In between bouts of "tapping" both legs III were raised vertically quickly and slowly lowered, before a renewed sequence of opisthosomal bobbing and tapping. On two occasions a male of *M. leo* was also observed raising its opisthosoma by about 45° (Figure 6), waving his legs III a couple of times and taking a few steps to the side. This resembled the fan dance of other species. The fact that this form of display was employed only rarely suggests that it is only of minor importance in the courtship of this species. Like other members of the *pavonis* group (*M. literatus*, *M. montanus*, *M. pavonis*, and *M. splendens*), male *M. leo* often flexed their legs III at the tibio-metatarsal joint at a rate of 1-8/s while vibrating legs III.





**Figure 6.** Display by the holotype ( $\sigma$  #1) *Maratus leo*. **1-3**, Partial elevation of the fan, with little or no lateral movement, was infrequently observed. **4-9**, Semaphore display was bilaterally symmetric as shown here, with pauses to vibrate the extended legs III up at down in a variety of different elevations, and bouts of tapping where the opisthosoma touched the substrate rapidly (20-22 cycles/s).



**Figure 7.** Display by the holotype ( $\sigma$  #1) *Maratus leo*. **1-3**, Single leg wave. This display or advertisement is thought to represent a way for the male to elicit movement of a female that may not be directly observable in the vicinity. After quickly elevating one leg to a near-vertical position, it would be lowered continuously to the side. **4-5**, This position, with one or both legs III extended to the rear, has been observed in other members of the *pavonis* group.

### *Maratus literatus*, new species

*Maratus pavonis*, variety *m-signitis* Otto & Hill 2012b, 2012c

*Maratus pavonis* : Otto & Hill 2013 (Figure 30:1-4)

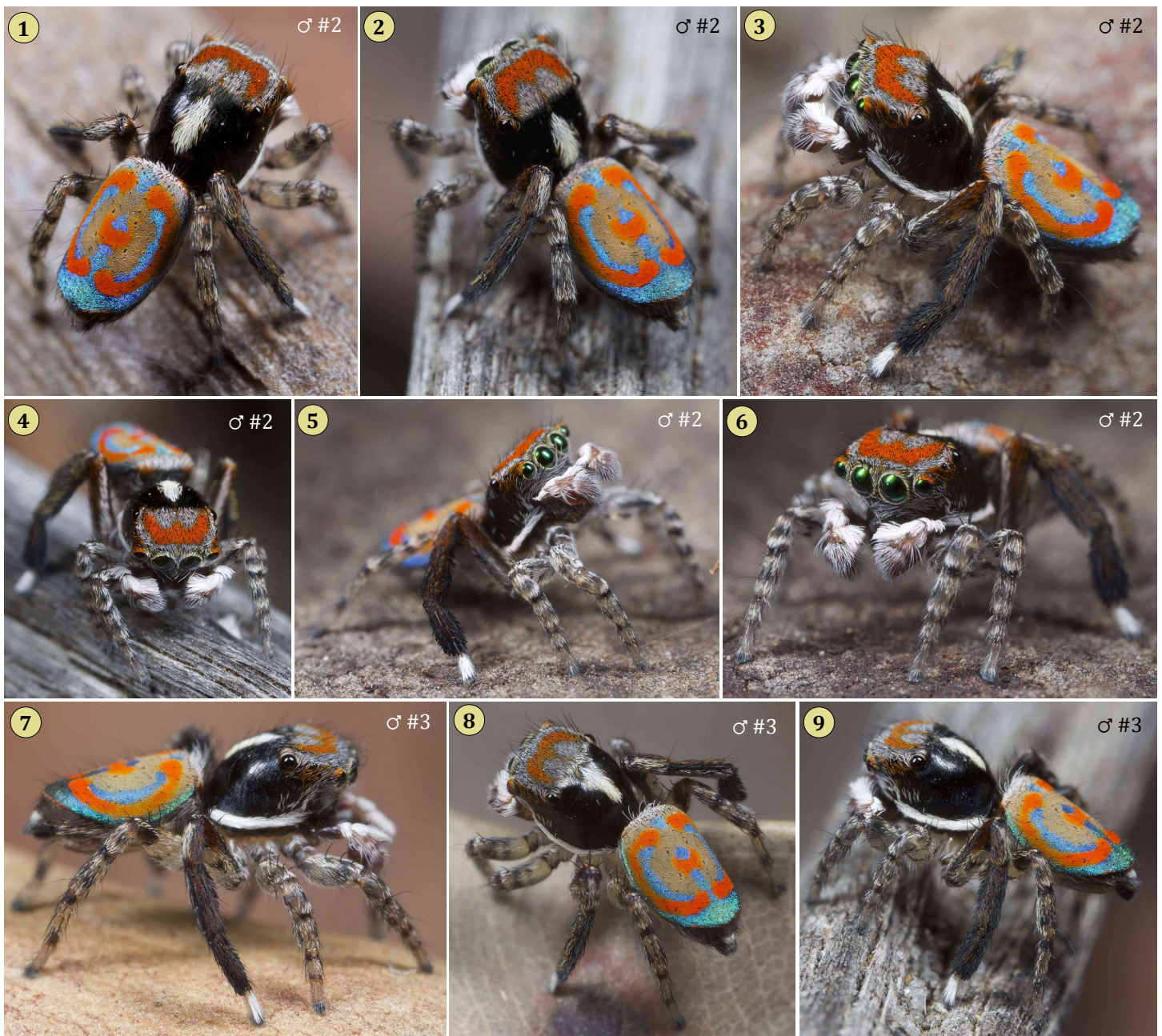
*Type specimens.* The holotype male ( $\sigma$  #2), one paratype male ( $\sigma$  #3) and one paratype female were collected as penultimates at Coleambally, New South Wales (S 34.87242°, E 145.94353°, 9 MAY 2014, J. Otto coll.). Another paratype male ( $\sigma$  #1) was collected earlier at the same location (20 SEP 2012, J. Otto coll.). All types will be deposited in the Australian Museum in Sydney.

*Etymology.* The species group name (*literatus*, adj., Latin) means *lettered*, a reference to the prominent 'm' figure (as viewed from the rear) of the eye region of males (less prominent in females).

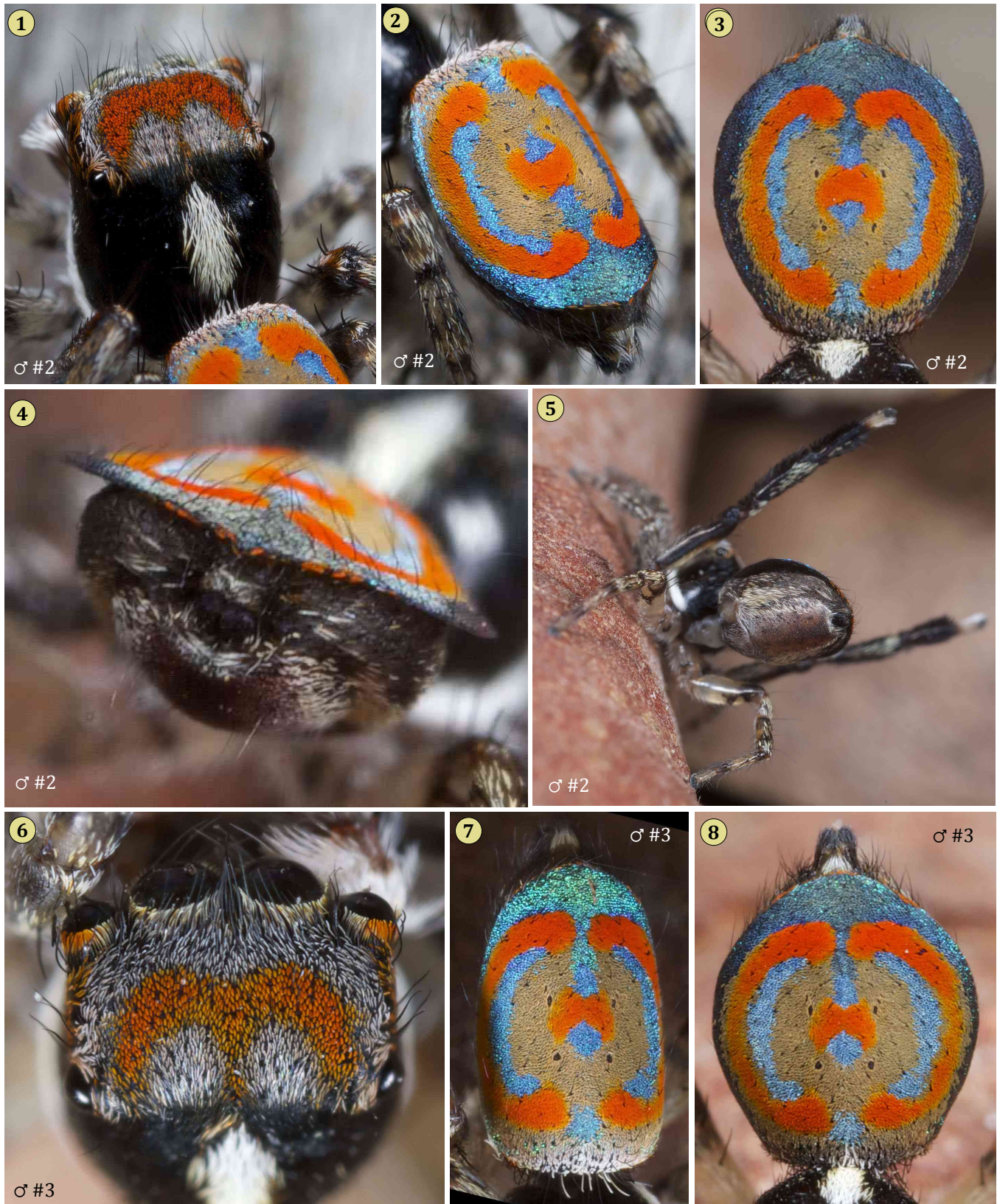
*Diagnosis.* Male *M. literatus* resemble the brightly coloured males of *M. pavonis* and *M. splendens* in many respects, but can be readily distinguished by the presence of a bright red-orange 'm' (as viewed from the rear) on a grey background of scales in the eye region. The eye region of *M. pavonis* is covered with uniform brown to orange-brown scales, while that of *M. splendens* bears a prominent crescent of blue iridescent scales on a bright red background. Legs I, II, and IV of *M. literatus* are ringed or banded with dark pigment at the proximal end of each segment, and many white setae or scales distally; those of *M. pavonis* and *M. splendens* are more translucent with relatively few markings. The median thoracic tract of

*M. literatus* is diamond-shaped (pointed at front and rear) like that of *M. splendens*; this tract is longer and rectangular in *M. pavonis*. Unlike the eastern *M. pavonis* (Dunn 1947), the fan of *M. literatus* males has lateral flaps that are expanded during display. *M. literatus* also have a heavy apex of the embolus (similar to *M. pavonis*), not clearly divided into two parts as in *M. splendens* (Figure 30 in Otto & Hill 2013). *M. literatus* females differ from those of *M. splendens* by the absence of a dark rim along margins of the carapace, from *M. montanus* and *M. watagansi* by the presence of a relatively wide band of scattered white setae along the margins of the carapace, and from *M. maritimus* by the lack of distinct white spots on the posterior opisthosoma.

*Description of male* (Figures 8-13). The holotype and paratype males (N=3) range from 3.96 to 4.27 mm in body length, not including the spinnerets.



**Figure 8.** Living holotype (♂ #2) and paratype (♂ #3) *Maratus literatus*. The bright colours resemble those of the related *M. pavonis*, but the prominent letter 'm' (red to red-orange on a grey background) of the eye region, the diamond-shaped median thoracic tract, and the banded legs I, II, and IV readily identify this species. The lateral flaps of the dorsal opisthosomal plate are not evident in these views (see Figure 9).



**Figure 9.** Details of the living holotype (♂ #2) and paratype (♂ #3) *Maratus literatus*. The lateral flaps can be seen in (4) and (5). Note the difference between retracted (2 and 7) and expanded (3 and 8, respectively) lateral flaps.

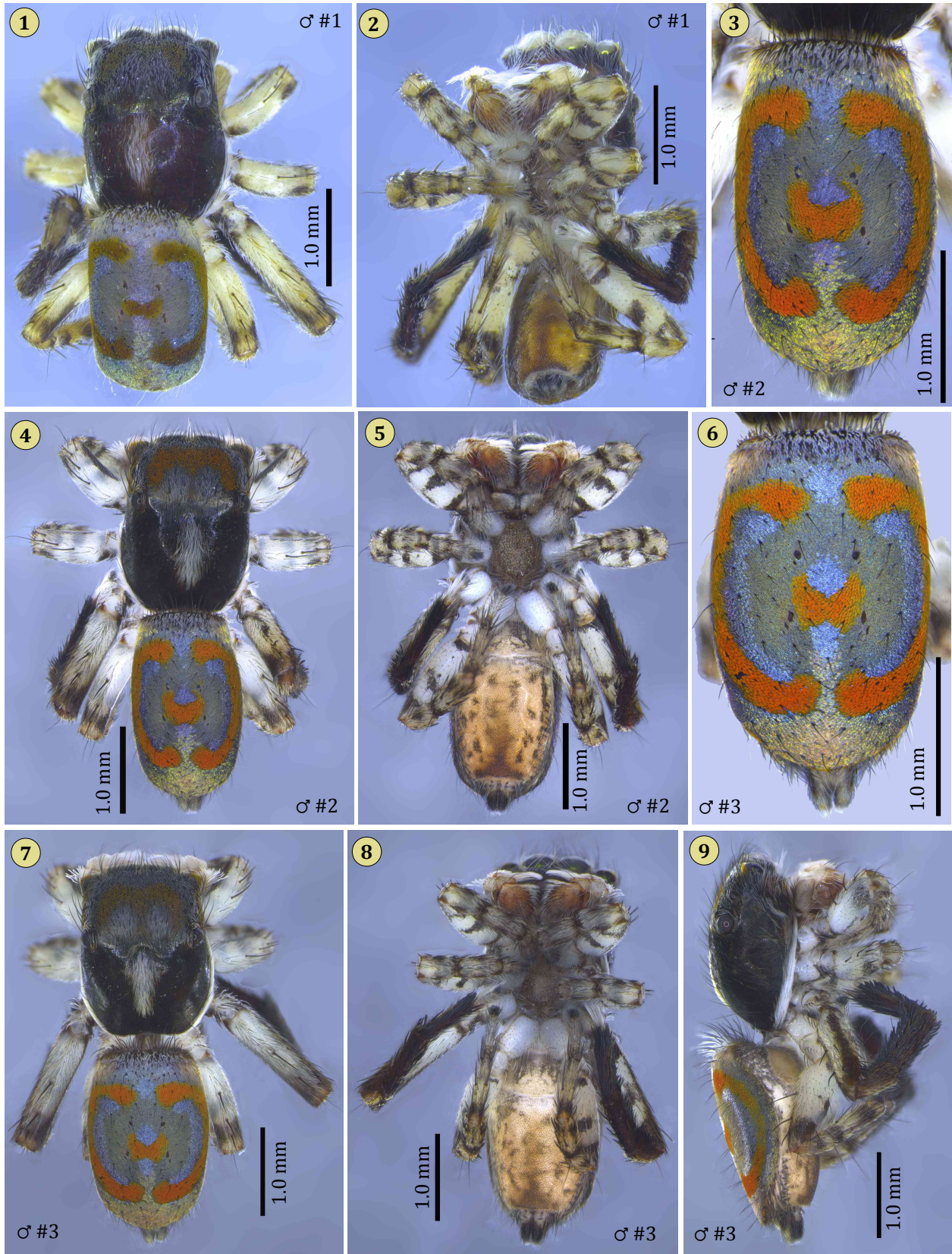
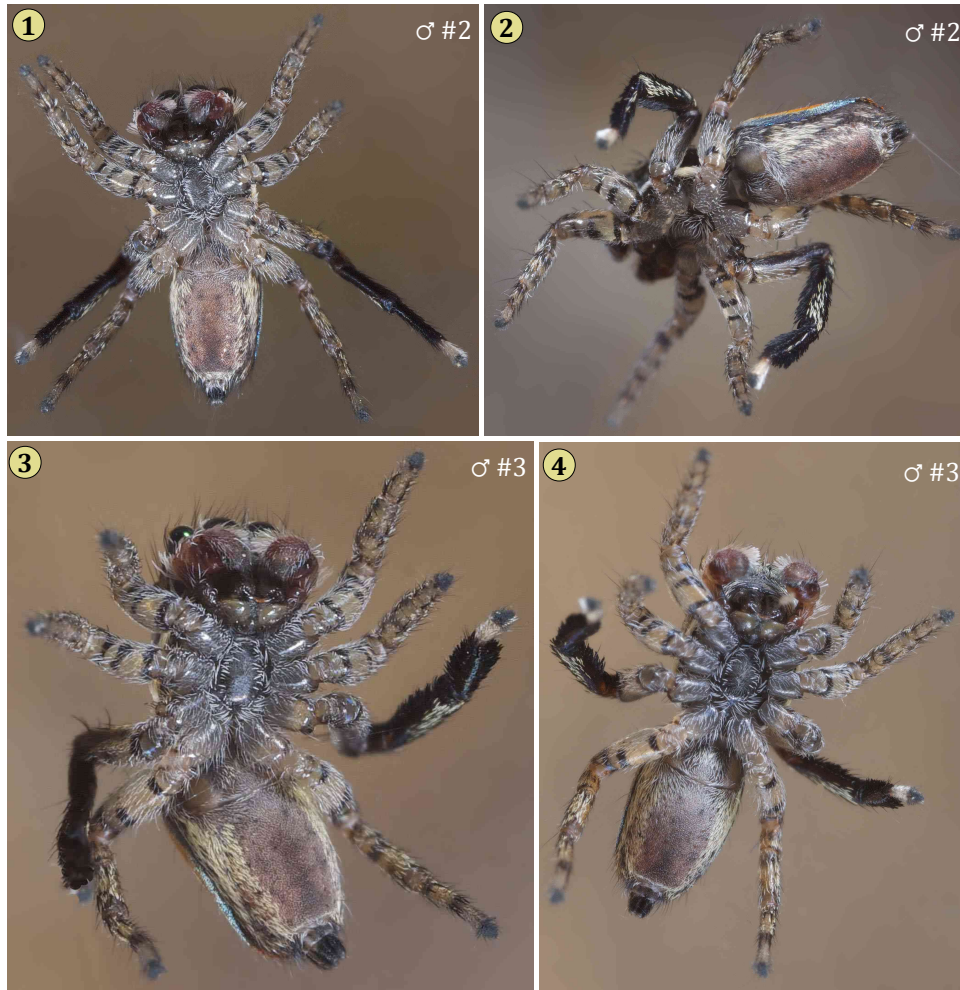
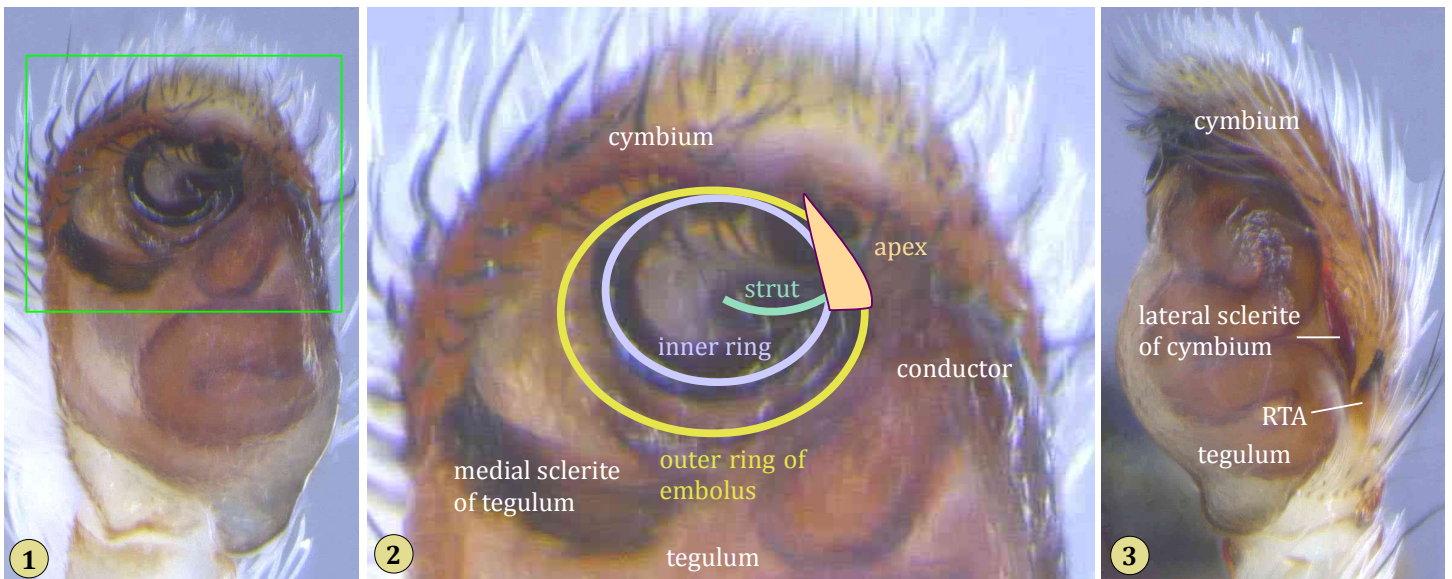


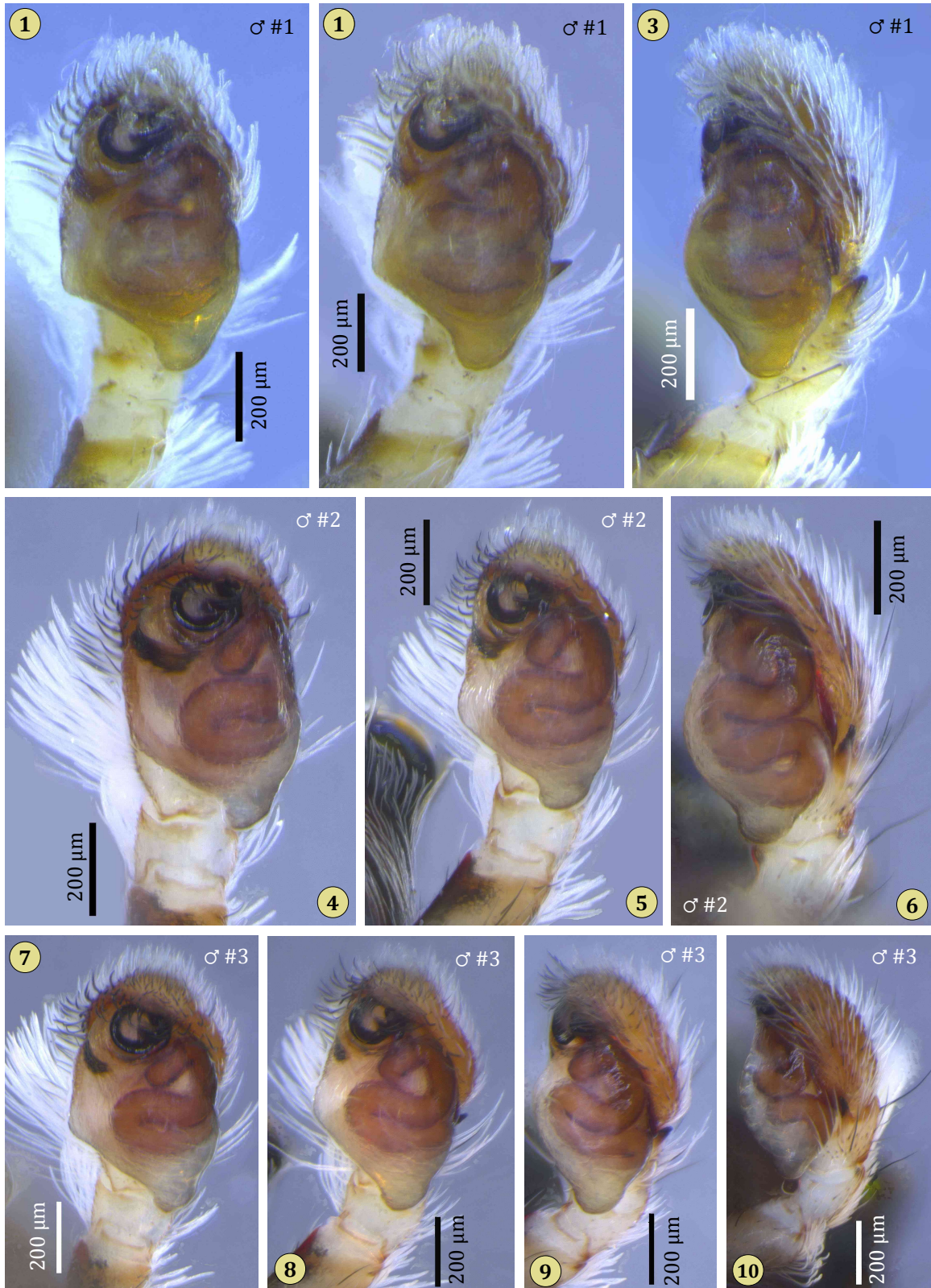
Figure 10. Holotype (3-5) and two paratype (1-2, 6-9) *Maratus literatus* in ethanol.



**Figure 11.** Underside of living holotype (1-2) and paratype (3-4) *M. literatus*.



**Figure 12.** Underside of the left pedipalp of the holotype ( $\sigma$  #2) *M. literatus*, showing important features. **2**, Diagrammatic detail of inset from (1). The apex associated with the ends of both inner and outer rings of the embolus is dark or heavy without distinct separation of an inner and outer apex as in *M. splendens*.



**Figure 13.** Underside of the left pedipalp of the holotype (♂ #2) and two paratype (♂ #1, 3) *Maratus literatus*.

The carapace and chelicerae are dark brown or black. The anterior eyes are bordered with grey scales above and below. Scattered but not dense long grey setae are present on the dark clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with uniform grey scales, bounded laterally by dark orange-brown scales along each lateral eye row, and bearing toward the rear a distinct 'm' (as seen from the rear) comprised of bright red to red-orange scales. Behind the PLE row, and

to the sides, the carapace is glabrous, except for a dense marginal band of bright white setae. The median thoracic tract is pointed toward the front and rear (not rectangular), comprised of bright white scales, and extends half-way to the rear margin from the posterior eye row. The PME are closer to the PLE than to the ALE.

The opisthosoma is oval to rounded in shape, with a brightly coloured dorsal plate similar to that of *M. pavonis* in appearance and colouration (background of iridescent blue-green and some mixed tan scales, outer parens and butterfly of bright red-orange scales, and inner parens of tan scales), but bearing distinct lateral flaps. Several stout white setae project forward from this plate which is otherwise fringed with only scattered setae. There is a small triangular tuft of grey setae just above the anal tubercle. Spinnerets are dark grey in colour. The ventral opisthosoma is brown with darker brown spots at the center, bordered laterally by tan setae of moderate length. The coxae, sternum, endites and labium are grey in living spiders, but fade to white in preserved specimens.

Legs I and II are about the same length, much shorter than legs III and IV. Legs III are by far the longest. Legs I, II and IV are similar, banded with darker cuticular pigment at the proximal end, and many white scales toward the distal end, of each segment. Femora of legs III are dark, black proximally and dark red distally in living spiders with a prominent white stripe anterodorsally and less prominent white stripes ventrally or posteriorly. The femora fade to white in ethanol. From the patella to the metatarsus legs III are dark red-brown, fringed with heavy black setae that are most prominent on the metatarsus. The tarsus is covered with bright white setae and the footpads (tenae or tenent setae) are grey.

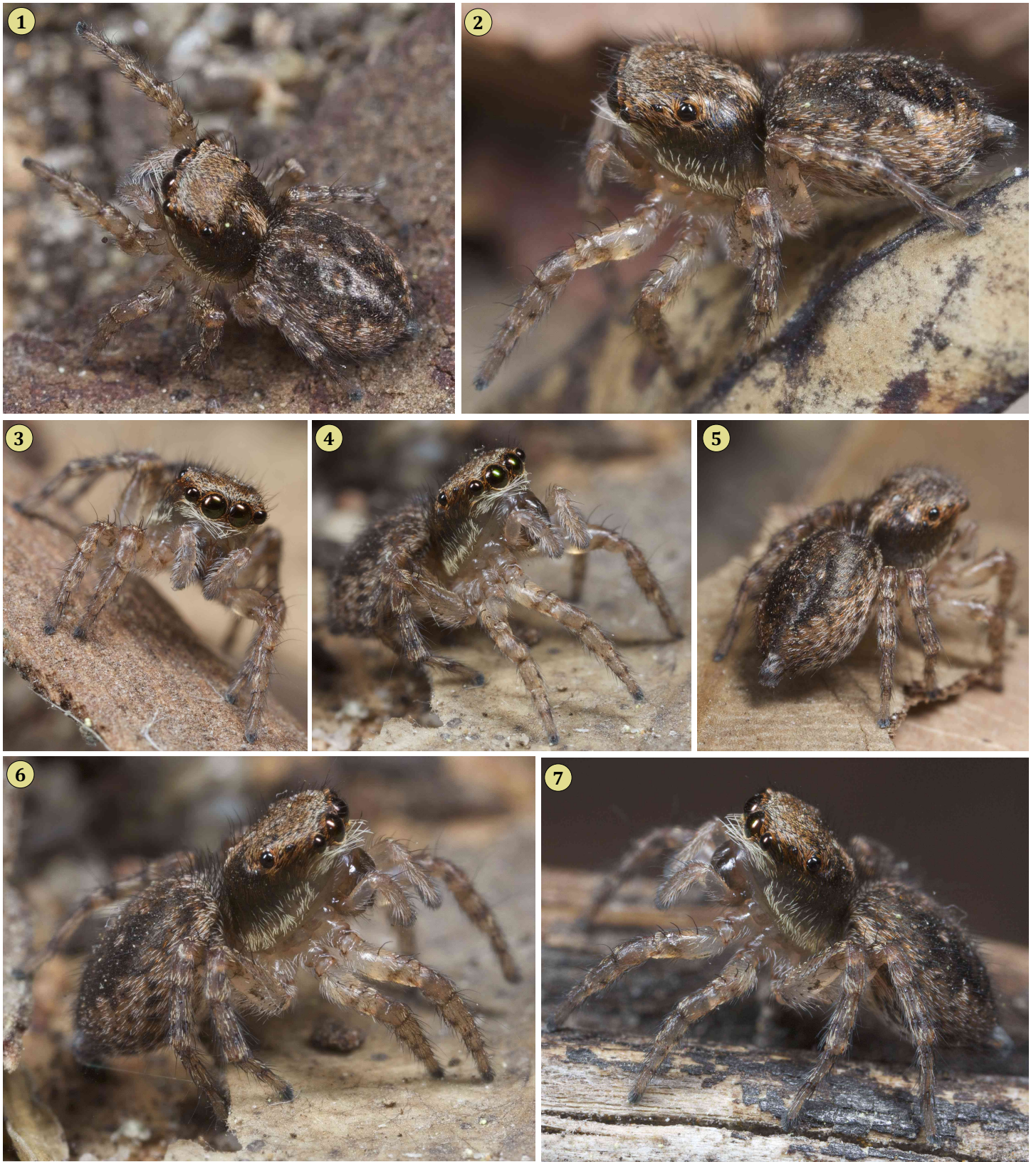
Proximal to the cymbium each pedipalp is fringed with many long, bright white setae, and each cymbium is distinctly darker with more sparse setation, distinctly separated proximally from the rest of the pedipalp by darker cuticle. When viewed from below (Figures 12-13), each pedipalp is typical for members of the *pavonis* group, with apices of the inner and outer rings of the embolus in close contact or fused to form a single heavy apex, a medial sclerite of the tegulum, sclerotization of the lateral margin of the cymbium where it makes contact with the tegulum, and a retrolateral tibial apophysis (RTA) with a dark, pointed apex.

*Description of female* (Figures 14-17). The single paratype female is 5.00 mm in body length, not including the spinnerets.



**Figure 14.** Carapace of the living paratype female *Maratus literatus*. **1**, Original photograph. **2**, Photograph (1) coloured to highlight an indistinct 'm' (actually comprised of brown scales) as viewed from the rear. Note the red-brown scales bordering the anterior eyes. The marginal band bears only scattered setae, and the median thoracic tract is much darker and less distinct than that of the male, but of similar shape.

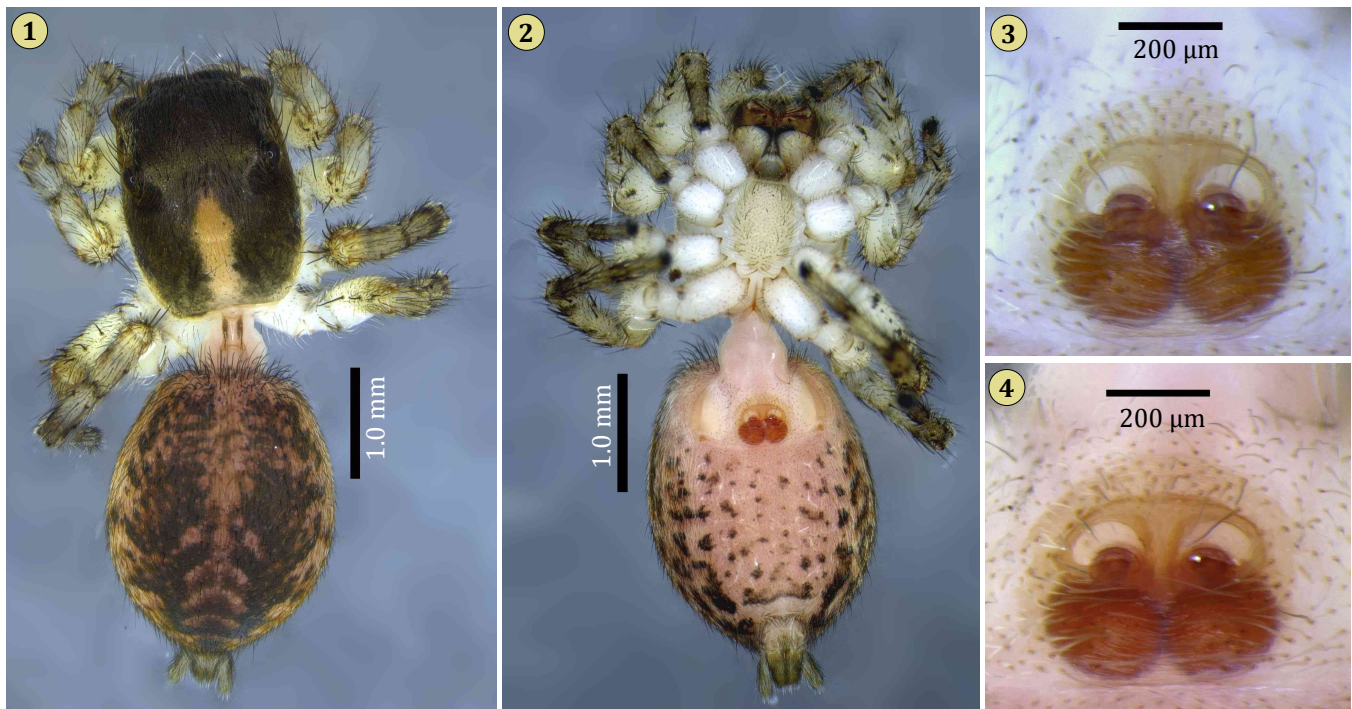




**Figure 15.** Living paratype female *Maratus literatus*. Note the broad marginal band of the carapace comprised of scattered long scales or setae, and the mottled sides of the opisthosoma. Banding of legs III-IV is more distinct than banding of legs I-II.



**Figure 16.** Two views of the underside of the living paratype female *Maratus literatus*.



**Figure 17.** Paratype female specimen, *Maratus literatus*. As with the male, the grey or brown colours of the underside of the prosoma and the legs fade to white in ethanol. **3-4**, Two views of the epigynum.

The carapace and chelicerae are dark brown. The chelicerae are glabrous. Anterior eyes are bordered with dark red-brown scales. Scattered but not dense long grey setae are present on the dark clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with mixed brown grey scales, bounded laterally by dark orange-brown scales along each lateral eye row, and bearing an indistinct 'm' (as seen from the rear) comprised of brown scales. Behind the PLE row, and to the sides, the dark brown carapace is mostly glabrous, with scattered red-brown to ivory scales and a distinct band of ivory scales along the margin. The median thoracic tract is pointed toward the front and rear (not rectangular), comprised of mixed ivory to tan or brown scales, and extends half-way to the rear margin from the posterior eye row. In ethanol this tract appears as a distinct white, unpigmented stripe. The PME are closer to the PLE than to the ALE.

The dorsal opisthosoma is dark brown and mostly glabrous with only scattered ivory to red-brown scale cover. The sides are mottled with brown spots and covered with ivory to tan setae of moderate length. There is a cover of short but not dense tan setae across the mottled venter. As in males, the coxae, sternum, endites and labium are grey in living spiders, but fade to white in preserved specimens.

Legs I and II are about the same length, much shorter than legs III and IV which are of similar length. The legs are mostly translucent, light brown and only weakly banded, with this indistinct banding more evident for legs III and IV.

Fossae of the epigynum are relatively small and oval or bean-shaped but separated by a wide septum and distinctly rimmed, about half of the diameter of the large, contiguous posterior spermathecae. Darkly sclerotized ducts visible through the fossae are rounded and about  $3/5$  the diameter of the fossae, situated at the rear of the fossae.

*Immatures.* Penultimate males and the penultimate female paratype are shown in Figures 18-19. At this stage, both sexes have the 'm' pattern of the eye region, but this is much less distinct than in the adult male. The penultimate male is more boldly marked than the penultimate female, and has the distinct banding of legs I, II and IV as observed in adults, but no special decoration of legs III. The female is much more translucent at this stage than the male, with only scattered setae comprising a less distinct marginal band on either side of the carapace.

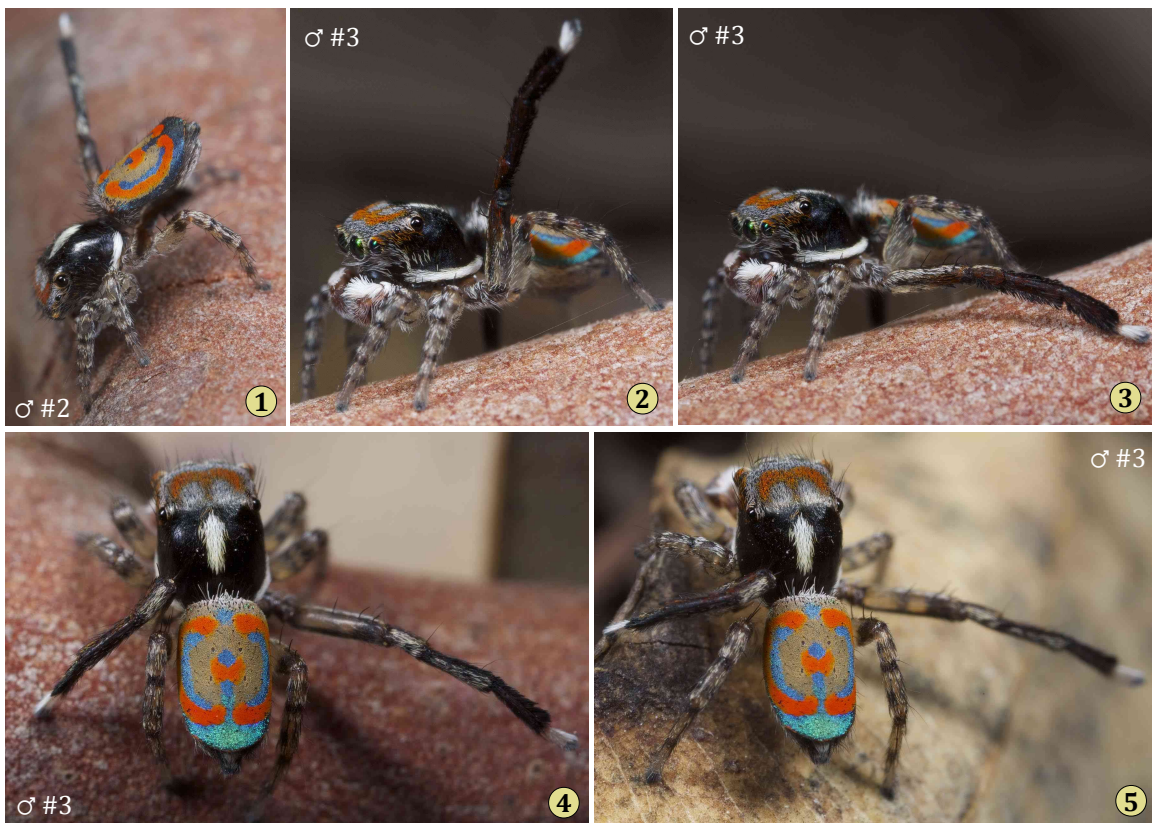


**Figure 18.** Penultimate holotype (1-2) and paratype (3-4) male *M. literatus*. At this stage the dark, glabrous sides of the carapace, the distinct marginal band, the banded legs, and some of the patterning of the dorsal carapace and opisthosoma characteristic of the adult male can be seen.

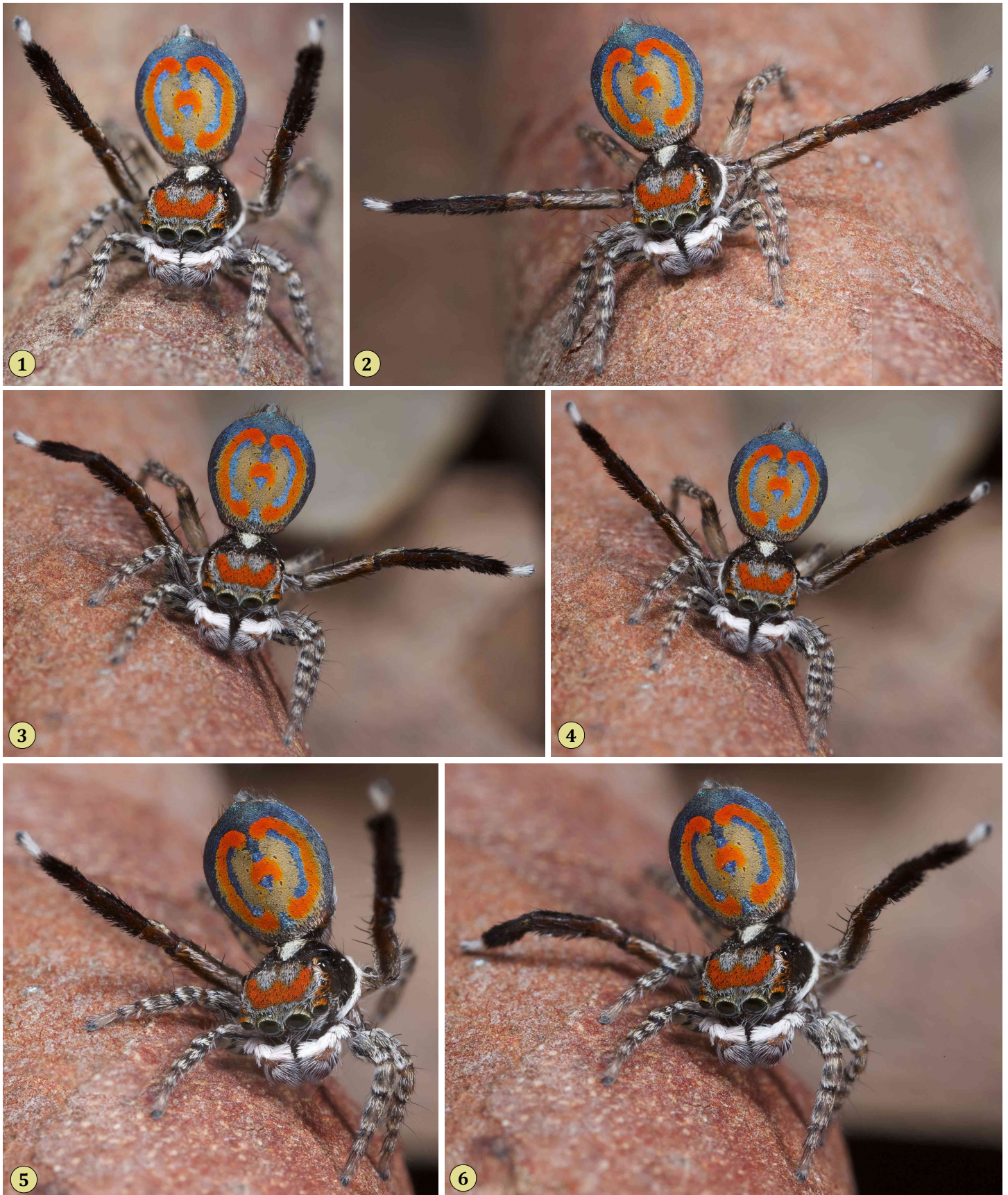


**Figure 19.** Penultimate female paratype, *M. literatus*. The penultimate female is relatively translucent with less bold colouration than the penultimate male.

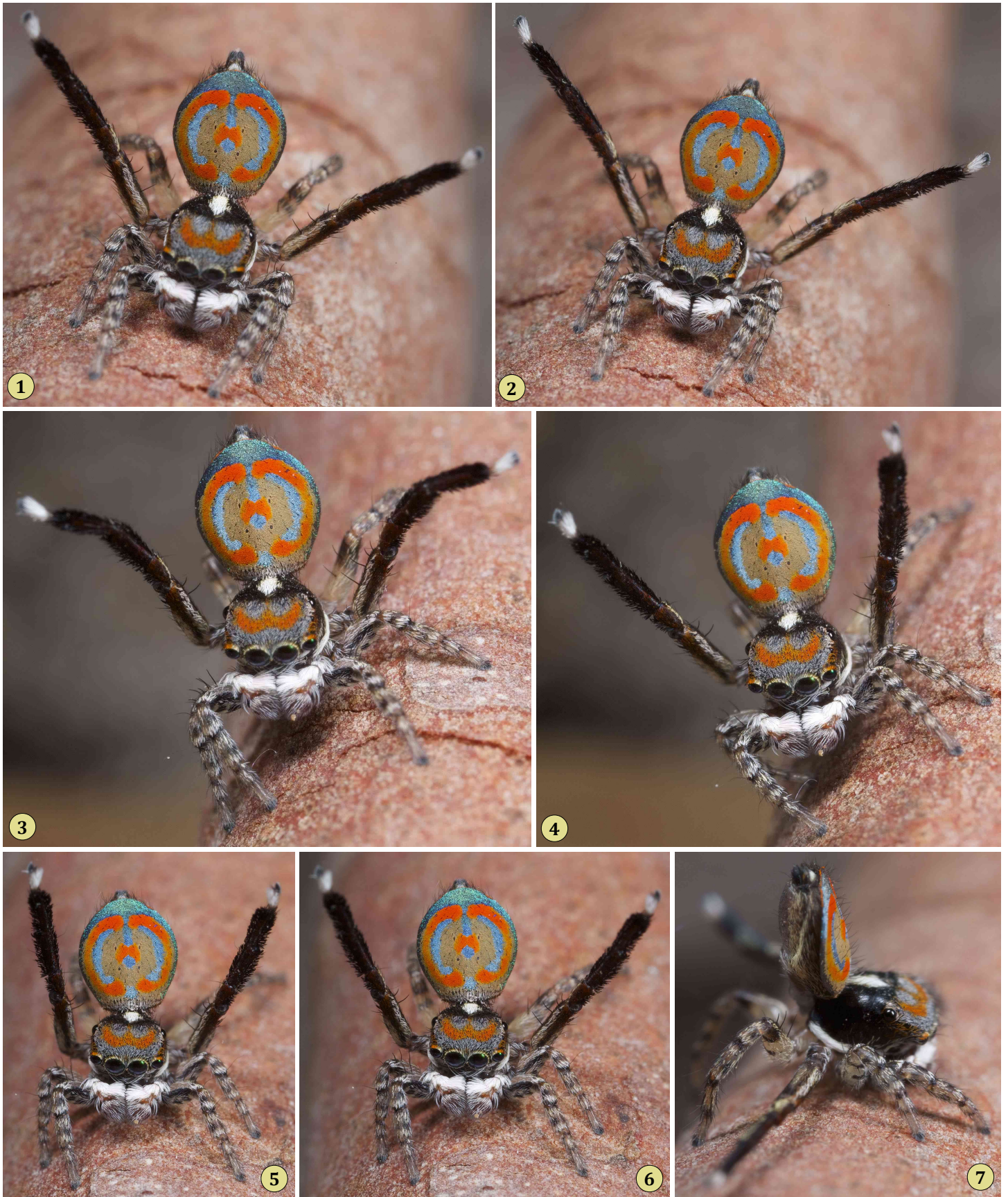
*Display by males* (Figures 20-22). The male *Maratus literatus* that we observed exhibited the range of display behaviour that we reported previously for *M. pavonis* and *M. splendens* (Hill & Otto 2011), with the exception that the bouts of rapid tapping (similar to those described for *M. leo*) appeared much more frequently in *M. literatus*. As with *M. pavonis* and *M. splendens*, the single leg wave of *M. literatus* was often accompanied by rapid (2-3 cycles/s) up and down movement of the two pedipalps in unison. During the fan dance, *M. literatus* males raised and flattened their fan with extended flaps, and like *M. pavonis* (but not *M. splendens*) continuously waved (5-10 cycles/s) the fan even when legs III were not moving. During the fan dance of all three species, legs III were waved up and down in a 'V' position (half elevated), and metatarsi were flexed as legs III were waved at a rate of 1-8 cycles/s.



**Figure 20.** Leg waving by male *Maratus literatus*. One or both legs III were held to the side and generally to the rear when waved up and down quickly during this display. This display is thought to be a general advertisement, used to elicit movement leading to the detection of a nearby female.

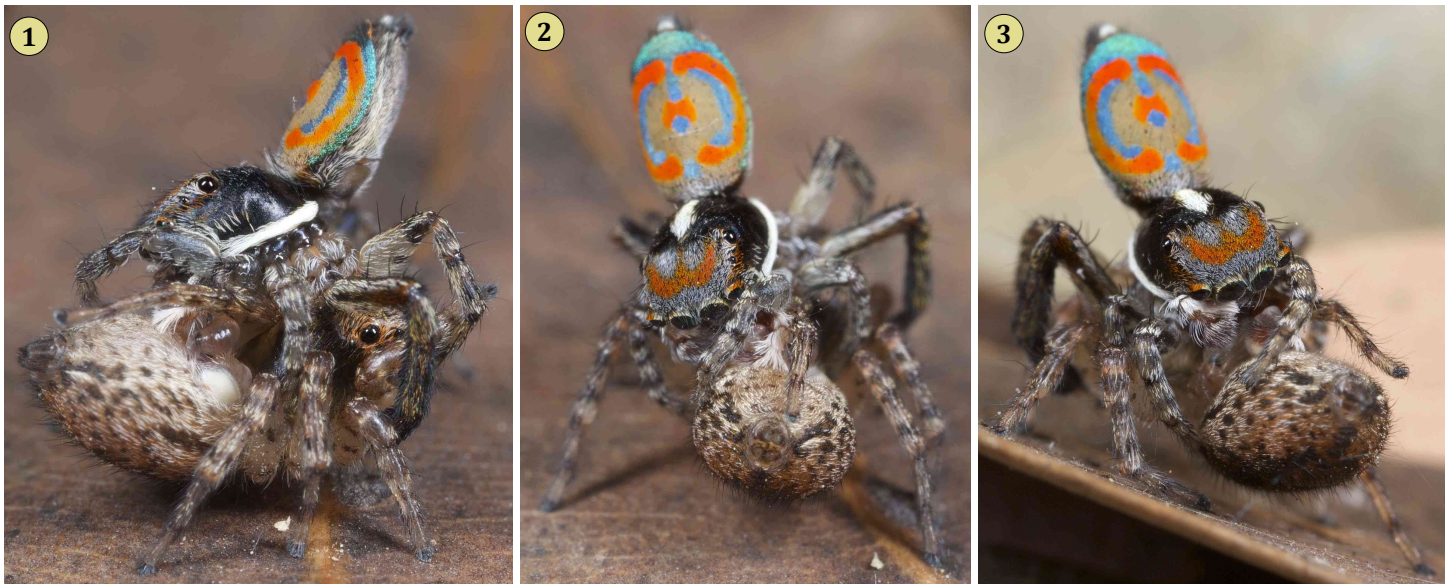


**Figure 21.** Fan dance by holotype ( $\sigma$  #2) facing the paratype female *M. literatus*. Note the flexion of the metatarsus in (3) and (6).



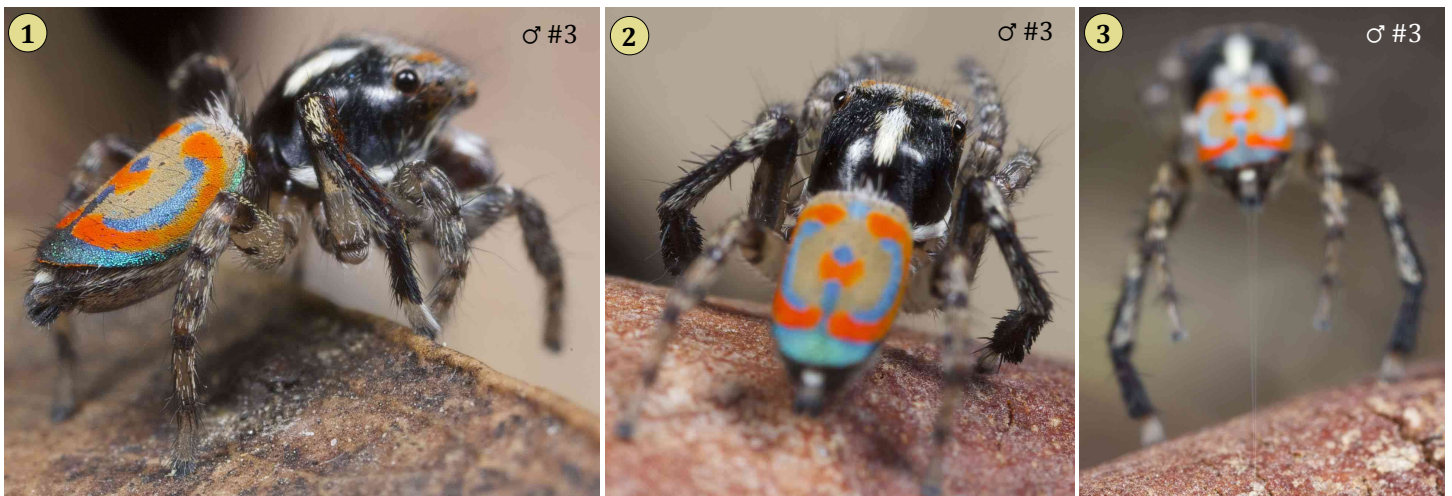
**Figure 22.** Fan dance by a paratype (♂ #3) facing the paratype female *M. literatus*. **1-2**, Note the change in orientation of the fan between these two positions. **3**, Flexion of the metatarsus (at the tibio-metatarsal joint) occurred as the extended legs III were waved in a transverse plane 1-8 cycles/s.

*Other behaviours.* As in all other *Maratus* species in which we have previously observed mating, the flexible female opisthosoma was rotated by 180° and the male inserted a pedipalp on one side, then the female opisthosoma was rotated by 360° in the opposite direction (through the original position) and the male would insert the other palp on the other side (Figure 23).



**Figure 23.** Mating by a paratype male (♂ #3) and the paratype female of *Maratus literatus*, showing rotation of the female opisthosoma.

We previously (Otto & Hill 2013) described kinematics of a jump by *M. watagansi*, essentially powered by the extension of legs III in a transverse or oblique plane to either side of the spider. Here (Figure 24) we show several stages during the jumps of a male *M. literatus*. This supports the earlier observation (Waldock 2007) that *Maratus* do not extend their flaps like wings to take flight.



**Figure 24.** Stages during three separate jumps by a male *M. literatus*. 1, Legs III flexed and positioned. 2, Legs I and II elevated as the spider prepares to rock forward with extension of legs IV. 3, Near-takeoff position, with legs III still extending well after legs IV have left the surface. Even though image (3) is out of focus, the flaps appear to be folded.

*Habitat.* *Maratus literatus* was found on small shrubs and litter surrounding a pond at the type locality near Coleambally (Figure 25).



**Figure 25.** Two views of the type locality of *M. literatus* near Coleambally, in the interior of New South Wales.

### ***Maratus maritimus*, new species**

*Type specimens.* The holotype male (♂ #5), five paratype males (♂ #2-3, 8-9) and nine paratype females (♀ #3-11) were collected at Pine Grove Holiday Park, Esperance, Western Australia (S 33.83208°, E 121.89040°, 9 OCT 2013, J. Otto coll.). Other paratypes include one female (♀ #1) from Woody Lake, Esperance (S 33.80695°, E 121.93526°, 6 OCT 2013, J. Otto coll.), one male (♂ #1) from Mullet Lake Nature Reserve, Esperance (S 33.79363°, E 121.98832°, 7 OCT 2013, J. Otto coll.), and two males (♂ #6-7) from Woody Island near Esperance (S 33.96145°, E 122.01980°, 8 OCT 2013, J. Otto coll.). One more male paratype (♂ #10) was recently found on Middle Island in the Recherche Archipelago (S 34.09415°, E 123.19925°, 4 SEP 2014, J. Otto coll.). All types will be deposited in the Western Australian Museum.

*Etymology.* The species group name (*maritimus*, adj., Latin) means *maritime*, and is a reference to the occurrence of this species near the Southern (Austral) Ocean.

*Diagnosis.* *Maratus maritimus* is the only species in the *pavonis* group in which the male opisthosomal plate has a relatively uniform cover of tan to dull orange scales, with only a very faint parens comprised of dark orange scales in some individuals. Species that are somewhat similar and may be confused with *M. maritimus* are *M. montanus* and *M. pavonis* var. *brunneis*. Apart from the opisthosomal scale cover *M. maritimus* males can be distinguished from *M. montanus* by having an opisthosoma that is more lanceolate (not oval, and not raised in display) and from male *M. pavonis* var. *brunneis* by the presence of a much wider thoracic tract as well as different colouration. Female *M. maritimus* have a set of three white markings posterolaterally on the opisthosoma, which in combination with other characters such as the white median thoracic band may be used to distinguish this species from other *Maratus* females. The female also differs from *M. splendens* females by the absence of the dark line along the carapace margin, from *M. literatus* females by the absence of a relatively wide band of setae along that margin, and from *M. watagansi* by the presence of a comparably dense band of white setae covering the clypeus.

*Description of male* (Figures 26-30). The holotype and paratype males (N=7) range from 4.20 to 4.95 mm in body length, not including the spinnerets. The males from Woody Island were larger than those from the mainland (♂ #6-7, body length 4.95 and 4.91 mm respectively).

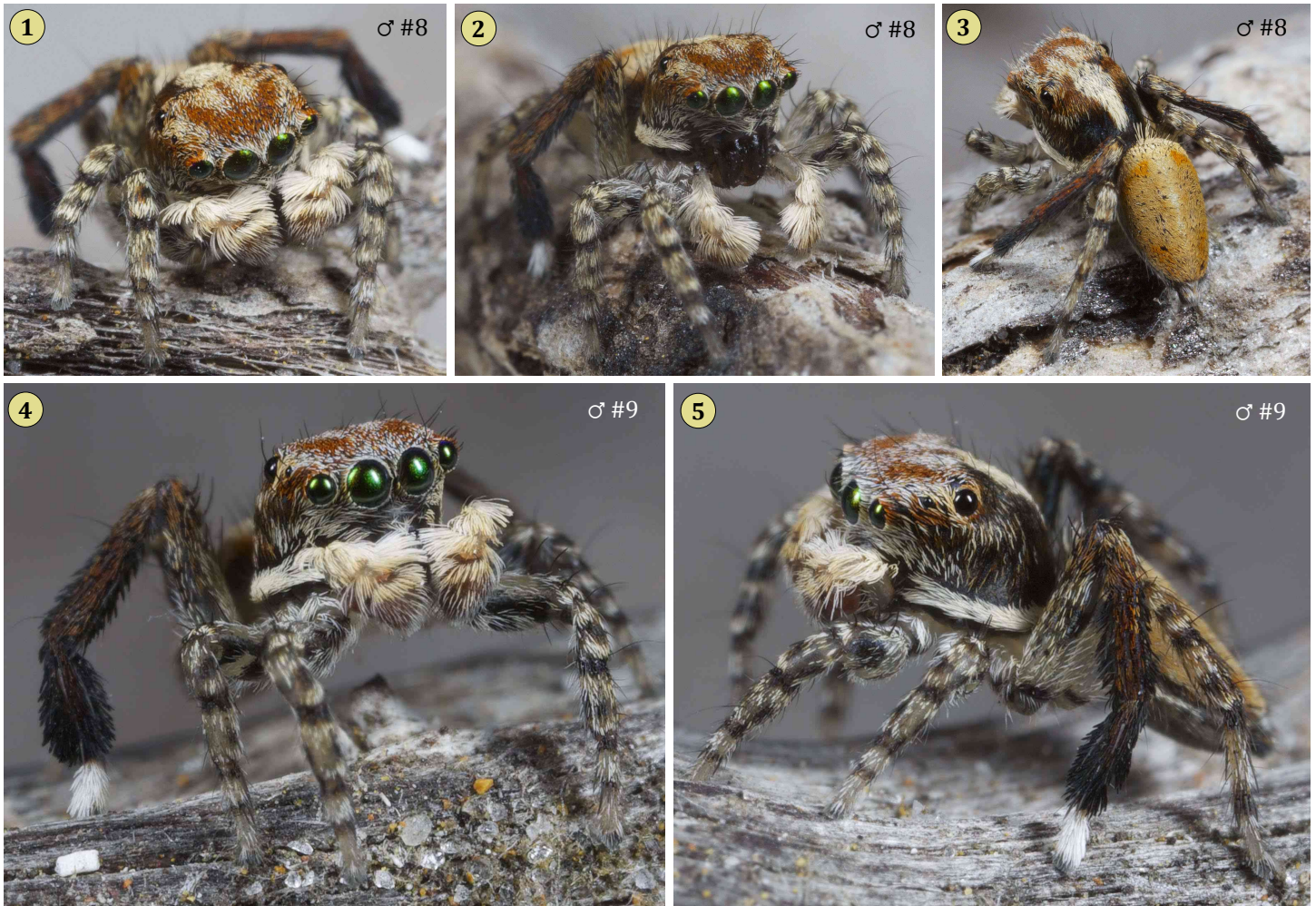




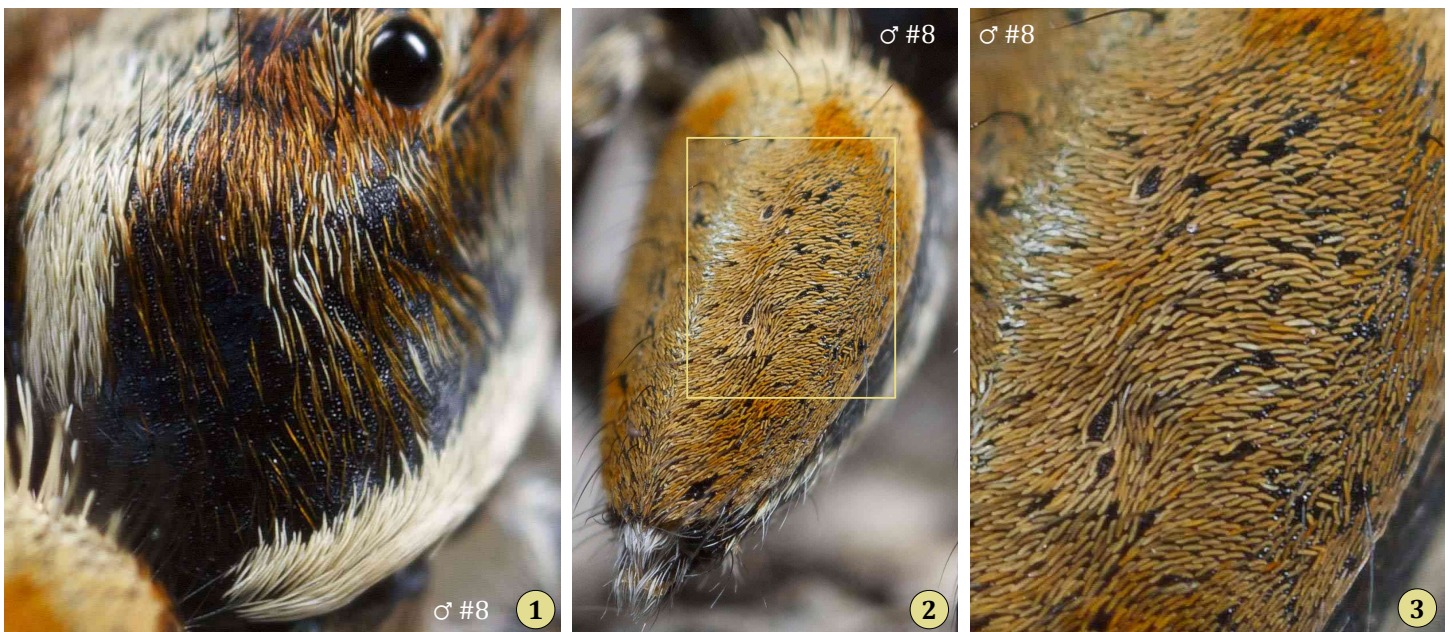
**Figure 26.** Three paratype male *M. maritimus* from (1-2) Mullet Lake Nature Reserve, and (3-6) Pine Grove Holiday Park, Esperance.



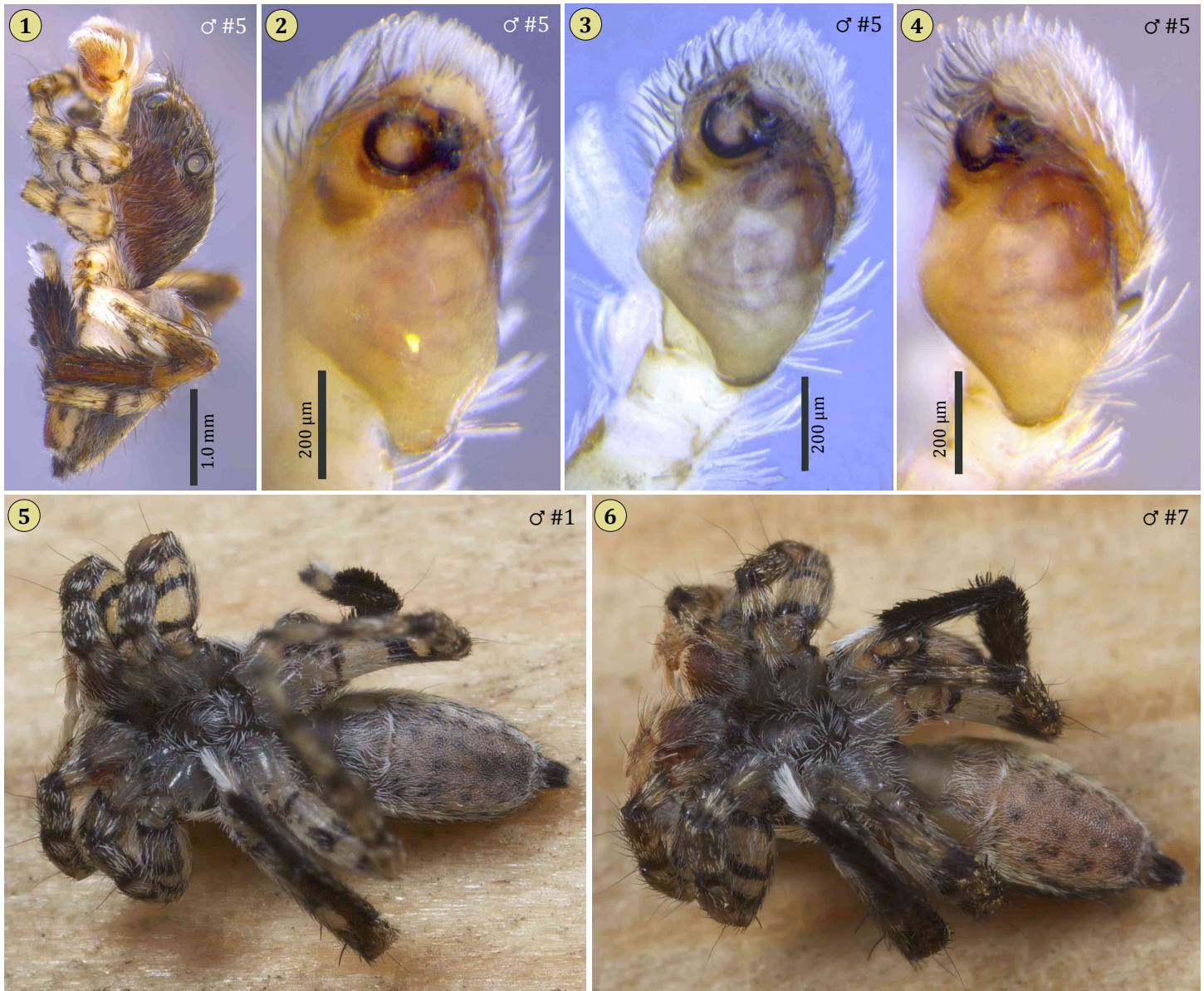
**Figure 27.** Living holotype (1-2) from Pine Grove Holiday Park, Esperance, and two paratype (3-6) male *M. maritimus* from nearby Woody Island.



**Figure 28.** Two living paratype male *M. maritimus* from Pine Grove Holiday Park, Esperance. **3**, Note the indistinct outer parans comprised of orange scales.



**Figure 29.** Detailed view of scale cover of a paratype male *M. maritimus*. **1**, Mixed white to ivory and red-brown scales on the left posterior side of the carapace, behind the posterior lateral eye. **2**, Predominantly tan or light-brown scale cover of dorsal plate. An indistinct outer parans of orange scales can be seen. **3**, Detail from inset in (2). A small number of iridescent blue-green scales can be seen along the median line, at upper left.



**Figure 30.** Holotype specimen (1-4, ♂ #5) and underside of two paratype male *M. maritimus* prior to fixation.

The carapace and chelicerae are dark brown or black. The anterior eyes are bordered with grey scales above and below. Scattered but not dense long grey setae are present on the dark clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with a mixture of grey and dark red-brown scales, extending laterally to surround the lateral eyes, and bearing toward the rear an indistinct 'm' (as seen from the rear) comprised of dark red-brown scales. Behind the PLE row, and to the sides, the carapace is covered loosely with many long grey or dark red-brown setae. There is a thick marginal band of bright white setae on either side of the carapace. The median thoracic tract is wider and comprised of mixed grey to ivory or white setae toward the front, tapering to a point toward the rear where it is more uniform white or ivory. The PME are closer to the PLE than to the ALE.

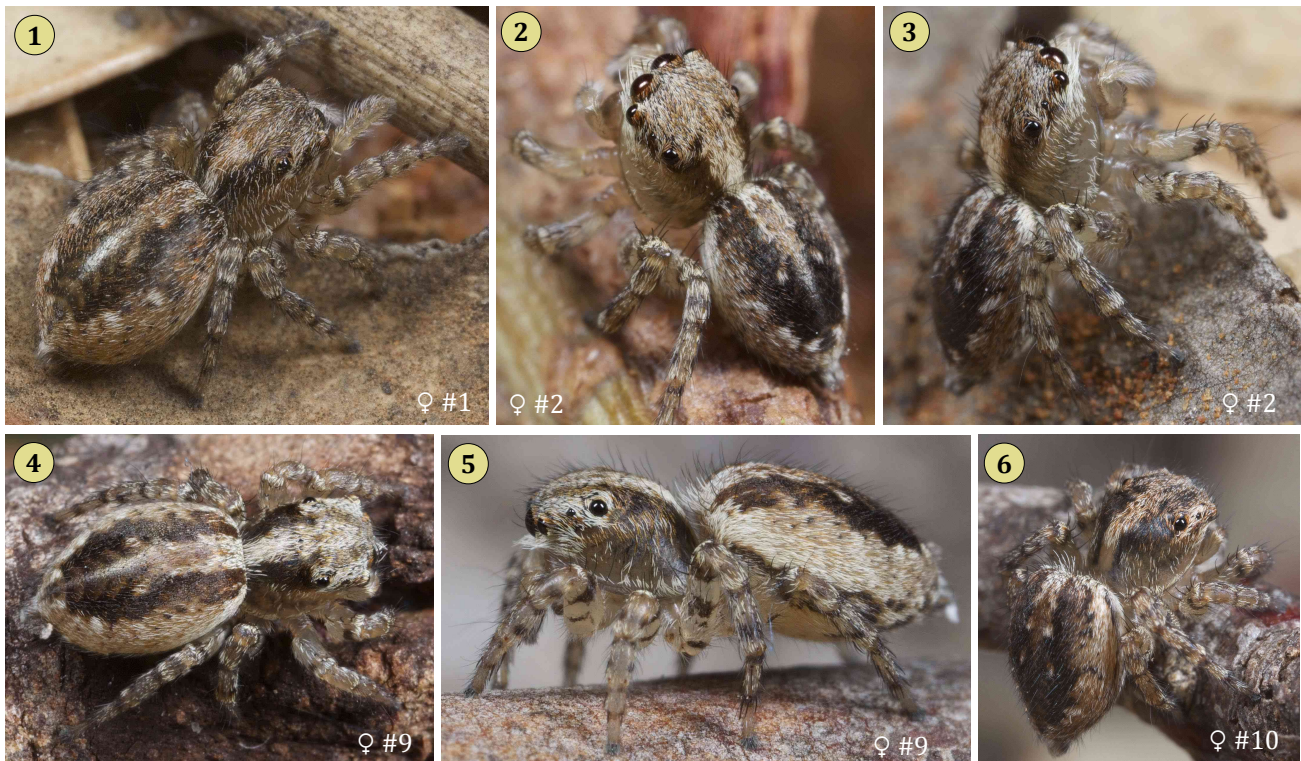
The opisthosoma is lanceolate or elongated, not oval. The dorsal plate is dominated by a relatively uniform cover of tan to dull orange scales, but some iridescent blue-green scales can also be seen, primarily along a narrow median tract. An indistinct outer parens comprised of darker, orange scales may be present. There are no lateral flaps or significant fringes on the lateral sides of the dorsal plate. Several stout white setae project forward from this plate which is otherwise fringed with only scattered setae. There is a small triangular tuft of white setae just above the anal tubercle. Spinnerets are grey in

colour, except for the posterior spinnerets that are white or ivory distally. The ventral opisthosoma is light brown, mottled with darker brown spots at the center, and bordered laterally by tan setae of moderate length. The coxae, sternum, endites and labium are grey in living spiders, but fade to white in preserved specimens.

Legs I and II are about the same length, much shorter than legs III and IV. From the underside, all femora are translucent with two prominent dark bands. Legs III are by far the longest. Legs I, II and IV are similar, strongly ringed or banded with darker cuticular pigment at the proximal end and in some cases the distal end of each segment, alternating with white scales. Femora of legs III bear many white setae proximally, and dark red-brown setae distally. The patella, tibia, and metatarsus III are dark red-brown with many stout, black setae forming a fringe beneath each tibia, and a thicker brush around each metatarsus. The tarsus is covered with bright white setae that overhang the pretarsus, and the footpads (tenae or tenent setae) are grey.

Proximal to the cymbium each pedipalp is fringed with dense ivory or tan setae antero-dorsally. This fringe appears as a bright line beneath the anterior eyes when the pedipalps are rotated and held together in front of the chelicerae in their usual position. A brown line of exposed cuticle at the proximal cymbium separates this fringe from a second fringe comprised of tan or ivory setae originating with the dorsal, proximal cymbium. The dorsal, distal cymbium bears fewer setae, and appears brown. When viewed from below (Figure 30), each pedipalp is similar to that of other members of the *pavonis* group, with apices of the inner and outer rings of the embolus in close contact or fused to form a single heavy apex, a medial sclerite of the tegulum, and sclerotization of the lateral margin of the cymbium where it makes contact with the tegulum.

*Description of female* (Figures 31-35). Females (N=3) ranged from 4.73 to 6.65 mm in body length, not including the spinnerets.



**Figure 31.** Four different living female *M. maritimus*. Compared to *M. montanus*, these are boldly marked with a median stripe running from the posterior carapace to the anterior opisthosoma, and pairs of bright marginal spots toward the rear.

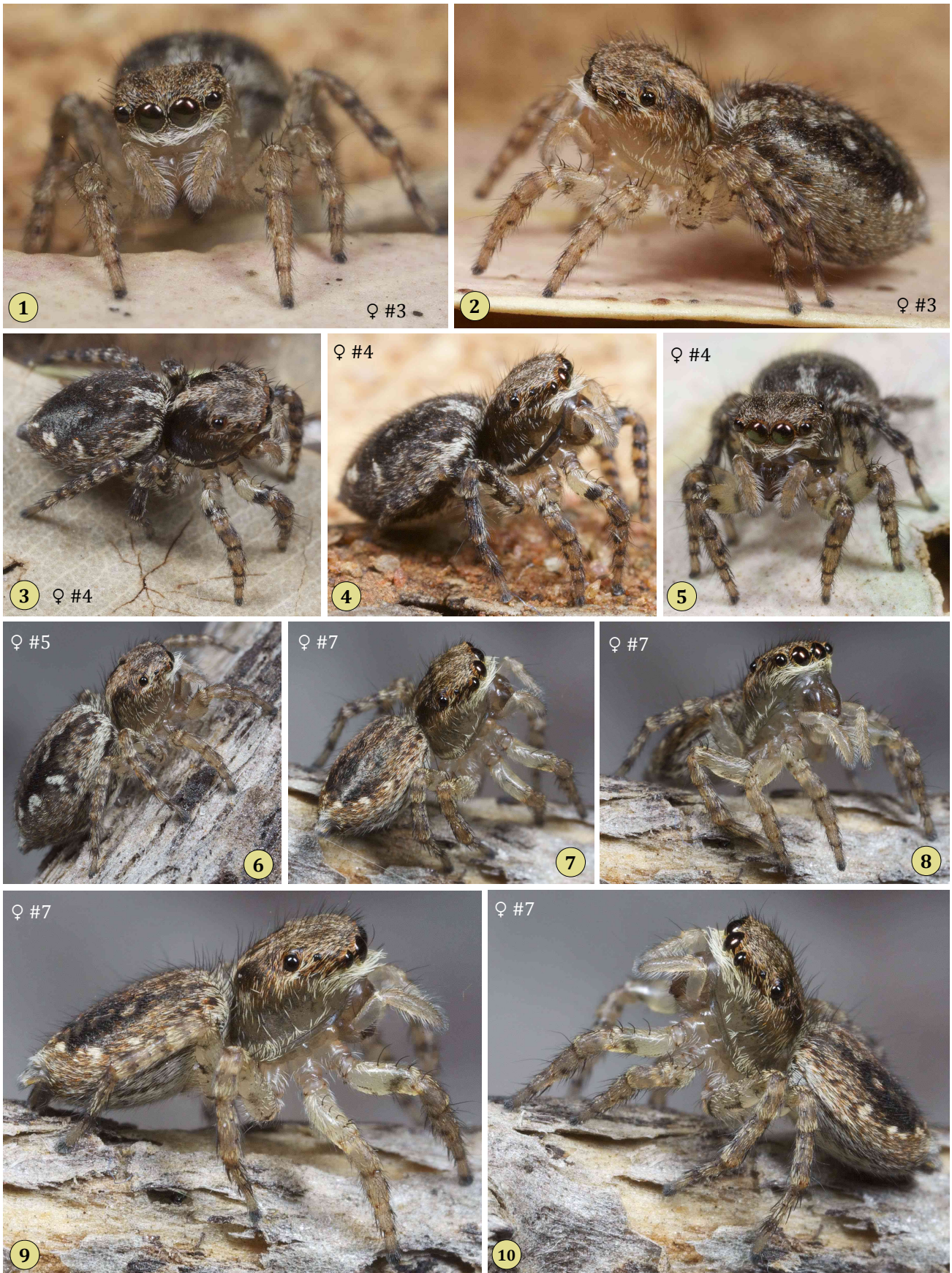
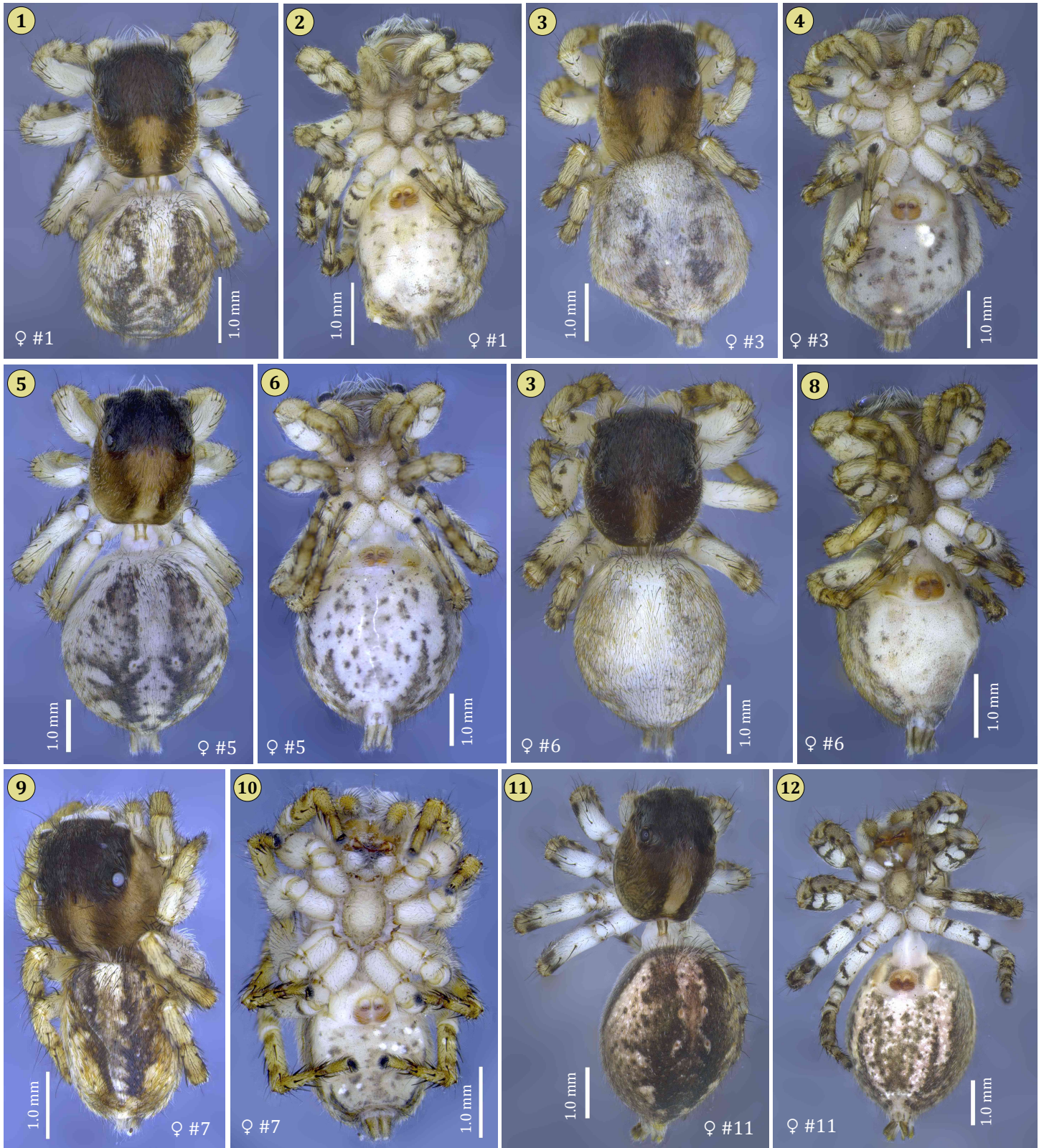
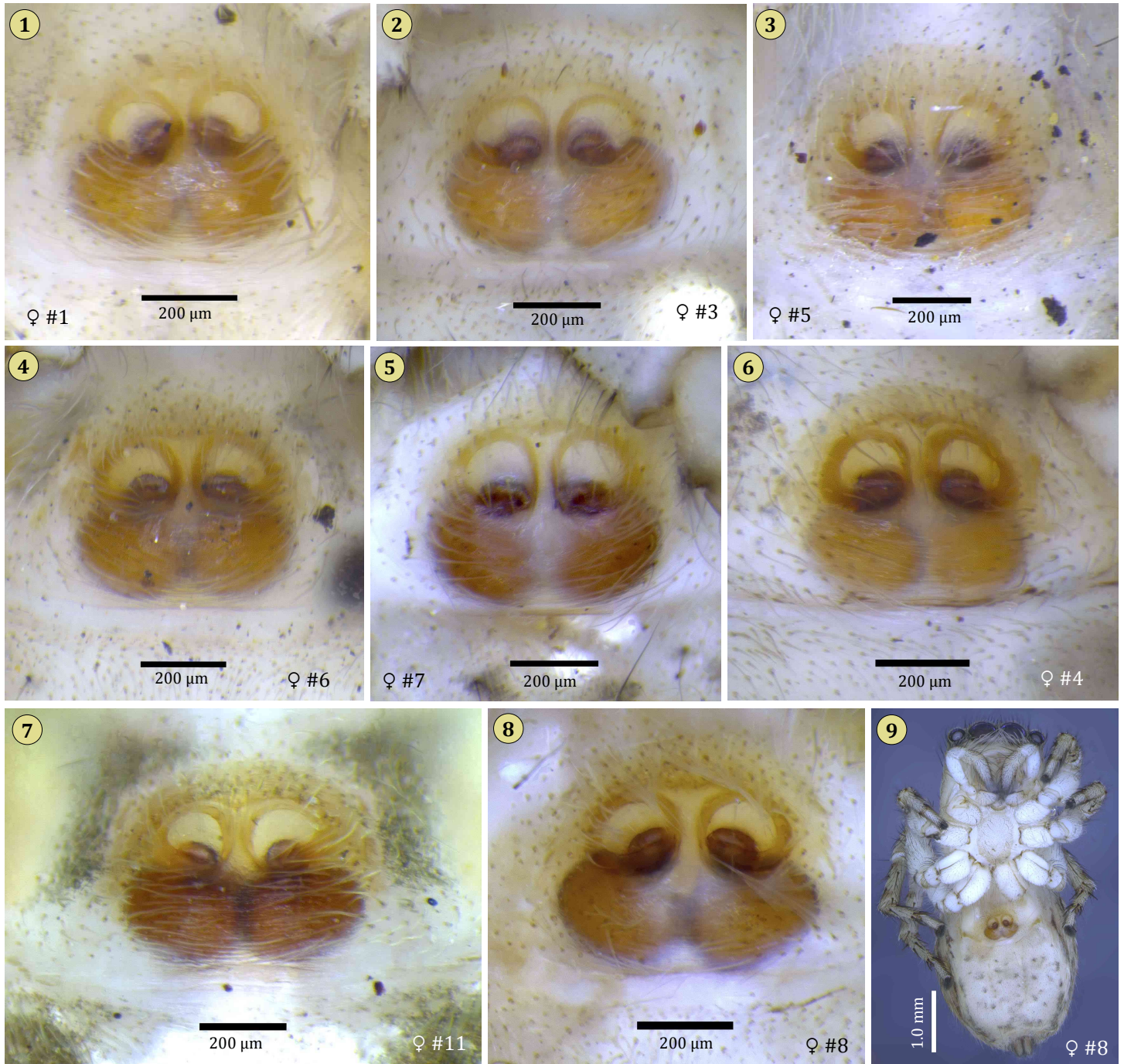


Figure 32. Four more living female *M. maritimus*.

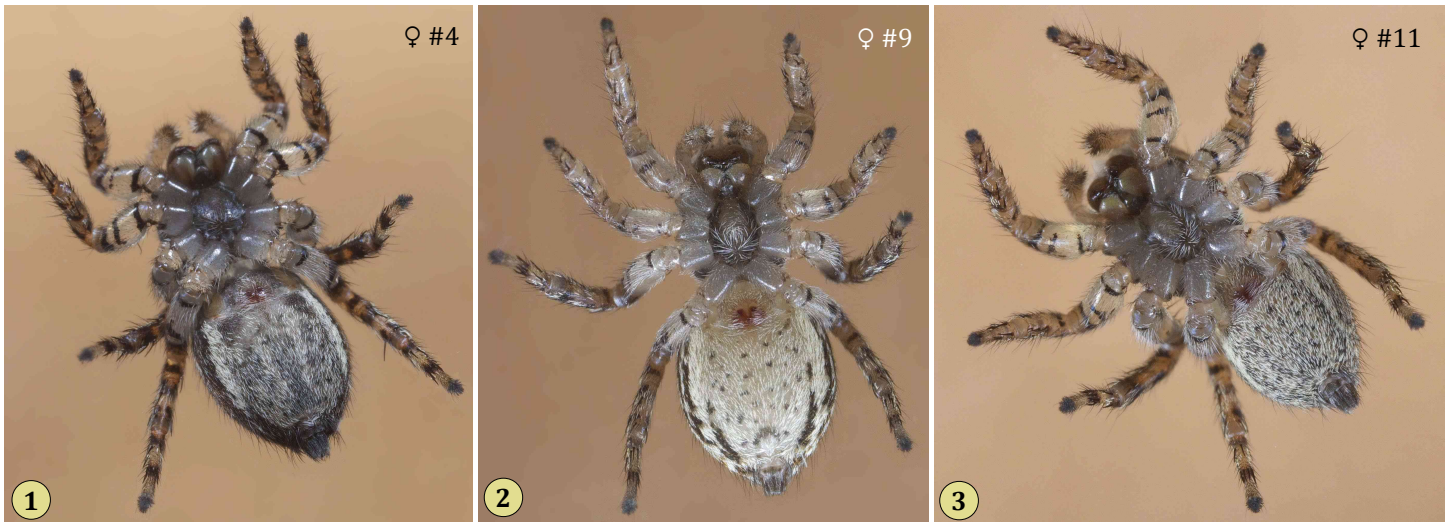


**Figure 33.** Six different female *M. maritimus* showing the loss of light brown pigment and translucence in ethanol. The characteristic, light-coloured median thoracic tract of the carapace, flanked by areas of dark pigment, is still evident in these specimens.



**Figure 34.** Epigyna of eight different female *M. maritimus*. Relative size and separation of the fossa varies, as does the placement of the dark or sclerotized ducts visible through the fossae, situated either posteriorly (e.g., 5), or medio-posteriorly (8).





**Figure 35.** Venter of three different living female *M. maritimus*, showing variations in general colouration associated with intensity of dark pigment and variable distribution of scale cover.

The carapace is darker in the eye region and behind the PLE, but otherwise the carapace, pedipalps, and chelicerae are light brown and translucent. The chelicerae are glabrous. Anterior eyes are bordered with brown scales above, white to ivory scales below. Long white setae are present on the clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with mixed brown and grey scales, and if present, an 'm' shaped pattern (as viewed from the rear), comprised of darker brown scales, is very indistinct. Behind the PLE row, and to the sides, the light brown, translucent carapace is mostly glabrous, with only scattered white to ivory setae, and only scattered ivory scales comprising a weak marginal band. The median thoracic tract is wide, wider at the front and narrower toward the rear, comprised of mixed ivory to tan or brown scales, and extends almost to the rear margin of the carapace. The PME are slightly closer to the PLE than to the ALE.

The dorsal opisthosoma is mostly dark brown and glabrous with only scattered ivory to red-brown scale cover, but bears a wide anterior median band of mostly ivory setae with as many as three paired lighter spots, and a lateral row of 2-3 bright white spots on either side. The sides and venter are of variable colouration, comprised of mostly ivory setae, or a mixture of ivory and brown setae. The coxae, sternum, endites and labium are grey in living spiders, but fade to white in preserved specimens.

Legs I and II are about the same length, much shorter than legs III and IV which are of similar length. The legs are mostly translucent light brown and legs III and IV may be more strongly banded with white scales alternating with darker pigment. In ethanol, legs fade to white.

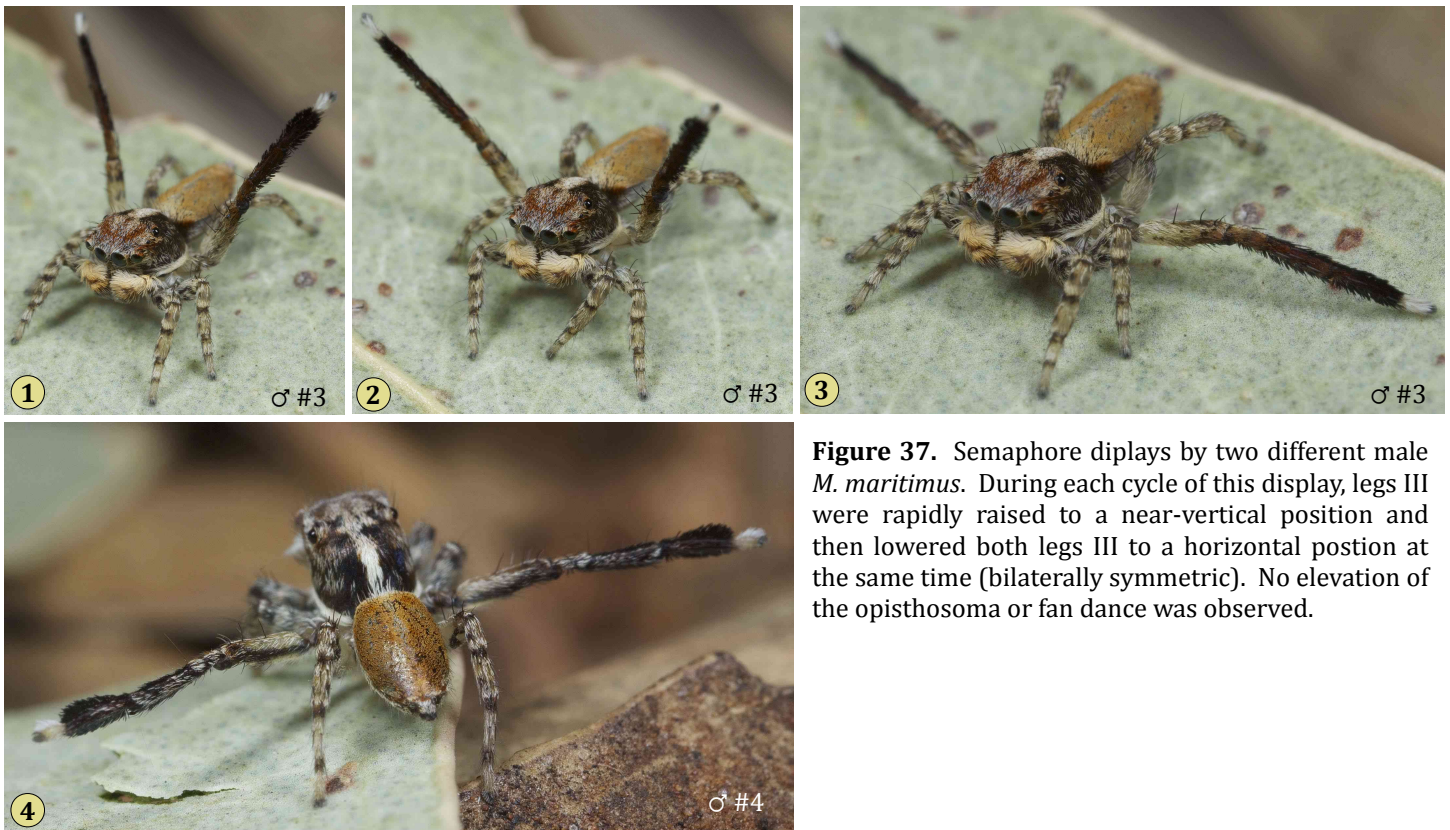
Fossae of the epigynum are rounded, oval or bean-shaped, rimmed, and separated by a septum of variable width. They are about half of the diameter of the large posterior spermathecae. Darkly sclerotized ducts visible through the fossae are rounded in appearance and are situated to the rear of the fossae (Figure 34).

*Immatures.* Immature male *M. maritimus* (Figure 36) are more boldly marked, with relatively larger paired spots on the dorsal opisthosoma, than are the adult females that they otherwise closely resemble.



**Figure 36.** Immature *M. maritimus* males. 1-3, Three earlier (not penultimate) instars. 4-6, Three penultimate instars.

*Display by males.* We have not observed any elevation of the fan or the movements associated with a fan dance in *M. maritimus*. Like other species in the *pavonis* group, male *M. maritimus* often performed rapid tapping, or quickly returned legs III from a horizontal position to a near vertical position at the end of each 0.3-1.0s cycle of semaphore display (Figure 37). Unlike *M. literatus* and *M. montanus*, however, we did not see them hold and vibrate legs III to the rear at the end of each display cycle.



**Figure 37.** Semaphore displays by two different male *M. maritimus*. During each cycle of this display, legs III were rapidly raised to a near-vertical position and then lowered both legs III to a horizontal position at the same time (bilaterally symmetric). No elevation of the opisthosoma or fan dance was observed.

*Habitat.* Most of the *M. maritimus* specimens were collected behind a cabin at Pine Grove Holiday Park in Esperance (Figure 38).



**Figure 38.** Two views of *M. maritimus* habitat behind a cabin at Pine Grove Holiday Park in Esperance (early October, 2013). These spiders were found on or near the ground.

### *Maratus montanus*, new species

*Type specimens.* The holotype male (♂ #2), one paratype male (♂ #1) and two paratype females (♀ #1-2) were collected on Mount Ragged in Cape Arid National Park, east of Esperance, Western Australia (S 33.44559°, E 123.47498°, 14 OCT 2013, J. Otto and D. Knowles coll.). All type specimens will be deposited in the Western Australian Museum.

*Etymology.* The species group name (*montanus*, adj., Latin) means *mountainous*, and is a reference to the occurrence of this species on Mount Ragged.

*Diagnosis.* Like the male *M. pavonis* var. *brunneis*, the dorsal opisthosoma of the male *M. montanus* is mostly covered with tan scales and anterior or posterior ends of the outer parans may be defined by brighter orange scales. However males of the two taxa can be distinguished by the width and shape of the thoracic tract (narrow and rectangular in *M. pavonis*, wide in *M. montanus*), and a mixture of grey scales with an indistinct 'm' pattern comprised of dark red-brown scales in the eye region of *M. montanus*. We have not found any male *M. montanus* with a central butterfly on the fan. Female *M. montanus* are similar to *M. maritimus* but do not exhibit the bold colour patterns seen in the latter. The fossae of the epigynum of *M. montanus* are also larger than those of *M. maritimus* and may have the same diameter as the posterior spermathecae. The female of *M. montanus* may be distinguished from that of *M. literatus* by the absence of a wide band of white setae along the margin of the carapace, and by having a more lightly coloured stripe along the midline of the dorsal opisthosoma. It differs from the female of *M. splendens* by the absence of a dark band along the carapace margin, and from *M. watagansi* by having a comparably dense fringe of white setae covering the clypeus.

*Description of male* (Figures 39-43). The holotype and paratype males (N=2) range from 4.35 to 4.51 mm in body length, not including the spinnerets.

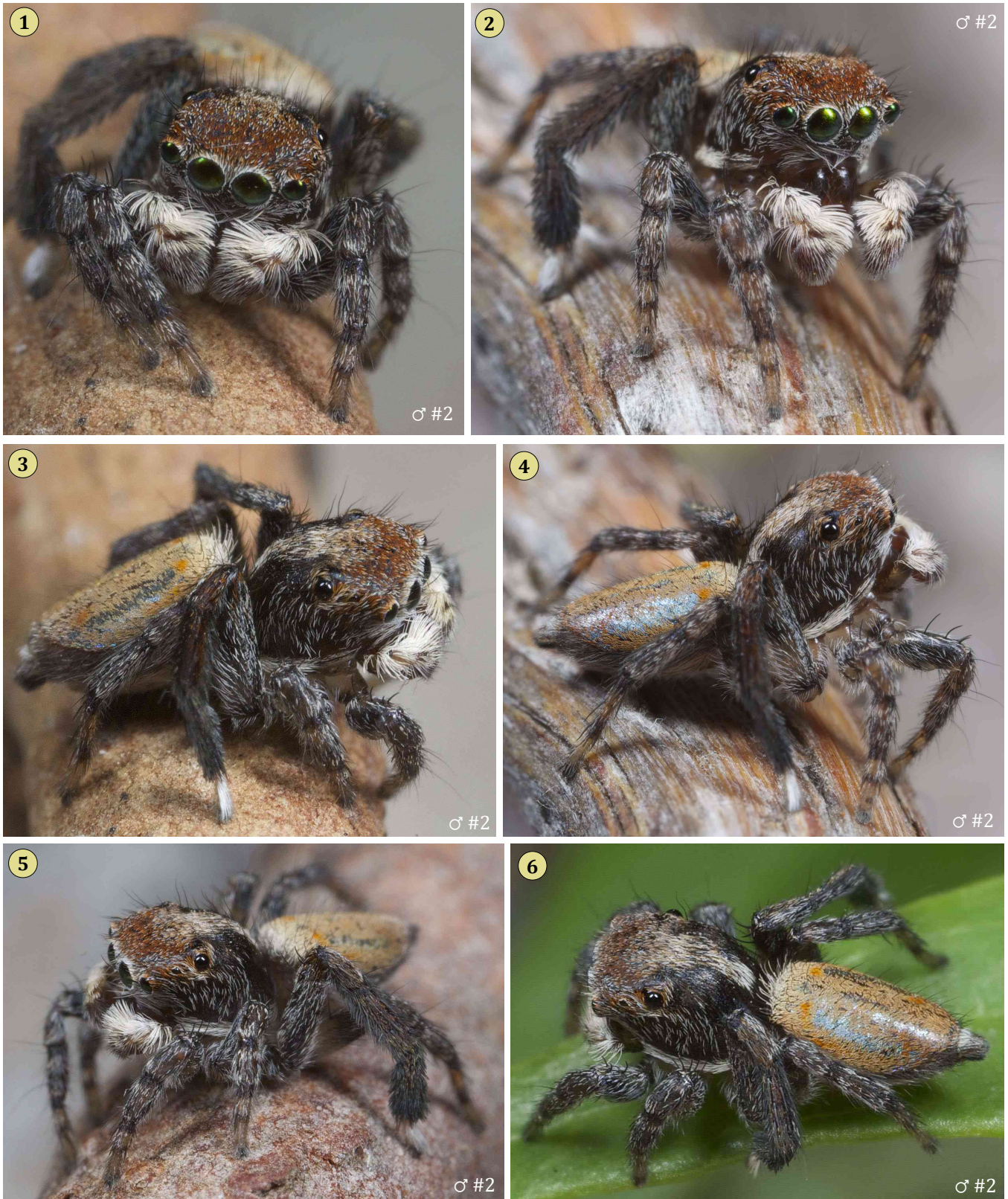
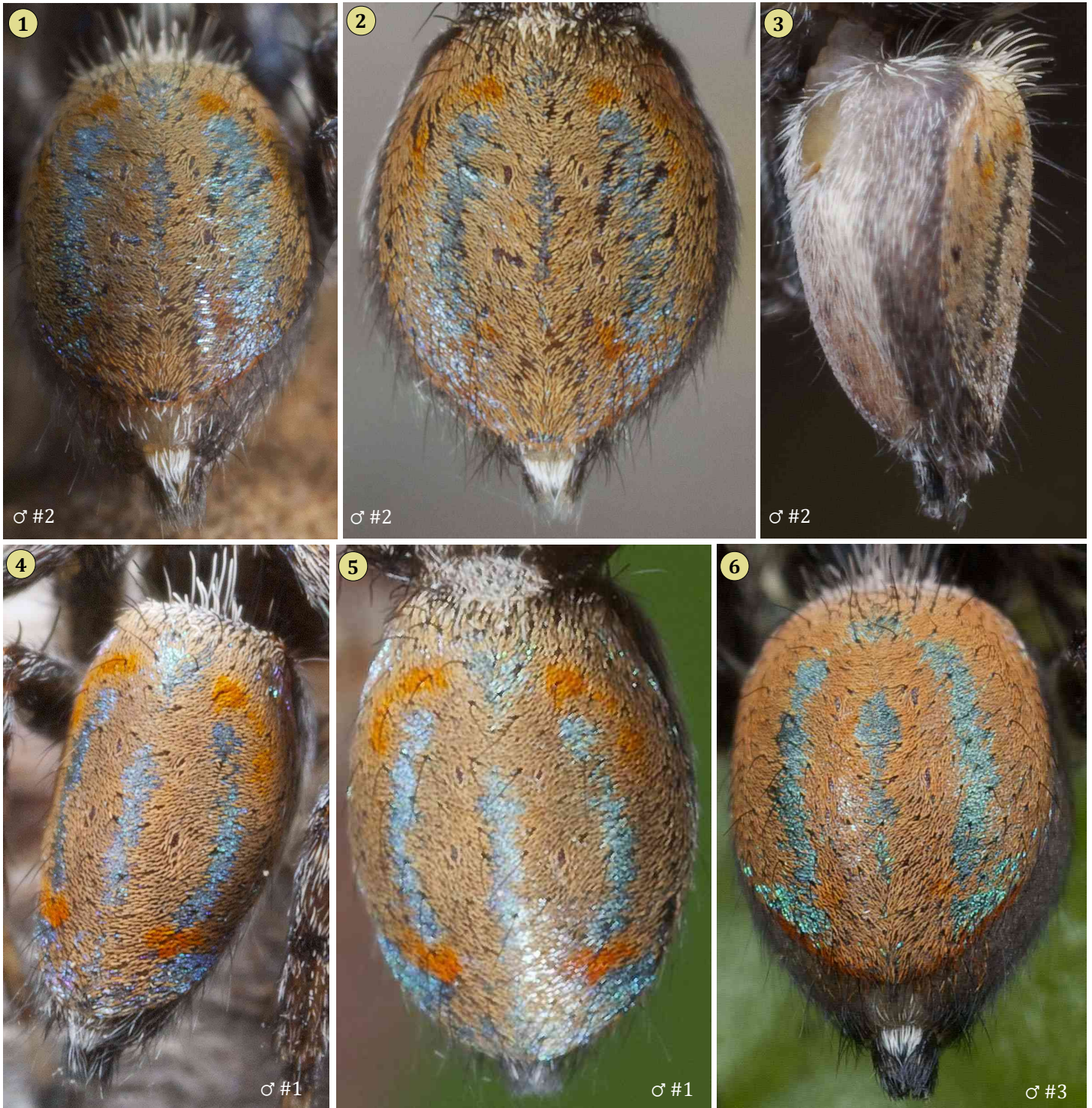


Figure 39. Living holotype (♂ #2) *M. montanus*.



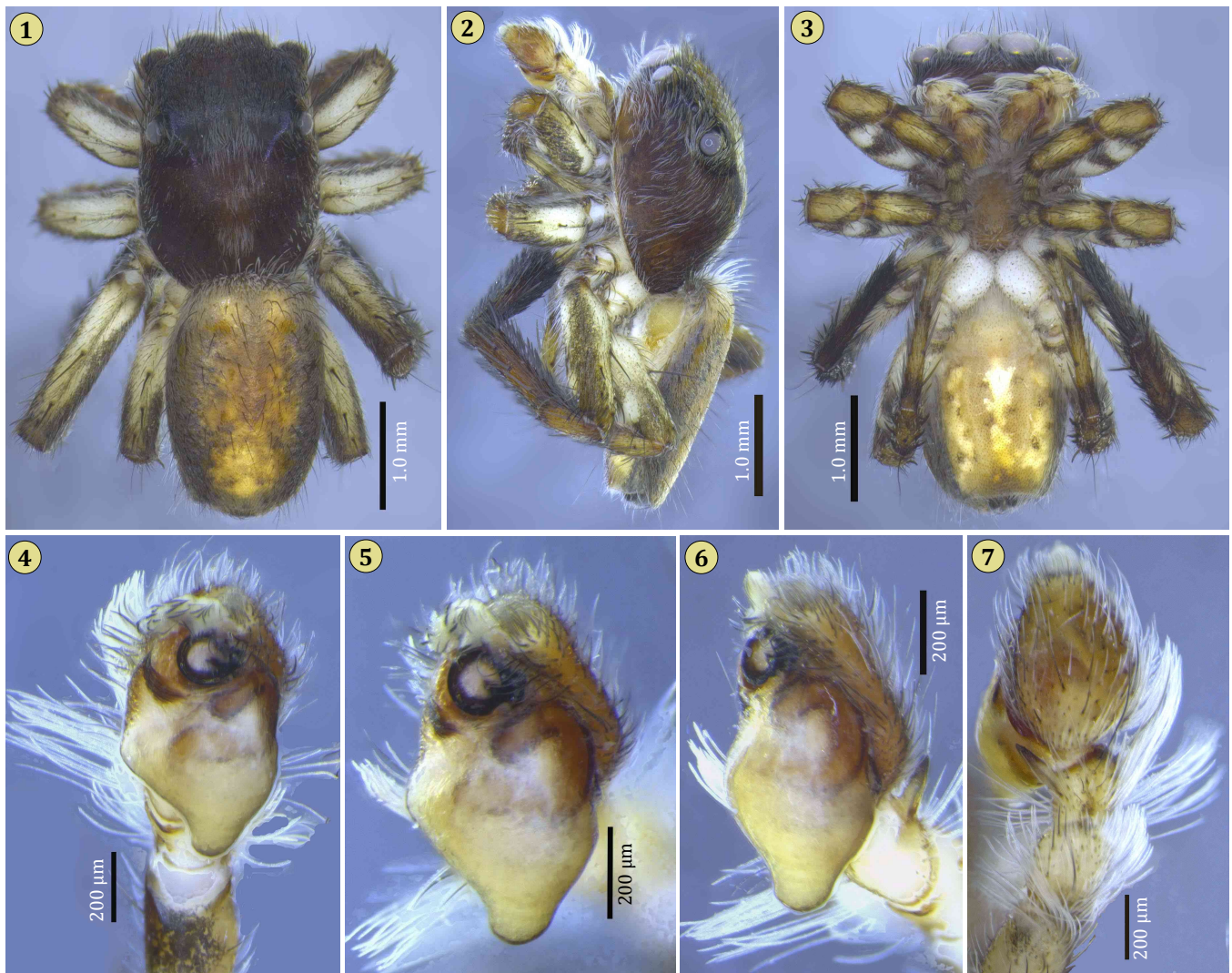
**Figure 40.** Male *M. montanus*. 1-5, Paratype. 6-8, Offspring of a paratype female, reared in captivity. This male emerged from the egg sac on 16 MAR 2014 and became an adult on 4 OCT 2014. A female that emerged on 16 MAR 2014 was also reared and became an adult on 9 SEP 2014, also consistent with the appearance of adults in the early spring.



**Figure 41.** Opisthosoma and fan of living *M. montanus*. **1-2**, Curved or retracted (1) and expanded or flattened (2) fan of holotype. **3**, Side view of opisthosoma of holotype. The depth of the opisthosoma varies with feeding condition. **4-5**, Curved or retracted (4) and expanded or flattened (5) fan of paratype. **6**, Fan of male reared in captivity. Pigmented scales comprising the inner and outer parens of this male were almost uniform light-orange, with darker red-orange scales along the posterior edge of the dorsal plate.



**Figure 42.** Underside of the holotype male (1), and anterior view of the extended left leg III of the paratype male (2). From below all femora are translucent with prominent dark bands or rings.



**Figure 43.** Holotype *M. montanus* specimen (♂ #2) in ethanol. 4-7, Four views of the left pedipalp.

The carapace and chelicerae are dark brown or black. The anterior eyes are bordered with grey scales above and below. Scattered but not dense long grey setae are present on the dark clypeus, several projecting forward over the chelicerae at the median. The eye region is covered with a mixture of grey and dark red-brown scales, extending laterally to surround the lateral eyes, and may bear an indistinct 'm' figure (as seen from the rear) comprised of dark red-brown scales. The relative abundance of grey or red-brown scales in the eye region varies. Behind the PLE row, and to the sides, the carapace is covered loosely with many long grey or dark red-brown setae. There is a thick marginal band of bright white setae on either side of the carapace. The median thoracic tract is wider at the front, comprised of mixed grey or ivory or white setae. The PME are closer to the PLE than to the ALE.

The opisthosoma is lanceolate to oval when the dorsal plate is not expanded, but wider and oval when that plate is expanded and raised during display. A background of blue-green iridescent scales is visible from above along three longitudinal tracts, one median and one lateral on either side. A wide inner parens comprised of tan, light orange, or brown scales, and an outer parens comprised of tan to light orange or red-orange scales, are present. The anterior and posterior ends of the outer parens may be red-orange and may appear as brighter paired spots. When not expanded, the dorsal plate is wrapped around the opisthosoma but does not have lateral flaps or significant fringes. Several stout white setae project forward from this plate toward the carapace. There is a small triangular tuft of white setae just above the anal tubercle. Spinnerets are grey in colour, except for the posterior spinnerets that are white or ivory distally. The ventral opisthosoma is light brown with scattered, small, darker brown spots, and bordered laterally by scattered ivory setae, mostly toward the front. The coxae, sternum, endites and labium are grey in living spiders, but fade to white in preserved specimens.

Legs I and II are about the same length, much shorter than legs III and IV. From the underside, all femora are translucent with at least two prominent dark bands. Legs III are by far the longest. Legs I, II and IV are similar, ringed or banded with darker cuticular pigment at the proximal end and in some cases the distal end of each segment, alternating with areas covered by white setae. Femora of legs III are covered with many white setae. The patella, tibia, and metatarsus III are dark brown with many stout, black setae forming a fringe beneath each tibia, and a thicker brush around each metatarsus. The tarsus is covered with bright white setae that overhang the pretarsus, and the footpads (tenae or tenent setae) are grey.

Proximal to the cymbium the pedipalp is fringed with dense white or ivory setae anterodorsally. A brown line of exposed cuticle separates this fringe from the dense white setae that cover the dorsal cymbium. When viewed from below (Figure 43), the pedipalp is similar to that of other members of the *pavonis* group, with apices of the inner and outer rings of the embolus in close contact or fused to form a single heavy apex, a medial sclerite of the tegulum, sclerotization of the lateral margin of the cymbium where it makes contact with the tegulum, and a darker apex of the retrolateral tibial apophysis.

*Description of female* (Figures 44-47). Females (N=2) ranged from 4.42 to 5.29 mm in body length, not including the spinnerets. The smaller specimen had just laid eggs.

The carapace is mostly covered with mixed grey to brown setae, but this cover varies and may be affected by rubbing during the life of the female. Cuticle of the eye region is darkly pigmented. Toward the margins, the carapace is more glabrous and lighter or translucent, without a distinct marginal band. The chelicerae are glabrous and brown. Anterior eyes are bordered with brown scales above, white to ivory scales below. A dense cover of long white setae is present on the clypeus, projecting forward over the chelicerae at the median. Apart from the cover of scattered setae, there is no distinct median thoracic tract. The PME are closer to the PLE than to the ALE.



The dorsal opisthosoma is dark brown and may be glabrous or bear scattered grey and brown setae, perhaps depending on condition as much as phenotype. Paired, lighter spots like those seen in *M. maritimus* females may be present, but these are much less distinct. The sides and venter have a fairly uniform cover of ivory to grey setae of moderate length, and many small dark brown spots can be seen on the venter. The coxae, sternum, and endites are light brown and translucent and the labium is darker brown in living spiders, but these fade to white in specimens kept in ethanol.

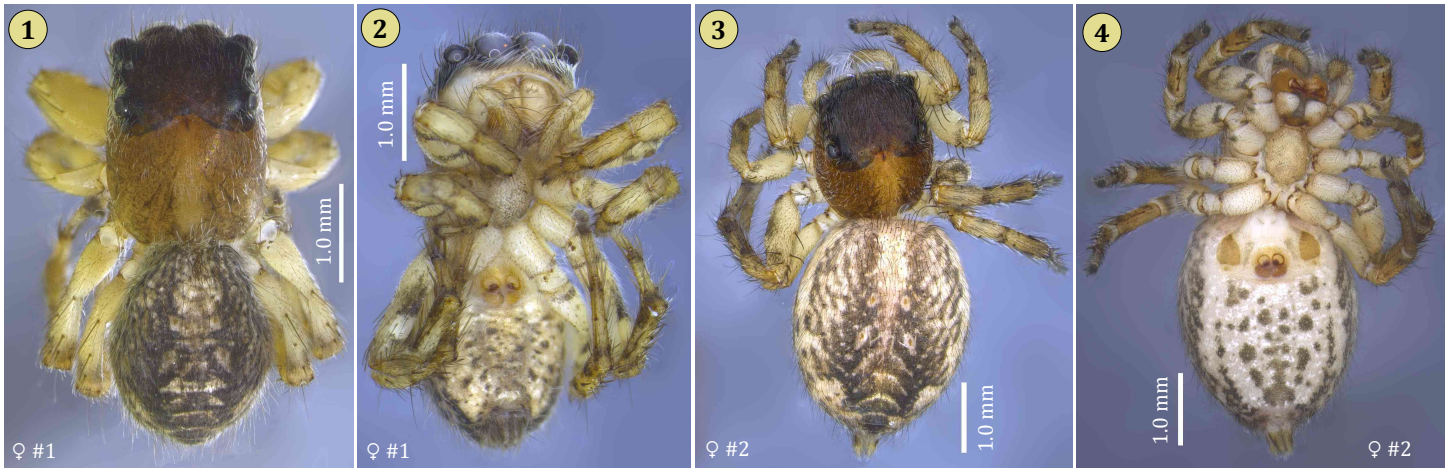
Legs I and II are about the same length, much shorter than legs III and IV which are of similar length. The legs are mostly translucent light brown and legs III and IV may be indistinctly banded with white scales alternating with darker pigment. In ethanol, legs also fade to white.



**Figure 44.** Three different female *M. montanus*. Compared to *M. maritimus*, colouration of females is uniform and subdued.



**Figure 45.** Venter of living female paratypes, *M. montanus*.



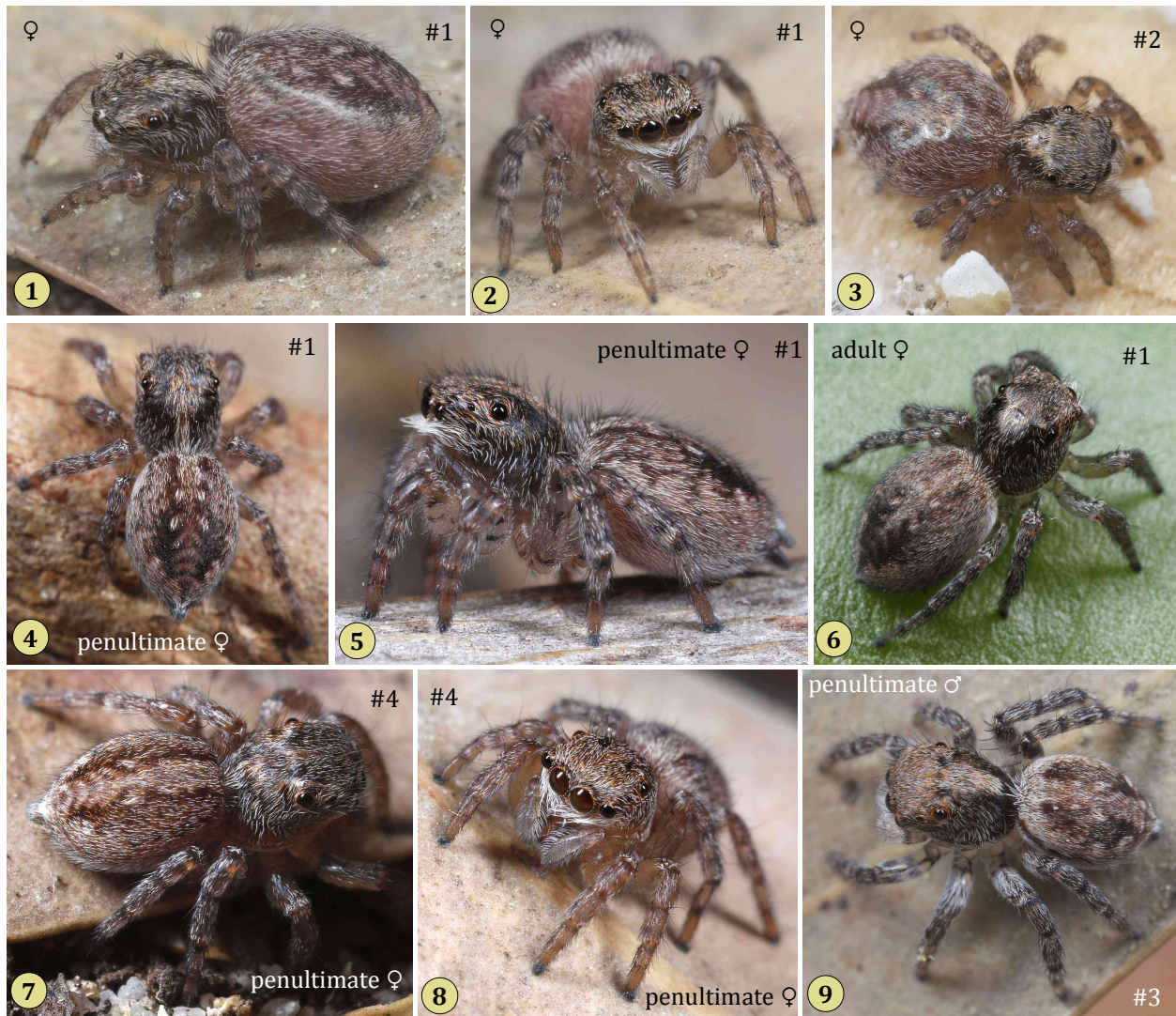
**Figure 46.** Paratype female specimens, *M. montanus*. The first (♀ #1) recently laid eggs.

Fossae of the epigynum are rounded, oval or bean-shaped, rimmed, and separated by a septum of variable width (Figure 47). They are more than half of the diameter of the large, contiguous posterior spermathecae. Darkly sclerotized ducts visible through the fossae are rounded in appearance and are situated to the rear of the fossae.



**Figure 47.** Epigyna of paratype female specimens, *M. montanus*.

*Immatures.* Immature *M. montanus*, like adult females, lack bold markings and their colouration is fairly uniform (Figure 48). The penultimate male (Figure 48:9) has the wide median thoracic tract that is characteristic of the adult.

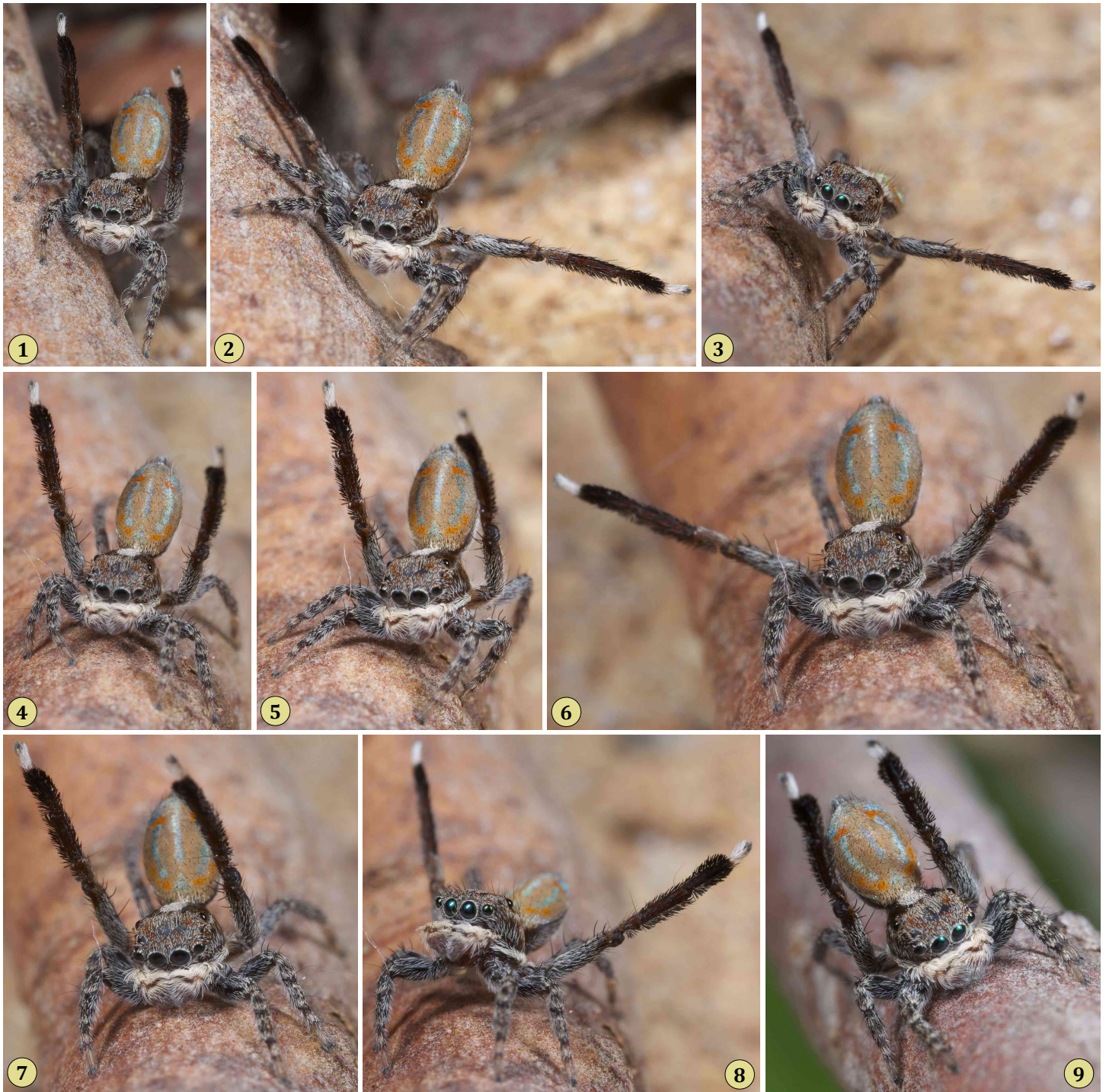


**Figure 48.** Developmental stages of *M. montanus*. 1-3, Early (not penultimate) instar females. 4-6, Penultimate and adult instars of immature #1. 7-8, A different penultimate female. 9, Penultimate male.

*Display by males* (Figures 49-50). During a single leg wave (advertisement), males often lowered one extended leg III from a near vertical to a horizontal, lateral position in a series of steps (lower, raise slightly, then lower more). They sometimes held it in an extended, lateral, horizontal position and rapidly (4-5 cycles/s) vibrated it up and down for extended periods, a behaviour we have not observed in other members of the *pavonis* group. The fan dances of *M. montanus* were generally quite similar to those of *M. literatus* and *M. pavonis*. For example, like *M. pavonis* (Hill & Otto 2011), they moved both extended legs III rapidly to a vertical position before lowering them to the sides while waving the fan rapidly (6-8 cycles/s) from side to side. Metatarsi III were occasionally flexed at the tibio-metatarsal joint as was also observed in the other species. We also observed that while fan movement in *M. splendens* always coincided with leg movements, in the other species of this group with a fan dance, including *M. montanus*, the fan was often moved while the legs were stationary.

Intermixed with the fan displays of *M. montanus* were bilateral semaphore displays in which legs III were rapidly raised to a vertical position, then lowered more slowly. They were then often held toward the rear

in a horizontal position and vibrated as the opisthosoma was bobbed up and down. Such displays were generally followed by bouts of rapid tapping. We have described this behaviour in more detail for *M. leo*. It occurs not only in all members of the *pavonis* group but also in some species outside this group (*M. harrisi*, *M. amabilis*).

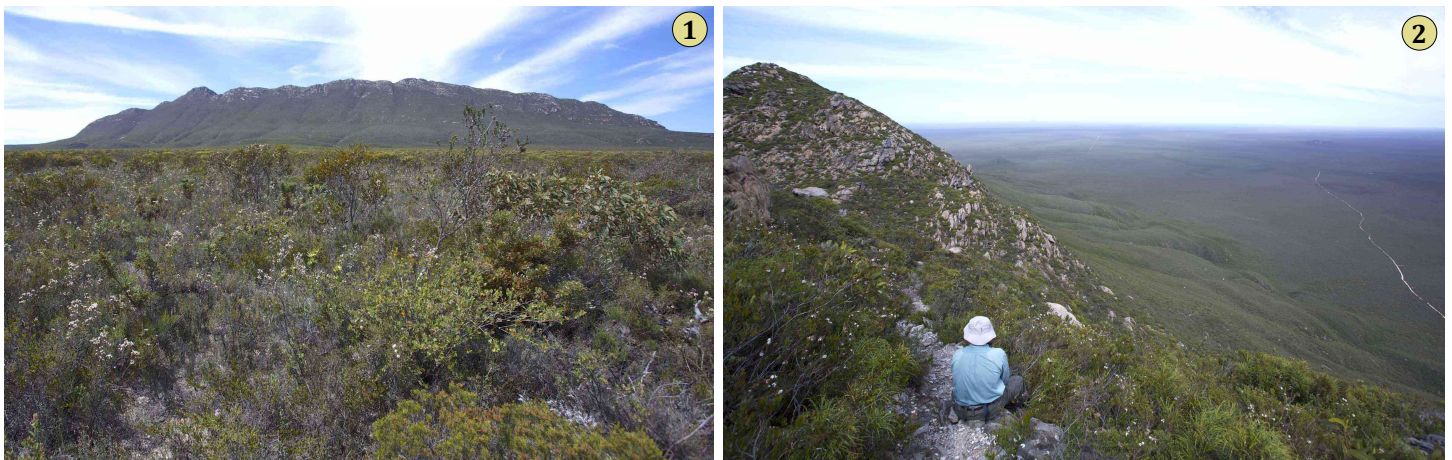


**Figure 49.** Photographs of display by the paratype ( $\sigma$  #1) *M. montanus* facing a female. During the semaphore display (3, 8) the fan was often not raised, or only partly raised, as legs III were lowered in a series of steps. During the fan dance, the elevated fan was waved from side to side as the elevated legs III were vibrated (up and down) rapidly in a transverse plane.



**Figure 50.** Photographs of display by the holotype ( $\sigma$  #2) *M. montanus* facing a female. **1-2**, Note the different degree of expansion or inflation of the fan in these two photographs. **3**, Typical orientation of legs III during a fan dance. **5**, Bobbing (opisthosoma moved up and down) position with legs III extended to the rear. This was also observed in *M. literatus*.

**Habitat.** The type locality is near the top of Mount Ragged in Cape Arid National Park, where *M. montanus* was found on or near the ground (Figure 51).



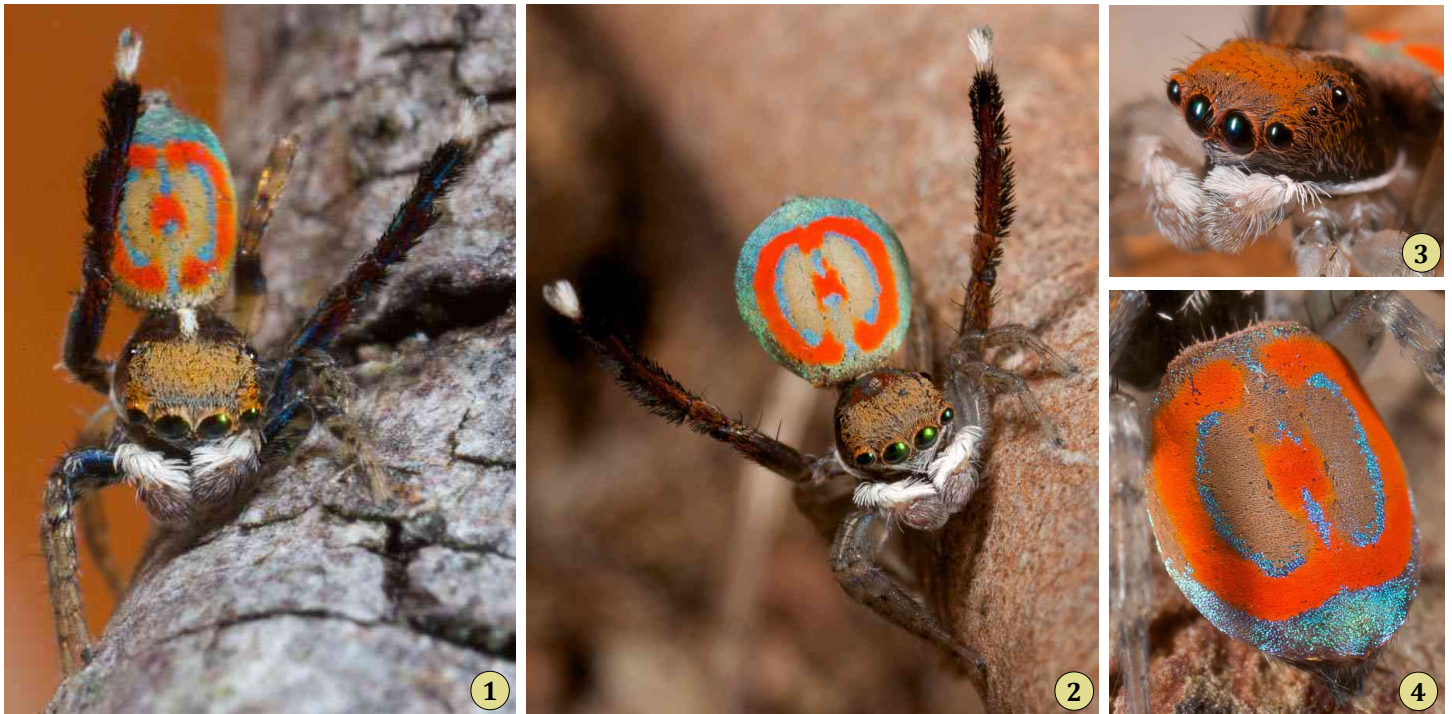
**Figure 51.** Mount Ragged locality for *M. montanus*. **1**, Mount Ragged in the distance. **2**, Type locality near the top of Mount Ragged. Photograph (1) was taken from the road that is visible in the distance (right, center) in photograph (2).

***Maratus pavonis* (Dunn 1947)***Saitis pavonis* Dunn 1947, 1957*Maratus pavonis* : Žabka 1991; Waldock 1993, 2007, 2008, 2013; Hill 2009, 2010; Otto & Hill 2010, 2011, 2012b, 2012c, 2013, 2014; Hill & Otto 2011; Girard *et al.* 2011; Metzner 2013; Platnick 2013; Prószyński 2013

**Type specimens.** Dunn (1947) listed six male specimens, all male, collected 20 OCT 1946 at Carnegie, Victoria, and one specimen from Altona collected 5 NOV 1946. He deposited a single type ('co-type') male in what is now the Museum Victoria, Melbourne, and another with Dr. V. V. Hickman of Tasmania. The remaining specimens remained in his personal collection. We previously published photographs of the type deposited in the Museum Victoria (Hill & Otto 2011), and it agrees with both Dunn's description and more recently collected *M. pavonis* from eastern Australia and Tasmania.

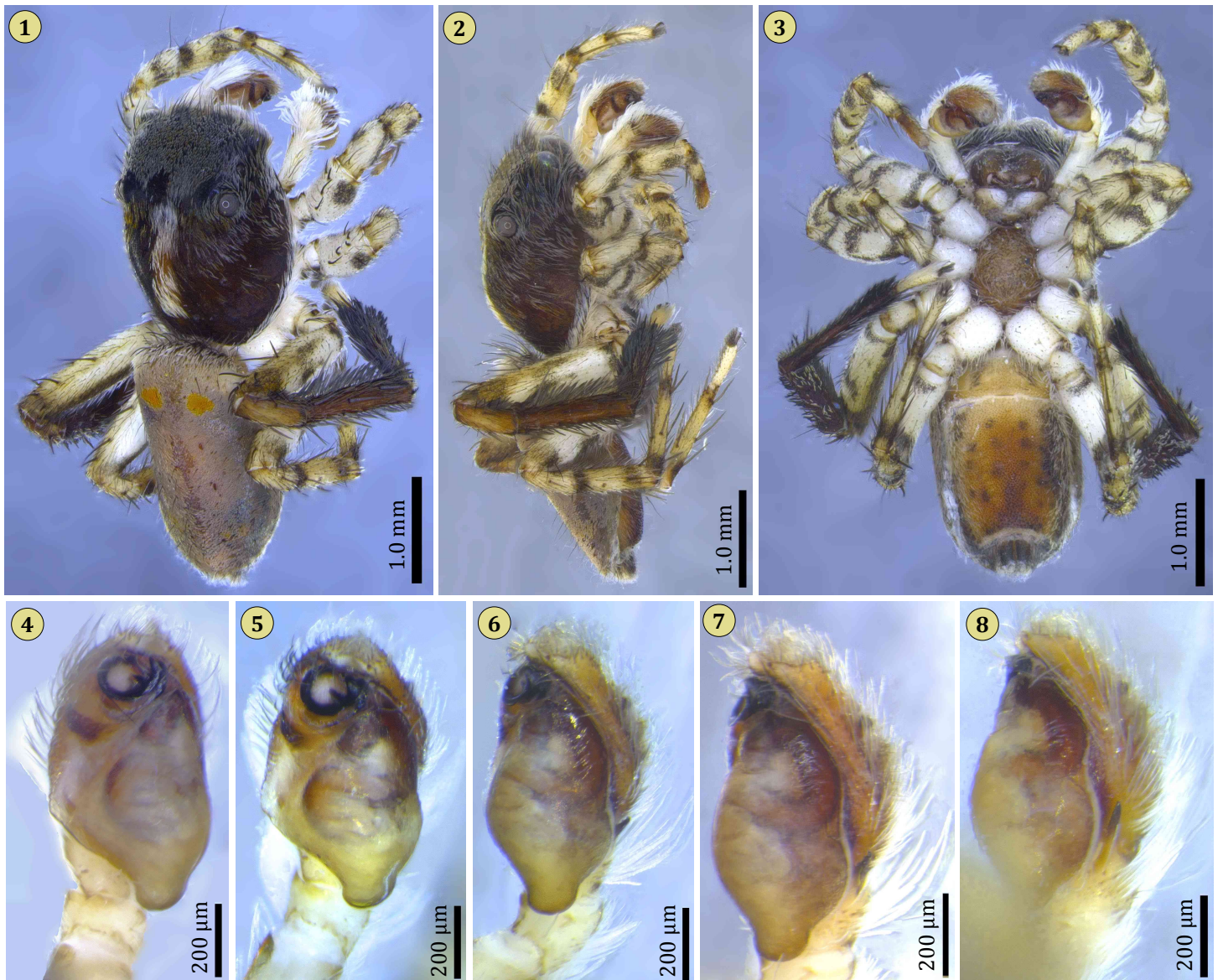
**Etymology.** The species group name (*pavonis*, nom., Latin) means *peacock*. This was a reference to the peacock-like display of males (Dunn 1957).

**Diagnosis.** See Hill & Otto (2011) for a detailed comparison with *M. splendens*. The uniform colouration of the eye region, the regular (long, narrow, rectangular) shape of the median thoracic tract, the relative lack of setae on the cymbium, and the relatively translucent legs I, II, and IV, with no white banding (dark bands may be present), separate males from other brightly coloured members of the *pavonis* group (Figure 52). Dunn used the lack of lateral opisthosomal flaps as an important distinction for *M. pavonis*, but we presently treat members of populations that do have these flaps as members of the same species.

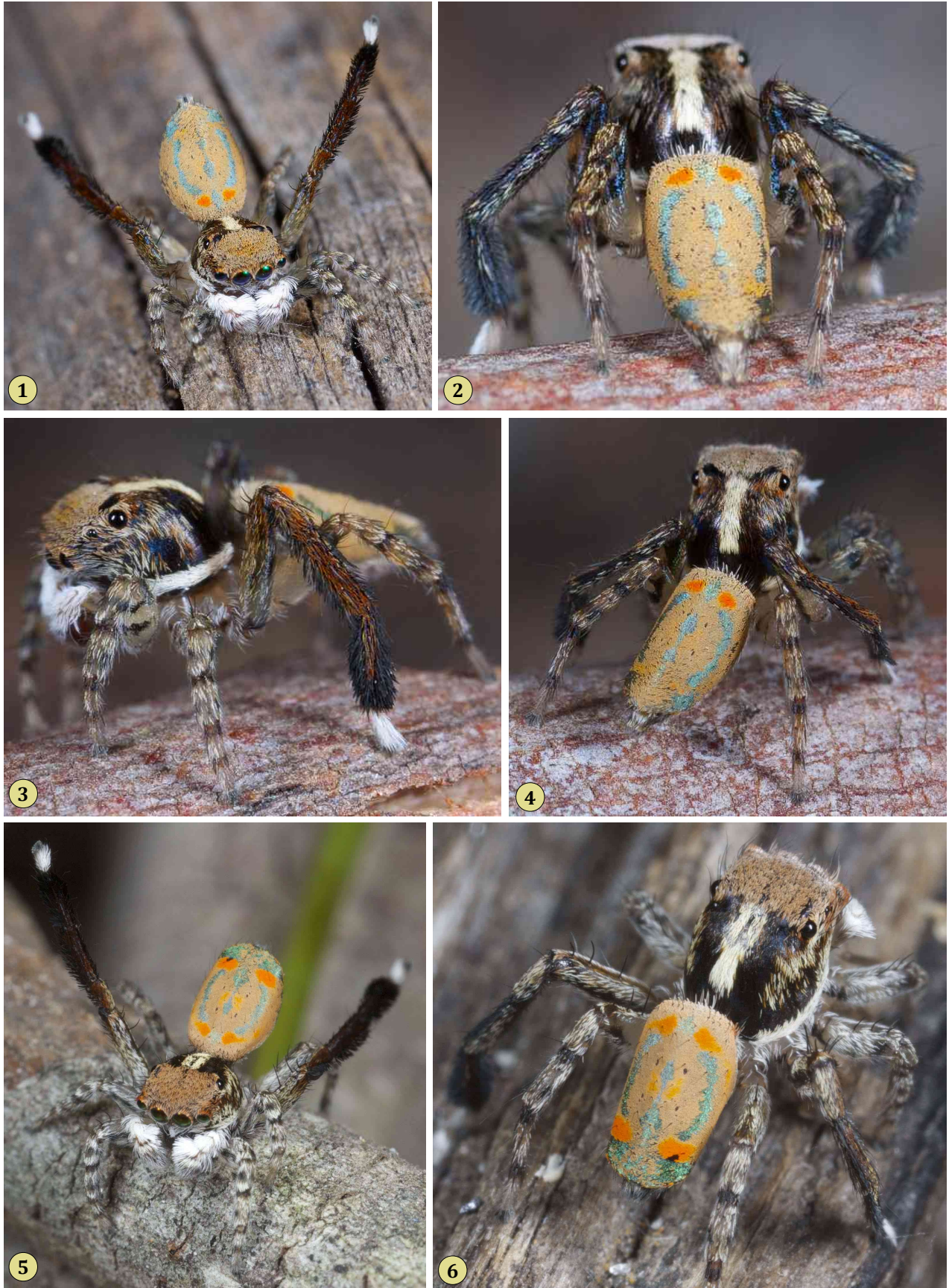


**Figure 52.** Colourful *M. pavonis* males. **1**, This displaying male, from Stanley, Tasmania is similar to Dunn's (1947) original description, as well as other *M. pavonis* found more recently in southeastern Australia. The fan is flattened or expanded during display but no lateral flaps are present. **2-4**, Colourful males from Western Australia often have orange to red-orange scales covering the eye-region (3), or comprising the inner parens (4). These may also have lateral flaps (2, 4), similar to those of *M. literatus*, that allow greater expansion of the fan during display.

We have previously identified a much less colourful variety of *M. pavonis* found north of Perth in Western Australia (*M. pavonis* var. *brunneis*; Otto & Hill 2012b, 2012c). This variety has only been found near Jurien Bay, not Watheroo National Park as reported in error. Males of this variety (Figures 53-54) resemble male *M. montanus* in having scattered scales on the sides of the prosoma, mostly light brown or tan scales on the dorsal plate, no lateral flaps and banded legs I-II, IV. Like other *M. pavonis*, however, the eye region is covered with scales of uniform colour, and the median thoracic band is narrower and of uniform width. We have seen one male with an indistinct central butterfly on the fan, and another male without this feature. At Tim's Thicket to the south of Perth the males are much closer to the 'typical' *M. pavonis* in general appearance and may even have lateral flaps, but the red-orange outer parens is interrupted by tan scales. Females of this intermediate form, like the males, have a median thoracic tract of uniform width (Figure 55). More detailed studies of the variation and distribution of *M. pavonis* will be needed to resolve whether *M. pavonis* can be divided into several different species.

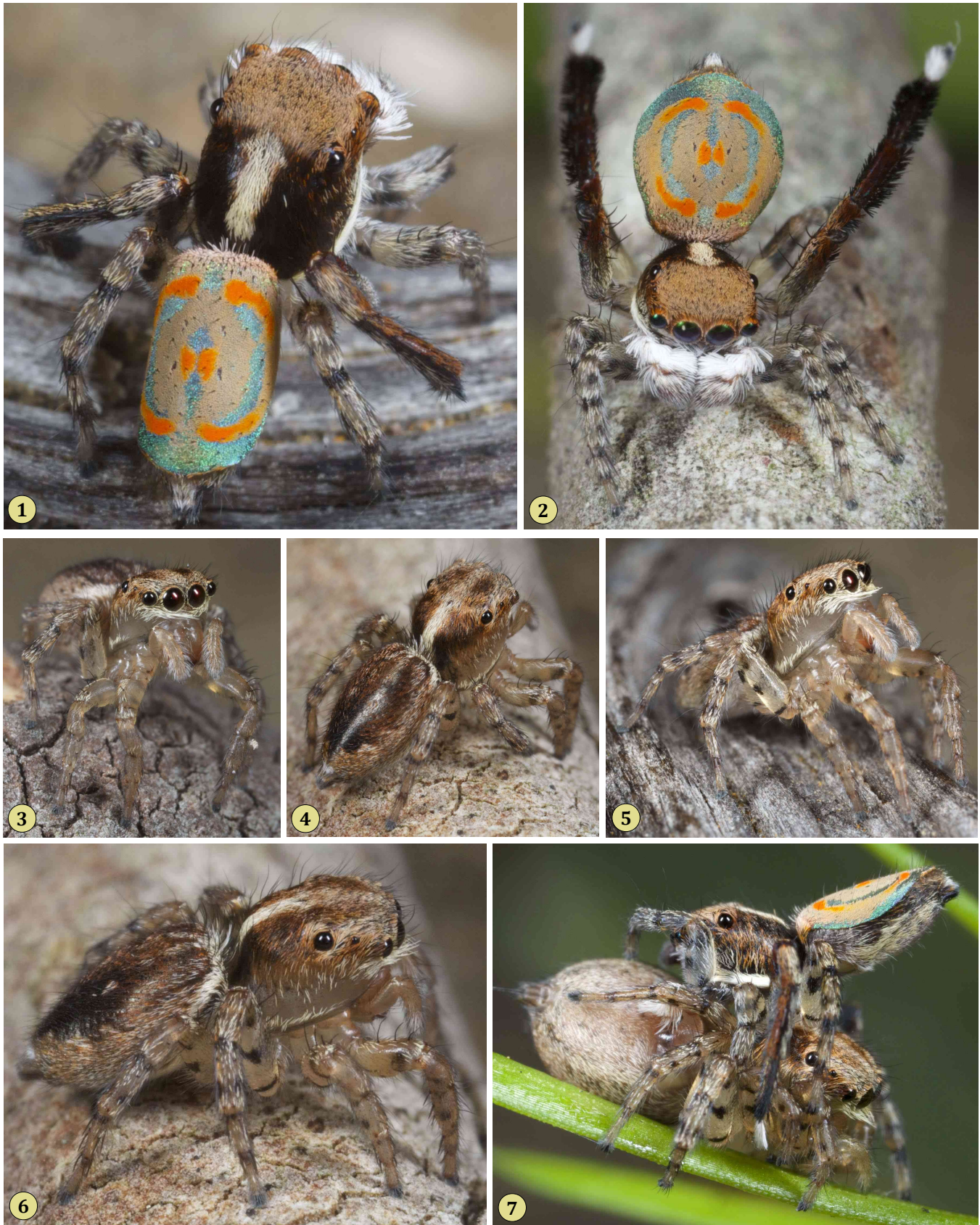


**Figure 53.** Male *M. pavonis* var. *brunneis* collected near Jurien Bay, north of Perth, Western Australia (S 30.30302°, E 115.11695°, OCT 2012, D. Knowles coll.). This male was 4.43 mm in body length, not including the spinnerets. **1-3**, Although the light-brown, translucent cuticle of the living spider appears white, dark pigment bands on the legs are still visible. **4-8**, Views of the left pedipalp. The heavy inner and outer apices of the embolus appear to be fused.



**Figure 54.** Male *M. pavonis*, var. *brunneis*, from the vicinity of Jurien Bay. **1-4**, Male (also shown in Figure 53) with a single bright red-orange spot at the anterior end of each outer parens. **5-6**, Another male, with less red and more white scales on the femur and patella of legs III. This individual also has an indistinct butterfly and a better-defined outer parens, the latter interrupted by tan scales in the middle.

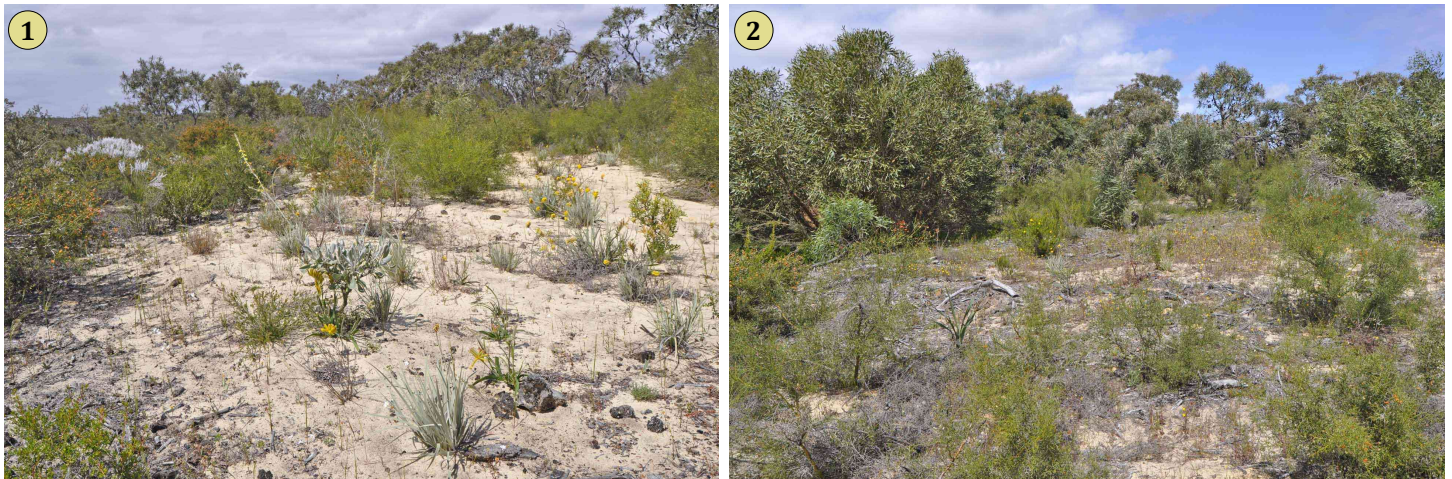




**Figure 55.** *M. pavonis* from Tim's Thicket. **1-2**, Two views of a male, showing well-defined butterfly but interrupted outer paracymbria, as well as banded legs I-II, IV. **3-6**, Four views of a female, showing the dark dorsal opisthosoma characteristic of *M. pavonis*, as well as the median thoracic tract of uniform width. **7**, Same male and female, mating.

*Display by males.* The fan dance of male *M. pavonis* that we have described (Hill & Otto 2011) is similar to that of *M. montanus*. Preliminary observations of the semaphore display of *M. pavonis* from Western Australia suggest that this display differs from that seen in eastern populations, with less waving of the fan, more rapid tapping or vibration of the extended legs III, and more metatarsal flexion.

*Habitat.* *M. pavonis* is widely distributed across southern Australia, from Tasmania to the Indian Ocean. The Jurien Bay locality, north of Perth, is an open woodland/shrubland association that includes *Banksia prionotes* and *Eucalyptus todtiana* (Figure 56; Knowles, pers. comm.). Specimens shown here were collected from the outside of a building in the vicinity of this habitat.



**Figure 56.** Two views of the Jurien Bay locality of *M. pavonis* var. *brunneis*, north of Perth, Western Australia, 290 m north of the location where individuals were collected on a building (S 30.30302°, E 115.11695°, elevation 69.0 m). Photographs by D. Knowles.

### ***Maratus splendens* (Rainbow 1896)**

*Attus splendens* Rainbow 1896

*Saitis splendens* : Simon 1901; Dunn 1947

*Saitis rainbowi* Roewer 1951

*Maratus splendens* : Žabka 1991; Hill & Otto 2011; Otto & Hill 2011, 2012b, 2012c, 2013, 2014; Girard *et al.* 2011; Metzner 2013; Zhang & Maddison 2013; De Angelis *et al.* 2013; Foelix *et al.* 2013

*Maratus rainbowi* : Waldock 2008, 2013; Hill 2009, 2010; Platnick 2013; Prószyński 2013; Australian Faunal Directory 2014

*Type specimen.* Rainbow (1896; see also Hill & Otto 2011) described a single male from Sydney, but did not designate a type specimen. Dunn (1947) referred to this species in his key, but also did not identify a reference specimen. The female has not been described previously.

*Etymology.* The species group name (*splendens*, adj., Latin) means *bright*, and is most certainly a reference to the 'bright colours' of the male in Rainbow's description. For purposes of stability, we continue to use Rainbow's *splendens* rather than Roewer's *rainbowi*. Whereas *rainbowi* still appears in a number of on-line catalogs, all published descriptions and studies of this spider to date have used the original name, *splendens*.

*Diagnosis.* See Hill & Otto (2011) for a detailed comparison with male *M. pavonis*. *M. splendens* males have relatively large flaps, circular in outline when extended (Figure 62). The curved band of iridescent blue scales between the PLE, bordered to the front and rear by uniform bright-red scales, is unmistakable.

These spiders are relatively small with almost unmarked, translucent legs I, II and IV. Females have a distinctive dark margin of the carapace, and a reticulum of dark pigment that can be seen through the sides of the carapace. Sclerotized ducts associated with the epigynum tend to be compact and situated at the posterior lateral corners of the fossae.

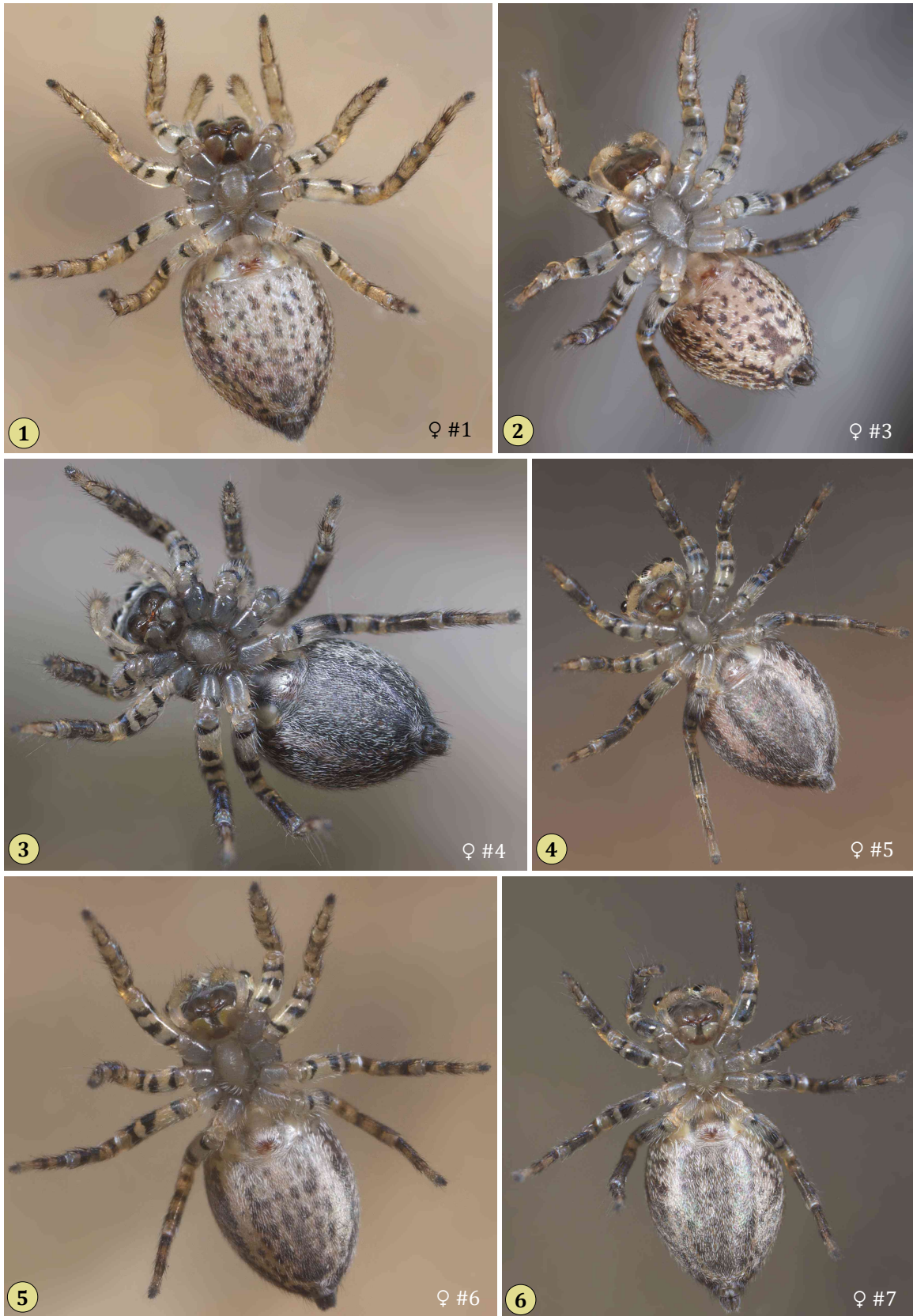
*Description of female* (Figures 57-61). Females (#1-7) described here are from Awabakal Nature Reserve near Newcastle and were found together with many male *M. splendens*. Body length of female specimens that were measured (N=5) ranged from 4.48 to 4.99 mm not including the spinnerets, and from 4.64 to 5.27 mm including the spinnerets.



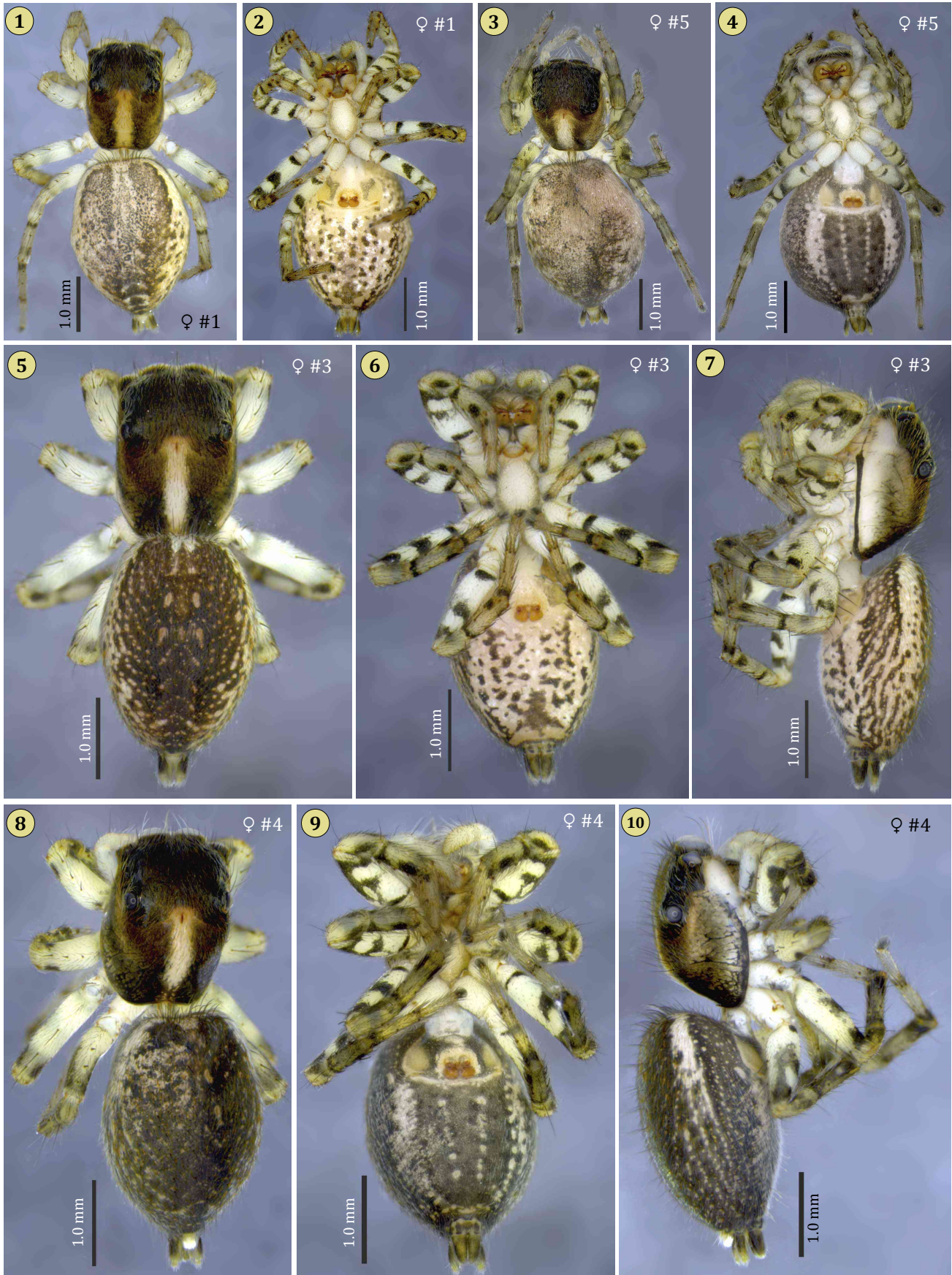
**Figure 57.** Three different female *M. splendens* from Awabakal Nature Reserve near Newcastle. The eye region of this species is more colourful than that of other *Maratus* that have been described. Note the marginal band of dark pigment and the dark reticulum visible through the sides of the carapace.



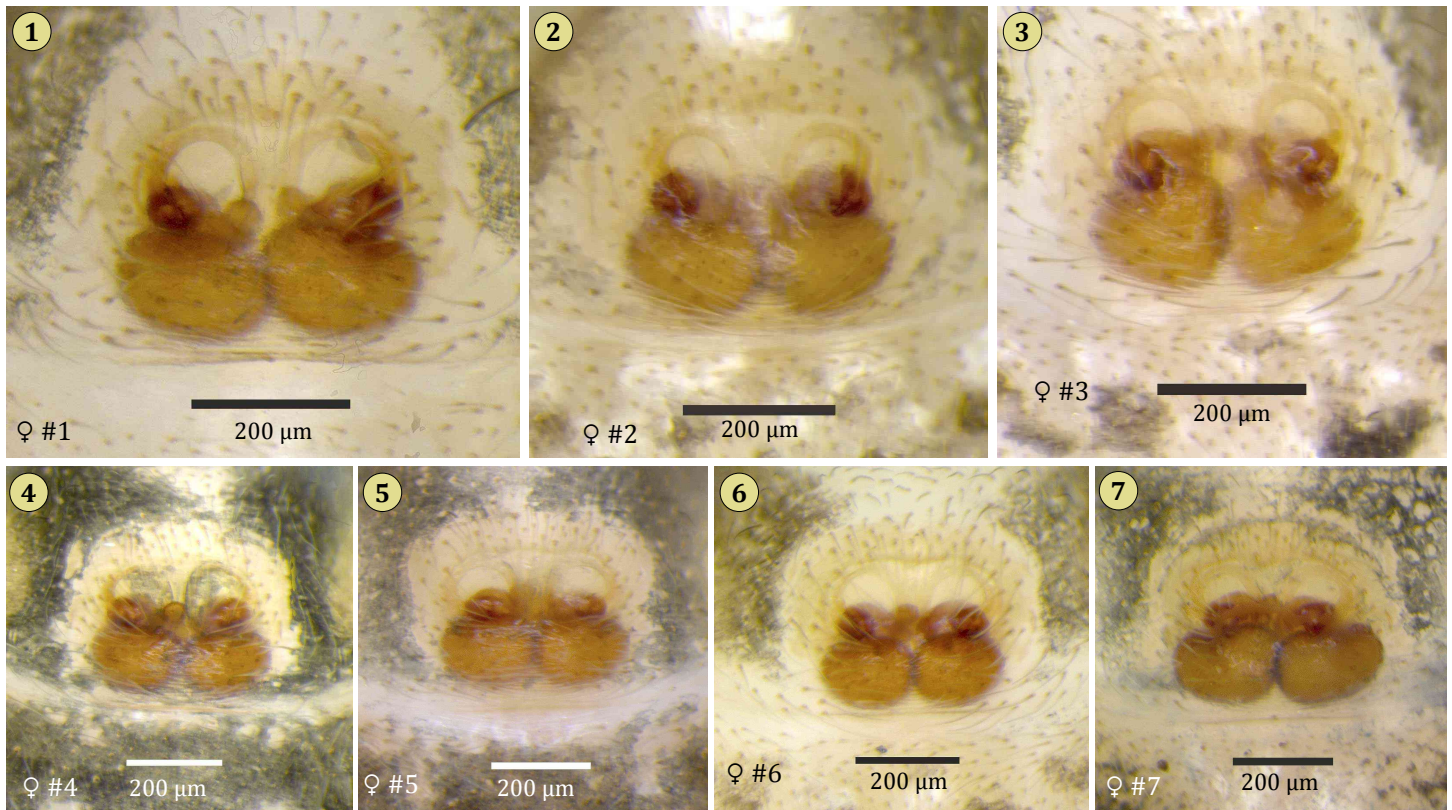
**Figure 58.** Four different female *M. splendens* from Awabakal Nature Reserve near Newcastle. **1-2**, This female was darkly pigmented, even on legs I and II.



**Figure 59.** Underside of six different female *M. splendens*. Note the variable light brown to grey colouration of the sternum, coxae, labium, and endites. Ventral opisthosomal spots were either distinct or indistinct, or completely obscured by dark pigment (3).



**Figure 60.** Four different female *M. splendens*. All translucent light brown to grey structures fade to white in preserved specimens. Pigmentation of the dorsal and ventral opisthosoma varies greatly.



**Figure 61.** Epigynum of six different female *M. splendens*. Fossae were relatively small compared to the spermathecae, and mostly circular. The darkest sclerotization of ducts was usually positioned at the posterior lateral corners of the fossae.

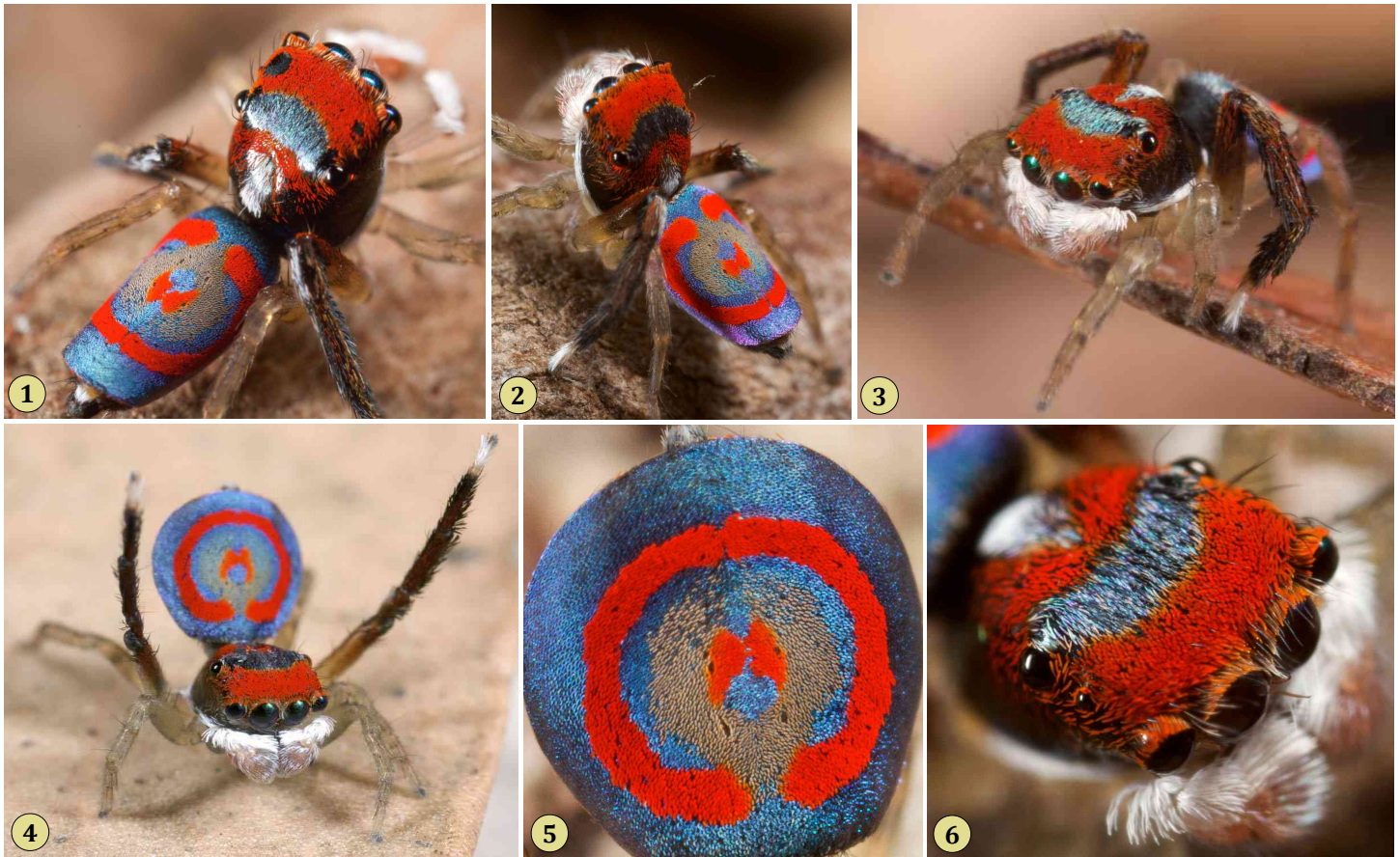
Chelicerae are brown to light brown and glabrous. A few long white setae, projecting anteromedially, may be present on the clypeus. The AME are bordered with ivory scales below and light orange scales above. The eye region is covered with light brown or tan scales surrounding a broad, darker band of brown or orange-brown scales behind each AME. Orange-brown scales also surround each lateral eye row. Behind the posterior eye row, a long median thoracic tract of uniform width, comprised of ivory or light brown scales, extends most of the way to the posterior margin of the carapace. On top of the carapace this is surrounded by mixed light-brown and orange-brown scales. The sides of the carapace are translucent, light brown and glabrous, revealing a reticulum of dark pigment inside of the prosoma. The carapace has no marginal bands, but each margin is highlighted by a distinctive narrow band of dark pigment. The PME are closer to the PLE than to the ALE.

The dorsal opisthosoma is dark brown with scattered white to light brown setae. Toward the sides, this may be mottled, and is bordered on each side by a wide band that is light in colour, covered more densely with white to light brown setae. The ventral opisthosoma may have distinct or indistinct brown spots, or it may be almost completely dark. The coxae, sternum, and endites are mostly glabrous and vary in colour from light brown to brown or from light grey to grey, but all fade to white in specimens kept in ethanol.

Pedipalps are light brown and translucent, with scattered white or light brown setae. Legs I and II are about the same length, much shorter than legs III and IV which are of similar length. Legs are mostly translucent light brown to grey. Femora are banded with dark pigment. Other segments of legs III and IV, and sometimes I and II, are also variably banded with dark pigment. In ethanol, legs also fade to white.

Fossae of the epigynum (Figure 61) are rounded, oval or bean-shaped, rimmed, and separated by a septum of variable width. They are 0.5-0.7x the diameter of the large, contiguous posterior spermathecae. Darkly sclerotized ducts visible through the fossae are rounded in appearance and are usually situated at the posterolateral corners of the fossae.

**Males** (Figure 62). We previously gave a detailed account of the display in this species (Hill & Otto 2011). The fan of the male *M. splendens* is only waved when leg III is waved during the fan dance. During semaphore display, lowering of legs III is not continuous, but interrupted.



**Figure 62.** Male *M. splendens* from Lane Cove National Park, Sydney. **4**, Displaying to female. **5**, Expanded fan showing circular outline and broad peripheral tracts of uniform, iridescent blue-green scales. **6**, Eye region, showing distinctive crescent-shaped band of iridescent blue scales between the PLE.

**Ritual male-male combat.** We previously (Otto & Hill 2012a) described the ritual (male-male) combat of *M. vesperilio* (Simon 1901). In Figure 63 we present frames from a video documenting what appears to be an agonistic approach of a male *M. splendens* toward a conspecific male. The approaching male held its expanded fan in a partly elevated position during this approach. The male that was approached jumped over the approaching male when it reached a distance of about 1cm.



**Figure 63.** Frames from a video (25fps) of a male *M. splendens* slowly approaching a second male to the left. During this approach the male maintained a crouching position without elevating any legs, and with the expanded opisthosomal fan in a partly elevated position.



***Maratus watagansi* Otto & Hill 2013***Maratus watagansi* Otto & Hill 2013, 2014

*Type specimens.* In addition to the male holotype, 7 male paratypes and 6 female paratypes, all from the type locality in Watagans National Park of New South Wales, have been designated and placed in the Australian Museum, Sydney (Otto & Hill 2013).

*Etymology.* The species group name (*watagansi*, nom., Latin form) means *of the Watagans*, a reference to the Watagans where this spider was found.

*Diagnosis.* Males have a distinctive dark red-brown or brown outer parens on an otherwise uniform tan dorsal opisthosomal plate (Figure 64). The apex of the male pedipalp is heavy and divided into three separate parts. Legs I, II and IV are banded with dark pigment but few white setae. The sides and rear of the carapace are mostly glabrous and dark brown.

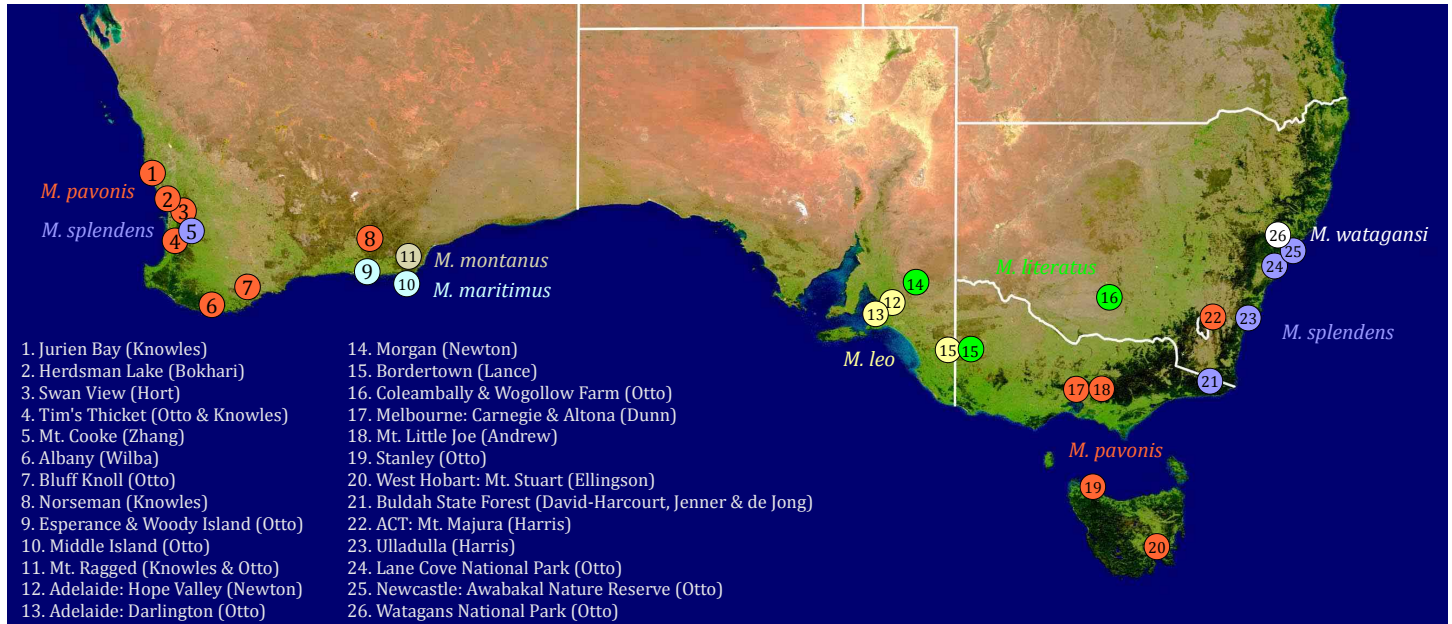


**Figure 64.** Male *Maratus watagansi* from Watagans National Park. **6.** Only a few scattered iridescent blue-green scales are present on the dorsal opisthosomal plate.

*Display by males.* Males do not raise the fan or perform a fan dance (Otto & Hill 2013), but like other species in the *pavonis* group engage in rapid tapping displays. As observed from high speed video footage, legs and body are rocked backward and forward, and each time that the opisthosoma reaches a rearward position it appears to touch, or is scraped against, the surface.

## Biogeography and speciation within the *pavonis* group

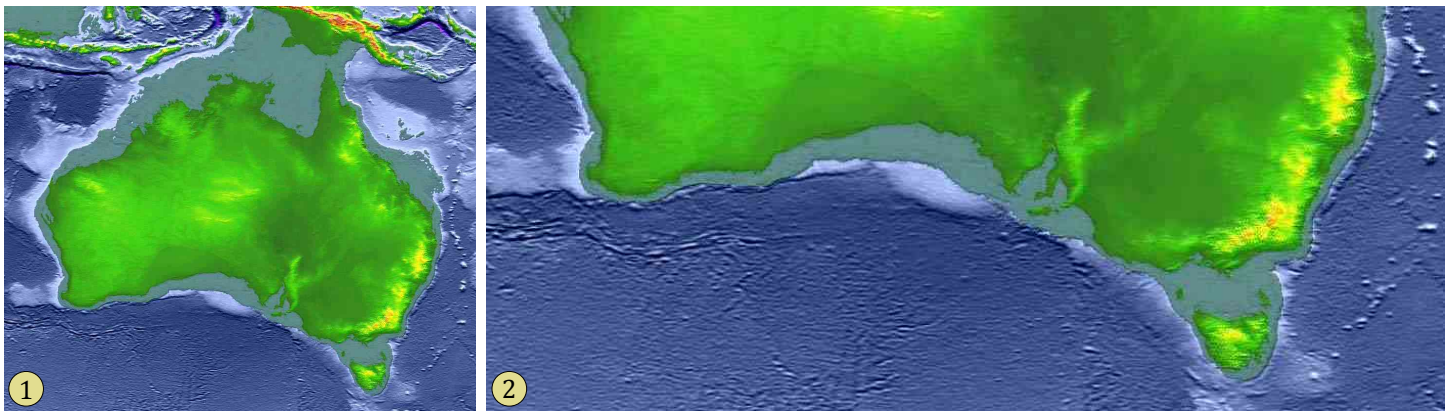
The seven species that we presently associate with the *pavonis* group of the genus *Maratus* are widely distributed across southern Australia (Figure 65). Many additional records for *M. pavonis* can be found in the Atlas of Living Australia (2014), in particular for Western Australia, but as we have not examined these specimens we cannot say whether they belong to *M. pavonis* or to a related species.



**Figure 65.** Localities where members of the *pavonis* group have been found, all in southern Australia. Localities are numbered and listed at lower left with collector or photographer names identified in parentheses. Some of these are based on earlier publications (Dunn 1947, Hill & Otto 2011, Otto & Hill 2012b, 2012c), some are new records, and others are based on more recent photographs posted at [www.flickr.com](http://www.flickr.com). (e.g., Harris 2014). In each instance we have viewed either the specimens themselves or unambiguous photographs. More details about these records may be obtained from the authors upon request. Background satellite image courtesy of NASA Visible Earth.

Our hypothesis is that all evolved from a common ancestor that was brightly coloured in the manner of *M. pavonis* and that bright colouration and in most cases the associated display behaviour was subsequently reduced in *M. pavonis* var. *brunneis*, *M. leo*, *M. maritimus*, *M. montanus* and *M. watagansi*. *M. watagansi* in the east and *M. maritimus* in the west no longer raise their opisthosoma at all. *M. leo* from South Australia only seems to have retained a reduced tendency to employ the opisthosoma in the display while *M. pavonis* var. *brunneis* and *M. montanus* have reduced colouration but have retained a fan dance that is similar to that of *M. pavonis*. Evidence for our hypothesis that drab colouration is apomorphic rather than plesiomorphic in the *pavonis* group lies in the fact that some blue-green iridescent scales can still be found on the dorsal opisthosomal plate (fan) of the males of most of these species and that bright colouration is the norm outside the *pavonis* group. Theoretically it is possible that reduction of bright colouration happened in the *pavonis* group only once, but for this to be the case all drab coloured species of the *pavonis* group would need to form a monophyletic group. We are unable to suggest any characters that would support such monophyly. We suspect that the main driver for this reduction in colouration has not been sexual selection in favour of less colouration by females (although female selection for bright colours would be expected to relax in these groups over time), but improved male survival through crypsis in certain locations. In some local populations, the price paid by males for their bright colouration may have been too great, and the balance shifted toward crypsis and survival during the search for females. Male ornamentation has long been associated with deleterious traits or pleiotropy that can reduce male survival (e.g., Darwin 1871, Brooks 2000).

Given our knowledge of changes in climate and geography during the Holocene, the species that we observe today most certainly had a very different distribution in the recent past. For example, the last glaciation (~50ka) was associated with much greater aridity across the Australian continent which resulted in a shift in the extent and distribution of vegetation types, and later, during the Last Glacial Maximum (LGM, ~20ka) sea levels were about 110m lower and a host of coastal islands in the south, as well as Tasmania, were part of a much larger continent (Figure 66). These changes or oscillations in climate and geography have occurred many times, alternately isolating and then connecting off-shore islands, and shifting vegetation. This has not only resulted in species shifting from one place to another but also contributed to speciation and subsequent hybridisation of populations. This process will be continuing into the future. However, the increasing fragmentation of habitats in modern times, and increasing isolation of species in local parks or nature reserves that serve as refugia (Campbell *et al.* 2011, Nistelberger *et al.* 2014, Schut *et al.* 2014) now may become more important to the future distribution of these species than shifting climate and geography.



**Figure 66.** Extent of Australian continent after a 110m drop in sea level. During the Last Glacial Maximum (LGM, ~20ka) New Guinea (1) and the many islands along the southern coast of Australia, including Tasmania (2), were part of a larger continent. Holocene climate has been generally warmer and wetter in temperate Australia (Petherick *et al.* 2013), where species of the *pavonis* group are now primarily associated with a wet winter/dry summer climate. Based on background maps provided by NOAA.

The results of shifts in climate and geography now manifest themselves not only in the distribution of the various species in the *pavonis* group but also in their morphology and behaviour, and just how the particular combinations of characters that we observe today may have arisen in the past is difficult to interpret. For example, the 'm' figure in the eye region can be found in a series of species over a geographical range, from the interior of New South Wales (*M. literatus*) to the southern coast of Western Australia (*M. maritimus*). This could well be the result of hybridization or gene introgression between species (Hedin & Lowder 2009), or alternatively certain genes corresponding to these characters were present over part of the range of an ancestral species that subsequently gave rise to multiple species that retained and now share these genes.

### The species problem

There are many different definitions of just what constitutes a species (Chung 2003, Wilkins 2003, Kutschera 2004, de Queiroz 2005, Haffer 2006, Mallet 2007, Naomi 2011, Singh 2012, Torstrom *et al.* 2014). Mayr's biological species concept (Mayr 1942, 1996, Coyne 1994, Chung 2003, de Queiroz 2005) is certainly the most widely-taught definition, based on the notion that a biological species is an evolutionary unit comprised of an interbreeding population of organisms. In the case of sympatric populations that differ significantly in morphology the existence of reproductive isolation is clear. We

therefore do not see any difficulty in assigning *Maratus splendens* and *M. pavonis* to different species, as they seemingly occur in relative proximity to one another. Likewise, *M. leo* and *M. literatus* are clearly different species, as they not only differ significantly in morphology but also occur close together. The problem with the biological species concept is to decide what to do when confronted with populations that differ morphologically but have allopatric distributions. We have remarked on this previously in regard to the members of the *M. mungaich* group, which are morphologically close and have an allopatric distribution (Otto & Hill 2014). In cases like this it is difficult to decide whether such populations should be assigned species status or instead be considered as subspecies or varieties. In the current instance of the *pavonis* group similar problems arise with *M. literatus* and *M. pavonis*. Both species are clearly very closely related but can be easily distinguished from one another. However, there is no evidence yet that they occur sympatrically and no evidence either way on whether *M. literatus* will interbreed with *M. pavonis*. The specimens from Jurien Bay that we have identified as *M. pavonis* var. *brunneis* could be considered a separate species for the same reasons. Our decision to treat *M. literatus* as a separate taxonomic species is subjective and others in the future may come to a different conclusion. Mere similarity is no sure indication that different populations belong to the same species, as even populations that are much alike may not interbreed. And even if two populations that are clearly isolated (*e.g.*, *Phidippus regius* in Florida and Easter Island; Edwards 2004) are shown to interbreed, there is the question of whether this will happen naturally and whether these populations now belong to different biological species simply by the nature of their isolation. Mating or breeding experiments to test the validity of proposed biological species (*e.g.*, Hebets & Maddison 2005) may appear useful but they are almost never performed and in addition may also not be conclusive, as it is virtually impossible to simulate the actual (physical and circumstantial) conditions associated with mating in a diverse natural environment. However, demonstrations of reduced hybrid fertility could be convincing.

Species in many spider genera have often been distinguished by differences, in many cases small or graded differences, in genitalic morphology. However, in few cases has populational variation in these characters been reported, even if this has been observed, and usually only a single type has been described. From our experience (see also Waldock 2013), interspecific variation in genital morphology is of limited use for the identification of *Maratus* species, where it appears that recent evolution has been focused on the secondary sexual characters, including both ornamentation and behaviour of males, and not on mating mechanisms. In isolated populations these secondary sexual characters may evolve rapidly (Masta & Maddison 2002, Oh & Shaw 2013).

### Acknowledgments

We thank David Knowles for his assistance in the collection of many specimens, Monique and Geoff Urbas for allowing the collection of *M. pavonis*, var. *brunneis* on their property at Jurien, Kevin and June Shields for allowing the senior author (Otto) to collect the *M. literatus* types on their property at Coleambally, Andrew Leo for sending the specimens described as *M. leo*, and Martyn Robinson for looking after juvenile spiders while the senior author was away on holiday. We also thank the Department of Parks and Wildlife of Western Australia (licence number SF008869), the National Parks and Wildlife Service of NSW (licence number SL100390), and the Pine Grove Holiday park in Esperance for permission to collect spiders. Unless otherwise indicated, all photographs presented here are copyright © J. C. Otto.

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