

# Notes on the jumping spider *Phidippus clarus* Keyserling 1885 (Araneae: Salticidae: Dendryphantinae)<sup>1</sup>

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## Introduction

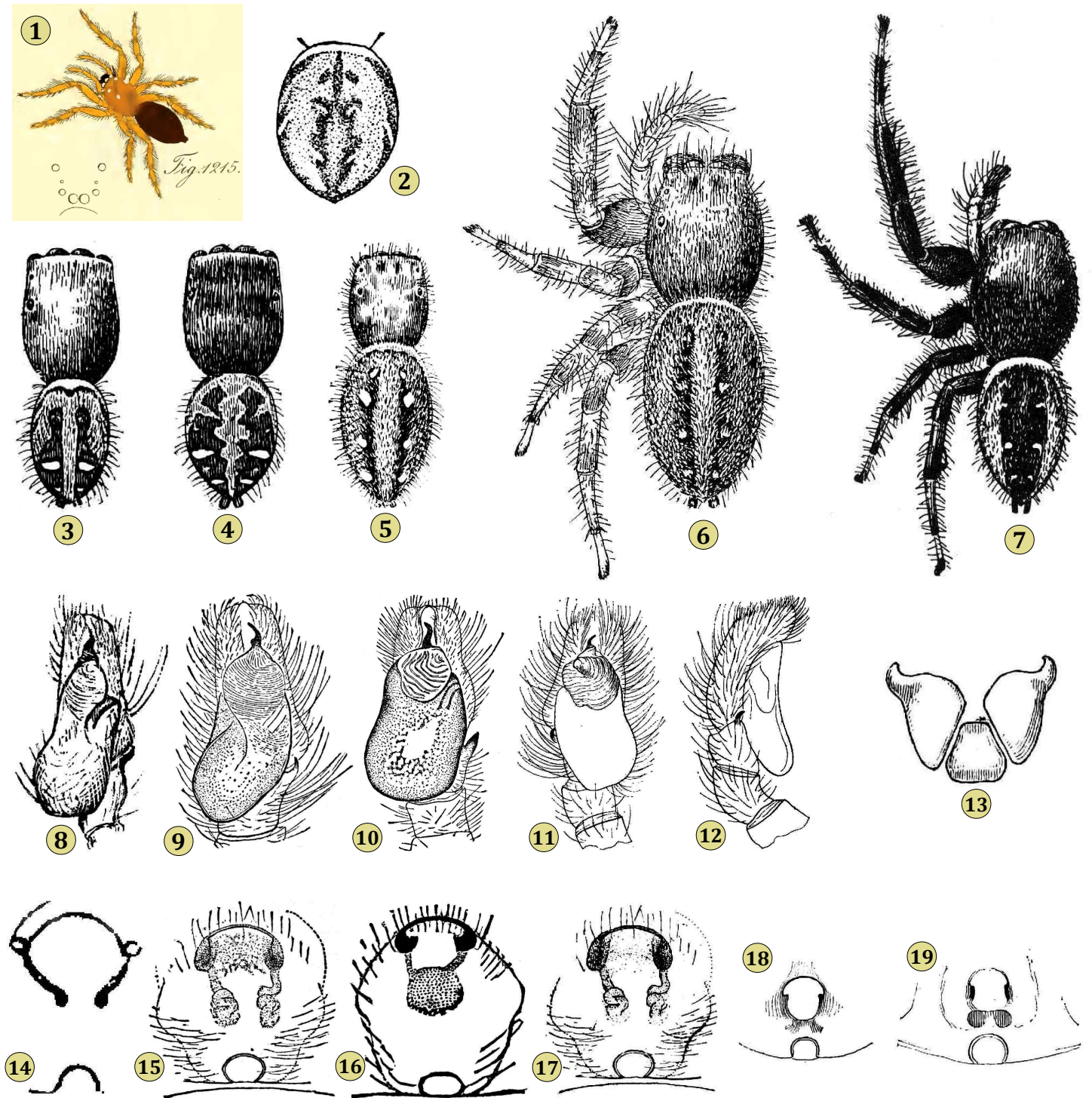
My study of salticid biology began in 1974, when I developed a strong interest in the behavior and neurobiology of these remarkable spiders (Hill 1975, 2006). I was soon familiar with the near-ground dwelling *Phidippus johnsoni* (Peckham & Peckham 1883) that frequent fallen logs in the oak (*Quercus garryana* and tall grass) savanna that once dominated the Willamette Valley of northwestern Oregon. The tall grass/herbaceous prairies there included large populations of a small, black, spotted salticid that I tentatively identified as a *Phidippus*. By August, the large adults of this species appeared in numbers at the tops of herbaceous plants, and I identified these as *P. rimator* (Walckenaer 1837) using the second edition of *How to Know the Spiders* (Kaston 1972). This identification was confirmed by Larry Pinter, then working on his revision of *Phidippus* as part of a Ph.D. program at Harvard. Much later, G. B. Edwards finally completed his revision of this large genus at Florida (Edwards 2004), and determined that Walckenaer's *Attus rimator* was best treated as a *nomen dubium*. Ever since, this important species of the North American tallgrass prairie has consistently been called *Phidippus clarus* Keyserling 1885.

With females that can vary considerably in appearance, even in a local population, *P. clarus* spiders have been given many different names in the past. Because of their relatively large size, the high visibility of adults and adult resting or brood sacs in tallgrass prairie or cleared (*old field*) habitats, their wide geographic distribution, and their locally high population density, these are one of the best-known jumping spiders in North America. The only species of *Phidippus* that might be better known is *P. audax* (Hentz 1845). As a result, they are also one of the most studied salticids, with many recent publications focused on their behaviour (Hoefler & Jakob 2006; Hoefler *et al.* 2006; Hoefler 2007; Elias *et al.* 2008, 2010a, 2010b; Kasumovic *et al.* 2009, 2010, 2011; Sivalingham *et al.* 2010). Here I will review some of this work in the context of my own experience with *P. clarus*.

## Identification

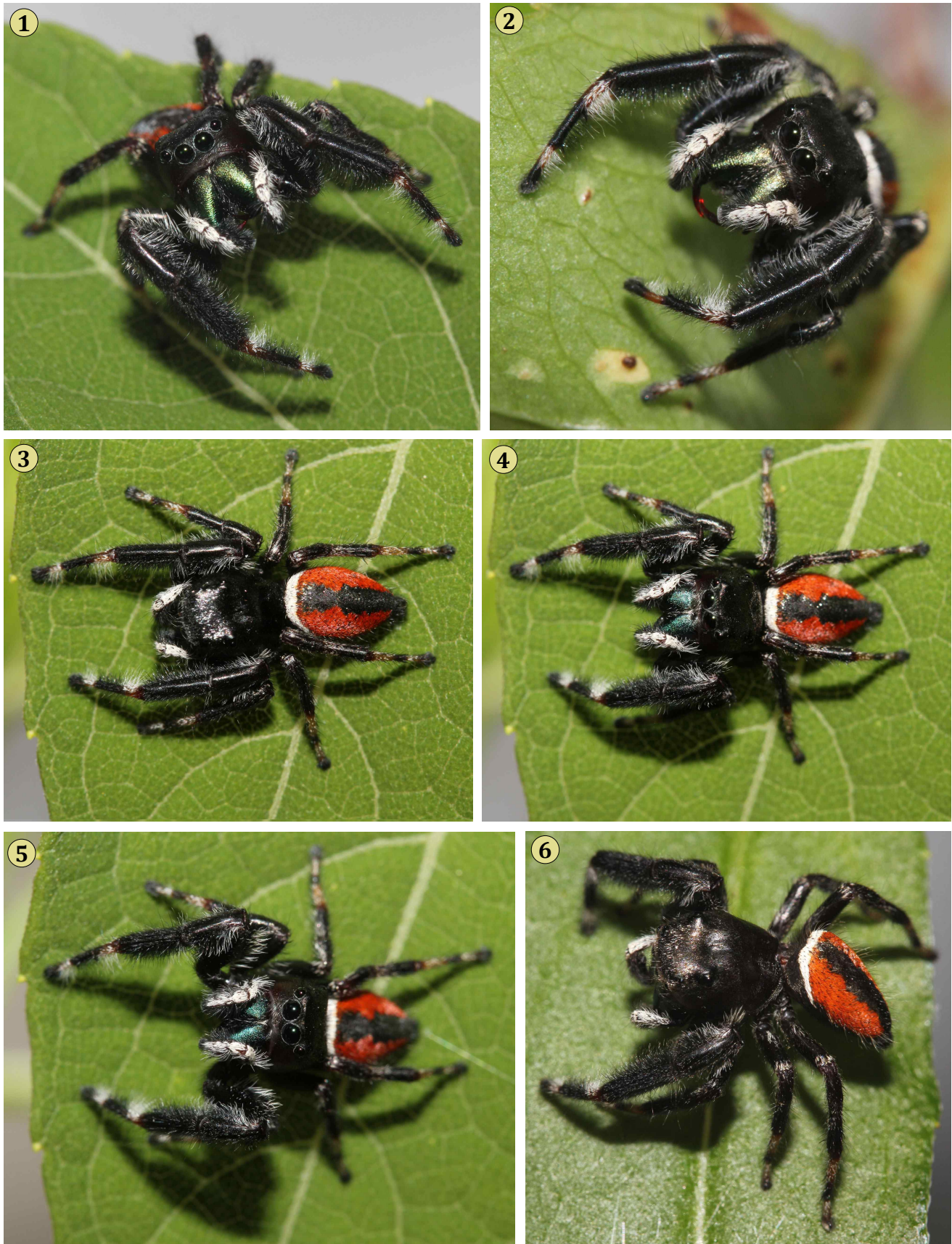
Edwards (2004) provides the definitive description and synonymy for *Phidippus clarus*. Emerton's line drawings (Figure 1:6,7) of the *habitus* correspond closely to its appearance, and thus this spider has usually been identified with little difficulty as either *P. rufus* Peckham & Peckham 1888 (not *P. rufus* Hentz 1845), *P. multiformis* Emerton 1891, or *P. clarus*. It should be noted in this context that although *rufus* was a favorite color in the descriptions of the Peckhams, few today are familiar with its older meaning, 'reddish', derived from the Latin.

*Adult male.* Adult male *P. clarus* (Figures 2-3) are easy to recognize, almost entirely black, with long legs I, a narrow band of white scales running along the top of each pedipalp, and a white anterior marginal band of white scales in front of broad lateral bands of red to red-orange scales on the opisthosoma.



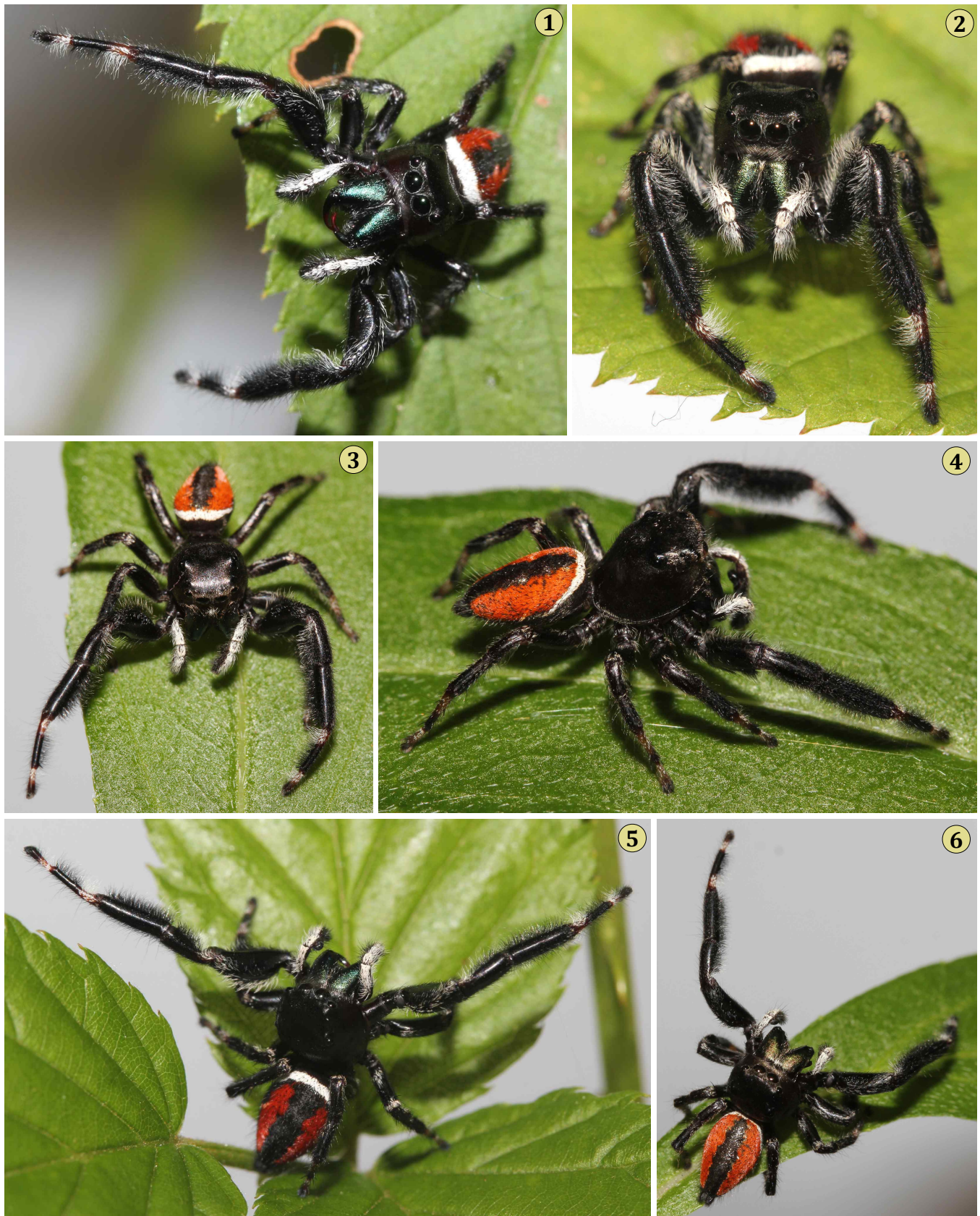
**Figure 1.** Early drawings representing *Phidippus clarus*. **1**, Female *P. testaceus* (after C. L. Koch 1846), length 0.4-0.45", name suppressed by Edwards 2004. This drawing is useless for species recognition. **2**, Dorsal opisthosoma, female *P. insolens* (after Peckham & Peckham 1888), width 4.5 mm. This shows the diagonal lateral stripes of females, not illustrated by Emerton. **3-5**, Immature *P. rufus* Peckham & Peckham 1888 (after Emerton 1891) or *P. clarus* (after Peckham & Peckham 1909). **6-7**, Habitus, adult female (**6**) and adult male (**7**), labeled variously as *P. rufus* Peckham & Peckham (after Emerton 1891), *P. multiformis* Emerton 1891 (after Emerton 1902) or *P. clarus* Keyserling 1885 (after Peckham & Peckham 1909). **8**, Left male pedipalp, *Attus flavus* (after Peckham & Peckham 1883), declared a *nomen oblitum* by Edwards (2004). **9**, Left male pedipalp, *P. insolens* (after Peckham & Peckham 1888). **10**, Left male pedipalp, *P. rufus* (after Peckham & Peckham 1888). **11-12**, Two views of right male pedipalp, *P. rufus* Peckham & Peckham 1888 (after Emerton 1891) or *P. clarus* (after Peckham & Peckham 1909). **13**, Mouthparts of male, *P. clarus* (after Peckham & Peckham 1909). **14**, Epigynum, *P. clarus* (after Keyserling 1885). **15**, Epigynum, *P. insolens* (after Peckham & Peckham 1888). **16**, Epigynum, *P. rufus* (after Peckham & Peckham 1888). **17-19**, Immature (**17**) and two other forms of epigynum (**18-19**), *P. clarus* (after Peckham & Peckham 1909).





**Figure 2.** Male *P. clarus* from southern Greenville County, South Carolina. Most males have relatively long legs I, but their relative length varies as does the size of the male. A well-defined dorsal band of white scales runs along the top of each pedipalp. The opisthosoma has a broad white anterior marginal band, and is flanked by large lateral tracts of red to red-orange scales. Its median is black, bearing a dense cover of transparent, reflective scales. The color of the iridescent chelicerae varies from bronze to dark green to blue-green. 3-5, Three sequential positions during the execution of a vertical ( $\beta$ ) turn (Hill 2010a) by a male with blue-green chelicerae.

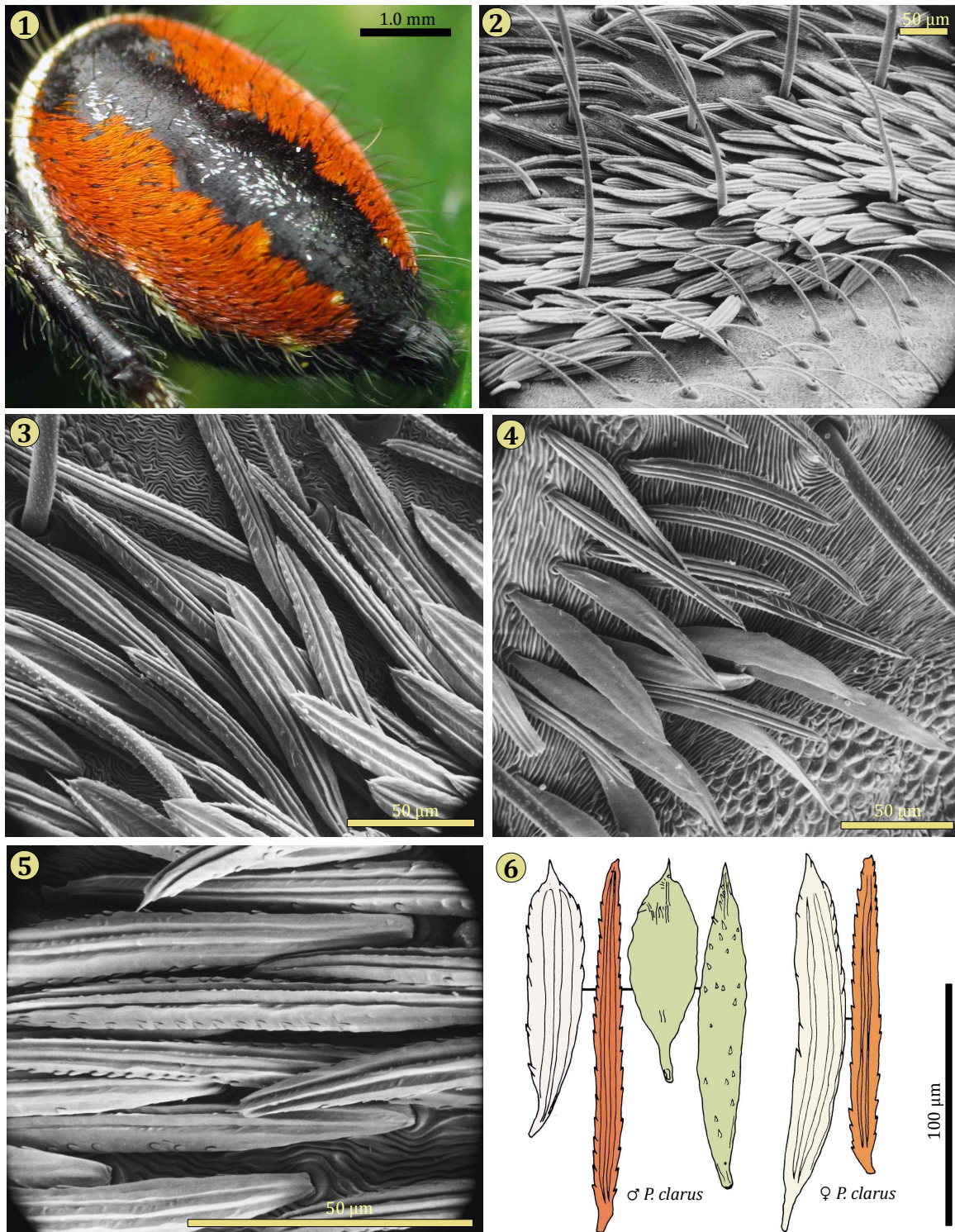




**Figure 3.** More views of male *P. clarus* from southern Greenville County, South Carolina. **6,** Male with bronze chelicerae preparing to jump up to a branch with legs IV flexed. Chelicerae are commonly bronze in color after the final molt, but usually they become green to blue-green within a few days.



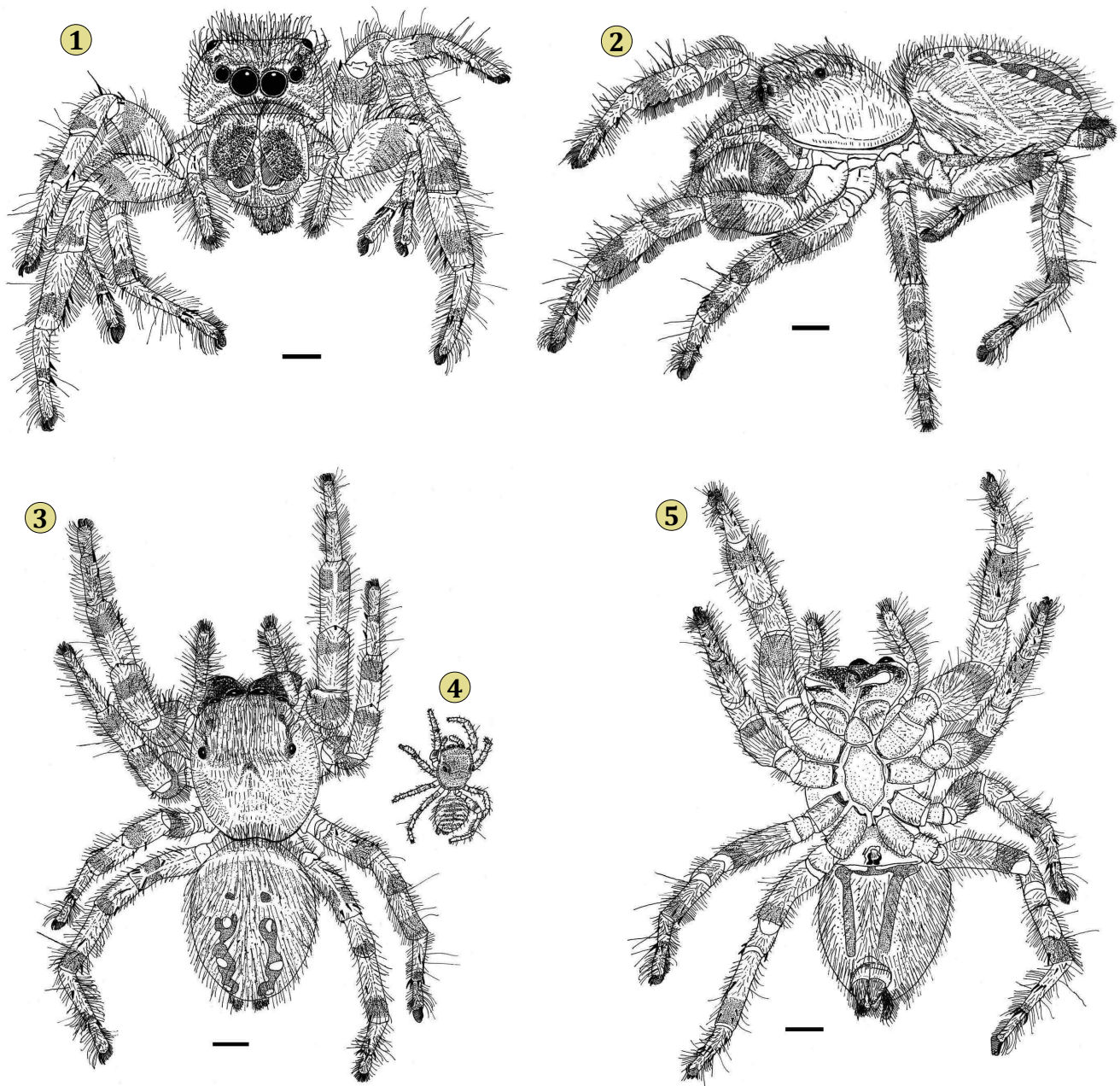
*Scale cover.* The red scales of the male are particularly long and narrow, and the white scales of the marginal band are much wider (Figure 4). Previously (Hill 1979a) I suggested that narrower scales are associated with selective absorption of certain wavelengths by colored pigments, and that wider scales are associated with reflectance across the broader spectrum.



**Figure 4.** Opisthosomal scales of *P. clarus*. **1**, Opisthosoma of living male from southern Greenville County, South Carolina. **2-5**, SEM views of male from Benton County, Oregon. **2-3**, Narrow red scales and wider white scales, both with three dorsal keels running along the shaft, and a characteristic pointed apex. **4**, Smooth, shiny transparent scales near long red scales. **5**, Detail of long red scales. **6**, *Camera lucida* drawing of scales from male and female (white to ivory pigmented, red to red-orange pigmented, and shiny, clear, transparent scales appearing olive green with transmitted light).



*Females* (Figures 5-9). Female *P. clarus* can usually be recognized by their bronze-red to gold scales on top of the carapace, white to ivory setae but not a well-defined clypeal band below the front eyes, eight spots in two longitudinal rows on the dorsal opisthosoma, and dark distal rings on the leg segments. Compared to males, they can vary greatly in coloration, even within a local population (Hill 2007). Most are cryptically colored, in varying shades of grey to tan, brown, or orange, but some are as brightly colored as the males, or even as dark as the males, with bright red to red-orange scales on the opisthosoma. This variability may result from a balance between two active forms of selection. Although crypsis in the vicinity of dry vegetation may help to conceal females from birds that would otherwise prey on them, aposematic (warning) coloration and movement similar to that of males may protect females from invertebrate predators that tend to avoid wasps. From year to year, or from place to place, the female forms that are favored might change, but maintenance of a diverse gene pool would ensure survival of at least some females.



**Figure 5.** Line drawings of an adult female (1-3, 5), and second instar (4) *P. clarus* from Benton County, Oregon (Hill 1975). These were drawn with a *camera lucida*. Each scale bar = 1.0 mm.





**Figure 6.** Adult female *P. clarus* with cryptic (red-brown to grey) coloration, from southern Greenville County, South Carolina. Note the tendency toward darker, reddish scales between the PLE. 5-6, Two views of a late-season (23 NOV 2013) nesting female with iridescent bronze chelicerae. Most females have iridescent dark green chelicerae. Leg segments of females have a ringed appearance, darker distally. Scale bars = 1.0 mm.





**Figure 7.** Darker female *P. clarus*. **1-2**, Two views of a dark nesting female (28 SEP 2012) from Laurens County, South Carolina. **3-6**, Three (3-4, 5, 6) different females from southern Greenville County, South Carolina. The pigmented scales of the dorsal opisthosoma of females can be just as intensely red or red-orange as they are in the males. Scale bar (5) = 1.0 mm.





**Figure 8.** Three female *P. clarus* (1-2, 3-4, 5-6) from Greenville County South Carolina, with bright red-orange scales covering the dorsal opisthosoma. Scale bar (3) = 1.0 mm.





**Figure 9.** Underside of four different female *P. clarus* from southern Greenville County, South Carolina. The medio-ventral opisthosomal band of lighter scales, flanked by dark lines, can be seen in all four. **2**, Note the relatively light-colored cuticle of this individual. Scale bar (2) = 1.0 mm.

*Immatures* (Figure 10; see also Walton 2013). Within their natural range, immature *P. clarus* can be readily recognized by their local abundance in the spring and early summer, and as relatively dark jumping spiders with 6-8 bright spots in two longitudinal rows on the dorsal opisthosoma. They are often the most abundant of all spiders in their old field or prairie habitat at this time. The color of the pigmented dorsal opisthosomal scales that comprise each lateral band varies from dark brown to brown, red-orange, or red, for both sexes. Adult males that have recently molted have bronze-colored chelicerae (Figure 10:4), but within a few days these usually become dark-green to blue-green.

It should be noted that large numbers of immature *Phidippus princeps* (Peckham & Peckham 1883) often appear in the same habitat during mid-summer when *P. clarus* adults appear. For one or two instars these resemble miniature adult female *P. clarus* in general coloration, but they are much smaller and bear a central spot or patch of scales on the dorsal opisthosoma. Under artificial lighting in the laboratory, it is possible to rear tiny fifth instar, adult *P. clarus* of about 5 mm in length, but I have never seen them this small in nature. This suggests that maturation in this species may be triggered by long day length. There is no evidence for this phenomenon in any other species of *Phidippus*.



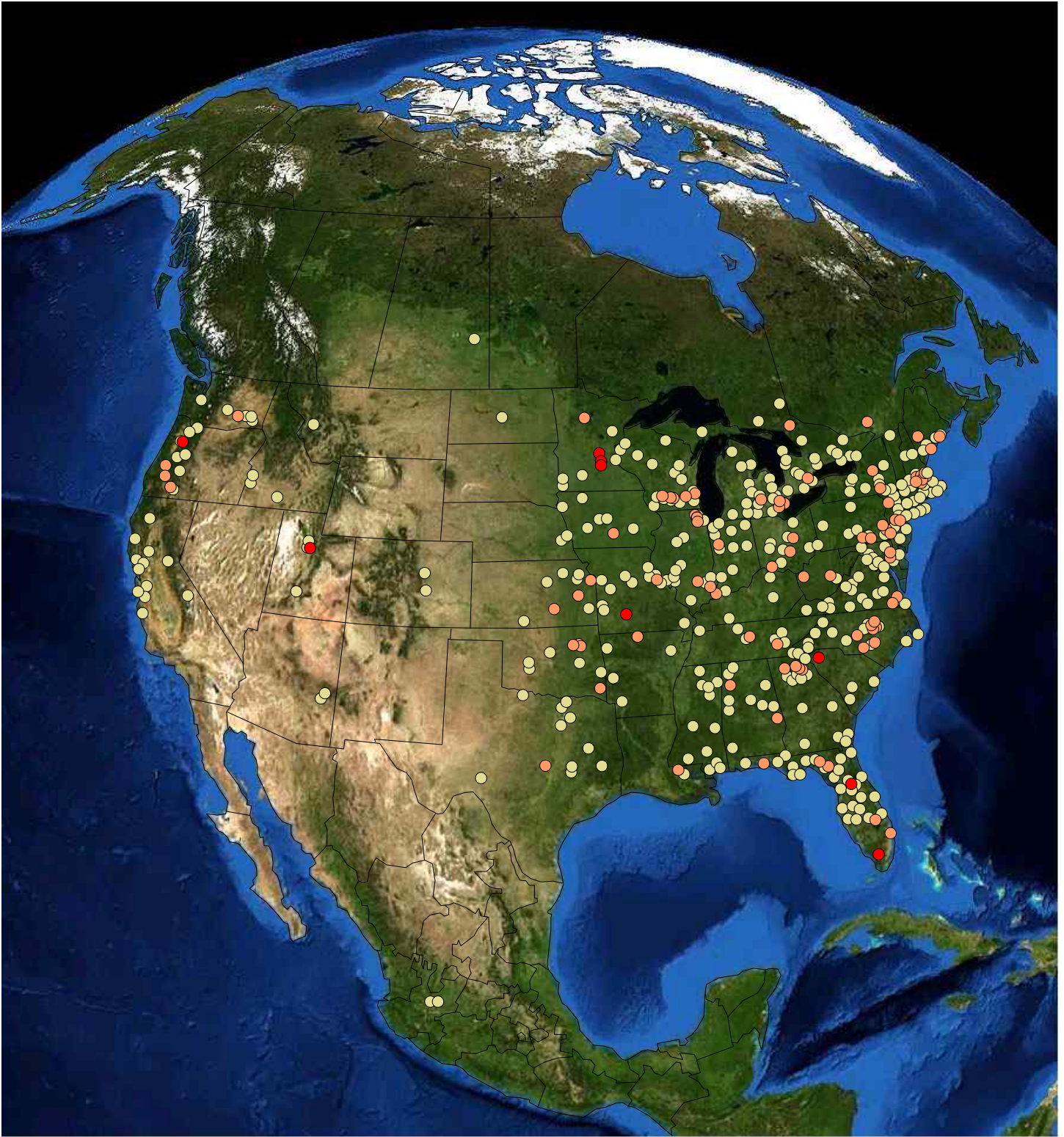


**Figure 10.** Immature *P. clarus* from southern Greenville County, South Carolina. **1**, Antepenultimate (23 MAY 2011). **2-3**, Penultimate male (12 JUL 2011). Note the dark carapace. **4**, Adult male soon after final molt. Within a few days the cuticle of this spider darkened and the chelicerae became dark green. Each scale bar = 1.0 mm.

### Distribution and habitat

*Phidippus clarus* are among the most common spiders in the old field or ruderal (disturbed, roadside) habitats of temperate North America, with a wide distribution across the continent, primarily in the east (Figure 11). They can be found in remnants of native tall-grass prairies or savannas, and probably originated as specialists in that habitat with respect to their use of the crowns or upper leaves of herbaceous plants or woody shrubs for their resting sacs and nests (Edwards 1980). They can complete their entire life cycle in this habitat. I have frequently found this spider in fields that had been completely cut over and baled in the previous year. This suggests that young *P. clarus* rapidly colonize surrounding areas after they emerge from their nests. Based on its tallgrass habitat, *P. clarus* must have moved north with the recent (since 15-20Ka) retreat of continental glaciers, perhaps from a refuge in southern Mexico or the western margins of the Gulf of Mexico (Hill & Edwards 2013). It should be recognized that the present inter-glacial period is exceptional and not the norm for the cool Pleistocene. For most of its existence *P. clarus* must have been a southern species with a much more restricted range.





**Figure 11.** Distribution of *Phidippus clarus* in North America. Localities identified by Edwards (2004) are shown in light yellow. New localities associated with photographs clearly identifiable as *P. clarus*, posted at FLICKR® (<http://www.flickr.com>) or BugGuide.Net (<http://bugguide.net>), are light orange, and localities where I have observed these spiders in a field setting are shown in red. With few exceptions, this species is predominantly found in old field, ruderal, or tall grass/herbaceous prairie habitats in temperate, less arid areas of the east and west. West coast populations may have been introduced. This background image, showing ground cover during the month of July, was generated with the NASA World Wind 1.4 mapping tool, available at <http://worldwind.arc.nasa.gov/download.html>.



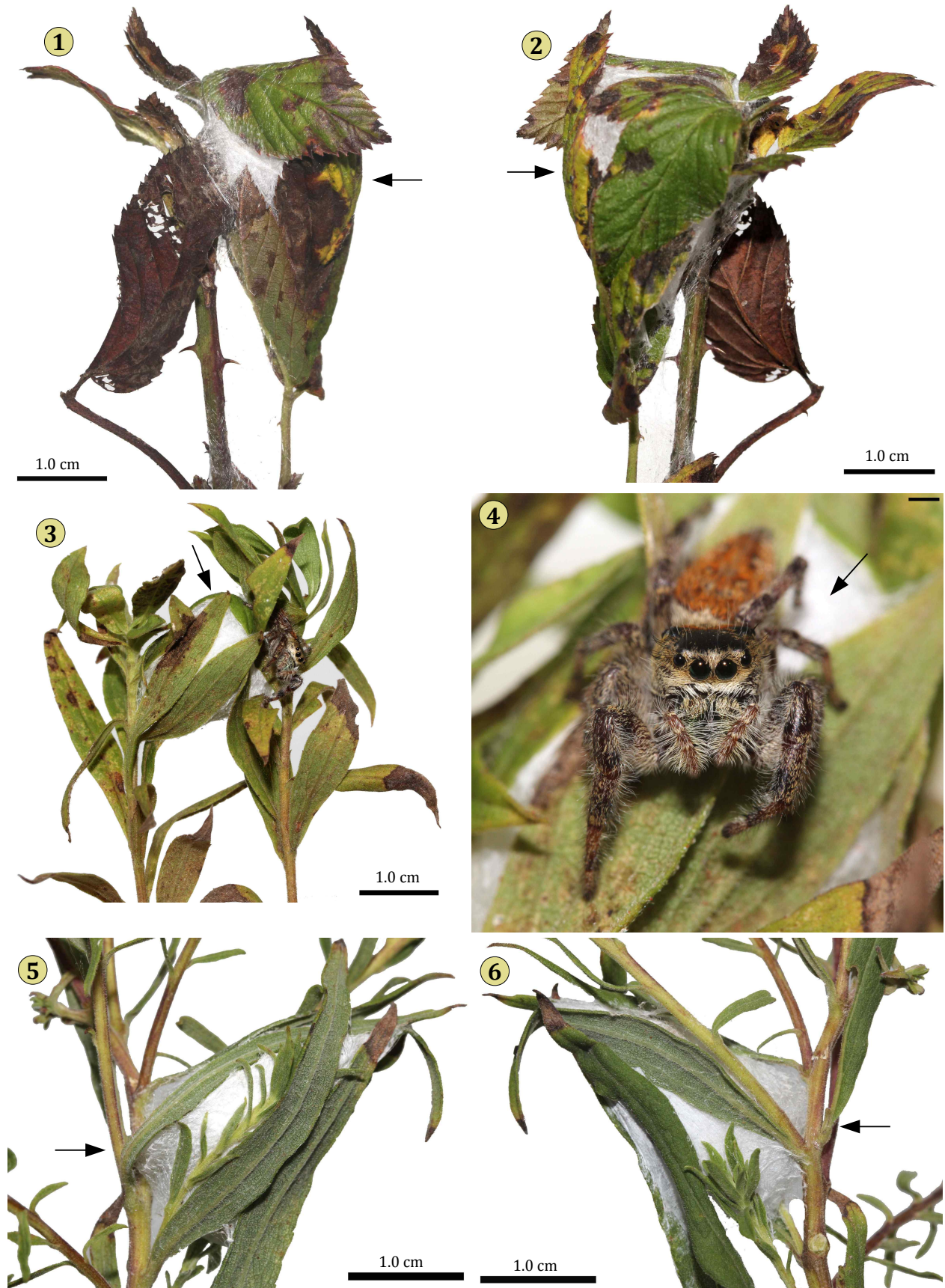
**Seasonality.** Edwards (1980) reported the maturation of *P. clarus* in the summer, with adults most often found between July and September. In the northern part of their range they may mature in June (Snetsinger 1955). Late summer maturation allows adults to make use of leaf clusters at the top of field plants that may persist into the late fall. In South Carolina I have found adult females tending their egg sacs from August to late November. According to Roach (1988), spiderlings disperse from September to January in South Carolina. *Phidippus cardinalis* and *P. pius* Scheffer 1906 share the tall-grass prairie with *P. clarus*, but adult *P. pius* are found in late spring to early summer, and adult *P. cardinalis* first appear in the fall and overwinter into the spring when the females lay their eggs (Edwards 1980, Roach 1988). I have usually found *P. cardinalis* and *P. pius* adults in association with heavy prairie grasses that retained persistent thatch near the ground during the winter, in more stable old field habitats.

**Nesting sites.** Female *P. clarus* can use one or more leaves near the top of shrubs and herbaceous plants, or even the nests of other spiders (Figures 12-14; see also Edwards 1980 and Johnson 1995). Leaves are connected with structural silk threads to establish a framework for the nest, and within this framework many layers of uniform silk are deposited to form a flattened tube. As in other *Phidippus*, one or more (usually two) openings to this tube are maintained, and can be opened and closed by the spider.



**Figure 12.** Resting sacs or nests constructed by female *P. clarus* in the leaves of shrubs in old field or ruderal habitats in southern Greenville County, South Carolina (8 OCT 2011). **1-2**, Two views of a nest between blackberry (*Rubus*) leaves, occupied by a female that had not laid eggs. **3-5**, Three views of a nest with eggs between two leaves of a shrub.





**Figure 13.** Nests constructed by female *P. clarus* in South Carolina. **1-2**, Two views of an occupied nest (arrows) at the top of a blackberry (*Rubus*) plant in southern Greenville County (23 NOV 2013). **3-4**, Two views of a female attending her nest (arrows) at the top of a goldenrod (*Solidago*) plant in northern Laurens County (30 SEP 2011). Scale bar in (4) = 1.0 mm. **5-6**, Two views of a different occupied nest (arrows) between *Solidago* leaves in northern Laurens County (30 SEP 2011).





**Figure 14.** Resting sacs or nests occupied by female *P. clarus* in southern Greenville County, South Carolina old fields. **1**, Female outside of her sac (arrow) below the top of *Solidago* (8 OCT 2011). **2**, Female looking out of open sac near at the top of *Rubus* (8 OCT 2011). **3**, Occupied nest below the top of a *Solidago* plant (9 SEP 2011). **4-5**, Female in sac at the top of a plant before (**4**) and just after (**5**) closing the entrance by pulling the top down. **6-7**, Two views of the cohabitating male that lived just below the top of the plant occupied by the female shown in (**4-5**).



### Related species

Terranova and Roach (1987) studied seven eastern species of *Phidippus* with gel electrophoresis. Their measurements of genetic distance between these species placed *P. clarus* outside of a clade that included *P. audax* and *P. putnami* (Figure 15:1). Edwards' subsequent (2004) grouping of *Phidippus* species, based on comparative morphology, depicted a very different view of the relationships between these species (Figure 15:2). Edwards placed *P. clarus* within a clade that he termed the *cardinalis* group (*tux* clade), and suggested that the southeastern *P. cardinalis* (Hentz 1845), and two Mexican species with a more restricted distribution (*P. mimicus* Edwards 2004 and *P. tux* Pinter 1970) were its closest relatives within the genus. All four of these species have been reported from southwestern Mexico (Edwards 2004). Comparison of the mitochondrial COI-5P gene of *P. clarus* with *P. audax* and *P. princeps* is also consistent with the hypothesis that *P. clarus* and its close relatives are not part of an *audax* group than includes *P. princeps* (Kaldari, pers. comm.).



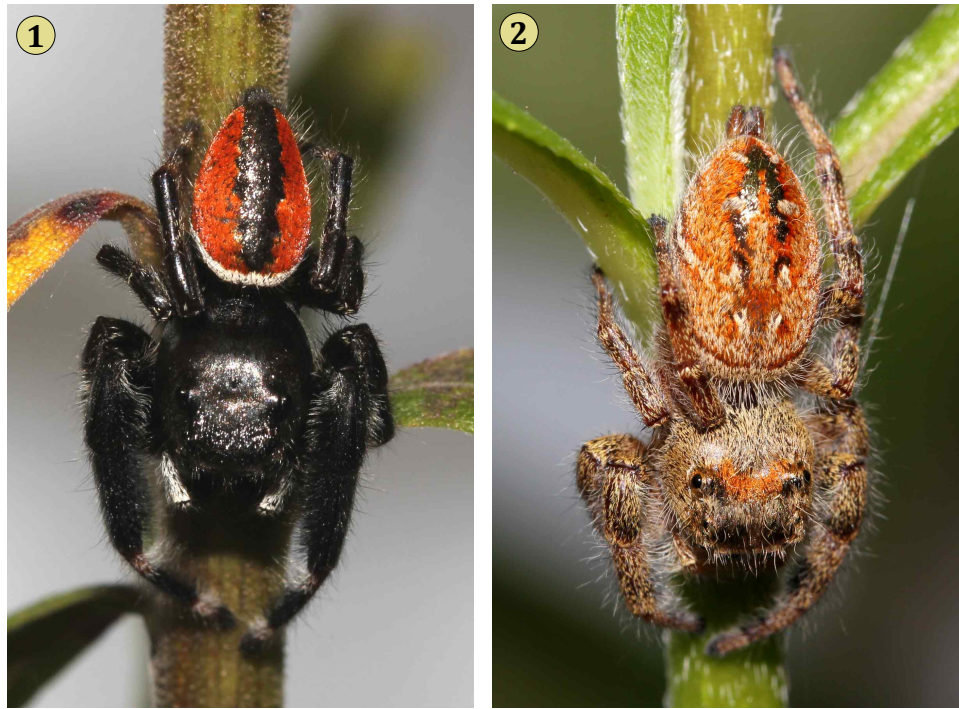
**Figure 15.** Cladograms depicting the hypothetical phylogeny of selected *Phidippus* species, based on gel electrophoresis (Terranova & Roach 1987) and comparative morphology (Edwards 2004).

### Behavior

*Hunting and spatial memory of location.* *P. clarus* was one of the species of *Phidippus* that I observed during my early study of hunting behavior and spatial memory (Hill 1978, 1979b, 2010). One male that I observed ran very long and fast pursuits out of sight of its prey, and I suspect that this kind of concealed approach is an important component of the hunting behavior of this plant-dwelling species. Hoefler & Jakob (2006) studied *nest site fidelity* or the tendency of *P. clarus* to return to previous nest at the end of a day away from the nest site. They found that late summer females were most likely to return to their nest site, and their experiments also indicated that colored landmarks (or *beacons*) in the vicinity of a nest could be used by a spider to find that nest. As with other *Phidippus*, I have frequently observed *P. clarus* waiting for prey in a face-down position near the top of the main stem of an herbaceous plant, away from the nest location (Figure 16; see also Edwards 1980, 1990), but this is not their only waiting or resting position.

*Defense of the nest by females.* Elias *et al.* (2010a) studied the defense of nest sites by females by staging combats, and found that 'desperado' or non-ritual fights between females were more likely to result in injury or death than were the more ritualized male-male combats that they observed.





**Figure 16.** Adult male (1) and adult female (2) *P. clarus* from southern Greenville County, South Carolina, in the face-down position on the main stem of herbaceous plants (18 AUG 2011).

**Predation.** Because adult *P. clarus* feed in the late summer, they have access to a large seasonal population of relatively large or adult insects (Schmitz & Suttle 2001; Schmitz 2008, 2009). In captivity, they readily feed on a wide variety of Orthoptera, Heteroptera, and Diptera (Figure 17; see also Hoefler *et al.* 2006). They will also take other spiders as prey (Hill 2009), but the specialized pursuit of spiders and other motionless prey does not appear to be one of their specialties as in *Thiodina* (Hill 2012). I have observed *T. puerpera*, another important spider of the tallgrass prairie or old field, feeding on small *P. clarus* in the spring. Edwards (1980) provides a comprehensive review of prey taken by *P. clarus*, and this agrees with my own observations. He also found that *P. clarus*, like other *Phidippus* species, jump at flies from a greater distance, but approach cabbage loopers (Lepidoptera: *Trichoplusia ni*) more closely before they attack. I suspect that a much greater repertoire of predatory behavior would be revealed by a more extensive field study. As with other salticids, our knowledge of prey taken by immatures is almost nil. Like adults, however, they readily capture a variety of insects commensurate with their size in the laboratory.

Hoefler *et al.* (2006) suggested that *P. clarus*, one of few *Phidippus* known to occur naturally in high population densities, might be of value in the control of insect pests. This would be incompatible with the use of insecticides and perhaps also with the application of herbicides as well. We are not certain how much *P. clarus* rely on direct intake of plant fluids for their survival, but I have observed immature *P. audax* taking fluid directly from *Rubus* leaves. Even if a maximum population density based on constraints of intraspecific competition and the required prey density could be established, *P. clarus* populations are subject to attack by many parasitoids in nature (Edwards 1980), and population stability might be very difficult if not impossible to attain. Edwards discussed the question of why this species exposes itself as much as it does at the top of plants, given the extent of parasitoid attack on nests. I hypothesize that, like many other prairie species, the survival of *P. clarus* depends on a high level of dispersal between generations. According to this hypothesis, each local population can succeed only until its predators and parasitoids build up their own populations, at which time the population of both *P. clarus* and its attackers would crash. As noted previously multiple female phenotypes may also contribute to this success.





**Figure 17.** Feeding *P. clarus* from South Carolina. **1**, Adult male feeding on bottle fly, southern Greenville County, 12 JUL 2011. **2**, Adult female feeding on bottle fly, southern Greenville County, 6 AUG 2011. **3**, Adult female feeding on bottle fly, Southern Greenville County, 11 JUL 2011. **4**, Adult female feeding on bush katydid, southern Greenville County, 23 AUG 2011. After jumping to capture this katydid, the spider held one of its legs between the endites as it hung from its dragline. **5**, Adult female feeding on tree cricket, southern Greenville County, 4 SEP 2011. **6**, Adult female feeding on bush katydid, northern Laurens County, 8 AUG 2012. **7**, Adult female feeding on leaf hopper, southern Greenville County, 18 AUG 2011. These are not field records of predation as each spider was captured and later offered its prey item in a controlled setting.

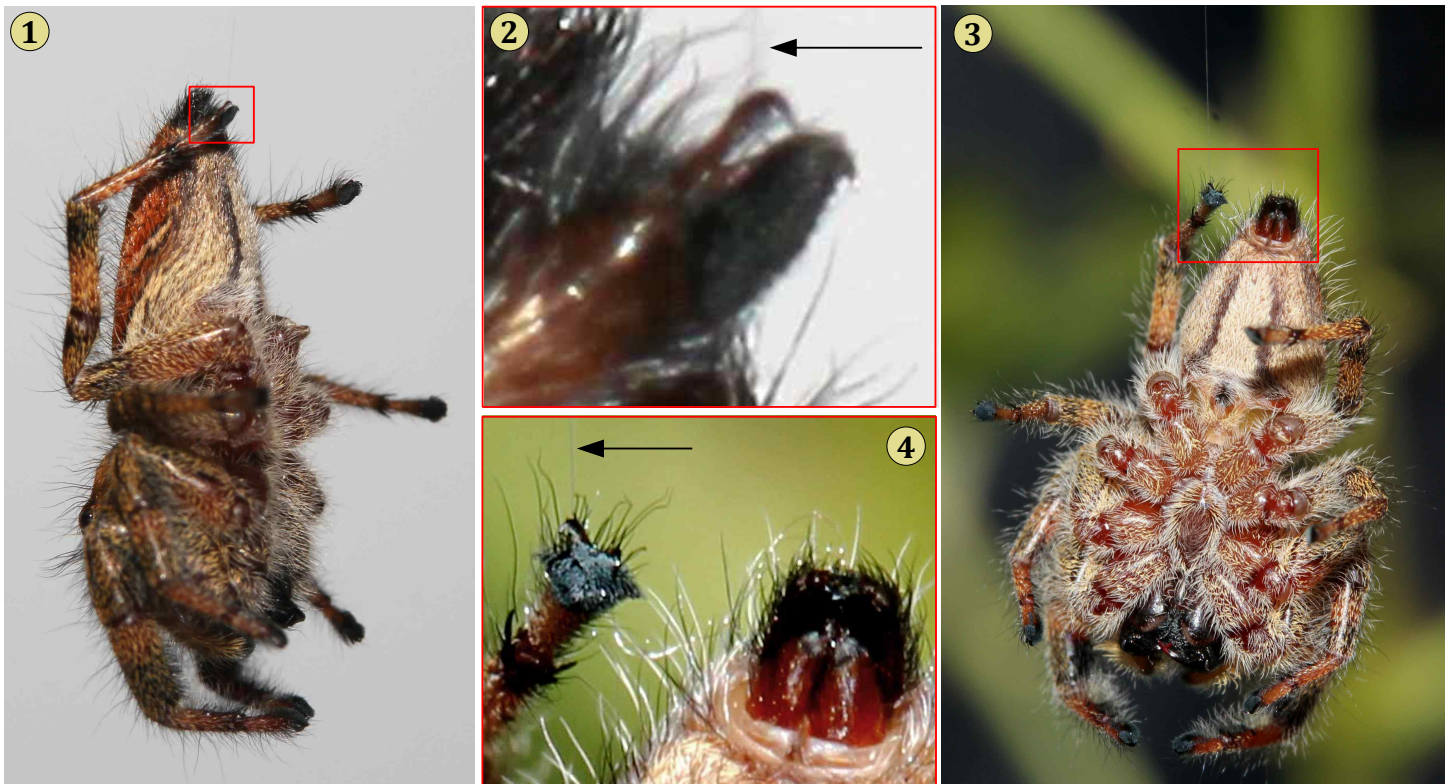


*Jumping.* Like other *Phidippus* (Hill 2010b) and probably the great majority of salticids, *P. clarus* power their jumps through rapid extension of legs IV, using legs III as a fulcrum during take-off (Figure 18).



**Figure 18.** Adult female *P. clarus* from southern Greenville County, South Carolina, preparing to jump down (1) and horizontally (2). In each example, legs IV were flexed against the surface of the underlying leaf, legs III were held against the surface, and legs I and II were raised off of the surface just before the jump.

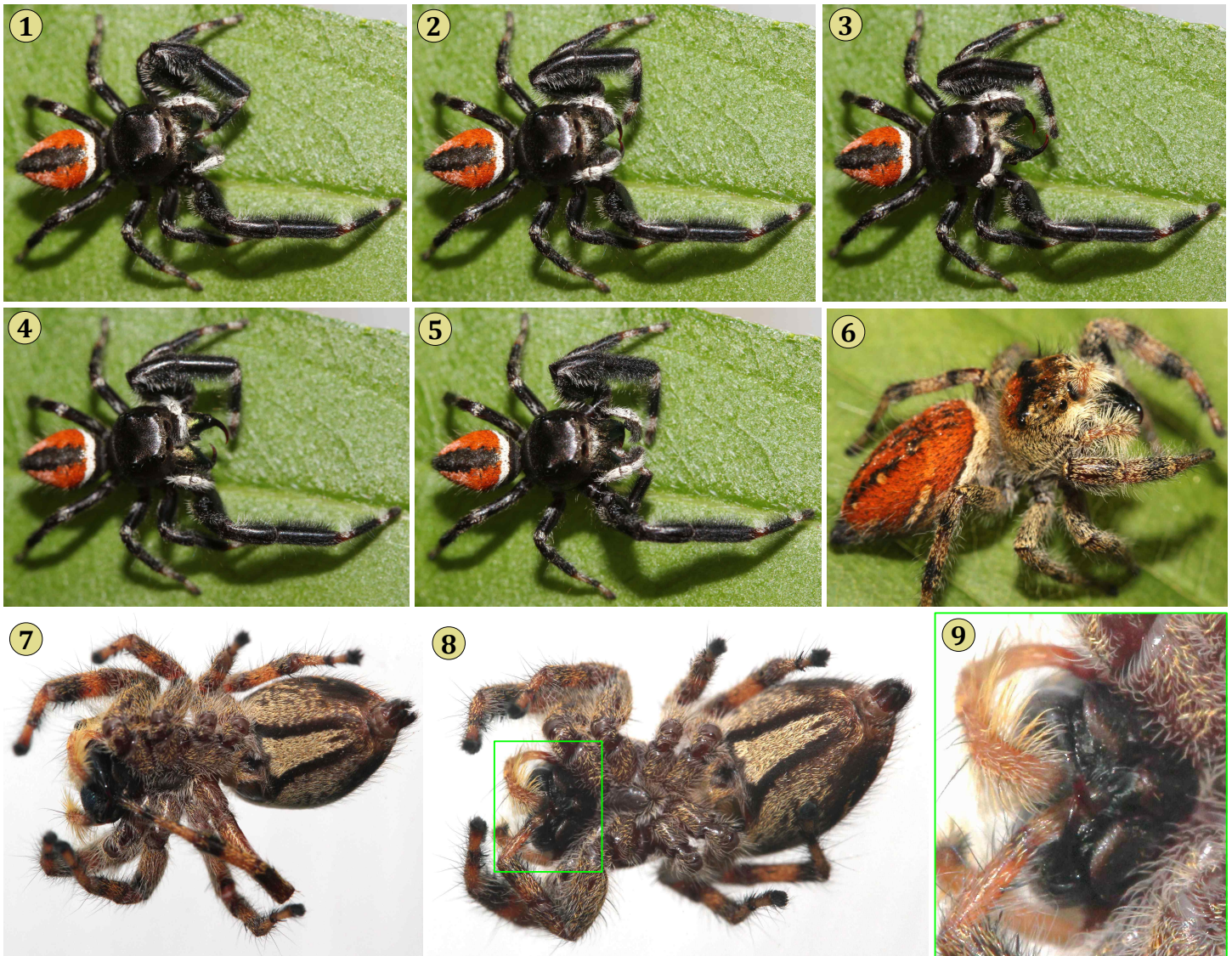
*Hanging on the dragline.* My hypothesis (Hill 2010c) has been that the closer spacing of teeth on the anterior claw of each salticoid leg corresponds to the use of the anterior claw to hold the dragline securely when the spider is hanging from it. Two examples of this use of the anterior claw of left leg IV by a female *P. clarus* are shown in Figure 19.



**Figure 19.** Two examples (1, inset magnified in 2, and 3, inset magnified in 4) of adult female *P. clarus* hanging from its dragline (arrows) with the extended anterior claw of left leg IV.



**Grooming.** Some examples of grooming by *P. clarus* are shown in Figure 20. As in other *Phidippus*, the front eyes and chelicerae are brushed with the pedipalps. The cheliceral base and fangs are often extended as these are groomed. The distal portions of all four pairs of legs and the pedipalps are pushed into the mouth as these are pulled under the fangs.



**Figure 20.** Some examples of grooming by adult male (1-5) and female (6-9) from southern Greenville County, South Carolina. 1-5, Sequential photographs of a grooming male showing (1) left leg I pulled under the fangs, (2) both fangs extended as the anterior surfaces were brushed with the pedipalps, (3-4) more extensive brushing of the extended fangs, and (5) right leg II pulled under the fangs. 6, Female brushing the anterior eyes and the extended left chelicerae with the left pedipalp. 7, Female pulling the distal part of right leg IV under the fangs. 8-9, Female pulling the tip of the right pedipalp under the right fang. In the inset detail (9) you can see the tip of this pedipalp pushed directly into the tip of the mouth. When grooming appendages with the chelicerae, the spider appears to be chewing them with its fangs. How this behavior contributes to the function of the legs or pedipalps, and the extent to which digestive fluid plays a role, is not known. However, behaviors like these are often observed after a spider has fed, and they may contribute to their hygiene.

**Mating success.** Behavior related to the success of male *Phidippus* has been the subject of a number of studies in the last 40 years, beginning with Jackson's many papers dealing with *P. johnsoni* in California (Jackson 1976a, 1976b, 1978a, 1978b, 1978c, 1979, 1980a, 1980b, 1980c, 1980d, 1981a, 1981b, 1986). Jackson's work was focused on the interactions of males and females, and he defined *type 1 courtship* as display outside of the nest, and *type 2 courtship* as interaction at the nest. He also studied the role of female pheromones in the location of females, and penultimate females in particular, by males. The cohabitation of male and female *P. johnsoni* observed by Jackson was described previously for *P. audax*



and *P. clarus* in Illinois by Snetsinger (1955), and similar behavior has also been reported for *P. otiosus* in Florida (Edwards 1990). Snetsinger described how male *P. clarus* located a female, built a nest on top of the female's nest, guarded that female from other males, and mated by extending its pedipalps through layers of silk to reach the female, sometimes mating multiple times. He also described the successful defense of a female by a male with a missing leg that was able to fend off four successive approaches by a larger male.

The role of sexual selection by a female jumping spider, based on female observation of male display or performance, has received much attention. In many salticids (e.g. *Habronattus*, Elias *et al.* 2006, and *Maratus*, Hill & Otto 2011) there is little doubt that females carefully scrutinize males, and in these genera males are usually highly ornamented, and perform an elaborate display in front of females. In many other genera including *Lyssomanes* (Tedore & Johnsen 2012) and *Thiodina* (Hill 2012) there is less evidence for scrutiny by females, and the ability of males to dominate rival males appears to play a larger role in their mating success. Several years ago I assisted in a televised production (PBS 2008) that included courting male *P. clarus*, but unfortunately the videographer decided to pair a male that I sent him with an aggressive female of a different *Phidippus* species. The result was portrayed as sexual selection by the female.

We can look at the probability of male mating success ( $P_{sm}$ ) as the product of four *somewhat* independent events with a simplified mathematical model:

$$P_{sm} = P_a P_f P_g P_m, \text{ where:}$$

$P_a$  = probability (0-1) that the male will live to adulthood  
 $P_f$  = probability (0-N) that an adult male will find an unmated female  
 $P_g$  = probability (0-1) that an adult male will be able to guard that female once found  
 $P_m$  = probability (0-1) that the male will be able to mate with that guarded female

These events are only *somewhat* independent. For example, maturation at an earlier instar might increase  $P_a$ , but reduce  $P_g$  if the male is smaller as a result. The probability of male mating success ( $P_{sm}$ ) is not independent of female mating success ( $P_{sf}$ ). If we assume that each female mates with only a single male, we can view each mating event of a male with a female as one unit of success for each:

$$P_{sm} = P_{sf} \sim 2/B, \text{ where:}$$

$B$  = average brood size per mated female

Assuming that the reproducing population is constant from year to year, the average probability of mating success for each sex is  $\sim(2/B)$ , since  $B(2/B)=2$  [corresponding to one mated male and one mated female]. If an unmated female is selective with respect to her choice of mate, then  $P_m < 1$ . As this clearly reduces the mating success of the male, it also appears to reduce the mating success of the female as well. The standard mathematical answer to this dilemma lies in the fact that, although a female reduces her own probability of mating success through her selectivity, the resultant mating success of her own offspring more than compensates for this loss. In addition, if males can find and mate with multiple females ( $P_f > 1$ ), multiple mating opportunities can overcome most of the risk associated with rejection of a single male ( $P_m < 1$ ). As a result, I hypothesize that, when *species averages* are compared, ( $P_f P_g$ ) and  $P_m$  will vary inversely. As the probability of a male-female encounter increases, female selectivity can also increase. If enough males are available to an unmated female, she can afford to be selective. But, if a male must defend a female from other males ( $1/P_g = \text{combat level} > 1$ ), then that female has fewer available males and should be less selective ( $1/P_m = \text{female selectivity} < 1$ ):

$$(\text{constant}) \cong (1/P_f) (1/P_g) (1/P_m), \text{ where:}$$

$1/P_f$  = search level  
 $1/P_g$  = combat level  
 $1/P_m$  = female selectivity



If males are scarce, or if they cohabit and guard individual females and thus reduce their search effort ( $P_f$  approaches 1), the penalty for higher female selectivity ( $1/P_m > 1$ ) becomes a real risk of reproductive failure for the female. In situations where population densities vary greatly from year to year, or from place to place, a female might reduce this risk by adjusting her own selectivity according to the number of males that she encounters. Within limits, failure to encounter a male after she molts to maturity might increase the receptivity of a female over time.

In the case of *P. clarus*, as with other cohabiting *Phidippus*, as well as *Thiodina* and *Lyssomanes*, I have observed that young, unmated females generally mate with the first male that they encounter (female selectivity close to 1). These spiders appear to have a higher combat level and lower female selectivity. In addition to cohabiting males (Figure 13), I have also observed adult male *P. clarus* displaying in the open, on top of leaves. Some males must find and mate with multiple females, as others are less successful.

*Male-male contests.* Recently Kasumovic *et al.* (2009, 2010, 2011) reported the results of a series of staged encounters between male *P. clarus*. They found that three factors increased the probability of male success in these contests: 'ownership' of a defended female, absolute size of the male, and prior experience in winning a contest. Experience at losing a contest reduced the probability of subsequent success. Males that were more closely matched in size were also more likely to engage in combat. This effect of experience may be adaptive in that males that lose may better put their time and energy into the search for a different female, perhaps one that has not been claimed. Earlier, Hoefler (2007) also found that larger males were more successful in combat than smaller males.

Whenever I have placed an adult male in the vicinity of another adult male *P. clarus*, they have engaged in a form of combat that involves two different postures (Figure 21). They moved quickly from display at a distance to approach, escalating to violent contact with extended fangs, and then rapid flight by one of the males. Just after this experience, the losing male in each instance was much less likely to engage in subsequent combat. I would characterize this combat as partly ritual (particularly with elevation to display a large size), and as partly a very dangerous attack on the other spider. Elias *et al.* (2008) associated the two postures with 'precontact' and 'contact' phases of the encounter, and also documented the *vibratory signalling* that accompanies each visual display.

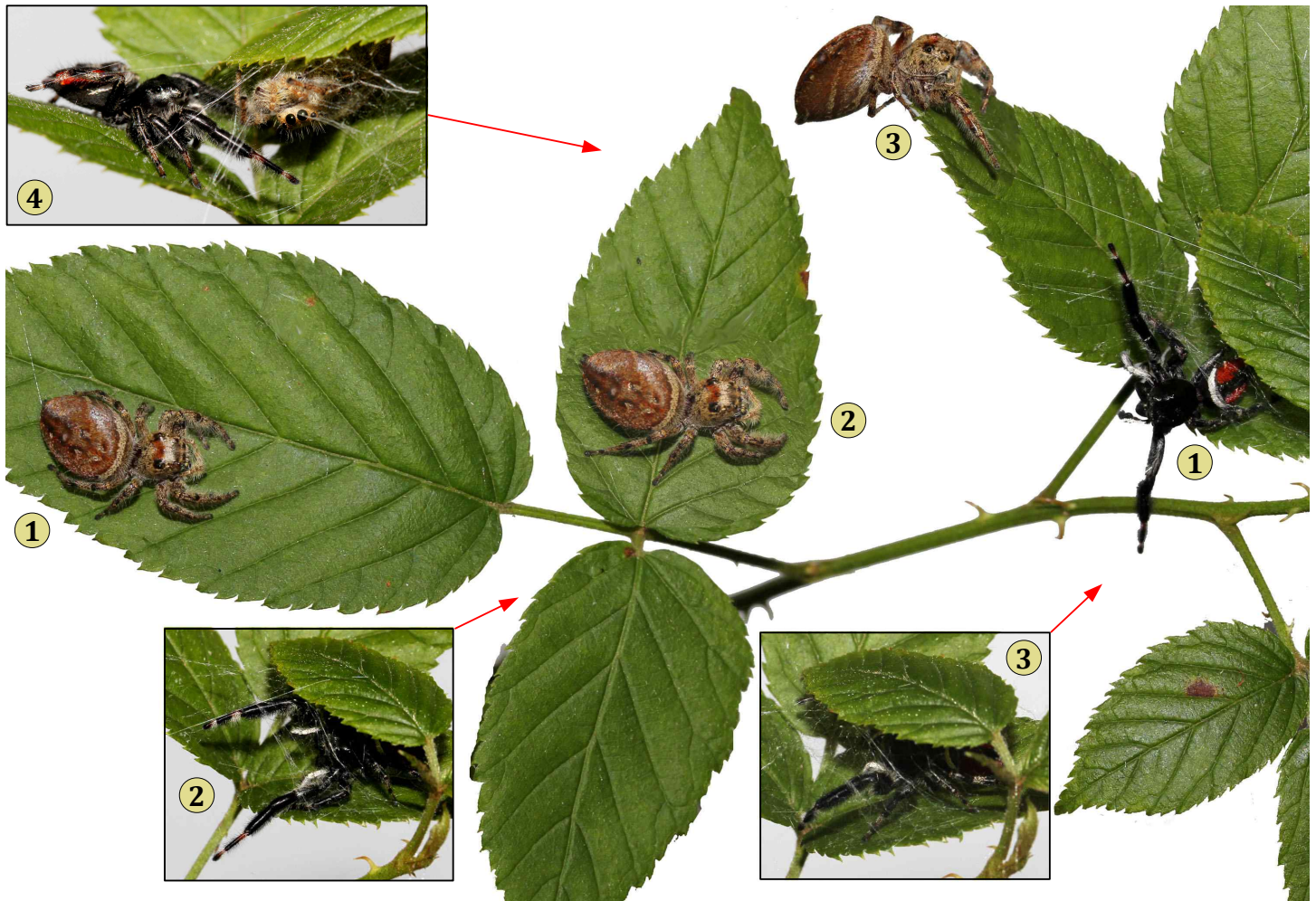
*Cohabitation of males and females.* Mate-seeking or courtship behavior of female salticids has not generally been reported, although Elias *et al.* (2010a) studied the violent defense of nests (*resources*) by females when approached by other females. I staged one encounter in the laboratory where I allowed a male *P. clarus* to construct a shelter under a leaf, and then introduced an unmated adult female (Figure 22). When this male saw the female, he displayed to her with exposed chelicerae and extended legs I, but did not approach as the female assumed a *receptive* posture facing the male, with opisthosoma turned to one side. As the male moved back into his retreat, the female approached him with no sign of either aggression or fear, and promptly moved into his retreat. Subsequently the male and female occupied this retreat together, and mated successfully several times. Clearly this staged encounter cannot be said to represent the normal situation in nature, where one tends to find an adult male cohabiting with a penultimate or mature female. But, it does demonstrate the remarkably 'amicable' and relatively long-lasting relationship that can be assumed by a male and a female of this species. This contrasts greatly with my many observations of the interactions of male and female *P. princeps* (Hill 1977). In that species, immediately after mating the female becomes a danger to the male, actively stalking a smaller male as prey. In the field, I have also observed many cases of 'cannibalism' in immature *P. princeps*. Cohabitation in *P. clarus* is easy to demonstrate in the laboratory (Figure 23).



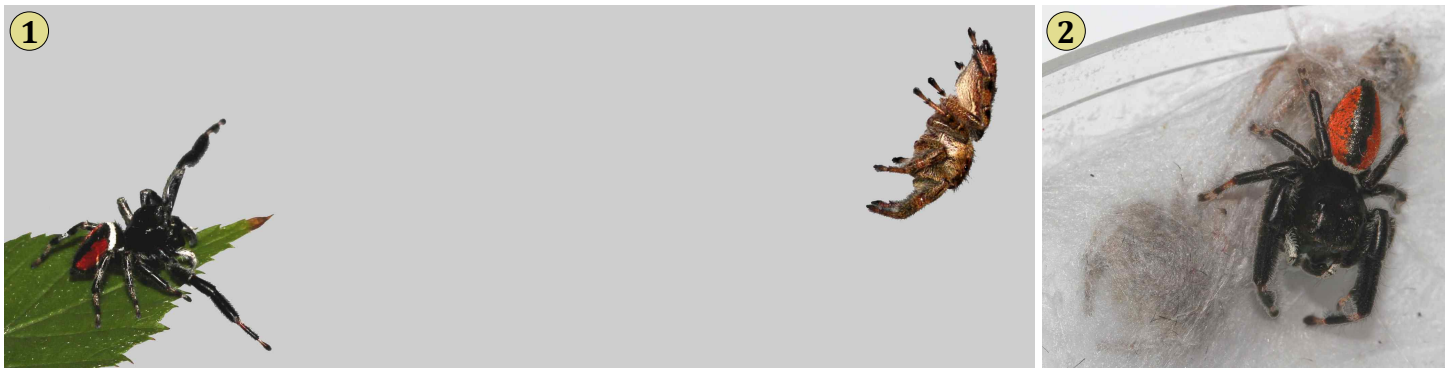


**Figure 21.** Combat between male *P. clarus* from southern Greenville County, South Carolina. **1**, Face-off. The larger male, at left, raised its body and exposed its chelicerae, as the smaller male began to extend its fangs. **2**, Both males extended their fangs. **3**, In close combat, males would move their pedipalps well to the side and attack with fully extended fangs. In some cases their chelicerae were in direct contact. **4**, Threat at a distance with extended legs I and exposed chelicerae. Note the slight extension of the fangs, something not seen in courtship display when the chelicerae are also exposed. **5-7**, Three other 'raised body' displays to a nearby male. All of these contests were staged by placing two males together on the same plant.





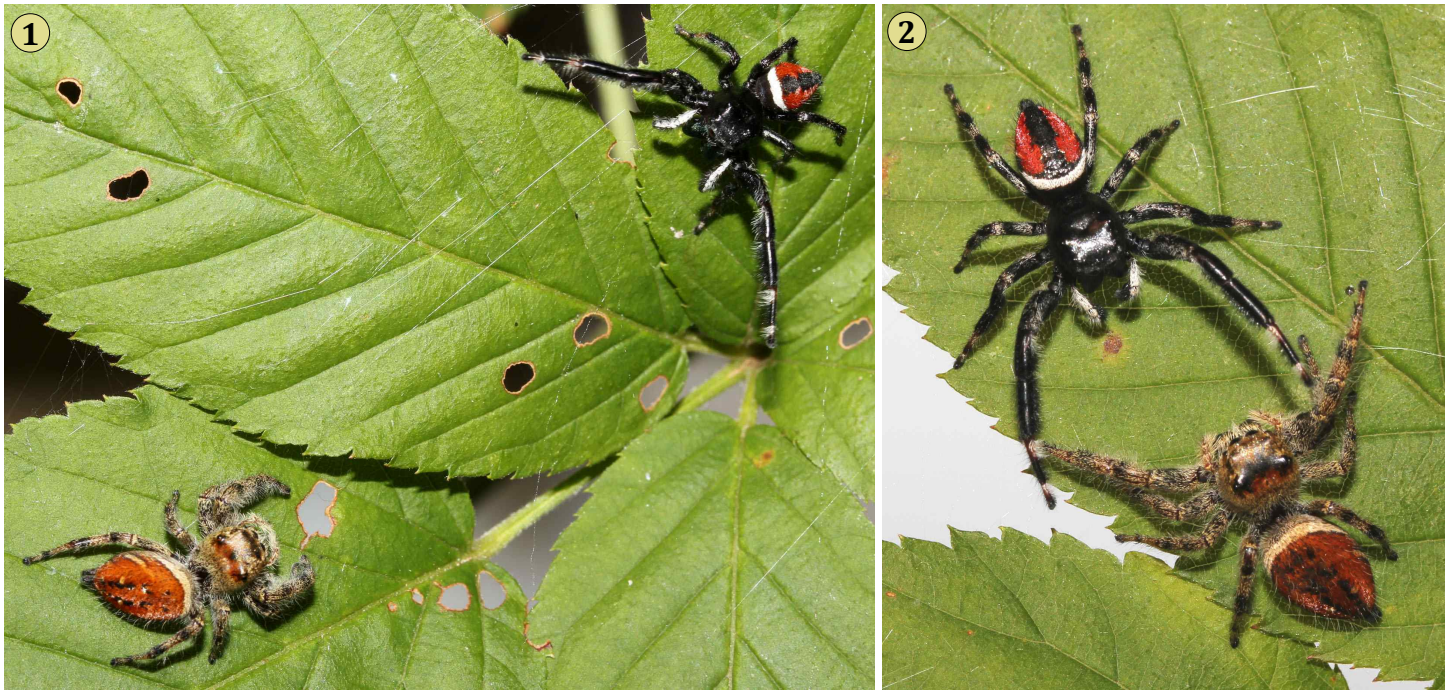
**Figure 22.** Photomontage showing four sequential positions (1-4) of a male and unmated female *P. clarus* near the top of a blackberry (*Rubus*) plant. The male (at right) was allowed to construct a shelter with silk before the female was introduced. **1**, As the male displayed from the entrance to its shelter, the female assumed an *available* position, with opisthosoma turned to the side. **2**, As the male retreated into its shelter, the female advanced and then stopped briefly, maintaining its available position. **3**, As the male retreated further into its shelter, the female continued to approach. **4**, After the female moved into his shelter, the male continued to accompany her. Later, they mated several times.



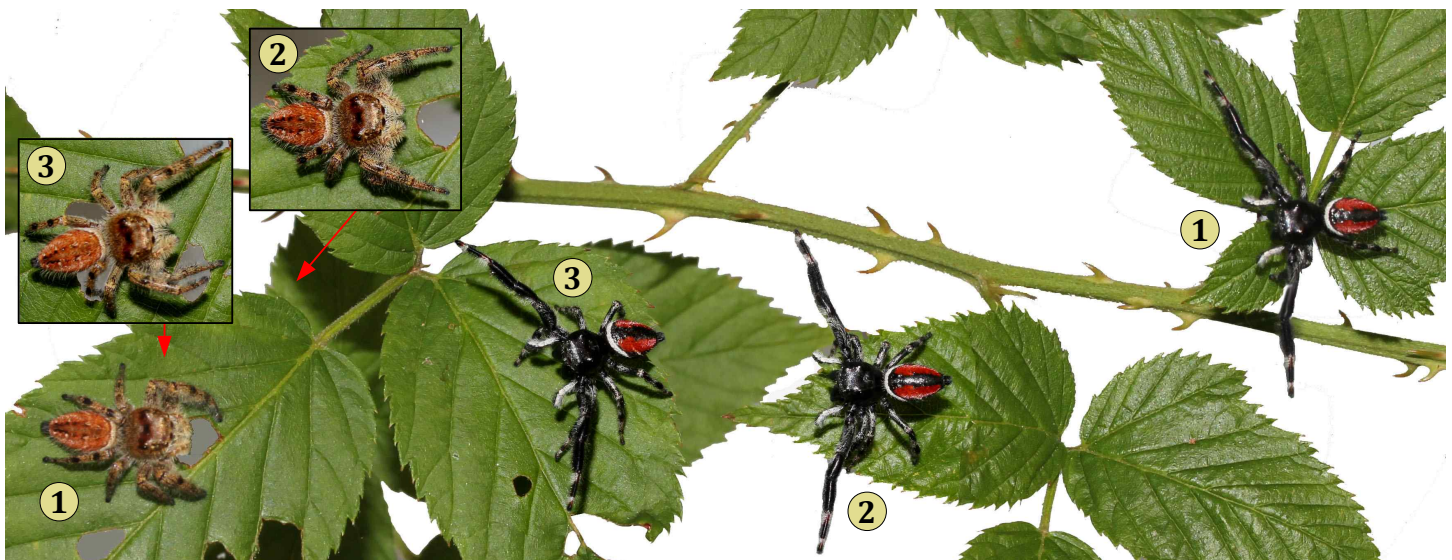
**Figure 23.** Male-female interactions. **1**, This male displayed to a female hanging from its dragline and tried to approach her on nearby leaves. Recognition of the female may have been facilitated by the presence of pheromones associated with silk in the area. **2**, Male cohabiting with a female in a petri dish. The male was introduced prior to the last molt of this female (exuvium at top right) and took up residence on top of her molting sac.



*Courtship display* (Figures 24-28). Here I describe the results of staged encounters that suggest that *P. clarus* males will court females that they encounter away from the nest, as do many other *Phidippus*. When a male *P. clarus* sights a female at a distance, he faces that female, extends his long legs I laterally as if to emphasize their length, and holds his pedipalps laterally to expose his iridescent chelicerae. Legs I may be moved quickly up and down to gain the attention of the female. This *advertisement* is not much different from the first phase of a male-male encounter, except that the fangs are not extended significantly. As in the male-male encounter, it probably represents an effective defensive position if needed. As the male approaches the female, legs I are brought closer together, and are finally directed toward the front to touch the female.

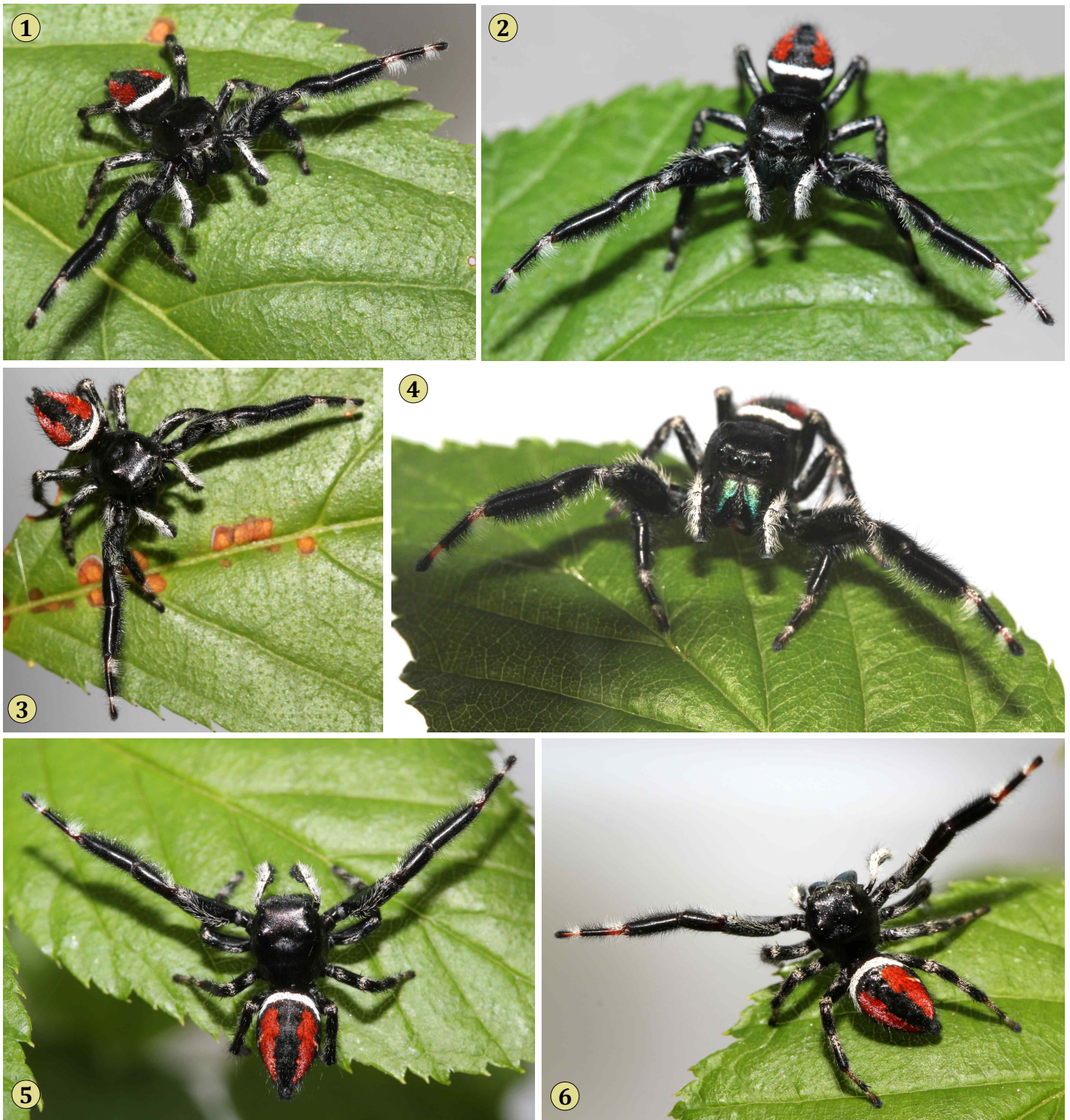


**Figure 24.** Two examples of a male *P. clarus* courting an unmated female in the open. **1**, The female in this case displayed a typical *receptive* position, facing the male with *opisthosoma* turned to one side. **2**, As this male approached the female, he brought his legs I together to touch the female. With legs I and pedipalps held to the side, this female assumed a defensive position, but the male persisted and they mated successfully. Southern Greenville County, South Carolina.



**Figure 25.** Photomontage sequence (1-3) showing a male *P. clarus* (right) displaying to and approaching an unmated female from a distance, with legs I held wide and the ends of the pedipalps held apart. Southern Greenville County, South Carolina.





**Figure 26.** Male *P. clarus* as they displayed to a females from a distance. Southern Greenville County, South Carolina. 4, The exposed chelicerae of this spider are only brightly iridescent when viewed from the front, as they would be seen by a female.





**Figure 27.** Sequence (1-6) showing part of an encounter between a male and female *P. clarus* from southern Greenville County, South Carolina. **1**, After mating on both sides, the male continued to face this female and maintained contact. **2**, Still touching the female, the male turned away to groom its chelicerae with its pedipalps. **3**, The male continued to court the female by bringing legs I closer together, as the female assumed a receptive position. **4**, Second mating of this pair. **5**, After mating, the male continued to touch the female, still in a receptive position. **6**, The male stepped back from the female and resumed courtship, resulting in a third mating of the pair. For some time afterward, the two spiders showed no fear of each other.

As do many other salticids, male *P. clarus* vibrate their opisthosoma up and down during courtship and mating. In staged encounters, Elias *et al.* (2010b) studied the relationship of vibratory signals associated with this 'tremulation of the abdomen' to the success of courting males. They were able to mute these vibrations by attaching the male prosoma to the opisthosoma with wax, and found that this did not prohibit mating, but it did reduce the success rate of males so treated. Their controls also had wax affixed in a similar position, but not in a manner that would stop vibrations. This finding supports but does not demonstrate the role of vibrations in courtship in *P. clarus*. It is possible that lack of freedom of movement of the opisthosoma altered the behavior of males so treated, and vibrations by the male may



not have any impact on female selectivity. At the same time, the fact that so many male salticids (and other spiders) exhibit this vibrating behavior suggests that it does have a function in courtship. For *P. clarus* at least, this should still be treated as a 'plausible hypothesis'. Sivalingham *et al.* (2010) also reported a positive correlation between male size and mating success, attributing this to female selectivity for the higher vibration rate associated with larger males.

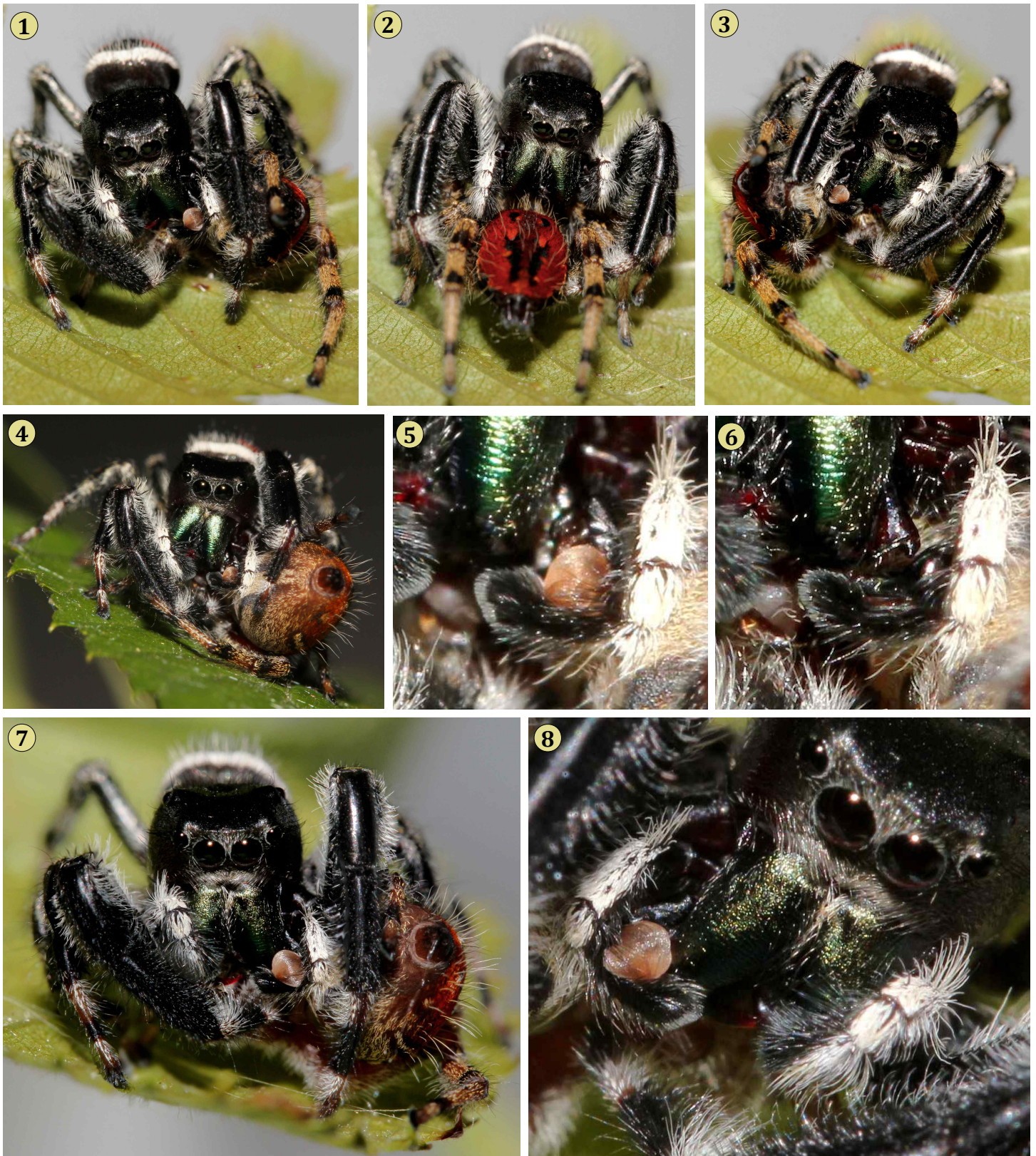
In a field study, Hoefler (2007, 2008) found that adult males initially outnumbered adult females as they cohabited with and guarded penultimate females. He found that larger males tended to be paired with larger females, and suggested that this 'size-associative pairing' could be the result of a preference of all males for larger females with greater fecundity, combined with the ability of large males to defend their preferred females from smaller males. In his study locations in the field were not mapped or correlated with spider size, and an alternative explanation for this 'size-associative pairing' is that the size of both male and female *P. clarus* varied according to resources available in different locations or microhabitats.



**Figure 28.** Courtship and mating by *P. clarus* from southern Greenville County, South Carolina. **1**, Display at a distance by male (left) with widely extended legs I. **2-3**, Two views of male displaying to a female that it faced, at a distance. **4-5**, Sequence showing a male bringing its legs I together as it approached a female in a receptive position.

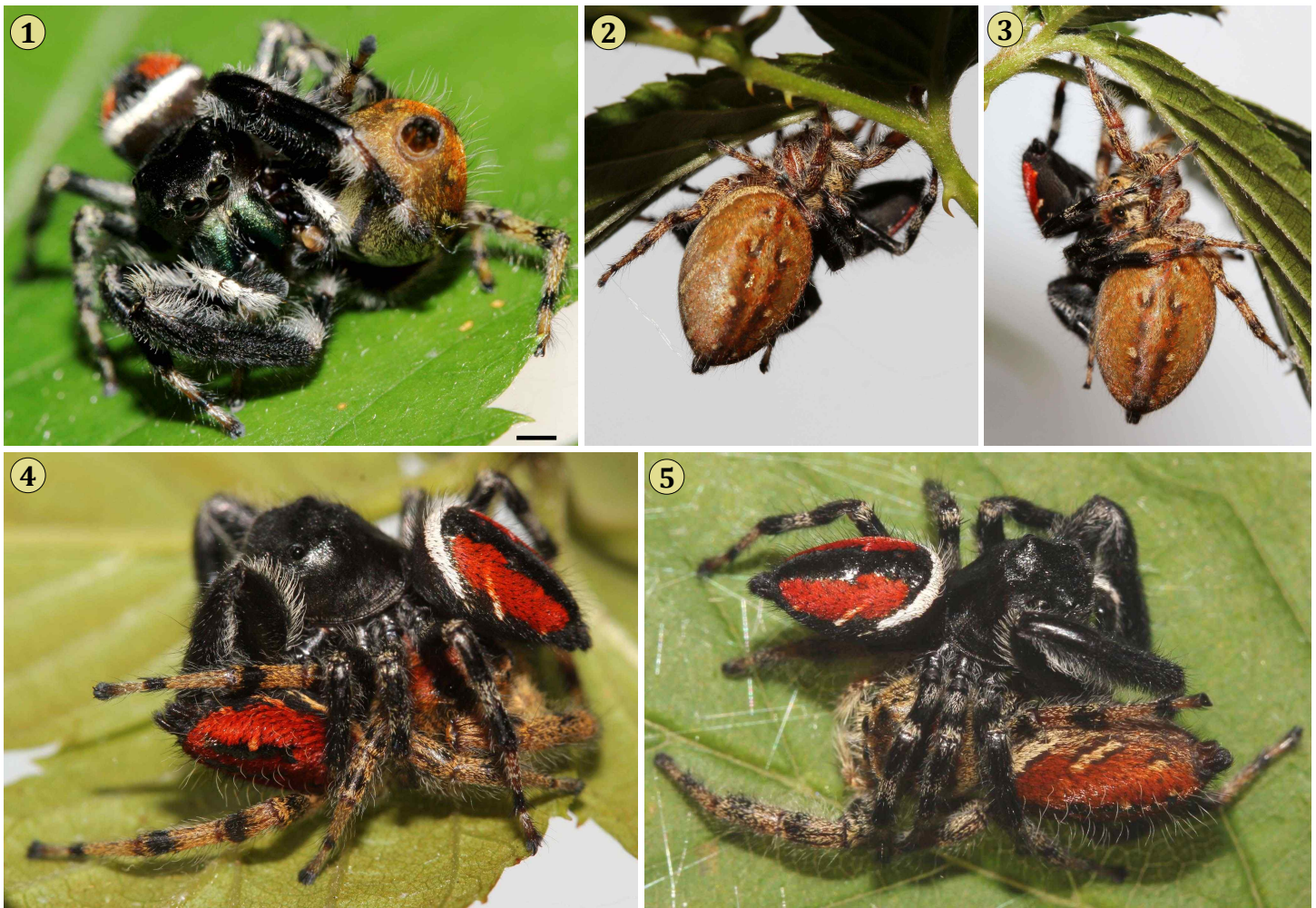
**Mating.** Several examples of mating behavior are documented here (Figures 29-30). Observed mating positions compared with those of other salticids, with the male climbing from front to rear over the female, rotating her opisthosoma to mate on one side, and then rotating her opisthosoma to mate on the other side. In staged encounters Sivalingham *et al.* (2010) found that females would mate with multiple males. I have observed multiple matings with a single pair (Figure 27), but have no information related to how long a female is receptive after she has mated.





**Figure 29.** Mating by *P. clarus* from southern Greenville County, South Carolina. **1-3**, Sequence showing a male mating first on the left side, then crossing over the female, and finally mating on the right side. **4-6**, Mating pair, showing details of cyclic palp expansion (**5**) and contraction (**6**) during the mating process. **7-8**, Two other pairs mating.





**Figure 30.** Mating by *P. clarus* from southern Greenville County, South Carolina. 2-3, This pair maintained a precarious foothold while moving between the two mating positions.

### Discussion

The relationship of day length (or other variables) to the rate of maturation in *P. clarus* needs more study and resolution before I would consider *P. clarus* to be an ideal laboratory animal. This species is however ideal for field studies of nest predator or parasitoid population dynamics, related to its high degree of exposure (Edwards 1980). Other areas for future study include the incidence of various female color forms (or associated genes when these can be identified) by population, and quantification of gene flow or dispersal between populations.

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