

Males of a new species of *Jotus* from Australia wave a paddle-shaped lure to solicit nearby females (Araneae: Salticidae: Euophryini)

Jürgen C. Otto¹ and David E. Hill²

¹19 Grevillea Avenue, St. Ives, New South Wales 2075, Australia, *email* jurgenotto@optusnet.com.au

²213 Wild Horse Creek Drive, Simpsonville, SC 29680-6513, USA, *email* platycryptus@yahoo.com

Abstract: The euophryine genus *Jotus* is reviewed. Characteristics and courtship behaviour of one new species from Australia, *Jotus remus*, are described. Males of this species display an unusual paddle-shaped modification of their distal legs III to females on the opposite side of a stem or leaf. High speed video recordings reveal that *J. auripes* and *J. remus* power their jumps by the extension of both pairs (III and IV) of rear legs.

Key words: courtship, euophryine, *Jotus auripes*, *Jotus frosti*, *Jotus remus*, jumping spider, salticid

Review of *Jotus*

Presently eight species are recognized in the euophryine genus *Jotus* L. Koch 1881 (Table 1; Figures 1-3), (WSC 2015).

Table 1. Species of *Jotus* L. Koch 1881 with published descriptions.

| species | additional references | localities | status |
|--|---|---|--|
| <i>Jotus auripes</i> L. Koch 1881 (TYPE) | Simon 1901; Žabka 1987; Davies & Žabka 1989; Otto & Hill 2012a, 2012b | various locations throughout New South Wales and Victoria | male is familiar but female not formally described |
| <i>Jotus braccatus</i> L. Koch 1881 | Žabka 1987 | Gayndah, Queensland | male and female described |
| <i>Jotus debilis</i> L. Koch 1881 | | Sydney, New South Wales | only female is described, epigynum does not look like <i>Jotus</i> |
| <i>Jotus frosti</i> Peckham & Peckham 1901 | | Victoria, here reported from Kangaroo Island, South Australia | only male is described, distinctive |
| <i>Jotus insulanus</i> Rainbow 1920 | | Lord Howe Island | only female is described, little detail in drawings |
| <i>Jotus maculivertex</i> Strand 1911 | | Kei Island, Indonesia | only male is described, does not look like a <i>Jotus</i> |
| <i>Jotus minutus</i> L. Koch 1881 | Žabka 1987 | Peak Downs, Queensland | male in original drawing looks like <i>Jotus</i> , but pedipalp drawn by Žabka (1987) does not |
| <i>Jotus ravus</i> (Urquhart 1893) | Bryant 1935 | Wellington, New Zealand | only male is described |
| <i>Jotus</i> sp. | Zhang & Maddison 2013, 2015 | Oakview State Forest, Queensland | male and female misidentified as <i>J. auripes</i> |

The type species for this genus, *J. auripes*, was originally described from Sydney but has recently been found at other locations in New South Wales and Victoria. The male *J. auripes* has a distinctive appearance, with many long, iridescent setae on the pedipalps and bright red-orange setae covering the anterior femora of legs I and II (Figure 1: 1; Figure 2; Otto & Hill 2012a, 2012b). The male pedipalp of this species appears in a number of published figures (L. Koch 1881; Žabka 1987; Davies & Žabka 1989; Otto & Hill 2012a, 2012b) but, apart from the presence of long iridescent setae, this is similar to the male pedipalp of other *Jotus*. Zhang & Maddison (2013, 2015) depicted a specimen that they identified as *J. auripes*, but in our opinion this represents another, yet undescribed species of *Jotus* (Figure 1: 10-11).

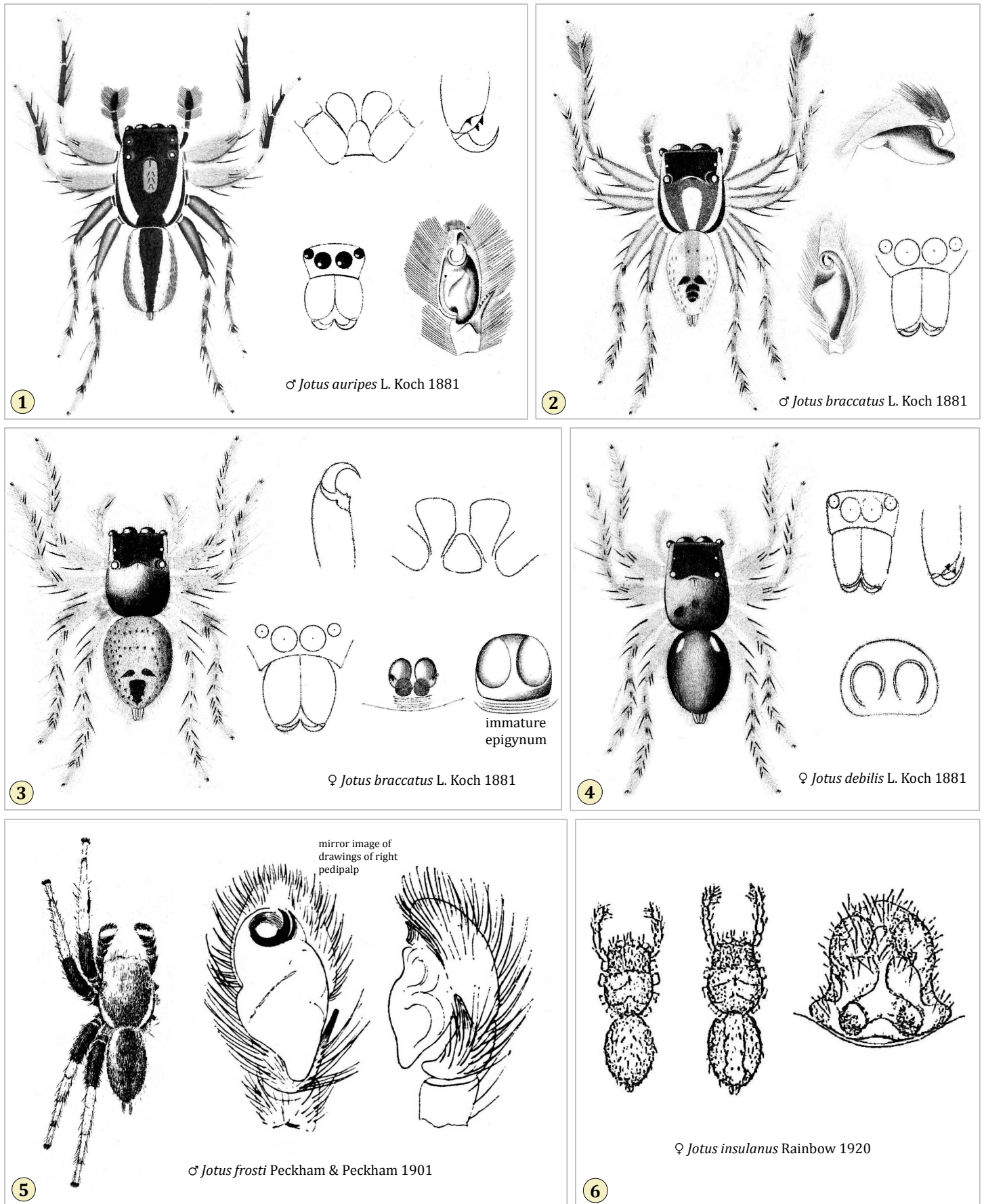


Figure 1 (continued on next page). 1-6, Drawings that accompanied the original descriptions of five *Jotus* species.

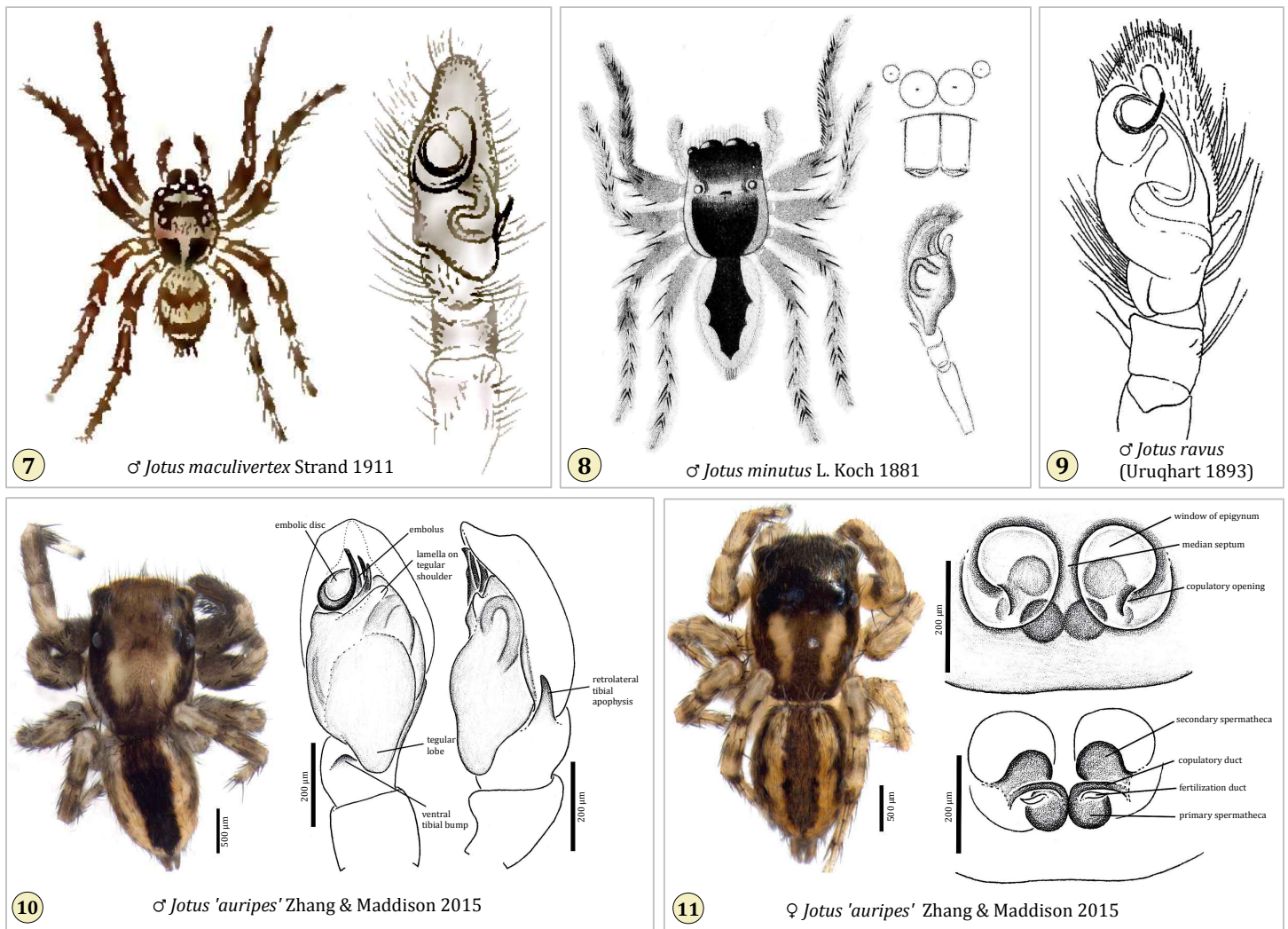


Figure 1 (continued from previous page). 7-8, Drawings that accompanied the original descriptions of two *Jotus* species. 9, Mirror image of drawing by Bryant (1935) of the right pedipalp of the male *J. ravus*. 10-11, Adaptation of Figures 491-496 used in the description of *Jotus 'auripes'* by Zhang & Maddison (2015). Unlike *J. auripes*, the carapace of this species does not have broad white lateral bands, but has narrower marginal bands. Figures 1: 10-11 Copyright © 2015 J. Zhang & W. P. Maddison, used here under a Creative Commons Attribution (CC-BY) 3.0 license.

The original drawings of male and female *J. braccatus* (Figure 1: 2-3; L. Koch 1881) are semi-schematic, but Žabka (1987) more recently redescribed the male and female genitalia of this species from the types and these are similar to those of *J. auripes*. We thus consider this spider to be correctly assigned. No individuals other than the type specimens are known to us. *Jotus frosti*, described by the Peckhams (1901) from a male collected in Victoria and carefully drawn by Emerton (Figure 1: 5), has a male pedipalp that agrees with that of *Jotus*, and a distinct white band across the pedipalps. Recently two male *J. frosti* were photographed at Kelly Hill Conservation Park on Kangaroo Island (Figure 3). As figured by Bryant (1935; Figure 1: 9) the pedipalp of the male *J. ravus* could also represent a *Jotus*. The status of the other species placed in this genus, all based on sketchy descriptions of a few specimens collected long ago, is less certain. The original illustration of *Jotus minutus* does seem to depict a species that is similar to other species in this genus with respect to the pattern on the carapace and opisthosoma, and the leg morphology. However, the male pedipalp in Žabka's (1987) redescription of *J. minutus* differs from other *Jotus*. Based on their limited descriptions, there is no reason to associate *J. debilis*, *J. insulanus* and *J. maculivertex* with this genus.

Jotus are common spiders and we believe that there are many similar, undescribed species in southern Australia (Figures 4-6).



Figure 2. Adult male *Jotus auripes* from Sydney. As viewed from above this type species for the genus *Jotus* is quite unremarkable and typical of males of this genus. From the front, however, the long iridescent setae of the pedipalps and the bright red-orange setae that cover the femora of legs I and II are distinctive. The female *J. auripes* is known but has not been formally described (Otto & Hill 2012a, 2012b).



Figure 3. Adult *Jotus frosti* males photographed on Kangaroo Island, South Australia, by Jürgen C. Otto (28 OCT 2015). This impressive species is readily identified by the transverse band of white setae across the front of each pedipalp, the dark iridescent anterior femur I (2), and the combination of long black setae above and long white setae below each femur I.



Figure 4. Undescrbed *Jotus* male (1-4) and a *Jotus* (conspicuous?) female (5-6) photographed at Barrington Tops National Park, New South Wales, by Jürgen C. Otto (1 NOV 2015). This male has a prominent black brush beneath tibia I, but no special ornamentation of the pedipalps. The pattern of scales on the carapace and opisthosoma is close to that of *J. frosti* and *J. remus*.



Figure 5. A different undescribed *Jotus* male from Barrington Tops National Park. The difference between this male and the one shown in Figure 4 may be in part due to wear, but this male is much darker without evident banding of the legs, and without white setae on metatarsus I. Differences between *Jotus* species may be quite subtle.



Figure 6. Undescribed male *Jotus* found near Denmark in Western Australia. This species has a distinct middorsal stripe on the opisthosoma, dark fringes under the femur, tibia, and metatarsus of legs I, and widely separated white stripes on the posterodorsal carapace. In most respects it is quite similar to the *Jotus* species that have been described from southeastern Australia.

Žabka (1987) lumped *Jotus* and a number of *Maratus* species (*Maratus* Karsch 1878) into the genus *Lycidas* Karsch 1878, but Davies & Žabka subsequently (1989) reinstated *Jotus*. Recently, Zhang & Maddison (2013, 2015) suggested that the genus name *Saitis* might be applied to a number of predominantly Australasian genera, including *Jotus*, that have been placed within a '*Saitis* clade' based on DNA sequencing (Figure 7). This clade may date back to the end-of-Eocene separation of Antarctica from Australia (ca. 33Ma, Hill 2009). Further studies of the relationships of spiders in this group are needed, but it is our view that there are many characters that can be used collectively to distinguish *Jotus* from the other members of this clade (Table 2).

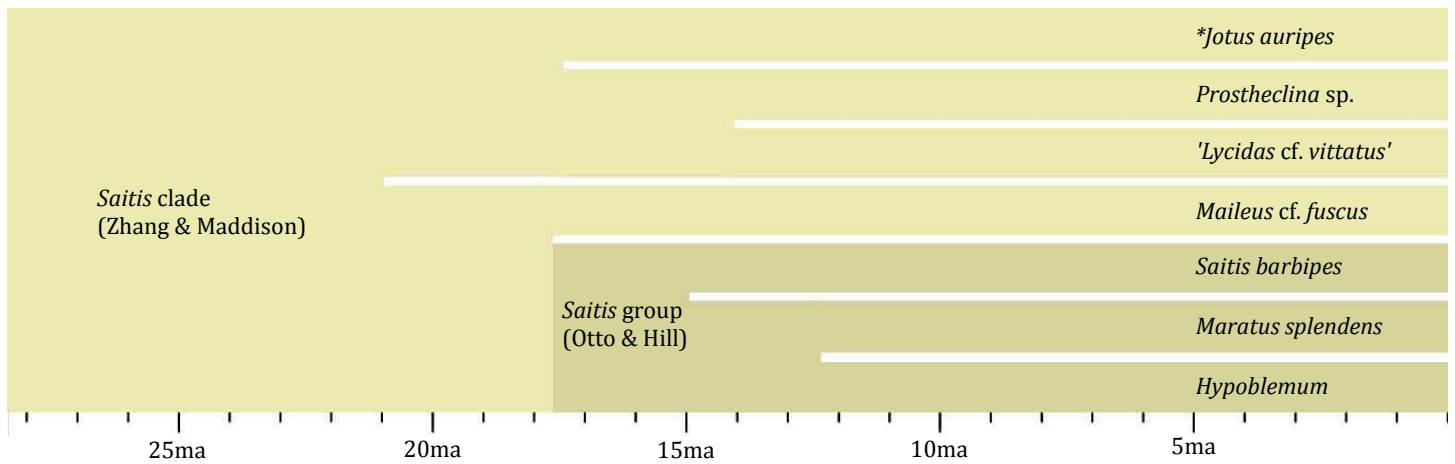


Figure 7. Estimated time line for divergence of genera in the *Saitis* clade, based on DNA sequencing and names used by Zhang & Maddison (2013). **Jotus* sp. misidentified as *J. auripes*.

Table 2. Important characters that can be used collectively to distinguish *Jotus*.

| character | <i>Jotus</i> | other euophryines in the <i>Saitis</i> clade |
|--|--|--|
| relative length of legs III and IV | legs III and IV nearly the same length or IV is slightly longer; usually no specialization of legs III; legs III usually not used in male courtship display; both legs extended to power jumps | legs III much longer, usually ornamented and raised in male courtship display, and their extension serves as the primary source of power for each jump by <i>Saitis</i> and <i>Maratus</i> |
| ornamentation and display of legs I by males | legs I raised in display; usually tarsi are white; often fringe of long dark setae under tibia, anterior of femur I and sometimes femur II brightly coloured or shiny | legs I usually like legs II, without ornamentation and not raised in display of <i>Saitis</i> and <i>Maratus</i> ; long, thin, and fringed in male <i>Prostheclina</i> (Richardson & Žabka 2007) |
| setation of carapace of male | broad lateral (not marginal) band of white scales on each side; mostly dark above or with mixed setae; white median thoracic tract wide or may bifurcate toward the rear | in <i>Maratus</i> often covered with bright scales and often with series of longitudinal stripes across the eye region; narrow marginal band but not lateral bands |
| opisthosoma of male | boldly and simply marked: dark medially with wide white to off-white lateral bands; opisthosoma without dorsal plate and not raised during courtship display | varies in <i>Saitis</i> ; <i>Maratus</i> males have a dorsal plate or scute that is usually brightly ornamented with pigmented and iridescent scales and waved when elevated; the opisthosoma often has long lateral fringes or flaps that represent lateral margins of the dorsal plate |
| embolus of pedipalp | proportionately smaller but heavy ring or spiral terminating in 2-3 distinct apices | spiral larger usually with two apices, not always distinct (<i>Maratus</i>), much larger (<i>S. barbipes</i>), or small with a single distinct apex (<i>Prostheclina</i>) |
| epigynum of female | anterior spermathecae relatively large, rounded, visible in fossae | fossae mostly clear without anterior spermathecae (<i>Maratus</i>), or with anterior spermathecae that are narrower and tubular (<i>Prostheclina</i>), or like <i>Jotus</i> (<i>Saitis</i>) |

Jotus remus, new species

Type specimens. The holotype male (♂ #5, collected as penultimate and reared to adulthood 13 JAN 2015), four paratype males (♂ #1-4), and nine paratype females (♀ #1-9) were collected at Gloucester Tops, Barrington Tops National Park in New South Wales (32.08969° S, 151.59412° E, 30 DEC 2014 - 1 JAN 2015, elevation 1159 m, coll. J. Otto). All types will be deposited in the Australian Museum, Sydney. Additional spiders were collected 1 NOV 2015 for the study of behaviour.

Etymology. The species group name (*remus*, Latin, m., nom., English translation *oar* or *paddle*) is a reference to the presence of a flat 'paddle' comprised of long setae associated with the modified metatarsus and tarsus III of the adult male.

Diagnosis. The presence of a paddle at the end of each leg III uniquely identifies this species. Otherwise, these are very similar to other *Jotus* with respect to structure of the male and female genitalia and general appearance. Male *J. auripes* and *J. frosti* are readily distinguished from *J. remus* by the distinctive appearance of their pedipalps and legs I (Figures 2-3). Females of most *Jotus* are unknown and it is thus unclear what characters may be used to distinguish them. Compared to the female of an undescribed *Jotus* species from Barrington Tops (Figure 4: 5-6), the carapace and legs of the female *J. remus* are distinctly darker in colouration.

Description of male (Figures 8-14). These are small to medium-sized jumping spiders, 4.86-5.69 mm in body length (N=5). Chelicerae are convex, of medium size, black and glabrous, with isolated medial setae and a distinct fringe of smaller, brown setae distally, above the dark red fangs (Figure 10: 1). The dorsal surface of the pedipalps is dark, covered with long white to dark brown (varies by individual) setae. Setae of the dorsal patella of each pedipalp are lighter in colour, white to light brown. The height of the clypeus is about 2/3 of the AME diameter. The clypeus bears many long white setae, most projecting ventromedially. The ALE are large, 1/2 to 2/3 of the AME diameter. The AME are contiguous. All anterior eyes are fringed with small white to light brown scales or setae. Scale cover of the eye region and carapace varies greatly between individuals, from dark brown or black and glabrous, to brown or red-brown at the front. This may be the result of aging or rubbing, as males collected earlier in the season (November) had a more complete scale cover like the holotype. A median thoracic tract of white scales or setae extends from the middle of the eye-region toward the rear, ending where the carapace drops off steeply midway from the posterior eye row to the posterior margin. When the scale cover is largely intact, this tract appears to be pointed at either end, resembling a stretched diamond. There is a broad lateral band of white scales or setae on either side of the otherwise dark carapace, extending from just below the PLE (but not in front of this) toward the rear. This band is near the margin on either side, but is not marginal. The carapace is about 3/2 as long as wide.

The dorsal opisthosoma is medially dark brown to black, narrower toward the rear. This area is flanked by broad lateral bands of white to off-white scales. Below, the opisthosoma is dark brown medially, and mottled light to dark brown laterally. The anterior spinnerets (Figure 10: 5-7) are long, black and glabrous. The posterior spinnerets are much shorter, covered with white to brown setae. From below, the coxae, sternum, labium, and endites are black and glabrous. From below the legs are also mostly black, with scattered white to brown setae.

Legs I and II are the shortest and of similar length, mostly black but with scattered patches of white to brown setae (variable by individual), most on the dorsal femora (Figure 10: 3). Again, this variation may be due to aging or rubbing. The distal tarsi of legs I are light-coloured as in other *Jotus*. Legs III and IV are similar in length, with legs IV slightly longer (Figure 11: 8). The metatarsi and tarsi of legs III are specially modified in the adult male (Figure 10: 8-11; Figure 11: 6, 8), with many long, off-white or light brown fringing setae on both the anterior and posterior margins forming a distinctive 'paddle'. The metatarso-tarsal joint is extremely narrowed, and the tarsus itself is somewhat flattened and of an atypical shape. The tarsi of legs I, II and IV also bear a very short fringe of stout setae (Figure 10: 3-5).

The male pedipalp (Figure 13) is typical for *Jotus*, with a relatively short but heavy spiral of the embolus. The apex of the embolus is divided into two or three heavy projections. The retrolateral tibial apophysis (RTA) is notched distally like that of other *Jotus* and related genera in the *Saitis* clade.



Figure 8. The five male types for *Jotus remus*. The holotype (σ #5) was lighter with a heavier cover of scales and setae. This may be due to the recent molt of this spider. A broad lateral band extends only from the rear of the eye region to the rear in this species. Other than a general appearance quite similar to that of other *Jotus*, the prominent proteral to retrolateral paddle associated with modifications of the metatarsus and tarsus of legs III is distinctive for this unusual species.



Figure 9. More views of the male holotype *Jotus remus*.



Figure 10. Details of living male *Jotus remus*. **1**, Above the dark red-orange fangs can be seen fringes of brown setae projecting from each distal paturon. **2**, Eye region of holotype male, covered with off-white to red-brown setae. **3**, Right legs I-III. Note the light colour of tarsus I and the fringes of short but stout off-white setae associated with the tarsi of legs I and II. **4**, Tarsus IV also has anterior and posterior fringes of stout, off-white setae. Note the erect spines associated with an increase of internal hydrostatic pressure as this spider prepared for a jump. Normally (5) these are not erect. **5-7**, The anterior spinnerets are black and glabrous, usually covered by the setose posterior pair (6). Note the release of a dragline from an anterior spinneret (7). **8-11**, Views of the distal right (8-9, 11) and left (10) leg III. Prominent anterior and posterior fringes form a paddle-like structure. The articulation of the metatarsus and tarsus is very narrow, and the tarsus is flattened somewhat.



Figure 11. Views of the holotype male *Jotus remus* in ethanol.

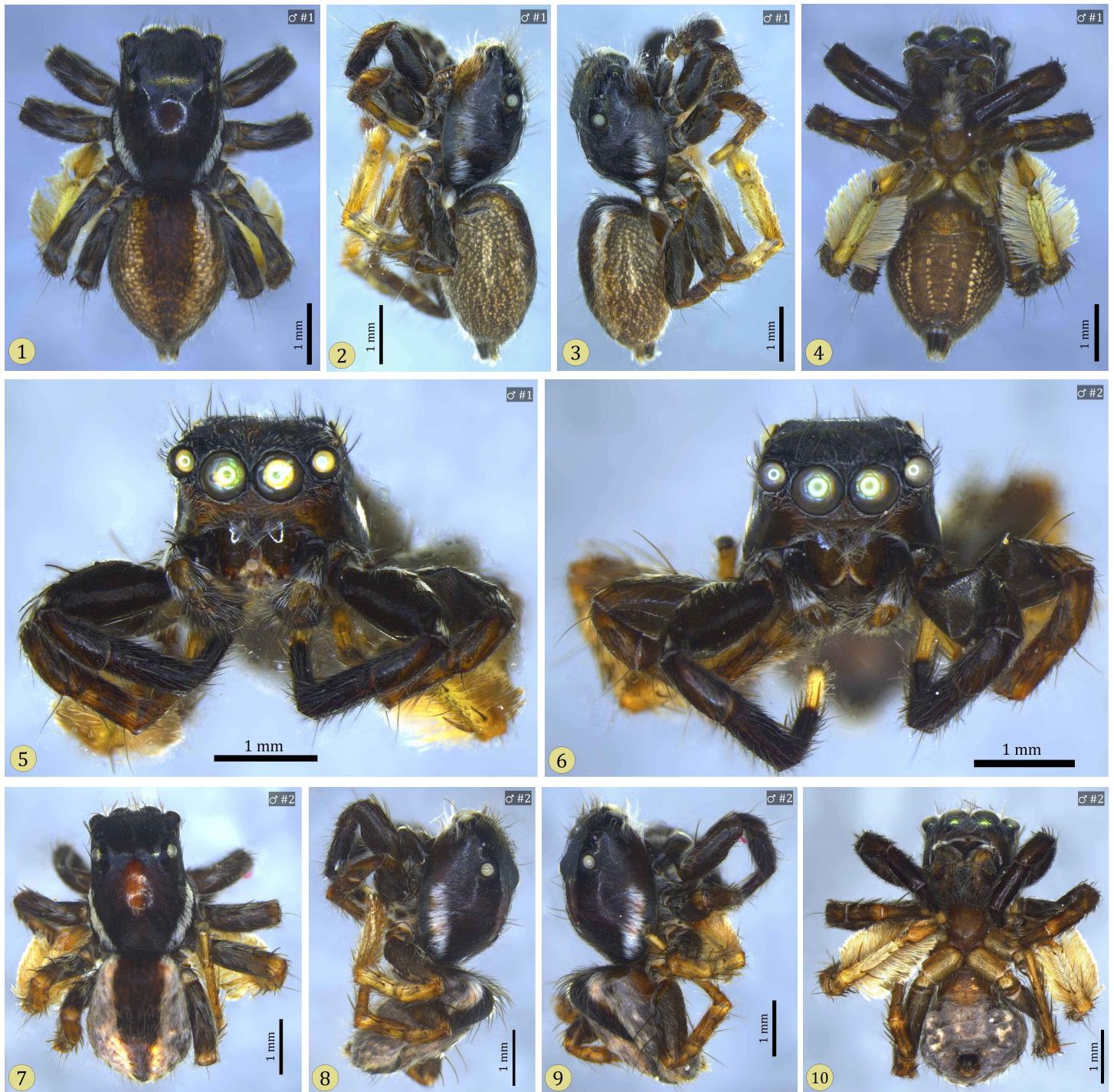


Figure 12. Two paratype male *Jotus remus* in ethanol.

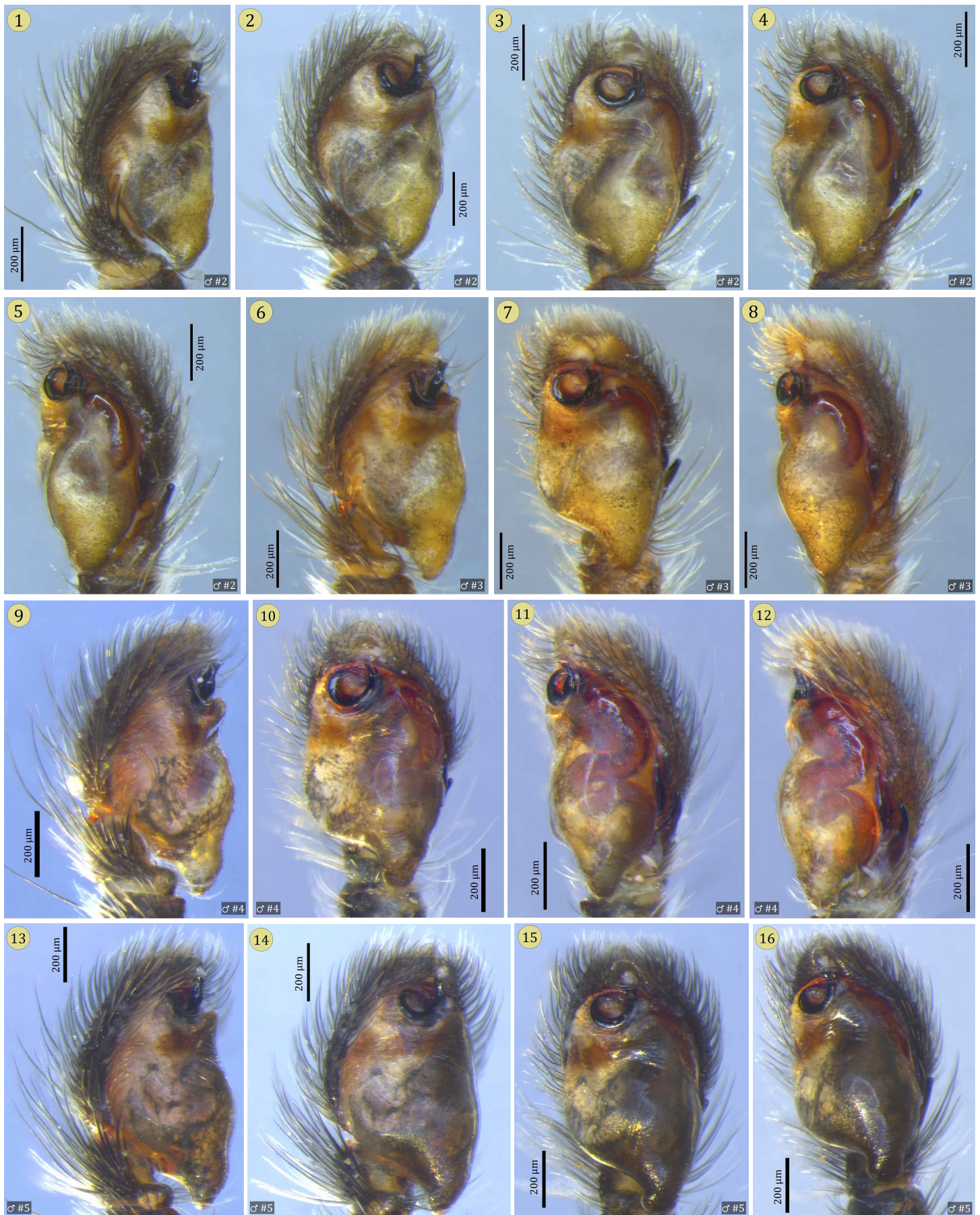


Figure 13. Views of the left pedipalp of four male *Jotus remus* types in ethanol.



Figure 14. Underside of the living male holotype *Jotus remus*.

Description of female (Figures 15-18). Female *Jotus remus* are somewhat larger (5.34-6.57 mm in length, N=9) and strongly resemble the males in colouration and general appearance, but lack any special modifications of legs III. The chelicerae are black, glabrous, and convex. The width of the clypeus is at least $2/3$ the diameter of the AME, and as in the male bears long white setae directed medio-ventrally. The pedipalps are black to dark brown and covered with white to off-white setae. The ALE are about half the diameter of the AME, and the AME are nearly contiguous. All anterior eyes are surrounded by light brown scales or setae. The carapace is black to dark brown with only scattered setae in the eye region, mostly around the lateral eyes. As in the male, a median thoracic tract of scales extends from the middle of the eye region toward the rear, ending at the beginning of the posterior slope of the carapace. There are also wide lateral, but not marginal, bands of white setae on the carapace. Again as in the male, these bands extend only behind the eye region, not in front of it.

The medio-dorsal opisthosoma is dark, but not as distinctly marked as the male. Laterally the margins are covered with brown to off-white setae and may be mottled somewhat. The anterior spinnerets are dark. From below the female is lighter in colour and more brown than the male, but darker in life (Figure 16). Legs I and II are shorter and similar in length. Legs III and IV are longer and also similar in length. Above, the legs bear scattered groups of off-white scales, most conspicuously on the dorsal femora.

As in other *Jotus* species, the epigynum of the female has a prominent pair of anterior spermathecae, visible through the fossae (Figure 18). These are similar in size to the posterior spermathecae.



Figure 15. Views of living female *Jotus remus*.



Figure 16. Views of the underside of three living female *Jotus remus*. From below, these spiders are brown to dark brown with a more or less distinct 'U' shaped mark under the opisthosoma (1-2). This may be obscured in darker individuals (3).



Figure 17. Views of four female paratype *Jotus remus* in ethanol.

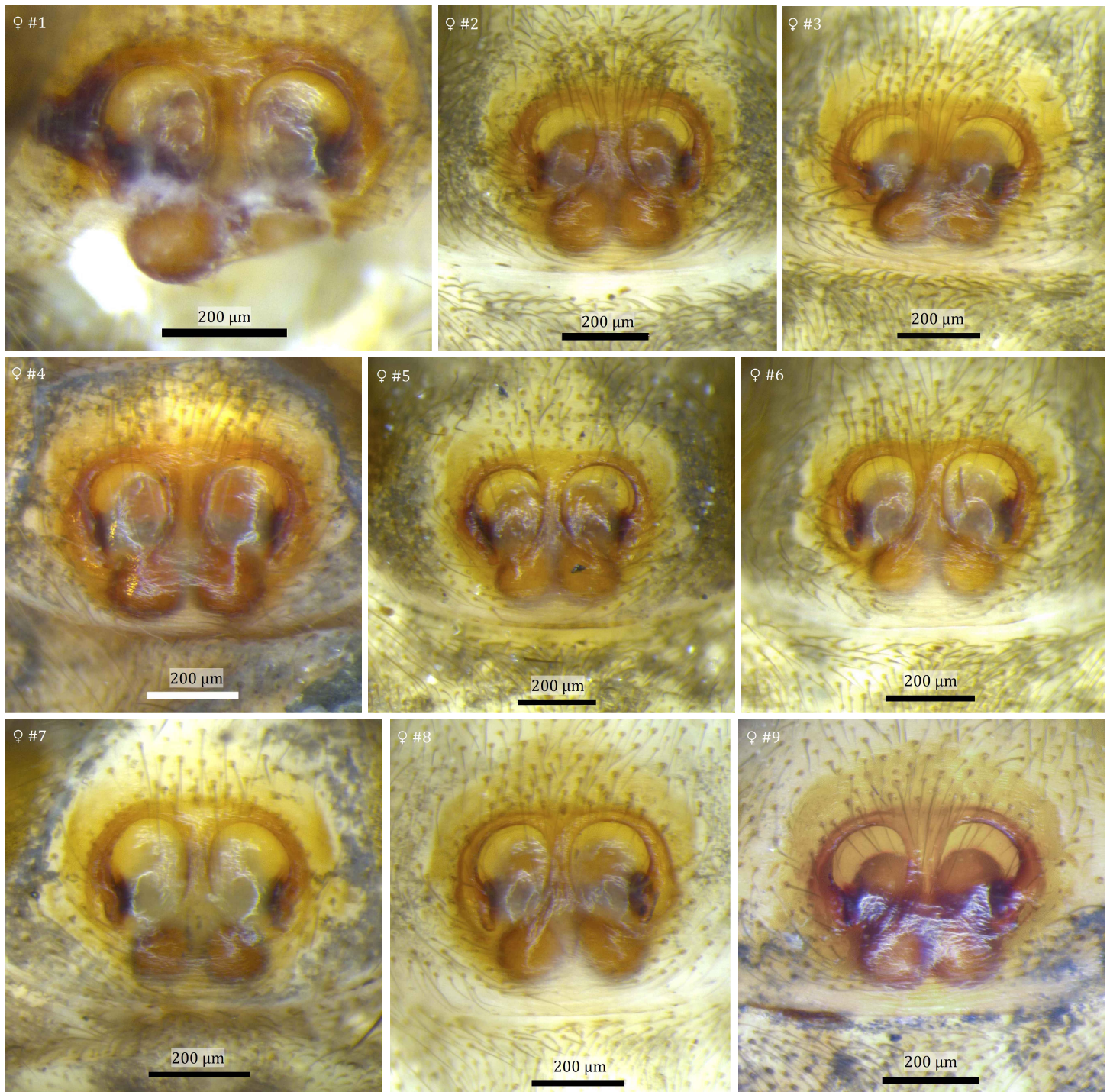


Figure 18. Epigyna of the nine female paratype *Jotus remus* in ethanol. The anterior direction is toward the top of the page. The anterior spermathecae are about the same size as the posterior spermathecae and are visible through the fossae. The septum between the fossae is generally wide.

Immatures. When compared with emergent (second instar) *Maratus*, *Jotus remus* are relatively dark and glabrous, with proportionately longer legs (Figure 19).

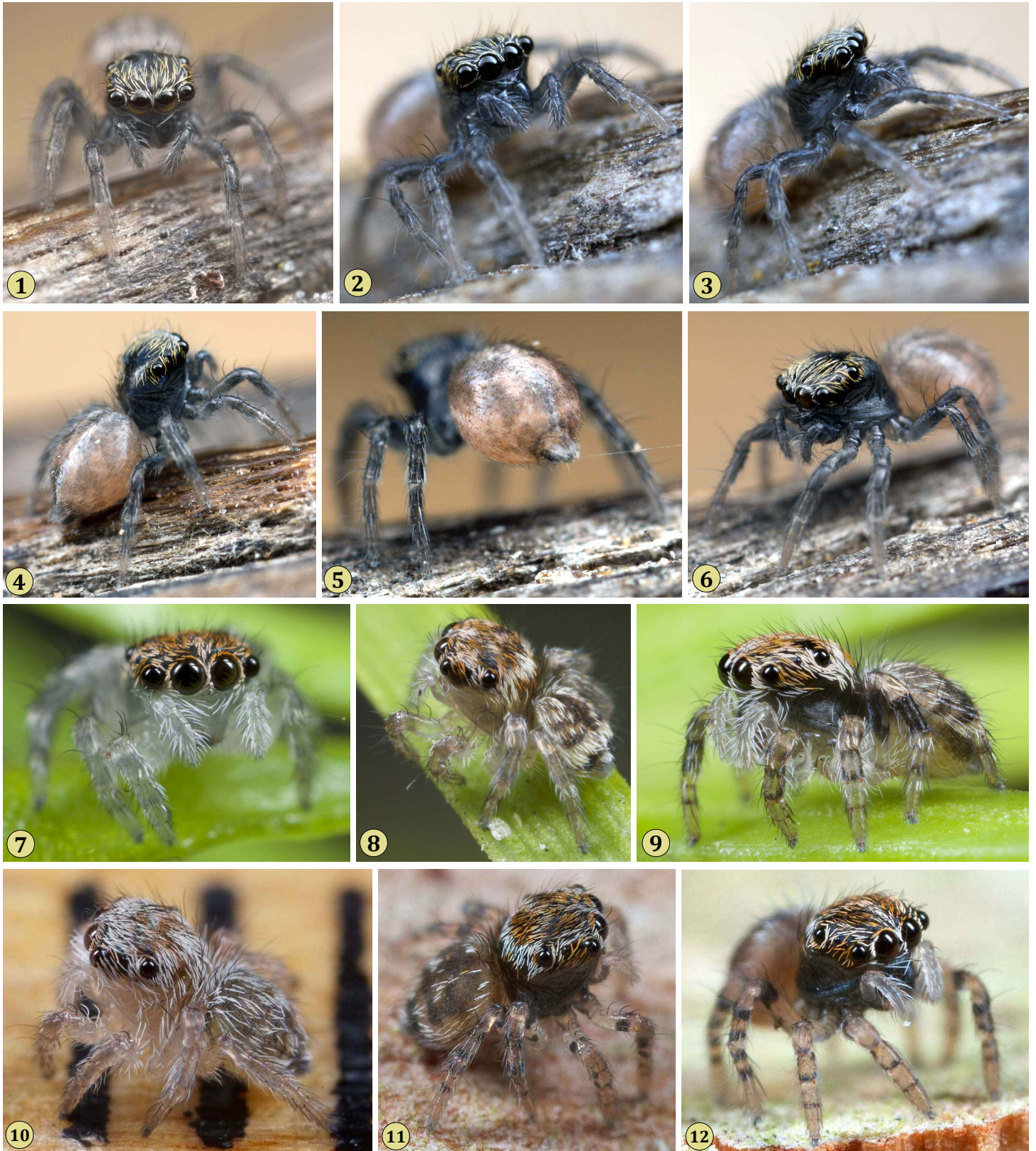


Figure 19. Emergent (second instar) young of *Jotus remus* (1-6), *Maratus personatus* (7-9), *M. pardus* (10), and *M. volans* (11-12). 7-12, After Otto & Hill (2014, 2015). *Maratus* juveniles are much more compact.

Male display and male-female interactions. The three behaviours characteristic of male courtship display are shown in Figure 20 and may be observed in two online videos (Otto 2015a, 2015b). These include 1) visual display in front of the female with legs I extended, 2) vibration in place on the opposite side of a leaf from the female, and 3) visual display of the paddle at the end of a leg III to a female on the opposite side of a leaf or stem.



Figure 20. Behaviours associated with the courtship display of male *Jotus remus* (sequential but not consecutive frames from a 25 FPS video). **1**, The male displayed directly in front of the female at a distance, with legs I elevated and extended. **2-5**, With the female on the underside of a leaf, the male vibrated in place by moving legs I up and down rapidly while bobbing the opisthosoma. **6-7**, The male waved one extended leg where the paddle could be observed by the female beneath the leaf.

The visual display in front of a female (Figures 21-22), often at a distance, was not elaborate. This simplicity corresponds to the lack of ornamentation. When performing this display the male stood in an erect posture with the white-tipped legs I held erect and waved slightly.

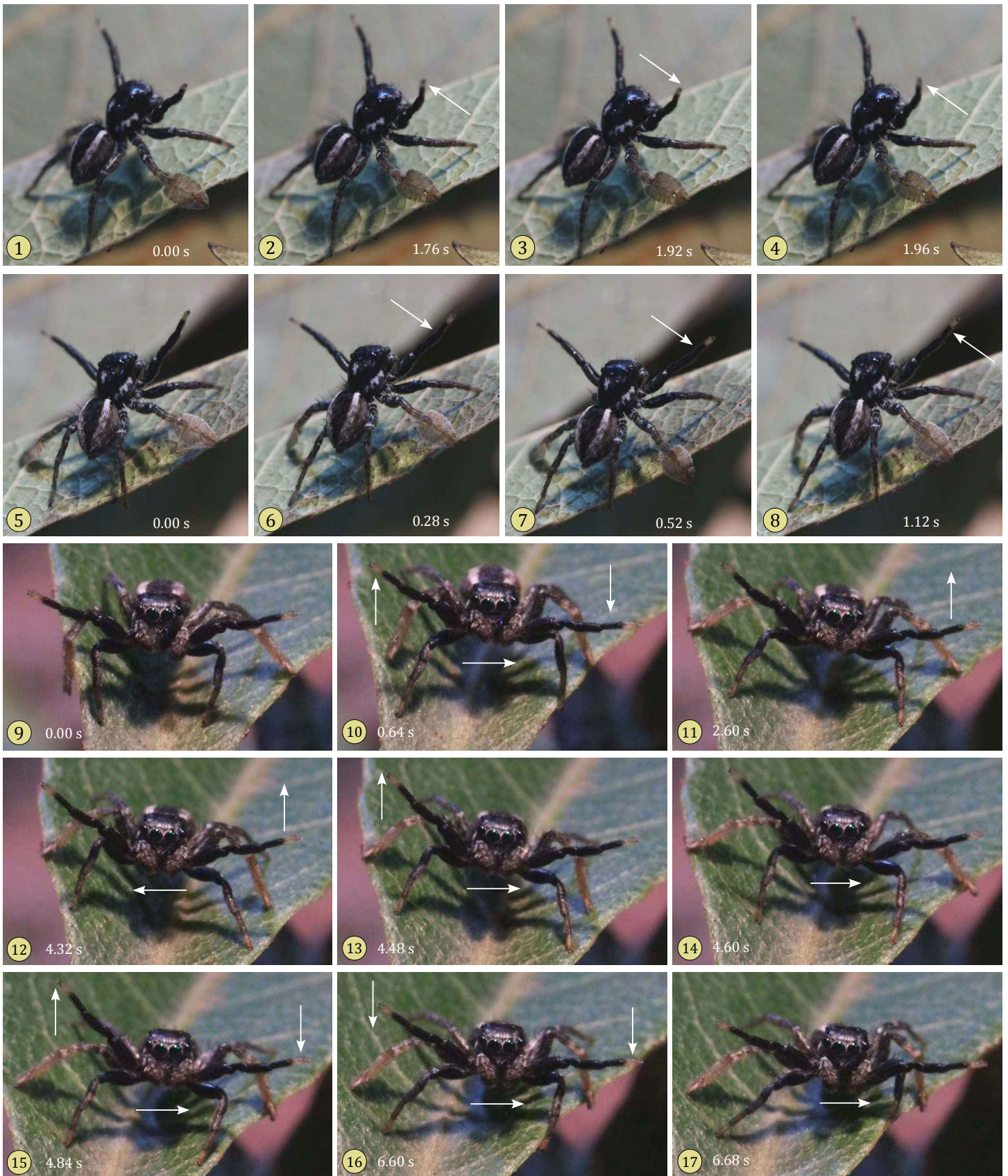


Figure 21. Three sequences showing the visual courtship display of male *Jotus remus* in front of a female (sequential but not consecutive frames from a 25 FPS video). Subtle movement of legs I and side-to-side movement of the body relative to the previous frame is highlighted with arrows.

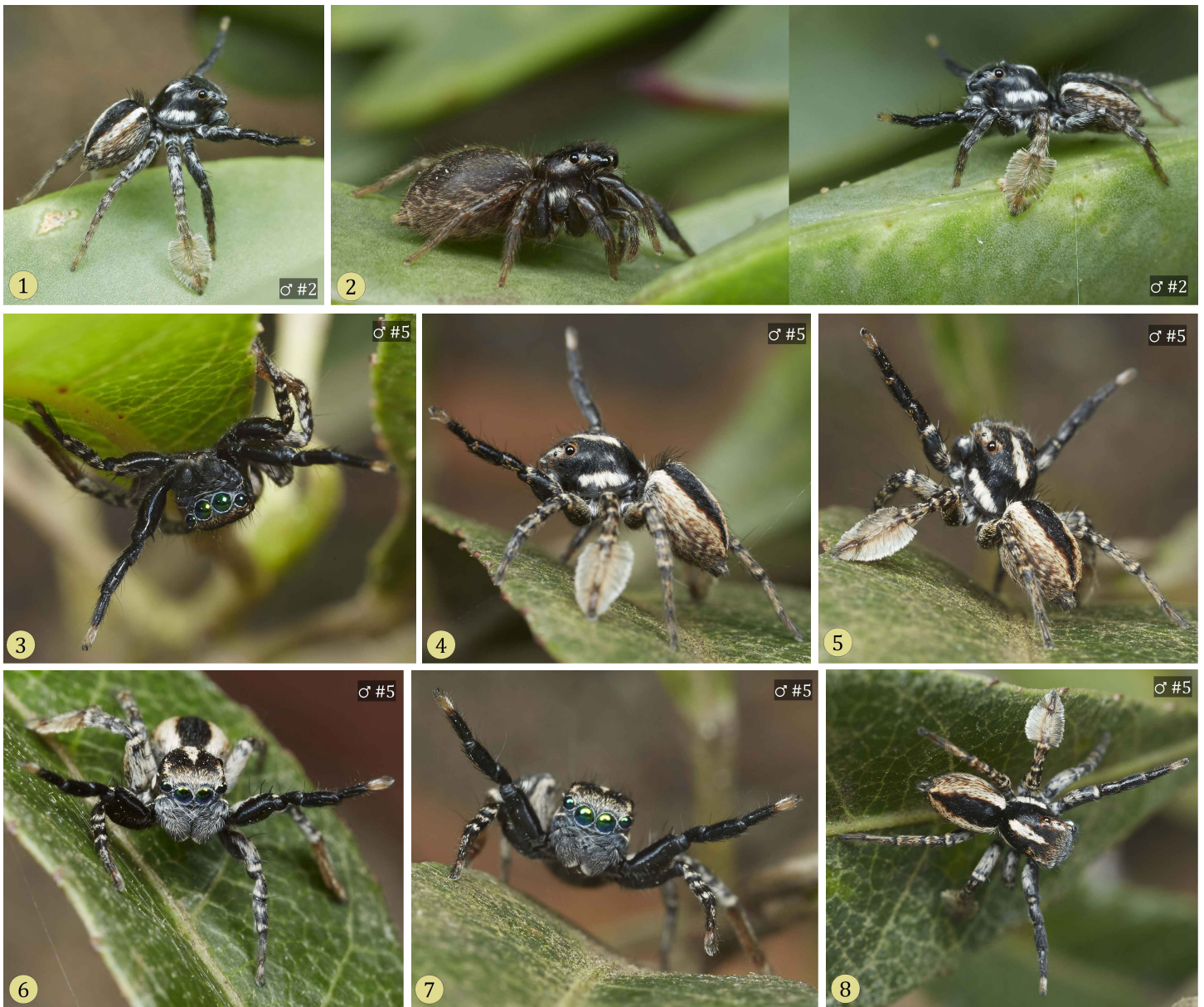


Figure 22. Photographs showing the visual courtship display of male *Jotus remus* in front of a female. **2**, The female (at left) watched the male .

The vibration display (Figures 23-24) was generally performed when the female was on the opposite side of a leaf or stem, out of sight of the male. This display involved rapid bilateral movement of the flexed legs I, with the tarsi near the mid-line, up and down. At the same time the opisthosoma was bobbed up and down rapidly. The cadence of this leg movement was distinctive, often repeated at a rate of $\sim 6/s$, with intermittent acceleration to twice this rate ($\sim 12/s$). This display was often interrupted as the male would reach over the edge of the leaf to display one of his paddles to the female.

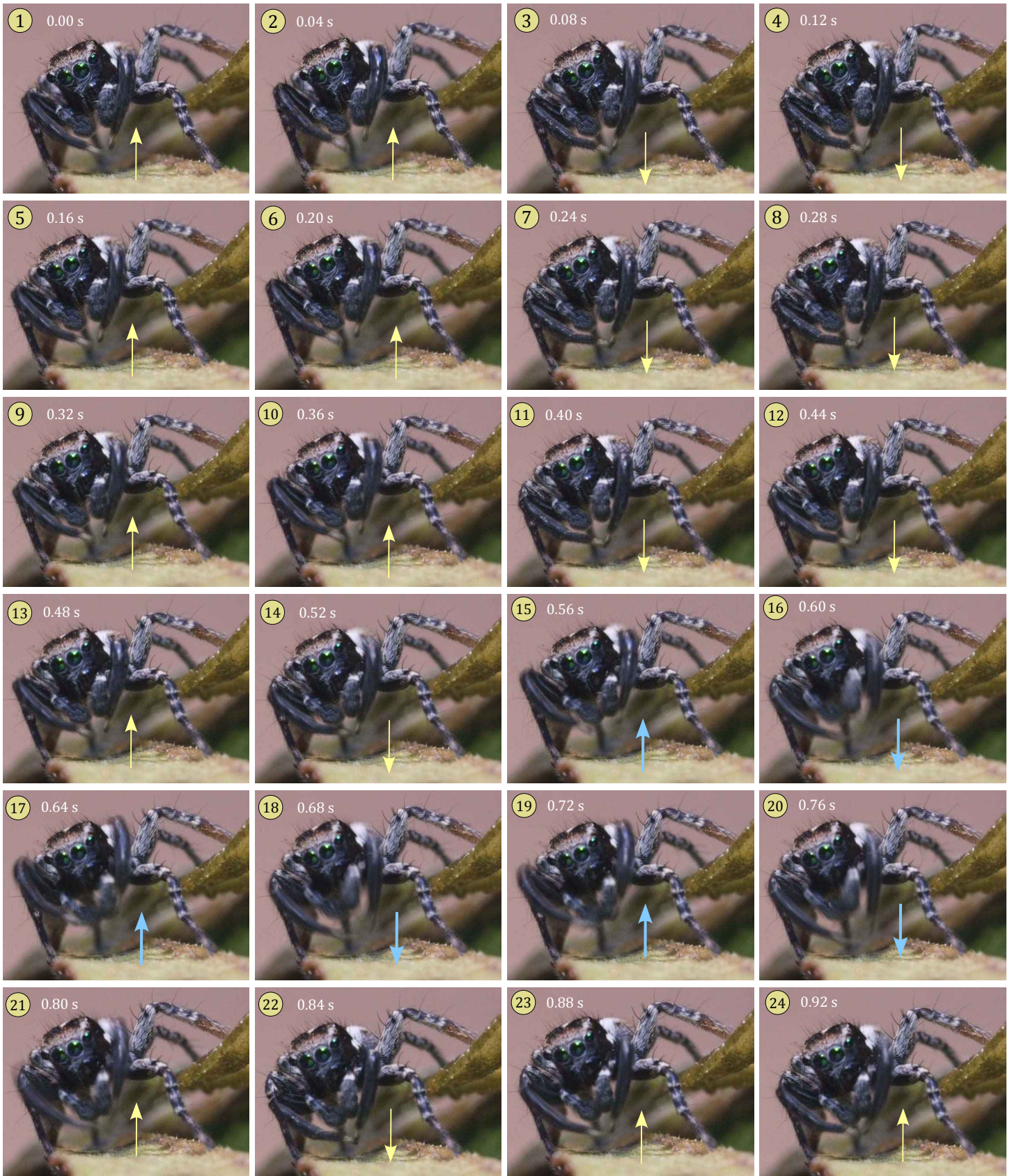


Figure 23. Consecutive frames (25 FPS video) showing the vibration display of a male *Jotus remus* on top of a leaf. The female was directly below this leaf. Arrows indicate the relative position of legs I in each frame (up or down). At times the $\sim 6/s$ cadence of this display doubled to $\sim 12/s$ (15-20).



Figure 24. Sequential frames (25 FPS video, not consecutive) showing alternation between paddle and vibration display by a male *Jotus remus* on top of a leaf. The female can be seen in outline below this leaf. **1-3, 12-14,** Display of the paddle by extending it over the edge of the leaf. **4-11, 15,** Vibration display. Arrows indicate position of legs I

Until we observed the behaviour of males in the presence of females, we could not understand how the paddle could be effective in visual display since it is flattened dorso-ventrally and thus would not be visible to a female in front of a male. In fact, this paddle is not used in face-to-face display by males, but is only used to attract the attention of a female on the opposite side of a leaf or stem (Figures 25-30). The extended paddle is moved forward and backward in front of a female, and females turn to watch the paddle and frequently attack it (Figure 30).



Figure 25. Sequential frames (25 FPS video, not consecutive) showing display of the paddle of one leg III by a male *Jotus remus*. Note the attention of the female on top of the leaf. At times (5) this display was interrupted and the female turned away.

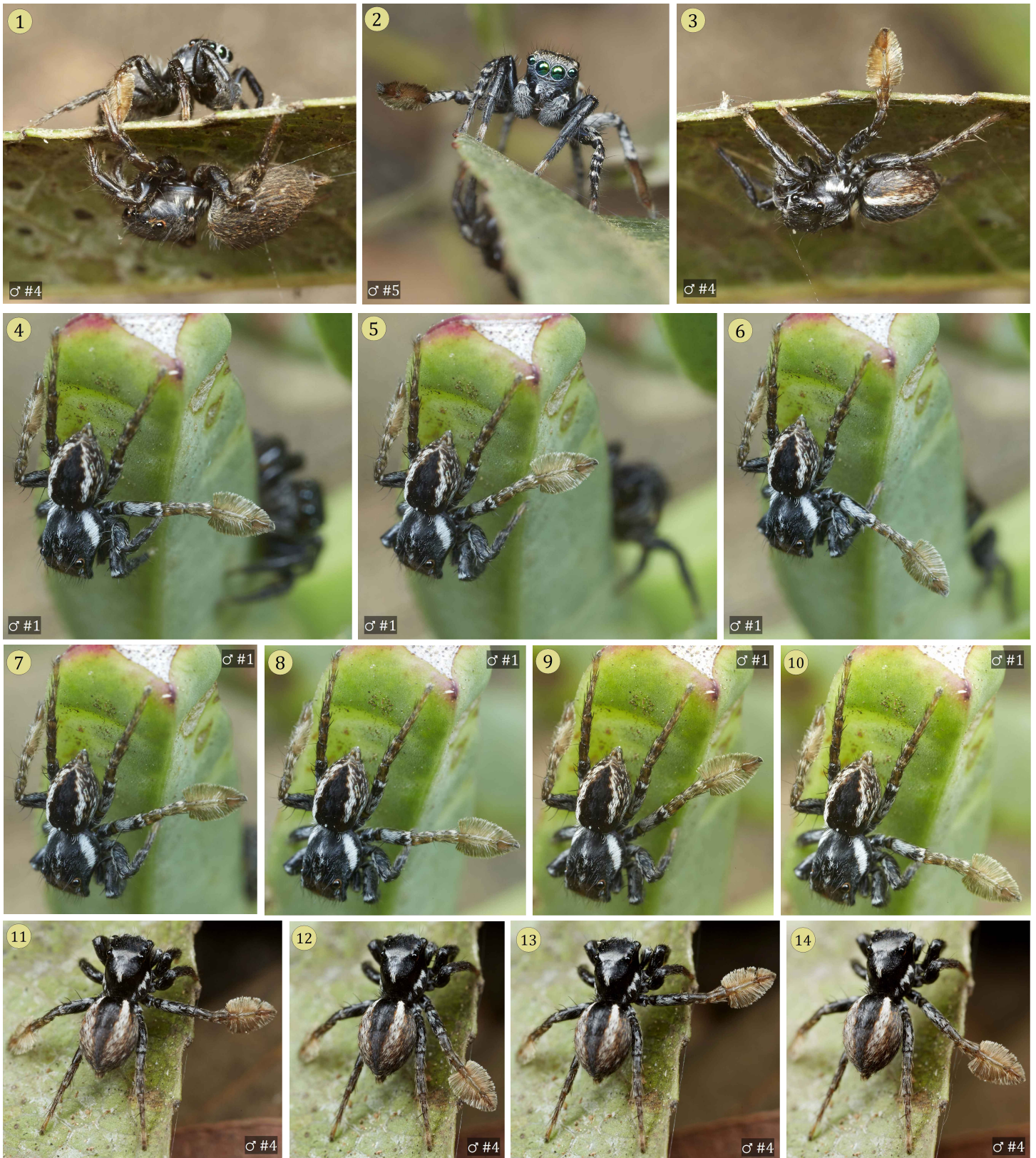


Figure 26. Photographs of display by a male *Jotus remus*. **1**, Male on opposite side of a leaf from a female. In this position males engaged in vibration display. **2**, Male displaying paddle to female beneath a leaf. **3**, Male displaying to a female on top of a leaf. **4-6, 7-10, 11-14**, Three sequences of paddle display by males.



Figure 27. Sequential frames (25 FPS video, not consecutive) showing display of the paddle by a male *Jotus remus*. 2-6, Here both paddles were displayed at the same time.



Figure 28. Sequential frames (25 FPS video, not consecutive) showing intermittent display of the paddle by a male *Jotus remus*. Note the attention of the female to the paddle when it was displayed. Paddle display alternated with vibration (3, 7-8).



Figure 29. Sequential frames (25 FPS video, not consecutive) showing a female turning to face the paddle of a male *Jotus remus*.



Figure 30. Sequential frames (25 FPS video, not consecutive) showing a female approaching and then jumping to attack the paddle of a male *Jotus remus*.

Females that continued to stalk and to attack the male paddle when it was displayed may have mated previously, but the males tended to be persistent and to continue this display nonetheless. Males were extremely skilled at evading the attacks of females and the nature of the paddle, comprised of long, soft scales, may make this difficult for the female to grasp. In many hours of observation of these male-female interactions not a single instance in which the male became injured or was caught was observed. Males appeared to have an uncanny awareness of the relative position and movement of females, even when out of sight. On the four occasions where mating was observed the female that was courted was a virgin and did not attack the paddle, but eventually stopped moving in response to movement of the paddle. The male then performed two very rapid and vigorous paddle strokes, the second approximately 0.6 s after the first. Approximately 0.6 s after the second stroke he dashed to join the female on the opposite side of the leaf and immediately mated with her. The entire procedure from the first vigorous paddle stroke to mounting the female for mating was extremely rapid, completed in just over 1.2 s (Figures 31-33). This procedure was followed on all four occasions. This double wave may be a signal to the female to indicate the intent of the approaching male, but it could also be a final and more extreme test of the receptivity of the female as indicated by her immobility. It should be noted that many other male salticids use the lack of movement or turning by a female as an indicator of receptivity. For example, *Colonus* (formerly *Thiodina*) males move from side to side in front of females, approaching only when the female stops turning to face them (Hill 2012). In the case of *Jotus remus*, however, males appear to be able to determine this lack of movement when the female is completely out of sight.

A mating pair of *J. remus* is shown in Figure 34. When mating, males tend to hold the female securely with their rear legs, wrapping one paddle around the carapace near the face of the female. Unlike other salticids such as *Maratus*, *J. remus* males only mated with a single pedipalp during each encounter.



Figure 31. Sequential frames (25 FPS video, not consecutive) showing a male *Jotus remus* making a first (1-4) and then a second (5-9) rapid swing of a paddle in front of a female on the opposite side of a leaf, then quickly flipping to the top of the leaf (10-11) to mount that female (12-16). White arrows indicate the position of the paddle during each rapid swing.

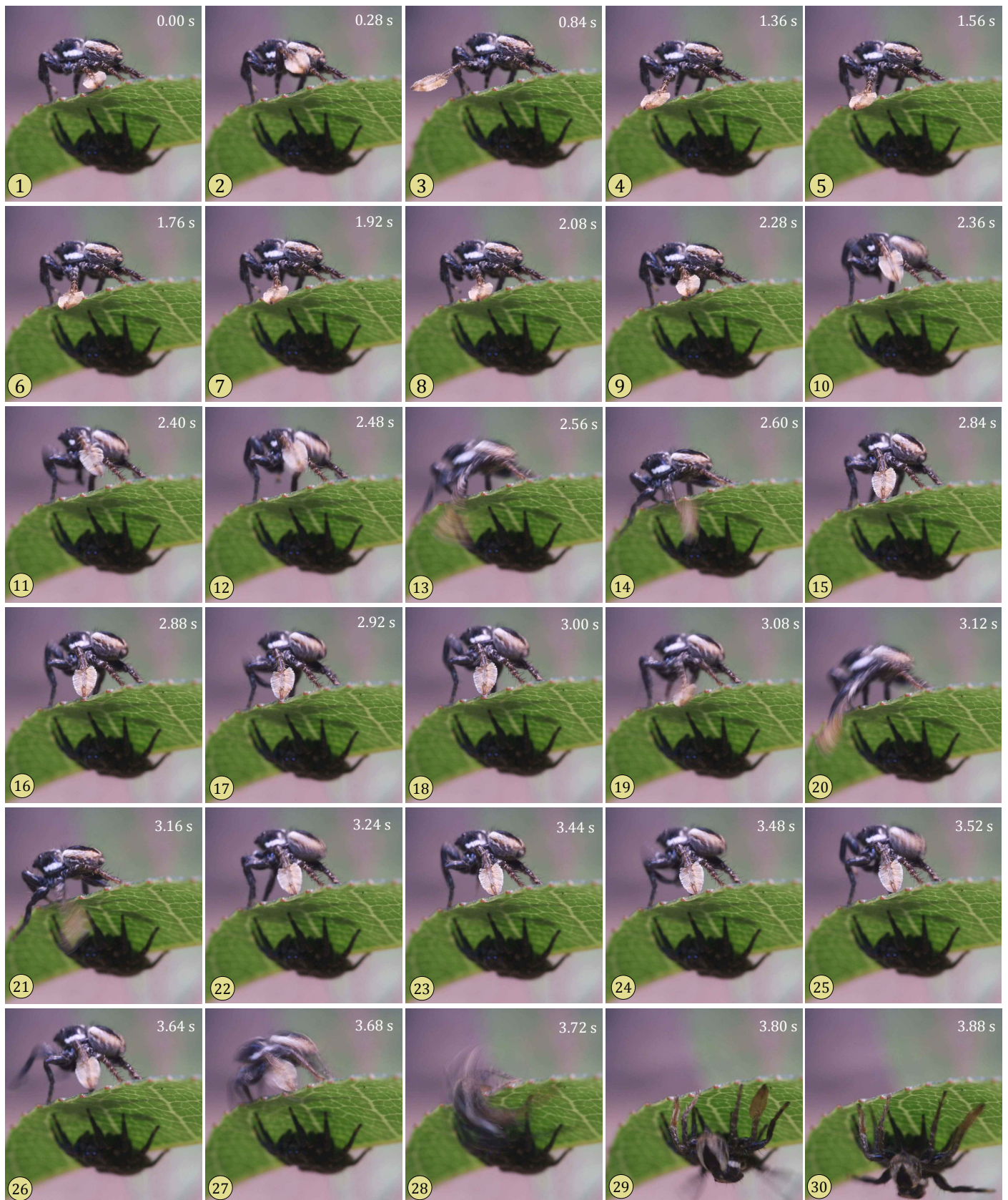


Figure 32. Sequential frames (25 FPS video, not consecutive) showing a male *Jotus remus* raising one paddle (1-2), quickly moving the paddle forward (3), moving the paddle more slowly through a series of increments to the rear in view of a female beneath the leaf (4-9), vibrating (11-12), making one rapid swing of the paddle (13-14), vibrating (15-18), making a second rapid swing of the paddle (19-21), vibrating (22-26), and finally quickly dashing beneath the leaf to mate with the female (27-30). As also shown in Figure 32, the two rapid swings of the paddle were completed in about half a second.

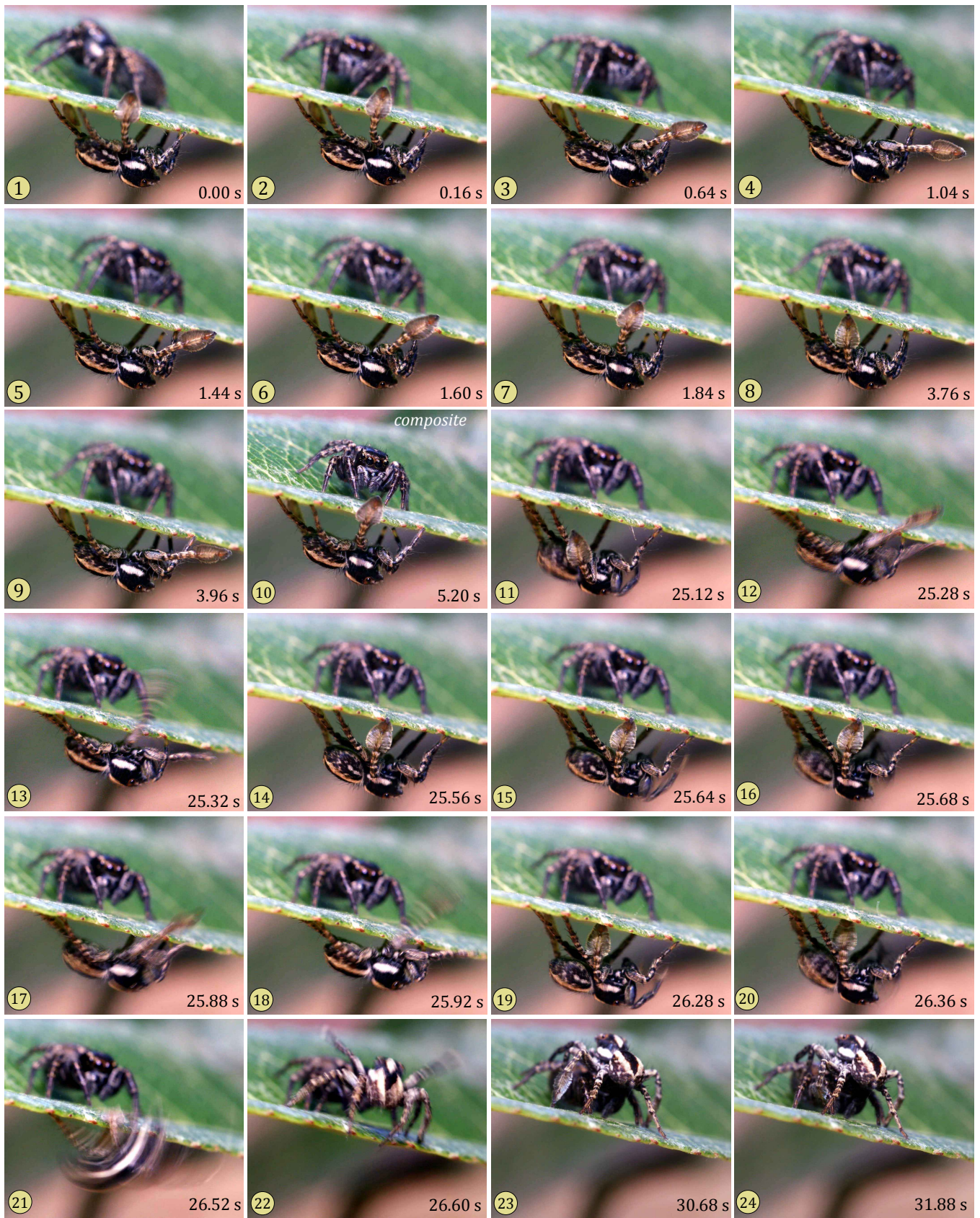


Figure 33. Sequential frames (25 FPS, not consecutive) showing a female *Jotus remus* on top of a leaf turning to follow the rapid forward and slower rearward movement of the male's paddle (1-10). With the female watching the male raised one paddle (11) to complete a rapid swing in front of the female (12-13), briefly vibrated (14-16), completed a second rapid swing of the paddle (17-18), vibrated (19-20), and finally flipped quickly around to the top of the leaf to join the female (21-24). Both rapid swings of the paddle were completed in little more than half of a second.



Figure 34. Photos showing two (1-3, 4-6) mating sequences of *Jotus remus*.

Habitat. *Jotus remus* were found on an exposed, higher elevation plateau at Gloucester Tops in Barrington Tops National Park, New South Wales (Figure 35). The major tree species in this area were Snow Gums (*Eucalyptus pauciflora*) and Mountain Gums (*Eucalyptus dalrympleana*). The ground cover was mostly Snow Grass (*Poa sieberiana*) and Mat Rush (*Lomandra* sp.). As legs III are extended during flight (Figure 36) there is a possibility that the paddles of the male allow these spiders to glide or parachute as they jump down from trees as has been found in a number of insects (e.g., Dudley *et al.* 2007, Yanoviak 2009). This could be effective at the higher velocities associated with a free fall, but appears to have little effect on normal jumps by these spiders (Figure 37). The paddles could also assist the males by improving their ability to secure a foothold or quickly flip to the underside of a leaf at the end of a jump (Figure 36: 2).



Figure 35 (continued on next page). Habitat of *Jotus remus* at Gloucester Tops.



Figure 35 (continued). 4, Note the male *J. remus* at the center of this photograph (inset).



Figure 36. Composite images showing selective frames of a jumping male *Jotus remus* (1000 FPS video). 1, After legs III were extended during take-off, they were moved laterally as the spider approached his target. 2, At the end of this jump, the paddle at the end of leg RIII wrapped around a leaf blade ([6], at 38 msec) and the male flipped around to land beneath that leaf blade.

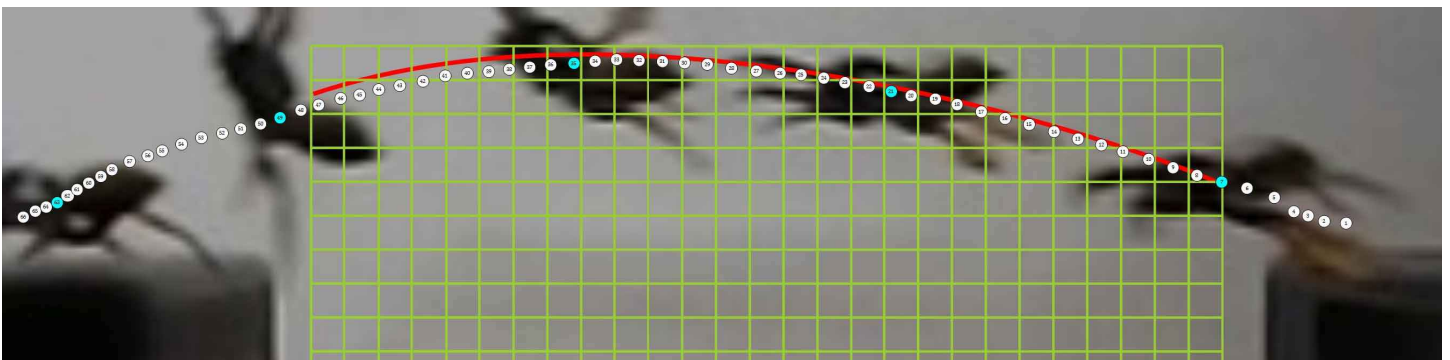


Figure 37. Selected composite images showing successive positions of a jumping male *Jotus remus* (1000 FPS video). The position of the pedicel was plotted with small circles at 1 msec intervals, superimposed on a grid of 1 mm squares (1 mm/msec corresponds to 100 cm/s). The take-off velocity (at position 7 at right side of grid) shown here was ~79 cm/s in a direction of 18.4° above horizontal (horizontal velocity ~75 cm/s, vertical velocity ~25 cm/s). The red line represents a ballistic flight trajectory from the take-off position, and the actual flight path (small circles) approximates this. Like other jumping spiders, *Jotus* use their dragline during these targeted jumps. Note the reversal of pitch (backward to forward) at the end of this jump.

Use of legs III and IV by *Jotus* to power their jumps

Jotus power their jumps through extension of legs IV followed by extension of legs III (Figures 38-45). Both leg pairs contribute to acceleration of these spiders. This contrasts with the almost complete reliance on extension of legs IV to power jumps in many salticids (Parry & Brown 1959, Hill 2010), and the almost complete reliance on extension of legs III to power jumps by *Maratus* and *Habronattus* species (Otto & Hill 2012c, 2013). In preparation for a jump, *Jotus* generally do not flex either legs III or legs IV to the extent that the species that specialize in leg III or leg IV jumps, respectively, do. In forward jumps extension of legs IV precedes extension of legs III, but in jumps with a greater vertical component both pairs of legs may be extended simultaneously. The ability to accelerate with both pairs of legs thus gives *Jotus* a great deal of versatility. The analysis shown here is based on the assumption that only extension, but not rotation, of legs III contributes significant acceleration to each jump.

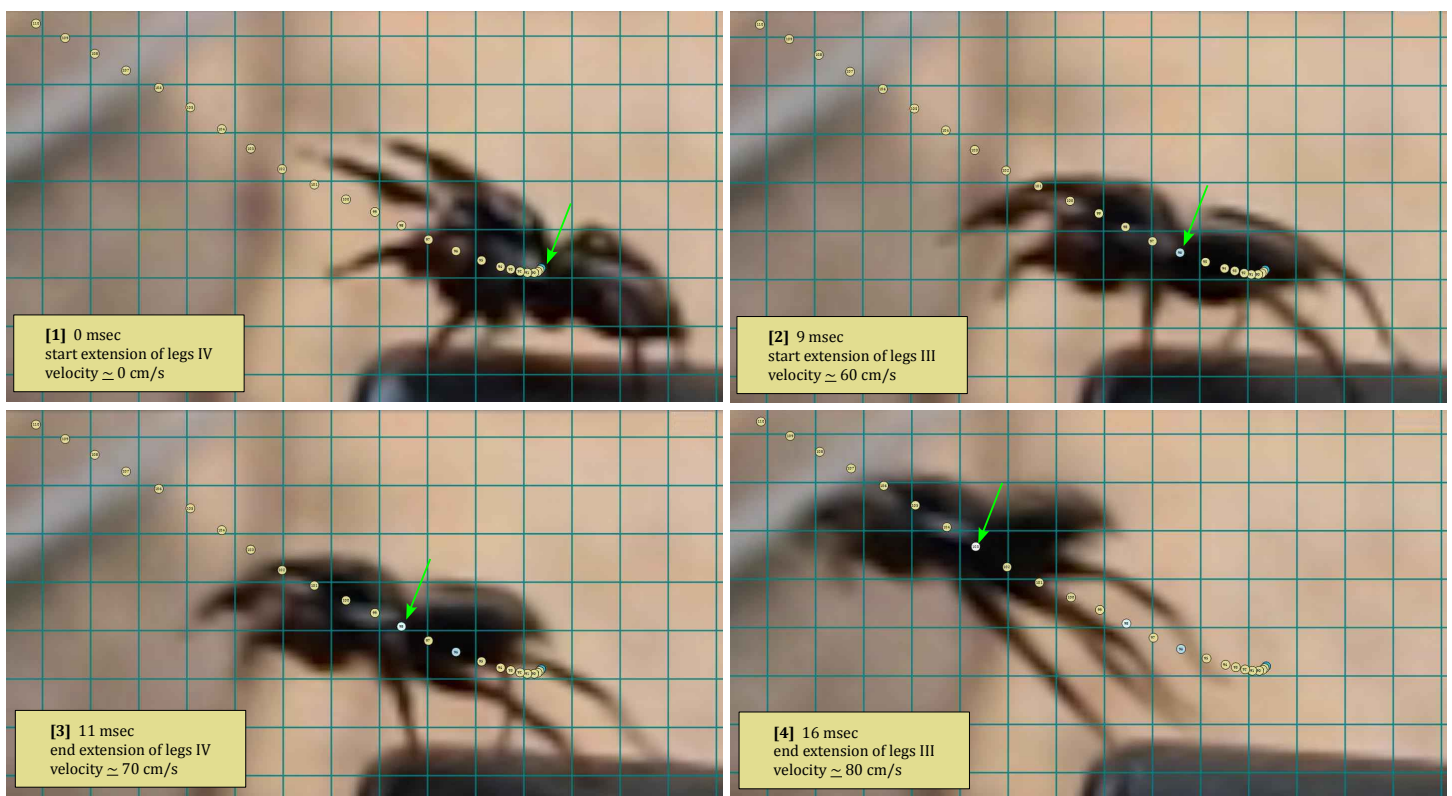


Figure 38. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this and in subsequent figures (Figures 31-36), four frames are shown to represent [1] the start position when extension of legs IV begins, [2] the start of extension of legs III, as legs IV continue to extend, [3] the end of extension of legs IV, when only legs III are still extending, and [4] the take-off position at which legs III are completely extended. Small circles show the position of a reference position on the spider (identified by the presence of the lateral band of white scales on the carapace) for each frame, separated by 1 msec. In the background is a 1 mm grid. In this example, the spider accelerated to \sim 60 cm/s with legs IV, then to \sim 70 cm/s with legs III and IV, and finally to \sim 80 cm/s with only legs IV. In this and in subsequent examples the spider crouched down against the surface before extending its legs.

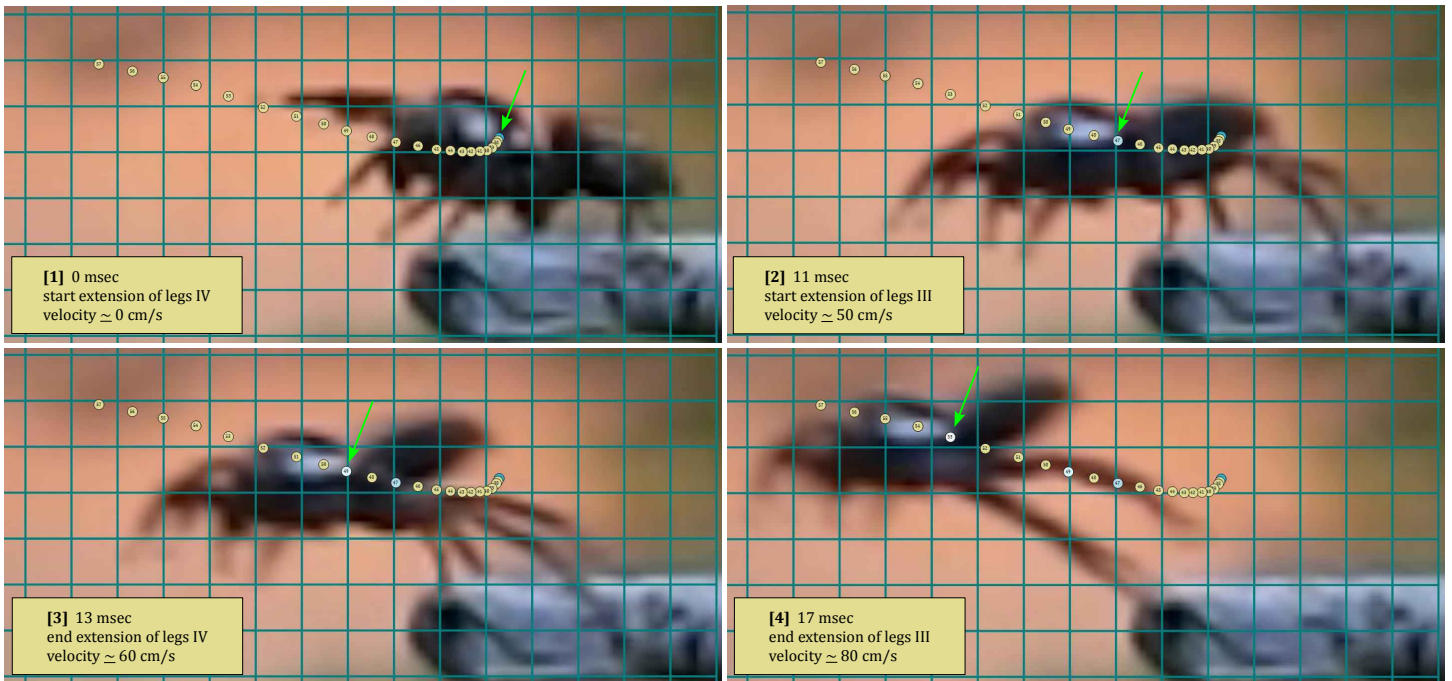


Figure 39. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this example, legs IV accelerated the spider to ~50 cm/s, then to ~60 cm/s, and extension of legs III brought this up to ~80 cm/s.

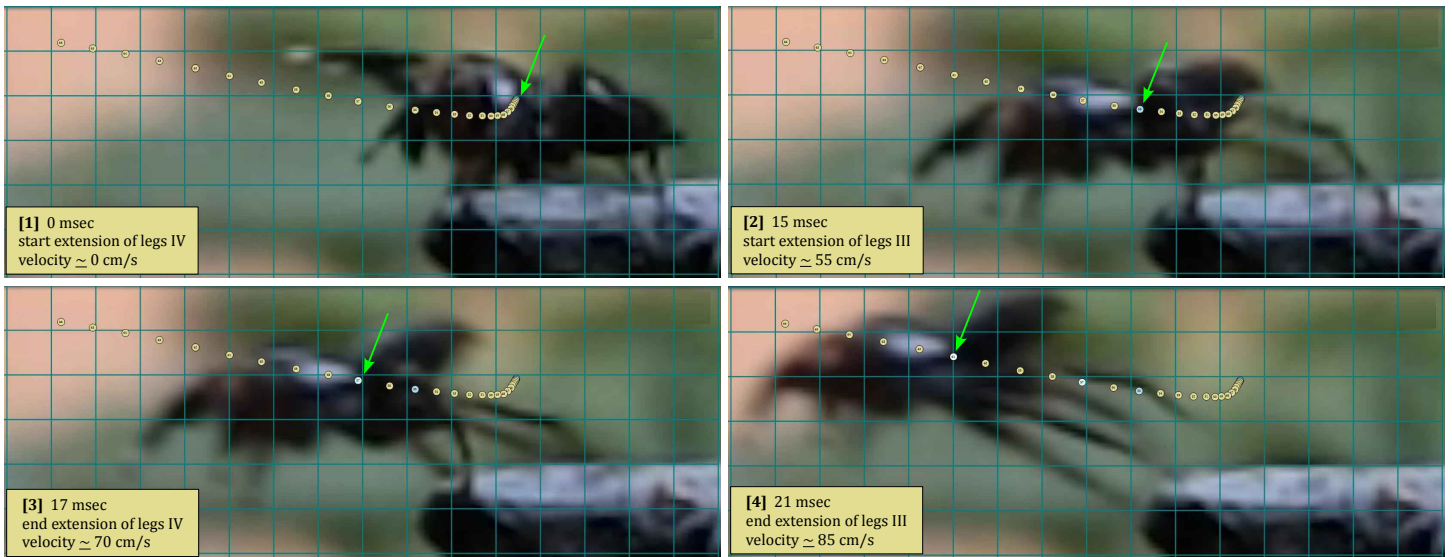


Figure 40. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this example, legs IV accelerated the spider to ~55 cm/s, then to ~70 cm/s, and extension of legs III brought this up to ~85 cm/s.

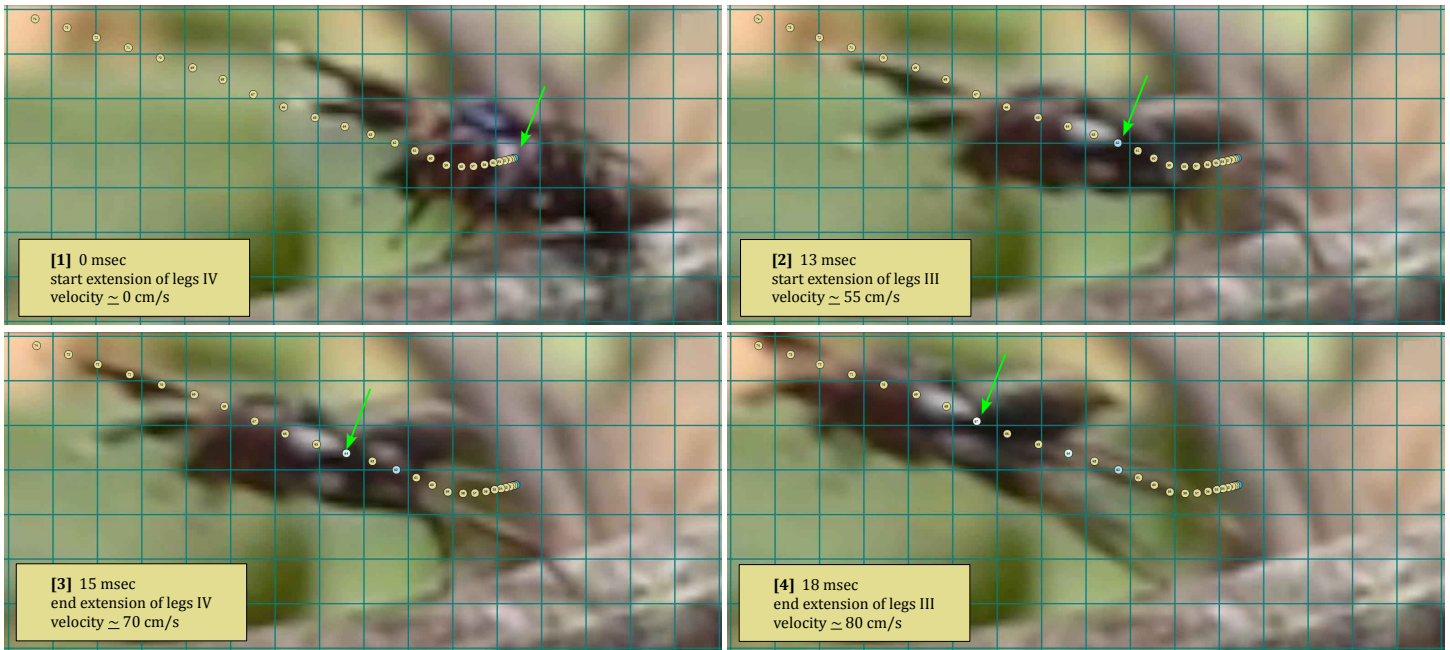


Figure 41. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this example, legs IV accelerated the spider to ~55 cm/s, then to ~70 cm/s, and extension of legs III brought this up to ~80 cm/s. Since vertical deceleration due to gravity takes place as the spider is accelerating, the actual acceleration due to vertical extension of the legs is somewhat greater than this.

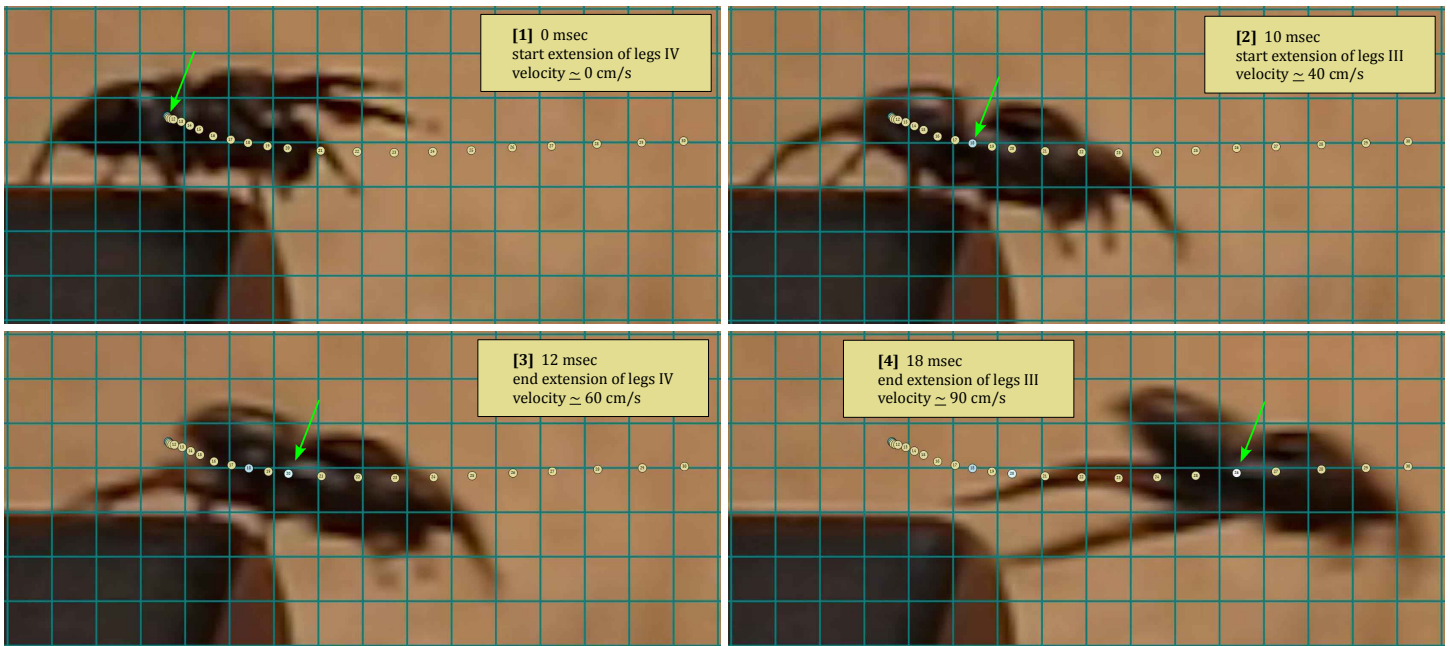


Figure 42. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this example, legs IV accelerated the spider to ~40 cm/s, then to ~60 cm/s, and extension of legs III brought this up to ~90 cm/s.

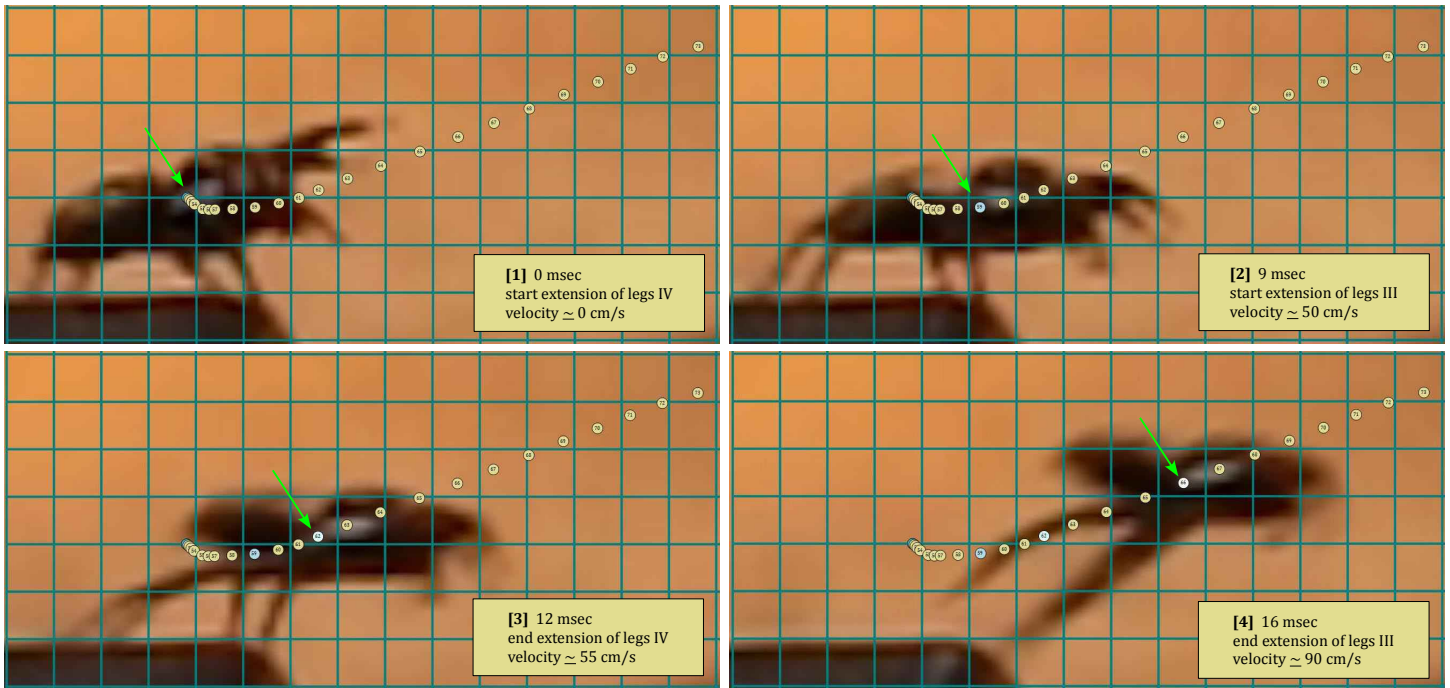


Figure 43. Take-off sequence by an adult male *Jotus auripes* based on analysis of high-speed (1000 FPS) video frames. In this example, legs IV accelerated the spider to ~50 cm/s, then to ~55 cm/s, and extension of legs III brought this up to ~90 cm/s.

Acceleration by an adult male *Jotus remus*, like that of *J. auripes*, used extension of legs IV followed by extension of legs III (Figure 43). Vertical jumps may be associated with simultaneous extension of all four hind legs (Figure 44).



Figure 44. Take-off sequence by an adult male *Jotus remus* based on analysis of high-speed (sequential frames at 1000 FPS), low resolution video frames. In this species legs III and IV are also close in length and both contribute to acceleration.

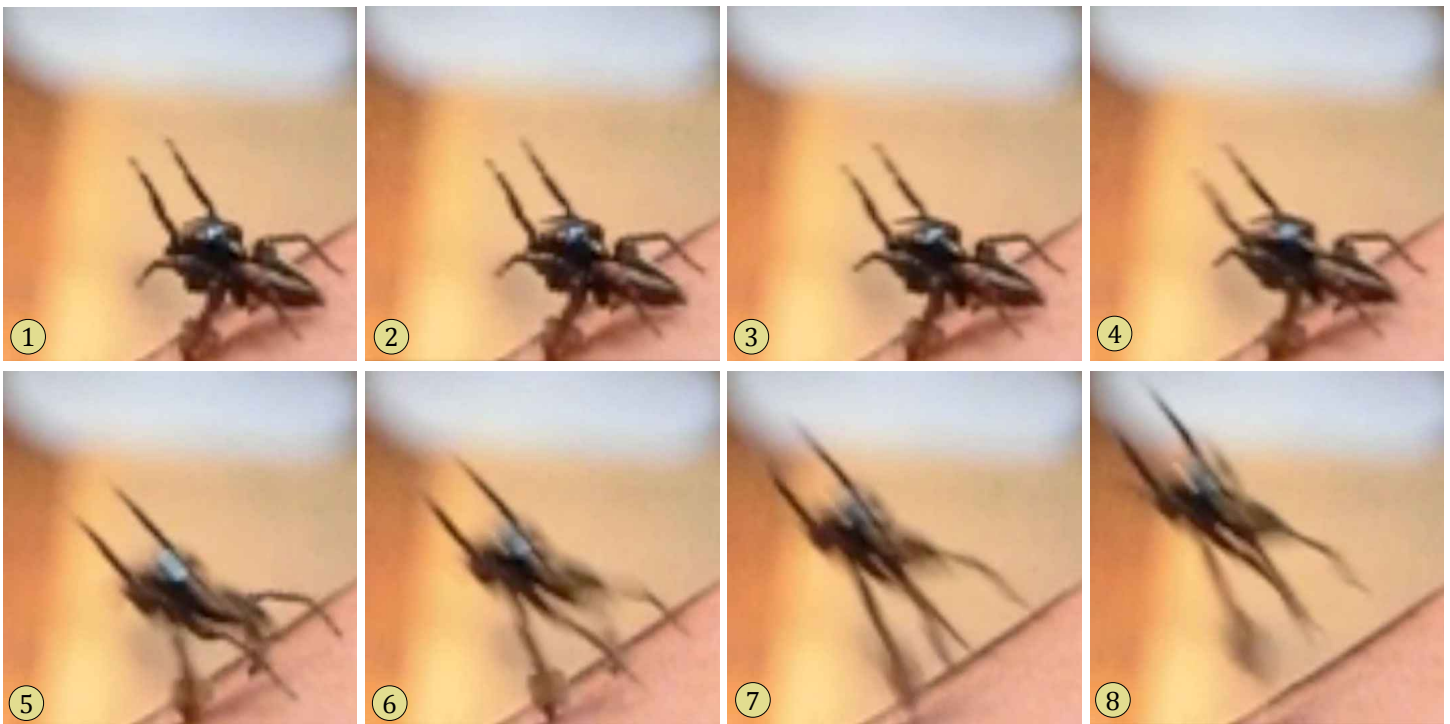


Figure 45. Take-off sequence by an adult male *Jotus remus* based on analysis of high-speed (sequential frames at 1000 FPS), low resolution video frames. Note the paddles on legs III. In this sequence, the spider crouched (1-4), then sprung off of the surface in a near-vertical trajectory, extending all four hind legs in about 3 msec.

Predation on ants by *Jotus* and other Euophryini

Quite a few euophryines are known to prey on ants. Some, like the New World *Anasaitis* and *Naphrys*, are considered to be ant specialists (Edwards *et al.* 1975; Cutler 1980; Li *et al.* 1996). Here (Figure 46) we include a photograph of a male *Jotus remus* taken in the field at Barrington Tops to document predation on what appears to be a small ant by this species.



Figure 46. Field records of predation on ants by a male *Jotus remus* at Barrington Tops (1), a female *Anasaitis canosa* from Greenville County, South Carolina (2), and a male *Naphrys pulex*, also from Greenville County (3). Although found on a different continent, *Naphrys* is thought to be more closely related to the Australian *Jotus* than to the *Anasaitis* that shares its leaf-litter habitat (Zhang & Maddison 2013). 2-3, Scale = 1 mm.

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References

- Bryant, E. B. 1935.** Notes on some of Urquhart's species of spiders. Records of the Canterbury Museum 4: 53-70.
- Cutler, B. 1980.** Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae), Zoologischer Anzeiger 204 (1-2): 97-101.
- Davies, V. T. and M. Žabka. 1989.** Illustrated keys to the genera of jumping spiders (Araneae: Salticidae) in Australia. Memoirs of the Queensland Museum 27: 189-266.
- Dudley, R., G. Byrnes, S. P. Yanoviak, B. Borrell, R. M. Brown and J. A. McGuire. 2007.** Gliding and the functional origins of flight: biomechanical novelty or necessity. The Annual Review of Ecology, Evolution, and Systematics 38: 178-201.
- Edwards, G. B., J. F. Carroll and W. H. Whitcomb. 1975.** *Stoidis aurata* (Araneae: Salticidae), a spider predator of ants. The Florida Entomologist 57 (4): 337-346.
- Hill, D. E. 2009.** Salticidae of the Antarctic land bridge. Peckhamia 76.1: 1-14.
- Hill, D. E. 2010.** Targeted jumps by salticid spiders (Araneae: Salticidae: *Phidippus*). Peckhamia 84.1: 1-35.
- Hill, D. E. 2012.** Notes on the jumping spiders *Thiodina puerpera* (Hentz 1846) and *Thiodina sylvana* (Hentz 1846) in the southeastern United States (Araneae: Salticidae). Peckhamia 99.1: 1-63.
- Koch, L. 1881.** Die Arachniden Australiens. Nürnberg. 1: 1213-1271.
- Li, D., R. R. Jackson, and B. Cutler. 1996.** Prey-capture techniques and prey preferences of *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae) from North America. Journal of Zoology, London 240: 551-562.
- Otto, J. 2015a.** Spid-a-boo. Online video at: <https://www.youtube.com/watch?v=HkiwPkjpYpA>
- Otto, J. 2015b.** Spid-a-boo 2. Online video at: <https://www.youtube.com/watch?v=r4YHf6nBbzE>
- Otto, J. C. and D. E. Hill. 2012a.** Notes on *Maratus* Karsch 1878 and related jumping spiders from Australia, with five new species (Araneae: Salticidae: Euophryinae). Peckhamia 103.1: 1-81.
- Otto, J. C. and D. E. Hill. 2012b.** Notes on *Maratus* Karsch 1878 and related jumping spiders from Australia, with five new species (Araneae: Salticidae: Euophryinae), version 2. Peckhamia 103.2: 1-82.
- Otto, J. C. and D. E. Hill. 2012c.** Two new Australian peacock spiders that display inflated and extended spinnerets (Araneae: Salticidae: Euophryinae: *Maratus* Karsch 1878). Peckhamia 104.1: 1-28.
- Otto, J. C. and D. E. Hill. 2013.** Three new Australian peacock spiders (Araneae: Salticidae: *Maratus*). Peckhamia 108.1: 1-39.
- Otto, J. C. and D. E. Hill. 2014.** Description of a new peacock spider from Cape Le Grand, Western Australia, with observations on display by males and females and comparative notes on the related *Maratus volans* (Araneae: Salticidae: Euophryinae: *Maratus*). Peckhamia 114.1: 1-38.
- Otto, J. C. and D. E. Hill. 2015.** *Maratus personatus*, a masked peacock spider from Cape Riche, Western Australia (Araneae: Salticidae: Euophryinae). Peckhamia 127.1: 1-30.
- Peckham, G. W. and E. G. Peckham. 1901.** Spiders of the *Phidippus* group of the family Attidae. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 13: 282-358.
- Rainbow, W. J. 1920.** Arachnida from Lord Howe and Norfolk Islands. Records of the South Australian Museum 1: 229-272.
- Richardson, B. J. and M. Žabka. 2007.** A revision of the Australian jumping spider genus *Prostheclina* Keyserling, 1892 (Araneae: Salticidae). Records of the Australian Museum 59: 79-96.
- Simon, E. 1901.** Histoire naturelle des araignées. Paris. 2: 381-668.
- Strand, E. 1911.** Araneae von den Aru- und Kei-Inseln. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 34: 127-199.
- Urquhart, A. T. 1893.** Descriptions of new species of Araneidae. Transactions of the New Zealand Institute 25: 165-190.
- WSC. 2015.** World Spider Catalog. Natural History Museum Bern, online at <http://wsc.nmbe.ch>, version 16.5, accessed on 24 OCT 2015.
- Yanoviak, S. P., M. Kaspari and R. Dudley. 2009.** Gliding hexapods and the origins of insect aerial behaviour. Biology Letters, Evolutionary Biology: doi:10.1098/rsbl.2009.0029
- Žabka, M. 1987.** Salticidae (Araneae) of Oriental, Australian and Pacific Regions, II. Genera *Lycidas* and *Maratus*. Annales Zoologici, Warszawa 40: 451-482.
- Zhang, J. and W. P. Maddison. 2013.** Molecular phylogeny, divergence times and biogeography of spiders of the subfamily Euophryinae (Araneae: Salticidae). Molecular Phylogenetics and Evolution 68: 81-92.
- Zhang, J. and W. P. Maddison. 2015.** Genera of euophryine jumping spiders (Araneae: Salticidae), with a combined molecular-morphological phylogeny. Zootaxa 3938 (1): 1-147.