

Jumping spiders of the *Phidippus princeps* group in the southeastern United States (Araneae: Salticidae: Dendryphantina)

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Abstract: A comparative study of adult and immature spiders of the *Phidippus princeps* group (*P. princeps* and *P. pulcherrimus*) from a series of local populations in the southeastern United States supports the hypothesis that this group represents a single *biological species*, with a wide and deep zone of hybridization between two distinct *typological species* or *geographical subspecies* (*princeps*-like and *pulcherrimus*-like, respectively). No significant niche separation of the two typological species has been identified, and no localities have been found where the two typological species coexist without significant evidence of interbreeding. Populations of the aposematically-colored *pulcherrimus*-like forms dominate in the subtropical southeastern coastal plain below the fall line and retain a juvenile pattern of scale cover into adulthood. Populations of the cryptically-colored *princeps*-like forms dominate in the eastern deciduous and mixed forest areas of temperate eastern North America above the fall line, with adults that replace the juvenile pattern with a more uniform pattern of scale cover. Historical research on the biology of these species is reviewed with an emphasis on temporal and microhabitat niche definition. Alternative hypotheses related to divergence of characters in this group and related implications for taxonomy are also discussed.

Key words: agonistic behavior, biological species, courtship, geographical subspecies, microhabitat, nest site fidelity, niche, *Phidippus audax*, *Phidippus clarus*, *Phidippus otiosus*, *Phidippus pulcherrimus*, *Phidippus regius*, predation, subspecies, trinomial nomenclature, typological species

Edwards (1980, 2004) identified the *princeps* group as a clade comprised of two relatively small and closely related allopatric species within the genus *Phidippus* C. L. Koch 1846:

***Phidippus princeps* (Peckham & Peckham 1883)**, assigned to genus by Peckham & Peckham 1901

Attus insolens Hentz 1845, *nomen nudum* by Edwards 2004

Phidippus castrensis C. L. Koch 1846, synonymy by Edwards 2004

Attus princeps Peckham & Peckham 1883

Phidippus brunneus Emerton 1891, synonymy by Bryant 1942

Phidippus insolens Peckham & Peckham 1909, ♂ only, after Edwards 2004

Phidippus dorsalis Bryant 1942, ♀ only, after Edwards 2004

***Phidippus pulcherrimus* Keyserling 1885**

Edwards (2004) also charted a gap between the ranges of the two species, with *P. pulcherrimus* restricted to the coastal plain below the fall line from Alabama to Georgia and *P. princeps* more widely distributed in the eastern forests from southeastern Canada west to the Great Plains (Figures 1-2). The female *P. dorsalis* Bryant 1942 (Southern Pines, North Carolina), bearing a distinctive middorsal stripe on the opisthosoma, was recognized as a southern form of *P. princeps*.

To further assess the relationship of *princeps* and *pulcherrimus* I have collected, reared, observed behavior, and photographed *princeps* group spiders representing a series of local populations that span the gap between the two species in the southeastern United States, ranging from northern South Carolina to central Florida (Figure 1, populations 1-10).

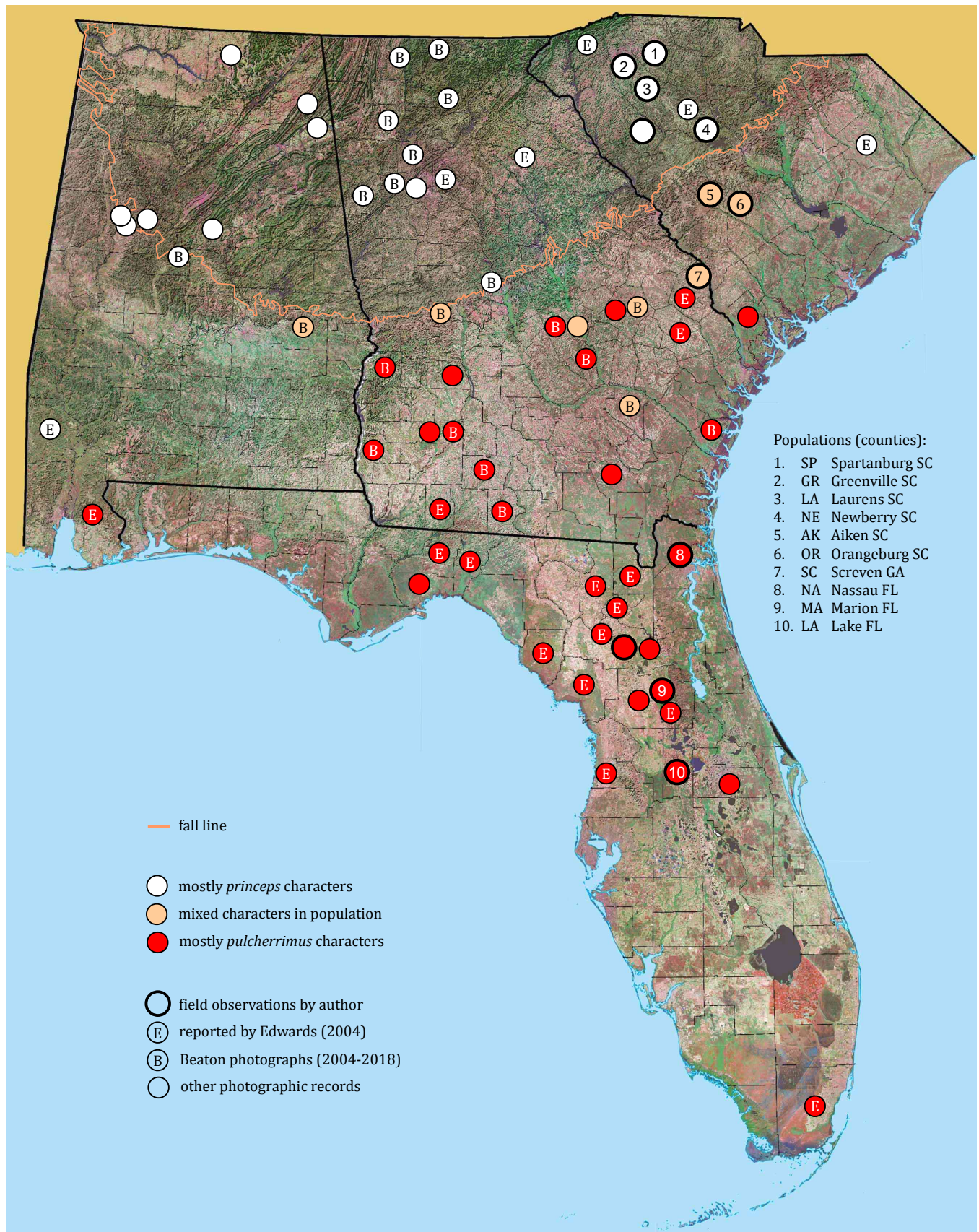


Figure 1. Distribution of the *Phidippus princeps* group in the southeastern United States. Study sites are identified with numbers (1-10). Records reported by Edwards (2004) are identified with an E. More recent records documented by Beaton are identified with a B. Other records are based on a review of photographs posted at BugGuide, FLICKR and iNaturalist sites on the internet. The background relief map was adapted from National Map/Landsat images.

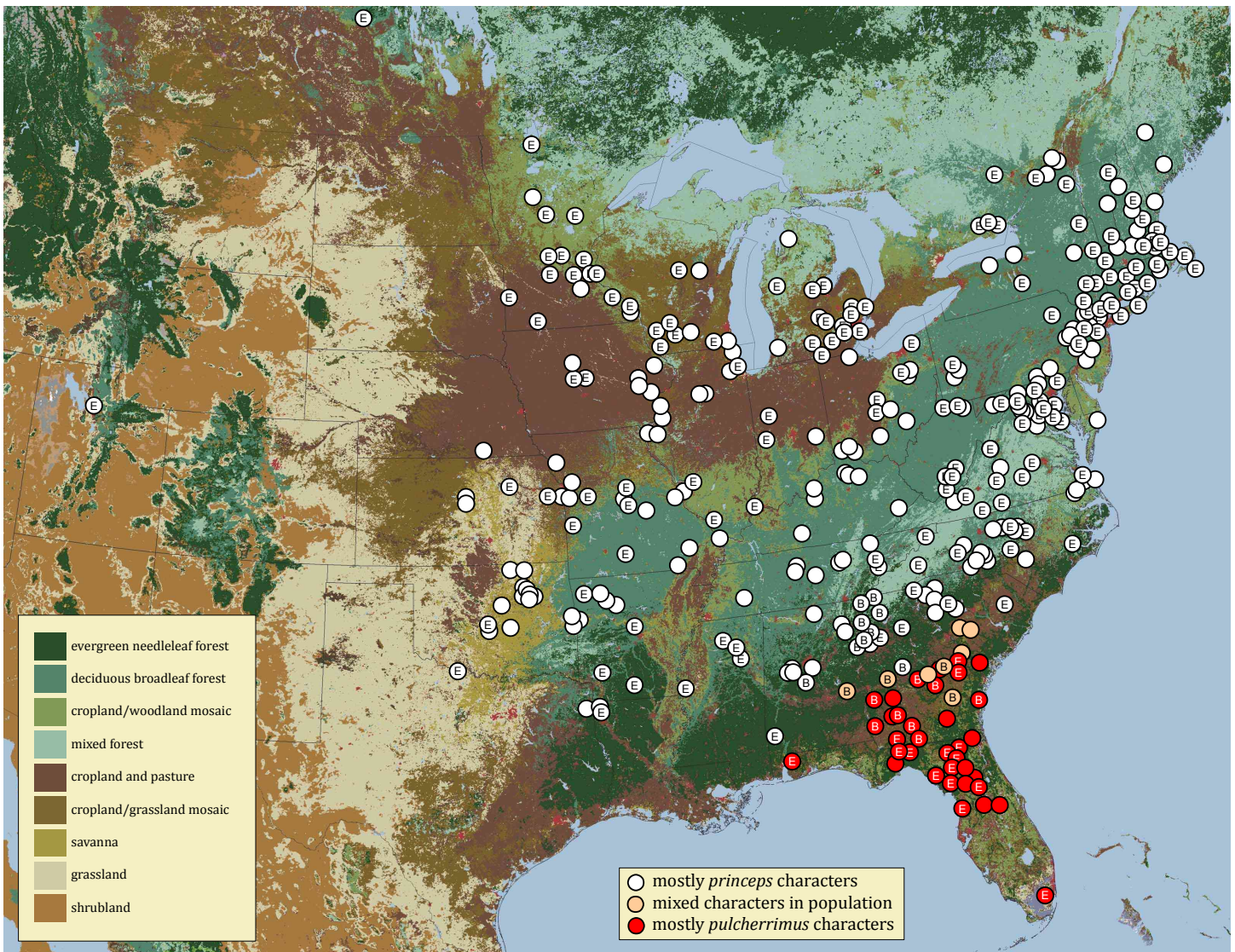


Figure 2. Distribution of the *Phidippus princeps* group in eastern North America. Sources for these records are described in Figure 1. Cedar Lake, Manitoba represents an additional record reported by Edwards (2004), to the north of this map. Note the western outlier near the Great Salt Lake of Utah. In Canada *P. princeps* has been reported from Saskatchewan, Manitoba, Ontario, Quebec and Nova Scotia (Paquin et al. 2010; Richman et al. 2012). *P. princeps* can be found in all parts of the eastern deciduous and mixed forest regions of North America, but is not known from the boreal forest to the north. *P. pulcherrimus* and many intermediate forms (or mixed populations) are mostly restricted to the southeastern coastal plain below the fall line. The background map of land usage, based on USDS 1992 1 km landcover data, was modified from images obtained with the online *National Atlas Map Maker*, no longer available.

A series of adult or immature representatives of the southeastern populations enumerated or identified with a B (based on photographs by Beaton) in Figure 1 are presented here in a series of figures (Figures 3-37). In general adults shown here represent individuals collected in the field and reared from the pre-penultimate or penultimate stages to maturity. Earlier instars were reared after successful mating of field-collected adults from the same locality.



Figure 3. Female *Phidippus princeps* collected as a penultimate (1-2) on an herbaceous plant in the deciduous woodland understory of Spartanburg County, South Carolina (locality 1), and reared to maturity (3-8). As in subsequent figures, each scale bar is 1.0 mm and identifiers in rectangles are used to associate images with respective spiders. Note the broad basal band, middorsal tract of scales, and relatively bright red-orange cover of the dorsal opisthosoma. Otherwise this is a fairly typical female *P. princeps*. 7-8, Suction (7) followed by regurgitation/maceration (8) phases of feeding.



Figure 4. Early instars of *Phidippus princeps* from Greenville County, South Carolina (locality 2). **1-6**, Emergent or instar 2 spiderlings. When placed on *Prunus* stems and leaves spiderlings sought out extrafloral nectaries (4-6). Note the uniform black color of the body and the relatively light, translucent legs and pedipalps of this stage. **7-9**, Early juvenile or instar 3. **10-12**, Juvenile or instar 4. Note the shiny gold scale cover of the carapace (10), typical of juvenile *P. princeps*.



Figure 5. Juvenile (instar 5) *Phidippus princeps* from Greenville County, South Carolina (locality 2). Juvenile *P. princeps* have flat, shiny scales on the dorsal opisthosoma like those seen in typical adult *P. pulcherrimus*.



Figure 6. Pre-penultimate (instar 6) *Phidippus princeps* from Greenville County, South Carolina (locality 2). Pre-penultimate *P. princeps* in this area can be quite dark with more scale cover over the dorsal opisthosoma, but their chelicerae are not yet iridescent.



Figure 7. Penultimate (nominally instar 7) female *Phidippus princeps* from Greenville County, South Carolina (locality 2). In this stage the face is still covered with a mask of dark red-brown scales around the anterior eyes, but the chelicerae are also iridescent as in adults. Except for one female (1-2), note the presence of distinct scale patterns on the dorsal opisthosoma, retained but not as obvious as they are in the juvenile stages.



Figure 8. Penultimate (nominally instar 7) male *Phidippus princeps* from Greenville County, South Carolina (locality 2).



Figure 9 (continued on next page). Adult female *Phidippus princeps* from Greenville County, South Carolina (locality 2). In this locality, adult females tend to have a white face, or white scales surrounding the anterior eyes. This makes the anterior eyes quite visible and most likely represents a device for intraspecific recognition or communication.





Figure 11 (continued from previous page). Adult female *Phidippus princeps* from Greenville County, South Carolina (locality 2). 31-32, Darker individual, with two pairs of posterior spots on the dorsal opisthosoma.



Figure 12. Adult female *Phidippus princeps* from Greenville County, South Carolina (locality 2). **1-5**, Ventral view of five females, showing variation in the appearance of the darker median band flanked by lighter bands. *P. pulcherrimus* females have essentially the same appearance. **6**, Detail of epigynum of female shown in (5). Here the posterior notch is semi-circular, but it can also be more shallow, angular or triangle-shaped. **8**, Detail from (7), showing grey rostrum between the chelicerae.



Figure 13. Adult male *Phidippus princeps* from Greenville County, South Carolina (locality 2). In this locality the carapace is completely black. Note the variation in scale cover of the dorsal opisthosom, from almost complete cover (3, 9, 12) to presentation of a black and red pattern (1, 5, 8). Iridescent chelicerae vary from green (2) to blue-green (11).



Figure 14. Immature *Phidippus princeps* from Laurens County, South Carolina (locality 3). 1-2, Juveniles. 3-6, Penultimate females. 7-12, Penultimate males.



Figure 15. Two adult female *Phidippus princeps* from Laurens County, South Carolina (locality 3).



Figure 16. Adult male *Phidippus princeps* from Laurens County, South Carolina (locality 3).



Figure 17. Female *Phidippus princeps* from Newberry County, South Carolina (locality 4). 1, Juvenile. 2-7, Views of adult.



Figure 18 (continued on next page). Two intermediate *Phidippus princeps-pulcherrimus* females from Aiken County, South Carolina (locality 5). 1, Pre-penultimate. 2-3, Penultimate, 4-10, Adult.



Figure 18 (continued from previous page). Two intermediate *Phidippus princeps-pulcherrimus* females from Aiken County, South Carolina (locality 5). 11-13, Penultimate. 14-21, Adult. 18, Note mantispid larva moving from spider prey to predator.

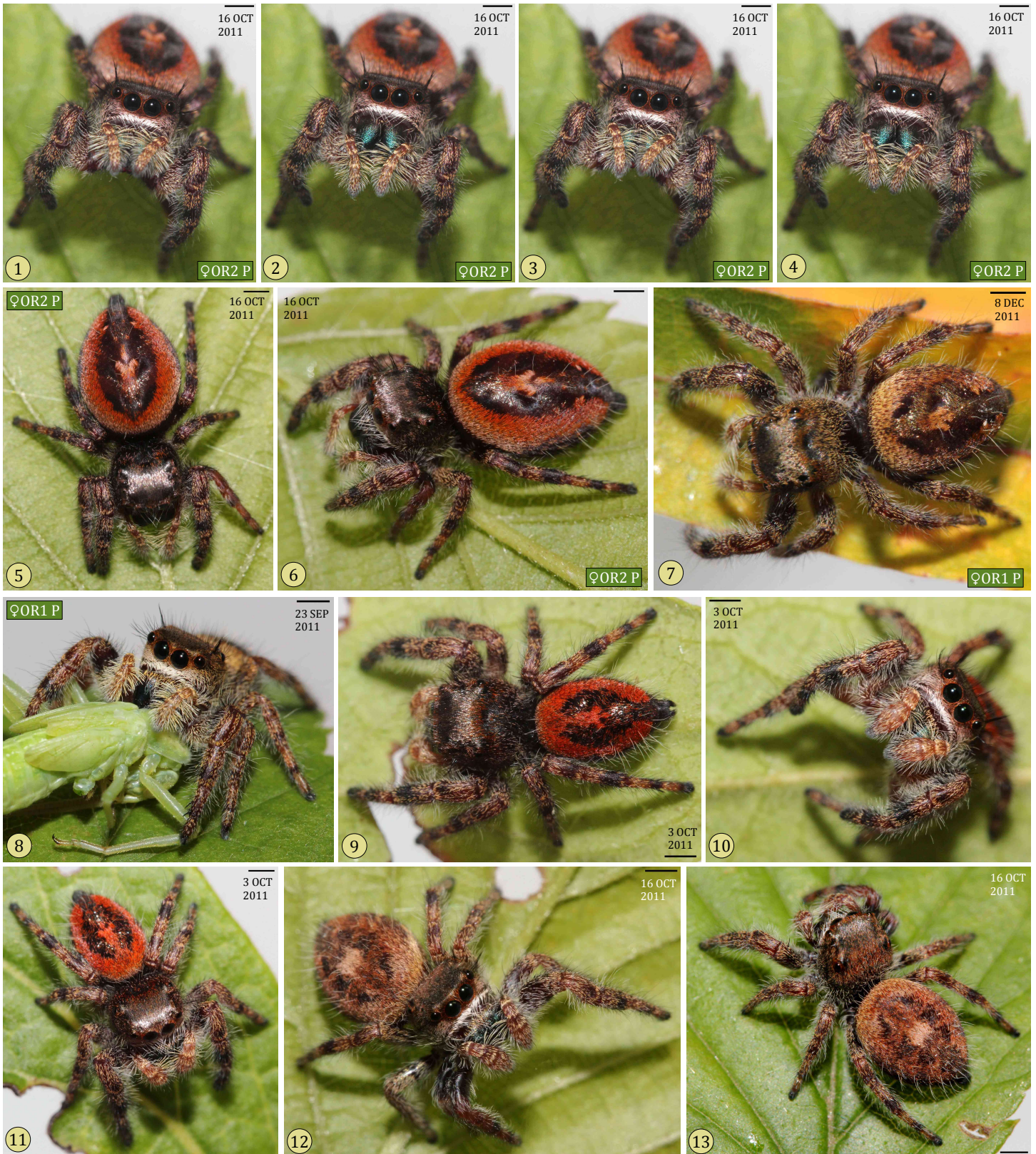


Figure 19. Penultimate intermediate *Phidippus princeps-pulcherrimus* from Orangeburg County, South Carolina (locality 6). 1-4, Sequential images of penultimate female, showing how pedipalps are moved down and up to flash the iridescent chelicerae toward the front. 5-6, Two dorsal views of penultimate female shown in (1-4). 7-8, Second penultimate female with more brown coloration. 9-11, Penultimate male. 12-13, Penultimate male with more brown coloration. Although one penultimate female (7-8) and one penultimate male (12-13) were brown, all had bright red-orange scales on the dorsal opisthosoma as adults (Figures 20-21).

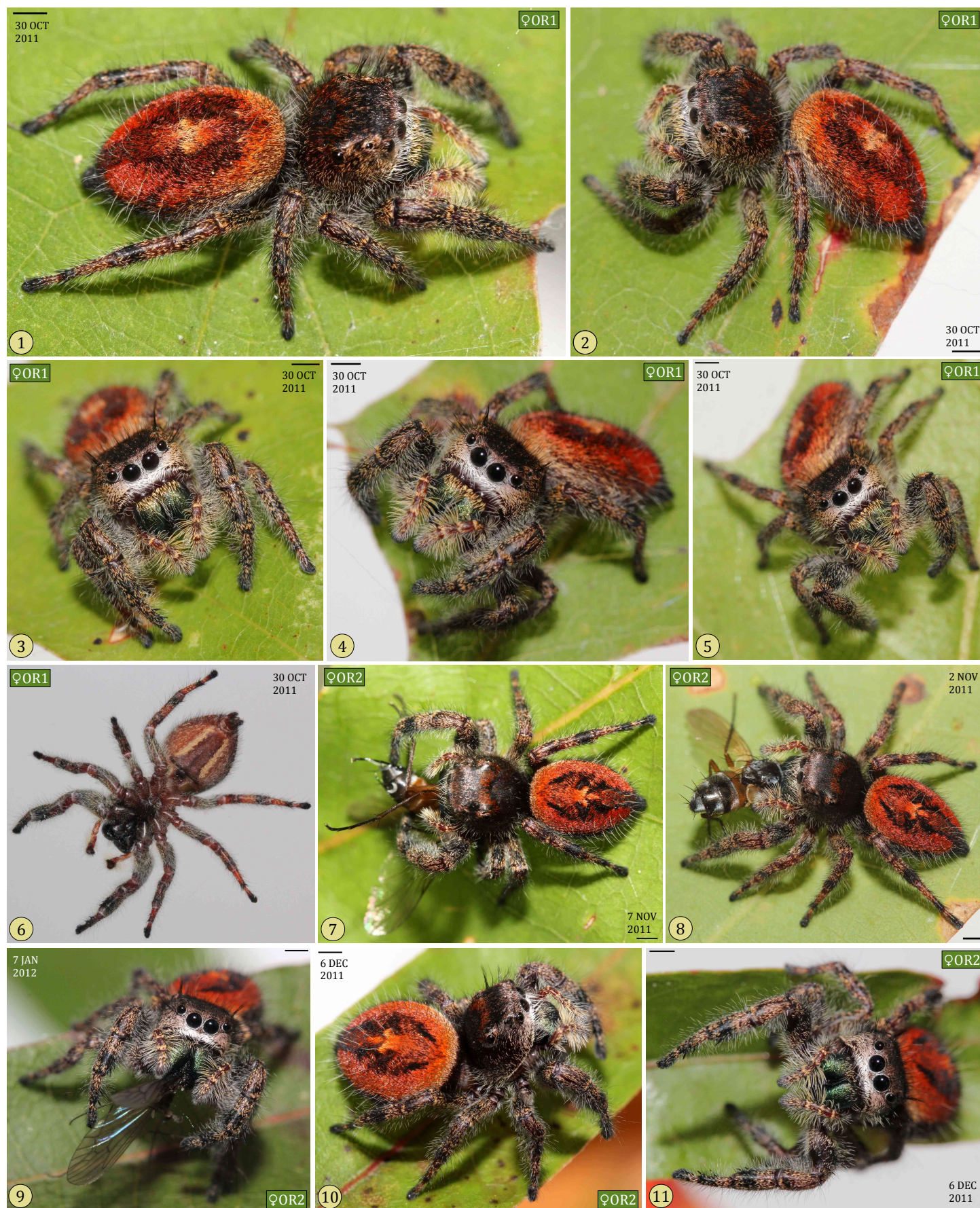


Figure 20. Adult female intermediate *Phidippus princeps-pulcherrimus* from Orangeburg County, South Carolina (locality 6).



Figure 21. Adult male intermediate *Phidippus princeps-pulcherrimus* from Orangeburg County, South Carolina (locality 6). 5-8, This male had small bands on the carapace below and behind the PLE. To the south these bands tend to be much larger in populations of *P. pulcherrimus*.



Figure 22. Emergent (instar 2) *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). **1-2**, In brood sac. **3, 8**, Some young had light-colored legs and pedipalps typical of *P. princeps*. **11-13**, Feeding at nectary when placed on a *Prunus* branch.



Figure 23. Early juvenile (instar 3, 1-8) and juvenile (instar 4, 9-15) intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). Early juveniles are primarily black with white scale patches. Juveniles were darker than typical *P. princeps*, but still had a cover of shiny scales in the eye region (13).

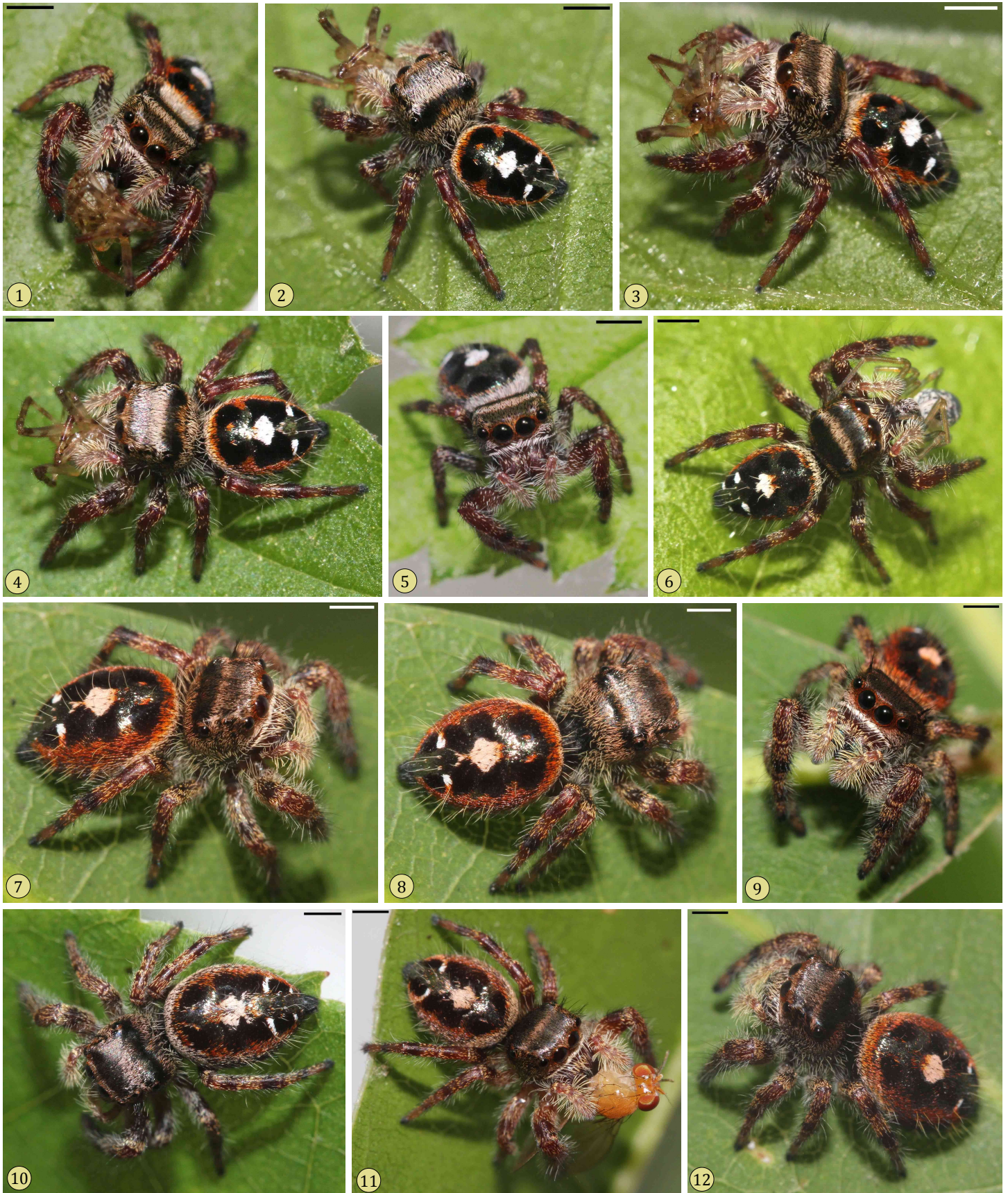


Figure 24. Juvenile (instar 5, 1-6) and pre-penultimate (instar 6, 7-12) intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). Like typical *P. pulcherrimus*, pre-penultimate spiders from this locality had iridescent chelicerae.



Figure 25. Penultimate female intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). Some penultimate females from this locality (1-2, 10-11) looked much like typical *P. pulcherrimus*. Others had more complex patterns of scale cover on the dorsal opisthosoma.



Figure 26. Penultimate male intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7).



Figure 27 (continued on next page). Adult female intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). Some females from this locality had scale patterns on the dorsal opisthosoma typical for *P. pulcherrimus* (12), but many had more complex patterns including an assortment of different scales along the middorsal tract, following the *dorsalis* pattern.

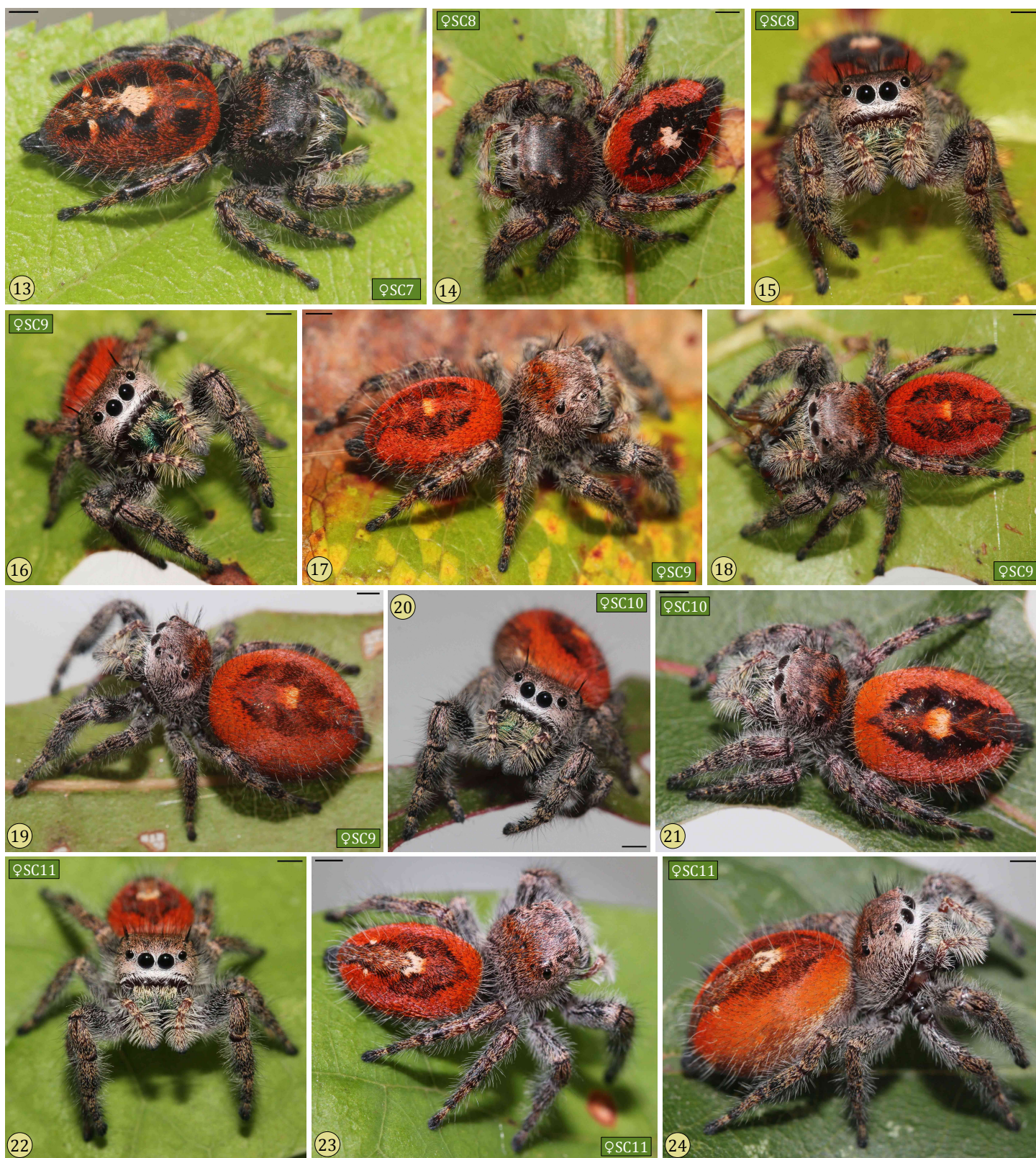


Figure 27 (continued from previous page, continued on next page). Adult female intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7).



Figure 27 (continued from previous page). Adult female intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7).



Figure 28. Ventral views of eight adult female intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7). 9-12, Detailed ventral view of epigynum for spiders shown in 5-8, respectively.



Figure 29 (continued on next page). Adult male intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7).



Figure 29 (continued from previous page). Adult male intermediate *Phidippus princeps-pulcherrimus* from Screven County, Georgia (locality 7).

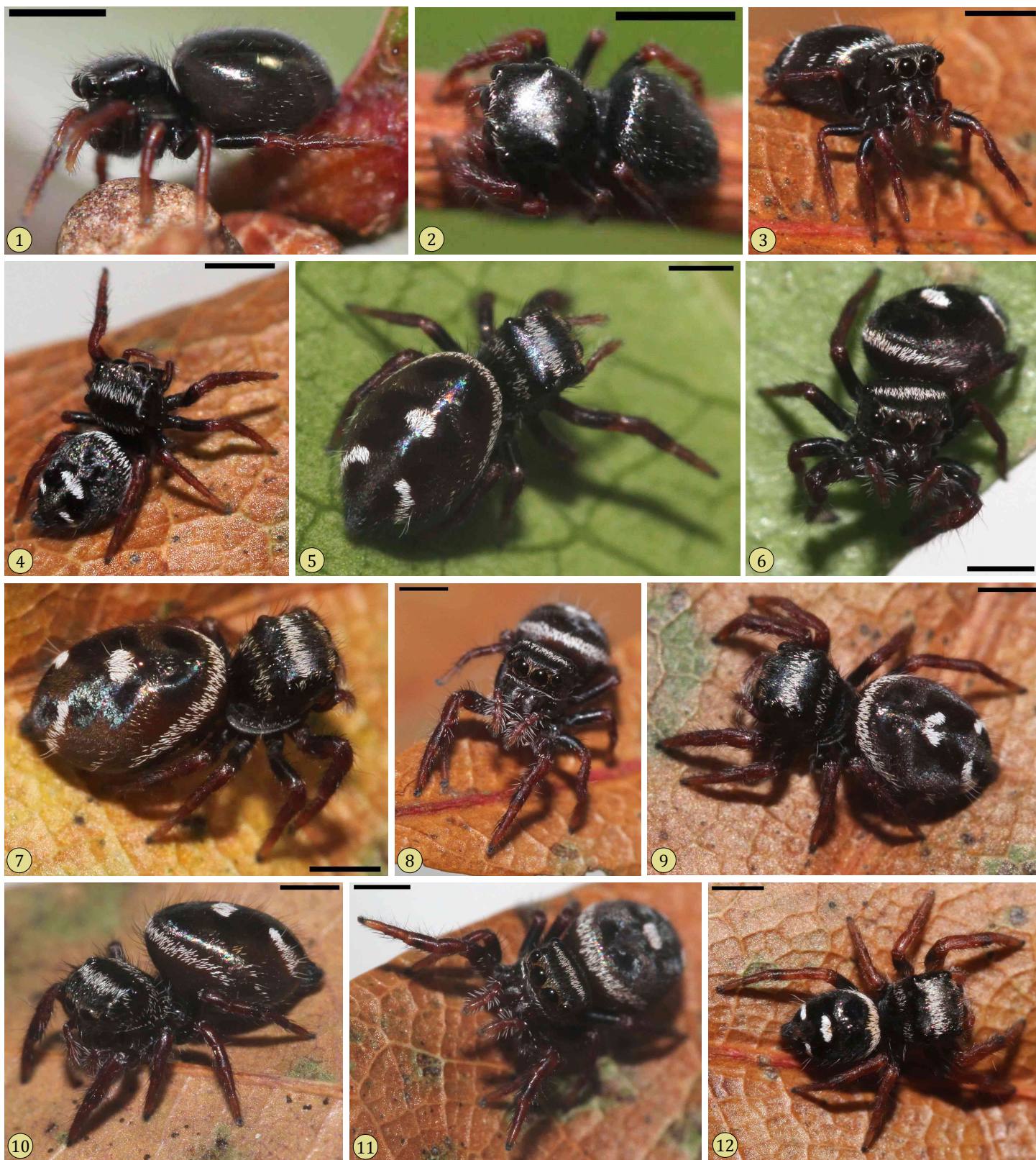


Figure 30. Emergent (instar 2, 1-2) and early juvenile (instar 3, 3-12) *Phidippus pulcherrimus* from Nassau County, Florida (locality 8).



Figure 31. Juvenile and pre-penultimate *Phidippus pulcherrimus* from Nassau County, Florida (locality 8). 1-4, Juveniles (instar 4). 5, Juvenile (instar 5). 6-12, Pre-penultimates (instar 6), with iridescent chelicerae.



Figure 32. Penultimate female (1-6) and male (7-12) *Phidippus pulcherrimus* from Nassau County, Florida (locality 8).

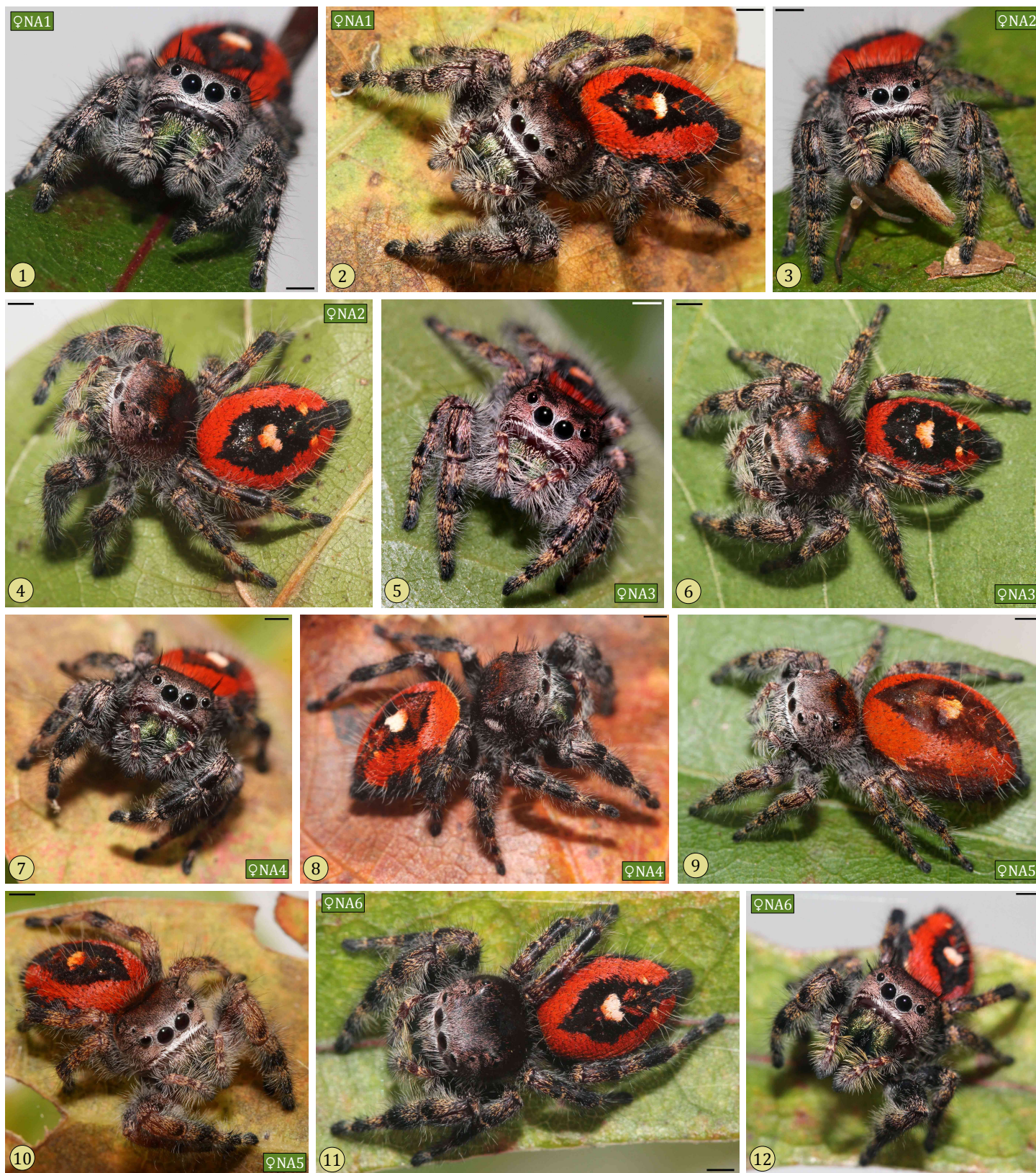


Figure 33 (continued on next page). Adult female *Phidippus pulcherrimus* from Nassau County, Florida (locality 8).

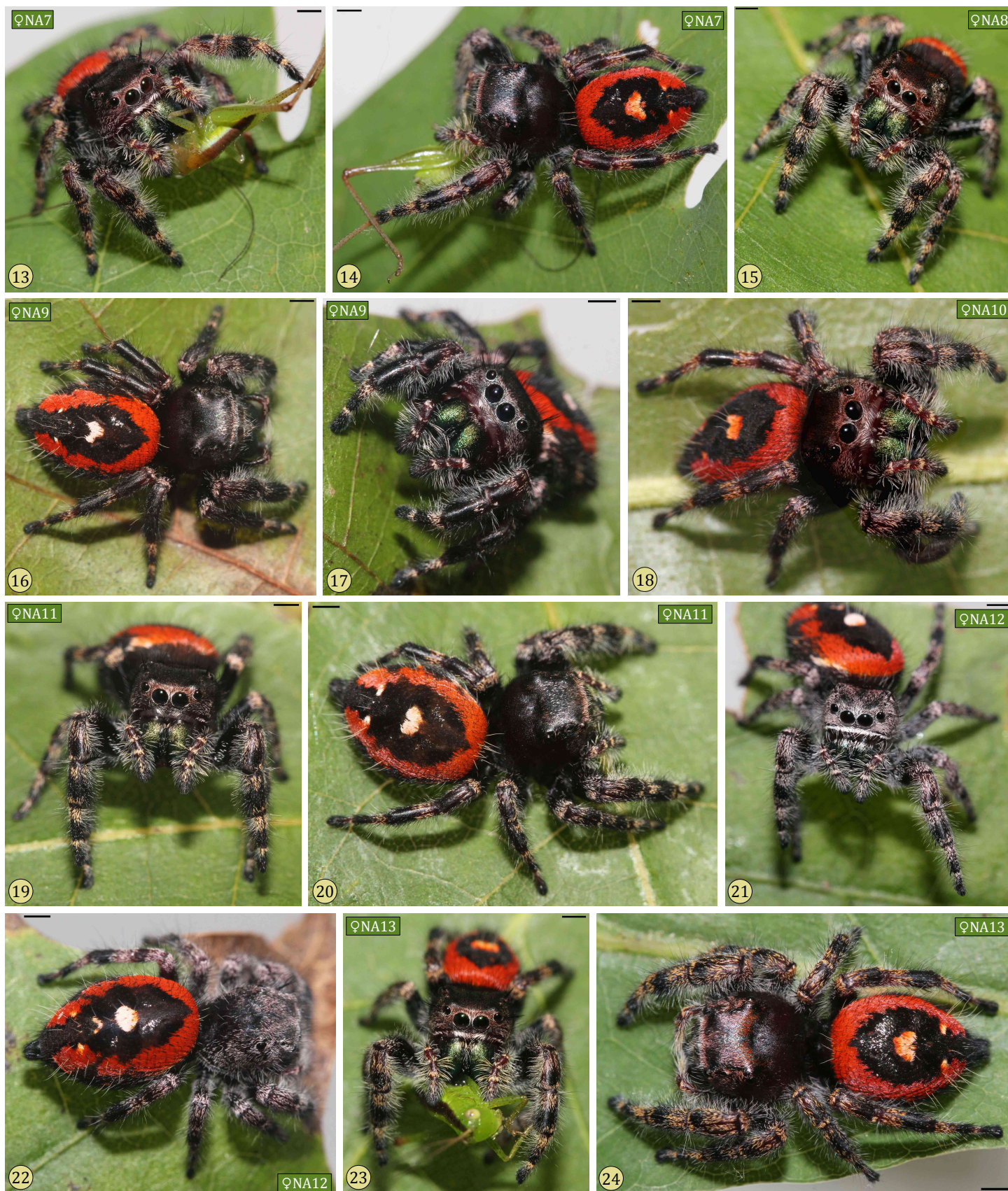


Figure 33 (continued from previous page). Adult female *Phidippus pulcherrimus* from Nassau County, Florida (locality 8).



Figure 34. Adult male *Phidippus pulcherrimus* from Nassau County, Florida (locality 8).



Figure 35. Adult female (1-6) and adult male (7-12) *Phidippus pulcherrimus* from Ocala National Forest (1978) in Marion County, Florida (locality 9).



Figure 36. Female *Phidippus pulcherrimus* from Tavares in Lake County, Florida (locality 10). **1-5**, Penultimate stage with distinct white clypeal line. **6-8**, Darker adult stage with few scales and no clypeal line on carapace.

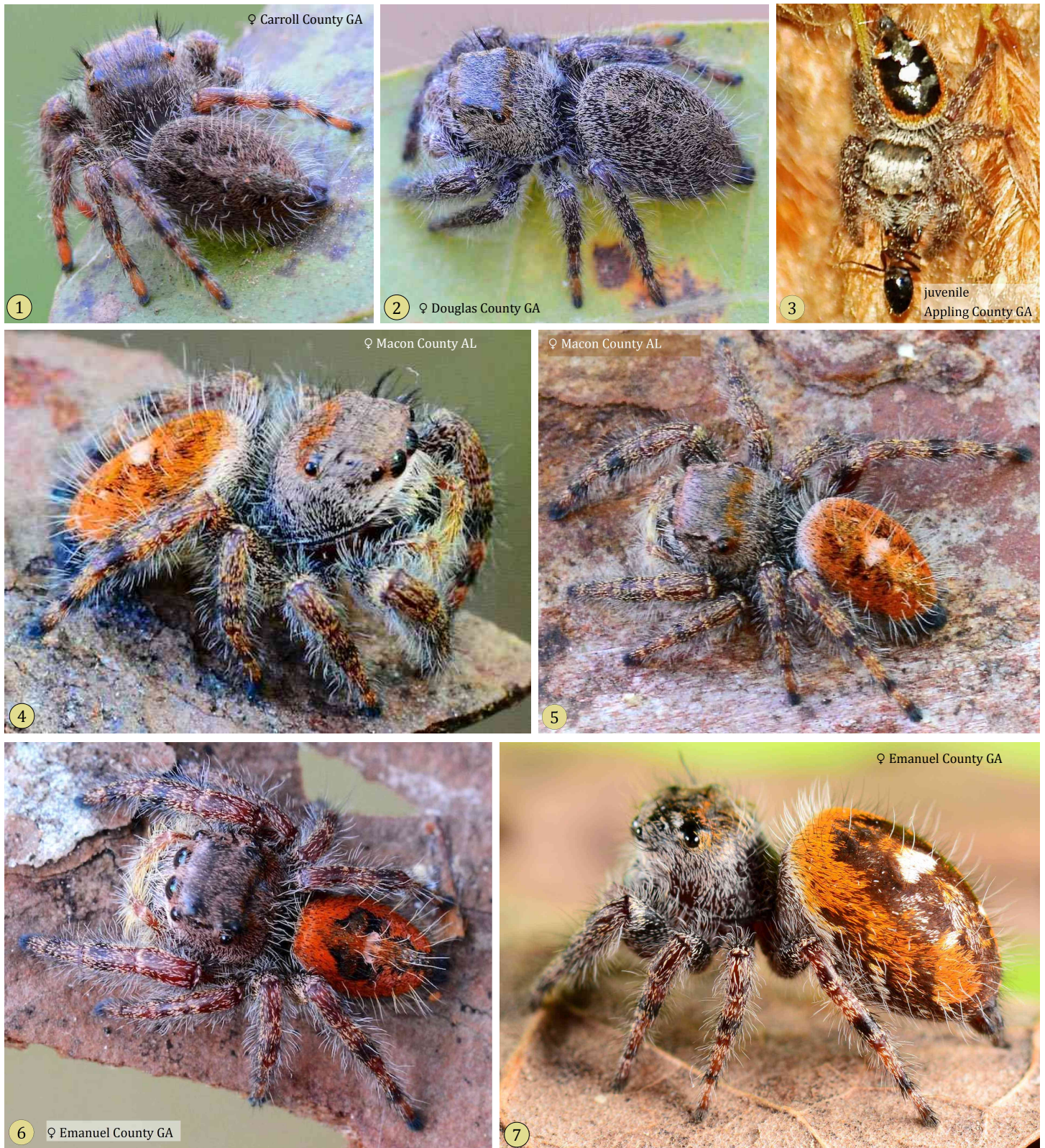


Figure 37 (continued on next page). Spiders from counties in Alabama and Georgia. 1-2, Adult female *P. princeps*. 3, Intermediate juvenile with golden carapace, feeding on captured ant. 4-7, Adult females from intermediate populations. Photos by G. Beaton, used with permission.



Figure 37 (continued from previous page). Spiders from counties in Alabama and Georgia. **8-9**, Adult females from intermediate populations. **10-12**, *P. pulcherrimus*. Photos by G. Beaton, used with permission.

Diagnostic characters. Since most individual spiders that I reared were tracked only by locality and not by individual, the exact instar could not always be determined. In these cases instar has been designated according to size and general appearance as shown in Table 1. Robertson & Stephens (2002) reared *P. princeps* from Macon County, Illinois in the laboratory and found that females needed 9 molts to attain maturity in the 10th instar. They suggested that males might mature earlier than females, by the 8th instar. I have found that southern spiders in this group of either sex can mature in the 8th instar. Actual instar count in the field may vary based on locality, hatchling size, climate and the length of each season.

Table 1. Nominal instar designations for spiders of the *Phidippus princeps* group.

instar	stage	CW mm	Greenville County, South Carolina (2)	Screven County, Georgia (7)
1	hatchling			
2	emergent	~0.8-1.0	uniform black with light appendages	uniform black with darker appendages
3	early juvenile	~1.0-1.2	four contiguous, large black spots on dorsal opisthosoma separated by paired white spots and central triangle	four contiguous, large black spots on dorsal opisthosoma separated by paired white spots and central triangle
4-5	juvenile	~1.2-1.8	dark red-brown mask around front eyes, brown scales around margins of dorsal opisthosoma	dark red-brown mask around front eyes, red-orange scales around margins of dorsal opisthosoma
6	pre-penultimate	~1.8-2.4	darker without iridescent chelicerae	darker with iridescent chelicerae
7	penultimate	~2.4-3.2	pattern of scales much like adult female except for dark mask, chelicerae iridescent	pattern of scales much like adult female except for dark mask, chelicerae iridescent
8	adult	~2.8-4.0	females with white face above white clypeal line	females with white face above white clypeal line

Drawings associated with earlier descriptions of these spiders are reproduced for reference in Figure 38.

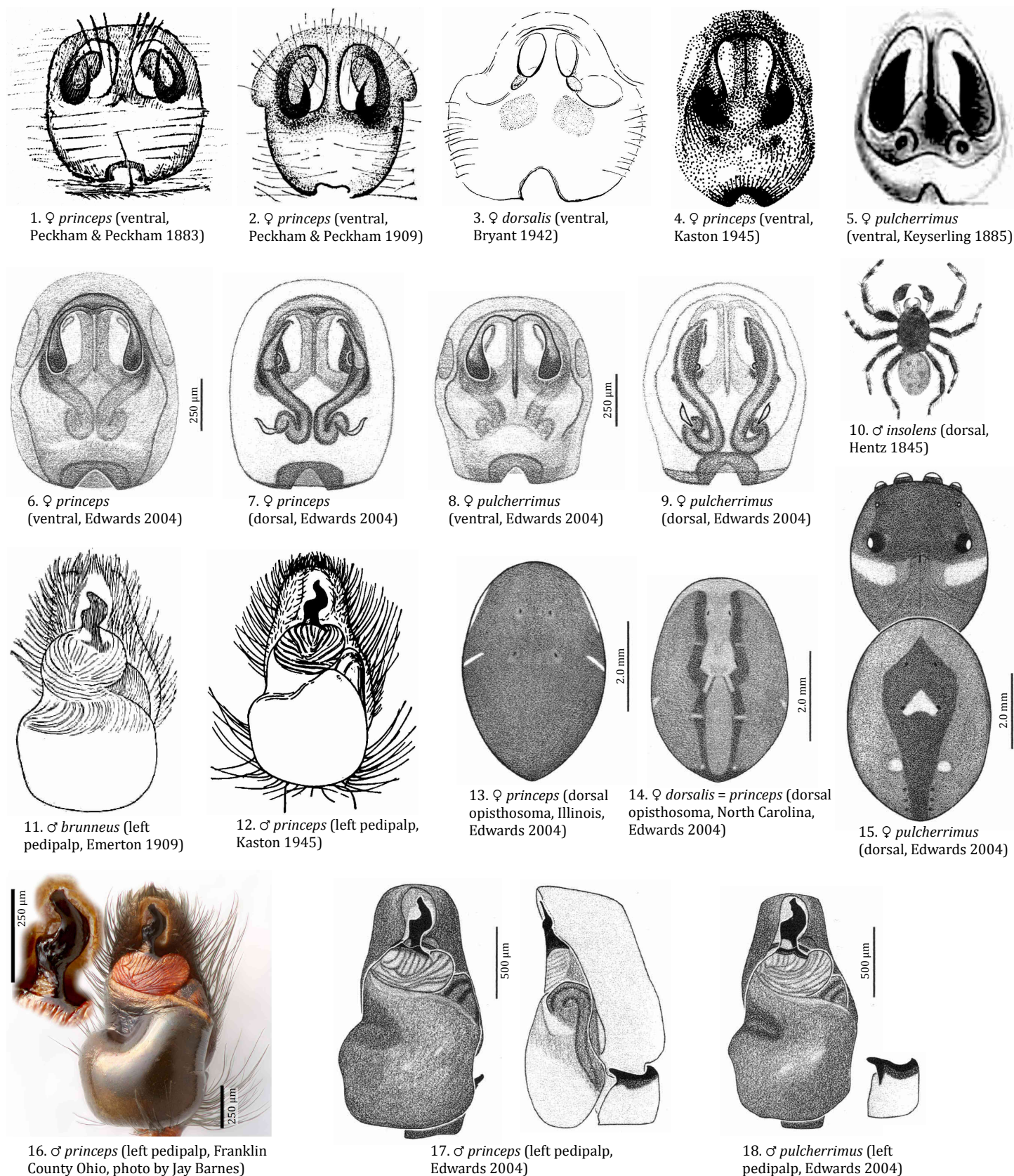


Figure 38. Illustrations published with earlier descriptions of *Phidippus princeps* and *P. pulcherrimus*. Composite photo by Jay Barnes (16) and drawings by G. B. Edwards (6-9, 13-15, 17-18) used with permission.

A comparison of characters for each southeastern locality that I have studied (1-10), mostly related to coloration and the distribution of scales, is presented in Table 3. Many of these characters, including the brown mask of juvenile spiders, the white face of adult females, and the presence of some males lacking white bands below and behind the PLE, could be found in almost all of these populations.

Table 2. Presence of diagnostic characters for the *Phidippus princeps* group by locality (1-10).

stage	character	<i>princeps</i> -like				mixed			<i>pulcherrimus</i> -like		
		1-SP	2-GR	3-LA	4-NE	5-AK	6-OR	7-SC	8-NA	9-MA	10-LA
emergent	yellow pedipalps		x					x	-		
	darker, red-brown pedipalps		-					x	x		
early juvenile	opisthosoma black with white or brown scales on margins and central white triangle, white paired posterodorsal spots		x					x	x		
	dark red-brown mask around front eyes		x		x			x	x		
juvenile	dorsal carapace covered with uniform shiny, golden scales		x		x			x	-		
	opisthosoma black with white or brown scales on margins and central white triangle, white paired posterodorsal spots		x		x			x	x		
	brown scales around margins of opisthosoma		x		x			x	x		
	red-orange scales around margins of opisthosoma		-		-			x	x		
	dark red-brown mask around front eyes		x	x				x	x		
pre-penultimate	chelicerae iridescent		-	-				x	x		
	chelicerae not iridescent		x	x				-	-		
	dorsal carapace covered with uniform shiny, golden scales		x	x		x		-	-		
	dorsal carapace covered with uniform brown scales		x	-		-		x	-		
	dorsal carapace dark and lacking scale cover		-	-		-		-	x		
	middorsal tract of pigmented scales on opisthosoma		x	-		x		-	-		
	dorsal opisthosoma black with wide margins		-	x		x		x			
	triangle (fused spots II) of lighter pigmented scales on opisthosoma		x	x		x		x	x		
penultimate	dark red-brown mask around front eyes	x	x	x		x	x	x	x		x
	line of white scales along clypeal margin	x	x	x		x	x	x	x		x
	lacking white scales along clypeal margin	-	-	-		-	-	-	x		-
	iridescent chelicerae	x	x	x		x	x	x	x		x
	dorsal carapace covered with uniform brown scales	x	x	x		x	x	x	x		x
	dorsal carapace covered with many grey to brown scales	-	x	-		-	-	x	x		-
	dorsal carapace dark and lacking scale cover	-	x	x		-	-	x	x		-
	dorsal opisthosoma covered with relatively uniform brown scales	-	x	-		-	-	-	-		-
	middorsal tract of pigmented scales on opisthosoma	x	x	x		x	x	x	x		-
	dorsal opisthosoma black with wide red-orange margins	x	-	x		x	x	x	x		x
adult ♂	triangle (fused spots II) of lighter pigmented scales on opisthosoma	x	x	x		x	x	x	x		x
	no band of white scales posterolateral to each PLE		x	x			x	x	x	-	
	distinct band of white scales posterolateral to each PLE		-	-			-	x	x	x	
	dorsal opisthosoma with fairly uniform cover of red scales		x	x			-	-	-	-	
	dorsal opisthosoma with black patterns interrupting scale cover		x	x			x	x	-	-	
	middorsal tract of pigmented scales on opisthosoma		-	-			-	x	-	-	
	dorsal opisthosoma black with wide red-orange margins		-	-			x	x	x	x	
adult ♀	triangle (fused spots II) of pigmented scales on opisthosoma		x	x			x	x	x	x	
	white face or cover of white scales around front eyes	x	x	x	x	x	x	x	x	x	-
	dark face without cover of white scales	-	-	-	-	-	-	-	x	-	x
	line of white scales along clypeal margin	x	x	x	x	x	x	x	x	x	-
	lacking white scales along clypeal margin	-	-	-	-	-	-	-	x	-	x
	dorsal carapace covered with uniform brown scales	x	x	x	x	-	-	x	-	-	-
	dorsal carapace covered with many grey to brown scales	-	x	-	-	x	x	x	x	x	-
	dorsal carapace dark and lacking scale cover	-	x	-	-	-	-	x	x	-	x
	no band of white scales posterolateral to each PLE	x	x	x	x	x	x	x	x	x	x
	distinct band of white or brown scales posterolateral to each PLE	-	-	-	-	-	-	x	x	x	-
	dorsal opisthosoma with fairly uniform cover of brown scales	-	x	x	-	-	-	-	-	-	-
	middorsal tract of pigmented scales on opisthosoma	x	x	x	x	x	x	x	-	-	-
	dorsal opisthosoma black with wide red-orange margins	-	-	-	x	x	x	x	x	x	x
	triangle (fused spots II) of pigmented scales on opisthosoma	x	x	x	x	x	x	x	x	x	x
	posterodorsal opisthosoma with one or two lighter, paired spots	x	x	x	x	-	-	x	x	x	-

Diagnosis of spiders in the *Phidippus princeps* group has relied primarily on coloration, scale patterns and genitalia. The distinctive female epigynum and male pedipalp have often been used to identify members of the *princeps* group (Kaston 1945, 1948; Edwards 1980, 2004; Paquin & Dupérré 2003), but only Edwards (1980, 2004) has compared the genitalia of both *P. princeps* and *P. pulcherrimus*. Even without a study of variation within and between populations, the described genitalia of both sexes are quite similar

and appear to pose no barrier to mating. Some *P. princeps* males (Figure 38:16) may have an apex of the embolus that is just as robust as that associated with male *P. pulcherrimus*. Edwards (1980) was able to mate the two species. In laboratory trials that I will not detail here I have found that some males and females nominally assigned to either species will court and mate with either species. This is only an anecdotal observation, but it appears that at least some female *P. princeps* find the larger male *P. pulcherrimus* to be particularly attractive. Males and females from intermediate (hybrid zone) localities successfully mated and produced broods with fertile offspring that I reared to the adult stage. No significant mortality of either eggs or juveniles was observed with respect to these broods.

To the casual observer the bright, aposematic colors of *P. pulcherrimus* clearly distinguish these from the dull and cryptic colors of northern *P. princeps*. However, as shown here, there are many intermediate forms that can be found far beyond the *hybridization zone* centered just below the southeastern fall line. These include variations on the *dorsalis* form (Edwards 2004) bearing a middorsal line of scales on the opisthosoma that can be found in individuals associated with both *P. princeps* and *P. pulcherrimus* populations. Comparison of juvenile with adult forms shows that while typical *P. pulcherrimus* retain a juvenile pattern of dorsal opisthosoma scales as they mature, this juvenile pattern tends to be replaced and obscured by a dense growth of relatively uniform or cryptic scales in the later instars of *P. princeps*.

Habitat. Juvenile to penultimate *Phidippus princeps* can be found living on herbaceous plants, shrubs, or young pine trees in open woodland or old fields, particularly in relatively undisturbed old fields or regrowth areas that border mature woodland (Edwards 1980, 2004; Roach & Edwards 1984; Roach 1988; Baker 2007; Stankowich 2009; Sourakov 2013; Hill 2016). In the southeast I have been most successful in finding these spiders, as well as *princeps-pulcherrimus* intermediates, on herbs in infrequently cleared utility corridors bordering mature forest. I have also seen dense populations of *P. princeps* in the north (Minnesota and New York) in old fields or prairie far removed from forest, in which large shrubs or young trees were present. In field trials *P. princeps* were found to selectively move toward taller, greener or more grass-like targets through vegetated corridors rather than over bare ground (Baker 2007; Baker et al. 2009). Juveniles mature in the late summer months, in the old field habitat occupied by adult female *P. clarus* (See Hill 2014), which they resemble (Roach & Edwards 1984; personal observations). It is possible that juvenile *P. princeps* gain some advantage during their juvenile instars through this kind of mimicry. We know little to nothing about where *P. princeps* overwinter and rear their young. I have observed pre-penultimate or penultimate *P. princeps* looking toward nearby tree trunks and then moving from herbs to those trunks (Hill 2010a). It is quite possible that the association of this species with mature forest or at least shrubs and young trees is related to the fact that they nest in these places, away from the herbaceous plants that they inhabit in their juvenile stages.

P. pulcherrimus immatures are also inhabitants of the open woodland understory and can also be found on shrubs in old fields or other transitional (field to forest) habitats in the southeast (Edwards 1980, 2004). They can often be found in large numbers on grass and herbaceous plants near pine flatwoods in Florida in the late summer or autumn months (Edwards 1980; personal observations). As with *P. princeps*, we know very little about their oviposition and brooding sites. However Edwards (1980, 1990) reported that Jon Reiskind found one female with her egg sac in a rolled sweet gum (*Liquidambar styraciflua*) leaf. This supports the hypothesis that *princeps* group spiders, unlike *P. clarus* that remain in the lower layer of herbaceous plants (Hill 2014), leave these plants to overwinter and to nest in trees.

Nesting. Immature spiders in the *Phidippus princeps* group construct flattened, tubular nests between leaves and stems of herbaceous plants, often near the top of these plants (Hill 1977b; Edwards 1980; Figure 39). Nests have 2-4 flattened entrances that can be opened and closed.



Figure 39. Nests constructed by *Phidippus princeps* (1-6, Greenville County, 7, Laurens County, both South Carolina) and a *princeps-pulcherrimus* intermediate in Orangeburg County, South Carolina (8-9). 1, 4, 6, 7, Arrows point to nest entrances. 2-3, Two views showing spider looking out of each entrance. 6, Detail of (5), nest with three entrances. 9, Detail of (8).

I have also seen an immature *P. princeps* nest with three entrances suspended on silk lines between herbaceous plants in woodland understory of Greenville County, South Carolina. In Tompkins County, New York I found many immature *P. princeps* nesting in the dry umbels of herbaceous plants in an open field. Hoeffler & Jakob (2006) also reported that the umbels of Queen Anne's Lace (*Daucis carota*) were a preferred site for nesting by *P. princeps*.

Nest site fidelity. Edwards (1980) described how *P. pulcherrimus* made short hunting forays and then returned to their nests. In Hennepin County, Minnesota, I once observed an immature *P. princeps* moving directly over a distance of more than 40 cm to reach its nest late in the day (Hill 1977b). In Greenville County, South Carolina I also observed an immature *P. princeps* carrying a captured moth down a stem and then over to a nearby plant where its nest was concealed, covering a total distance of more than 50 cm.

Phenology. Seasonal activity of northern and southern populations must vary as the growing season in the subtropical southeast can be more than twice as long as the growing season far to the north. However longer daylight hours in the north can compensate for this somewhat and it appears that both *P. princeps* and *P. pulcherrimus* follow an annual life cycle. In South Carolina I have found abundant juvenile instars for both *P. princeps* and intermediate forms from mid- to late summer, followed by the pre-penultimate and penultimate stages in October. Kaston (1948) found that *P. princeps* in Connecticut mature from late April to early May, with adults living at least until July. Edwards (1980, 1990, 2004) reported that North Carolina *P. princeps* mature from April to June and lay eggs from May to July, while Florida *P. pulcherrimus* mature from March to April and lay eggs from April to July. The earlier maturation of *P. pulcherrimus* in Florida can be associated with an earlier spring season there. In South Carolina, Roach (1988) described an even earlier maturation for *P. princeps*, with eggs laid from February to April and dispersal of emergent instars between 9 March and 10 July. Both species appear to share the same temporal niche, overwintering in the late stages of development to mature in the spring.

In the laboratory Robertson & Stephens (2002) reported three successive clutches for each *P. princeps* female, averaging 63 eggs for the first clutch and then 37 to 16 eggs in subsequent clutches. Kaston (1948) counted two clutches for Connecticut *P. princeps*, one of 43 eggs and the second of 115 eggs. Edwards (1980) found an average of 59 and a maximum of 61 eggs for each brood of *P. pulcherrimus*. Population density for these spiders can be quite high for the juvenile stages, although Edwards (1980) reported a significant drop in Florida *P. pulcherrimus* after instar 4. Baker (2007) noted that the population density of *P. princeps* in western Massachusetts can be as high as 3-5/m².

Predation. Spiders of the *Phidippus princeps* group feed on many different prey in the laboratory (Figures 40-45). They are known as ambush predators that face downward on stems of herbaceous plants as they watch for prey (Hill 1977b, 2010a; Edwards 1980, 1990). They will often wipe insects that secrete noxious chemicals against a leaf until those chemicals have dissipated. They reject toxic milkweed bugs (*Oncopeltus fasciatus*) that have fed on milkweed (*Asclepias*) on contact, and can learn to avoid these aposematic insects for at least several hours (Hill 2014), but this avoidance appears to be lost with a change in location or context (Skow & Jakob 2006). Jakob et al. (2008) also found that some individuals were skilled at associating prey locations with either red or blue colors. Long et al. (2012) found that avoidance of toxic fireflies (*Photuris*) by *P. princeps* could be associated with a flashing LED, suggesting that these spiders can learn to associate the flashing of fireflies with their unpalatability. Both *P. princeps* and *P. pulcherrimus* readily find and navigate detours to reach sighted prey (Hill 1977b, 2010a), and adjust both the relative direction and velocity of their jumps to reach that prey with their fangs and outstretched legs (Hill 2006a, 2010b, 2018). I have also seen *P. princeps* attempting to intercept a running ant, and conducting a tactile exploration of flower heads with their front legs (Hill 1977b).



Figure 40. Staged encounters with prey by *Phidippus princeps* in Greenville County, South Carolina. Spiders were placed with prey on plants in containers. **1-2**, Adult female preparing to jump on a nearby spider (1), and after capture of this spider (2). **3-5**, Adult females feeding on captured spiders. **6**, Adult female feeding on a captured Elephant Mosquito (*Toxorhynchites rutilus*). **7**, Juvenile feeding on a spider. **8**, Juvenile feeding on a Red-banded Leafhopper (*Graphocephala coccinea*). **9**, Adult female watching a pisaurid spider (*Pisaurina mira*). This spider was not attacked. **10**, Adult female watching a snout beetle that it did not attack.

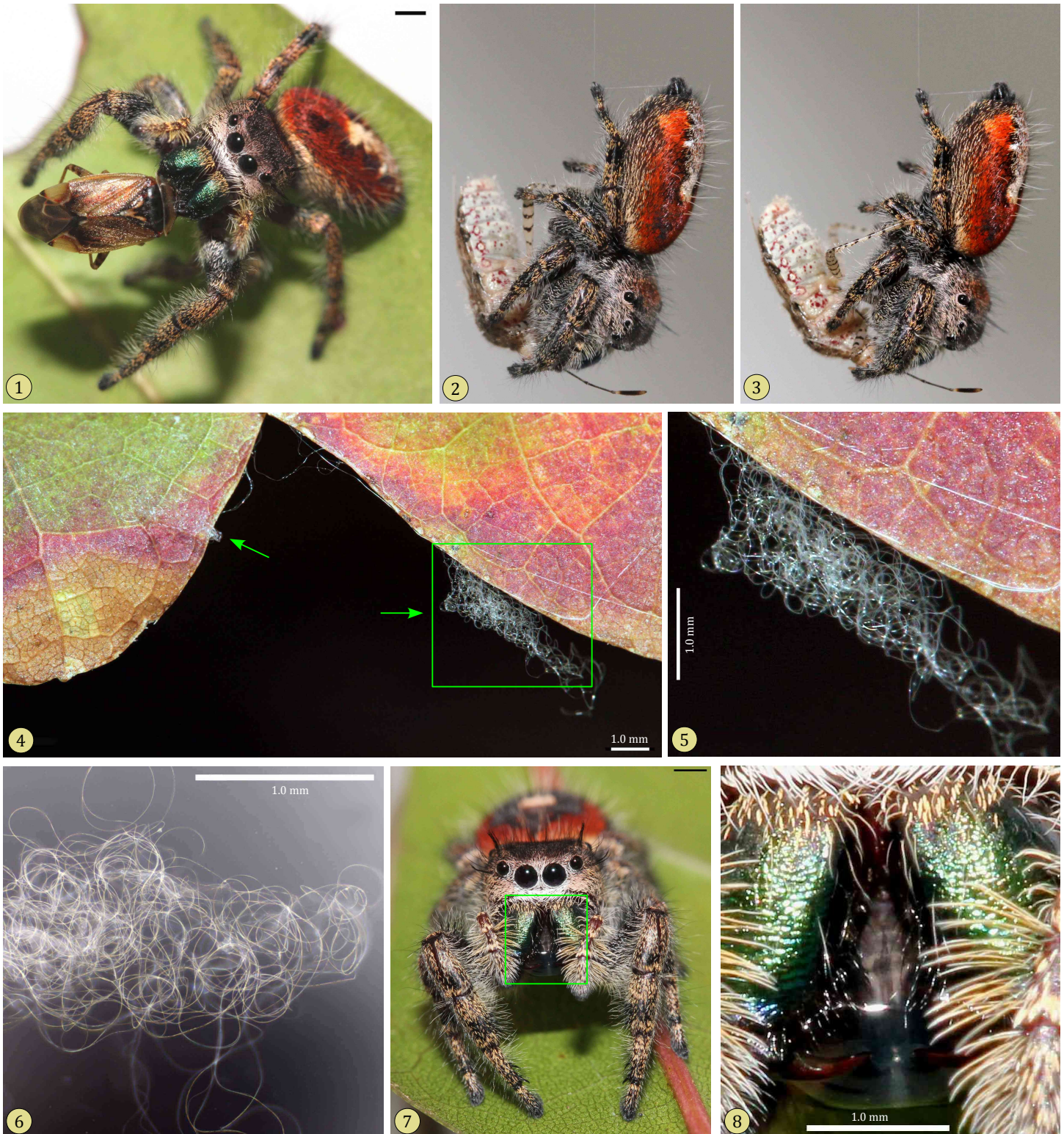


Figure 41. Behavior of adult female *princeps-pulcherrimus* intermediates from Screven County, Georgia, in the laboratory. **1**, Pedipalps and legs I were held to the sides until irritating compounds released by this heteropteran dispersed after the bug was rubbed against a leaf. Many heteropterans release a mixture of aldehydes and other volatile compounds (source of the distinctive "bug" odor) when attacked (Aldrich 1988). **2-3**, Two views of a spider feeding on a captured heteropteran while suspended on her dragline. The dragline was held with claws of right leg IV, stabilizing this spider as she fed. **4**, View from above of two tufts of wound dragline silk discarded by a spider after she jumped from and then climbed back up to respective leaves. When a salticid climbs a dragline, that dragline is wound up as shown here, perhaps with assistance of the toothed serrula that lines the outer margin of each endite. **5-6**, Detailed views of wound silk from tuft shown in (4, inset). **7-8**, Sometimes spiders regurgitate fluid after feeding, perhaps to clean the mouthparts. Up close (8) the grey rostrum can be seen.



Figure 42. Results of staged encounters between *Phidippus pulcherrimus* from Nassau County, Florida, and insect or spider prey. **1**, Adult male rubbing a Buffalo Treehopper (*Stictocephala bisonia*) against a leaf to remove defensive chemicals. **2-4**, Adult female feeding on a captured heteropteran. In a closer view (**3**) the grey rostrum of this spider can be seen between the chelicerae. **5**, Adult female feeding on a pisaurid spider (*Pisaurina*). **6**, Adult male feeding on an oxyopid spider (*Oxyopes*).

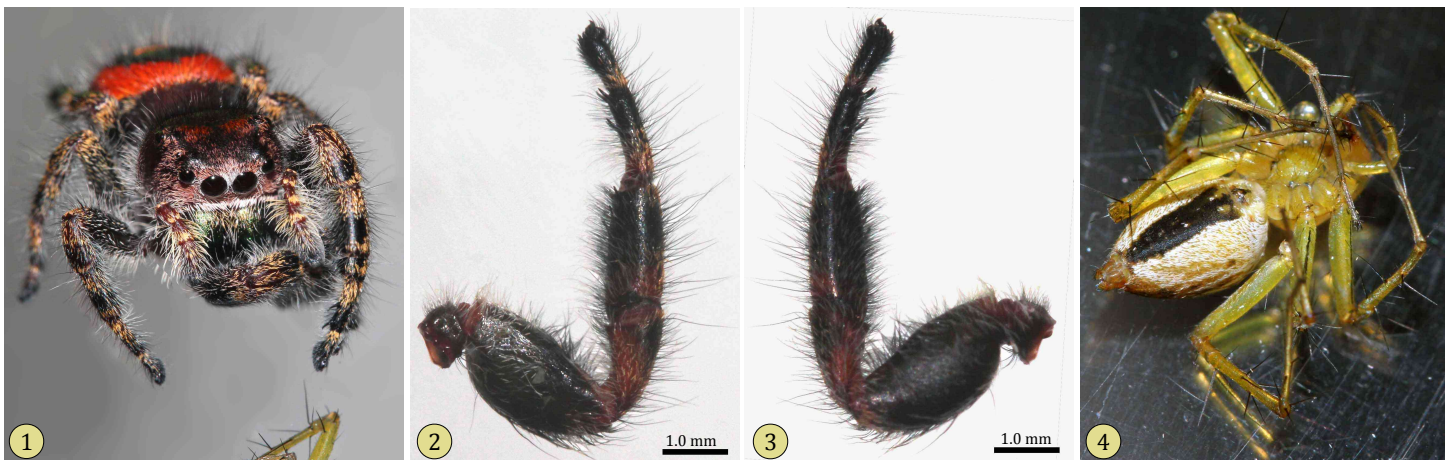


Figure 43. Autophagy after a staged encounter between an oxyopid spider (*Oxyopes*) and an adult female *Phidippus pulcherrimus* from Nassau County, Florida. **1**, Female *P. pulcherrimus* feeding on her own left leg I (autophagy) after removing it (auto-amputation) when it was injured during an attack on an adult female *Oxyopes*. **2-3**, Prolateral (**2**) and retrolateral (**3**) views of the amputated leg, showing amputation proximal to the trochanter. **4**, This adult female *Oxyopes* was killed in the attack.



Figure 44. Feeding by an adult female *Phidippus pulcherrimus* from Tavares in Lake County, Florida. All encounters with prey shown here were staged in the laboratory. **1, 5-6,** Feeding on brachyceran flies. **2-3,** Feeding on a sawfly (Hymenoptera: Symphyta). This sawfly buzzed or vibrated loudly when captured but that did not deter the spider. **4,** Feeding on a mayfly (Ephemeroptera). **7,** Feeding on a bee. **8,** Feeding on a spider. **9,** Feeding on a caterpillar.

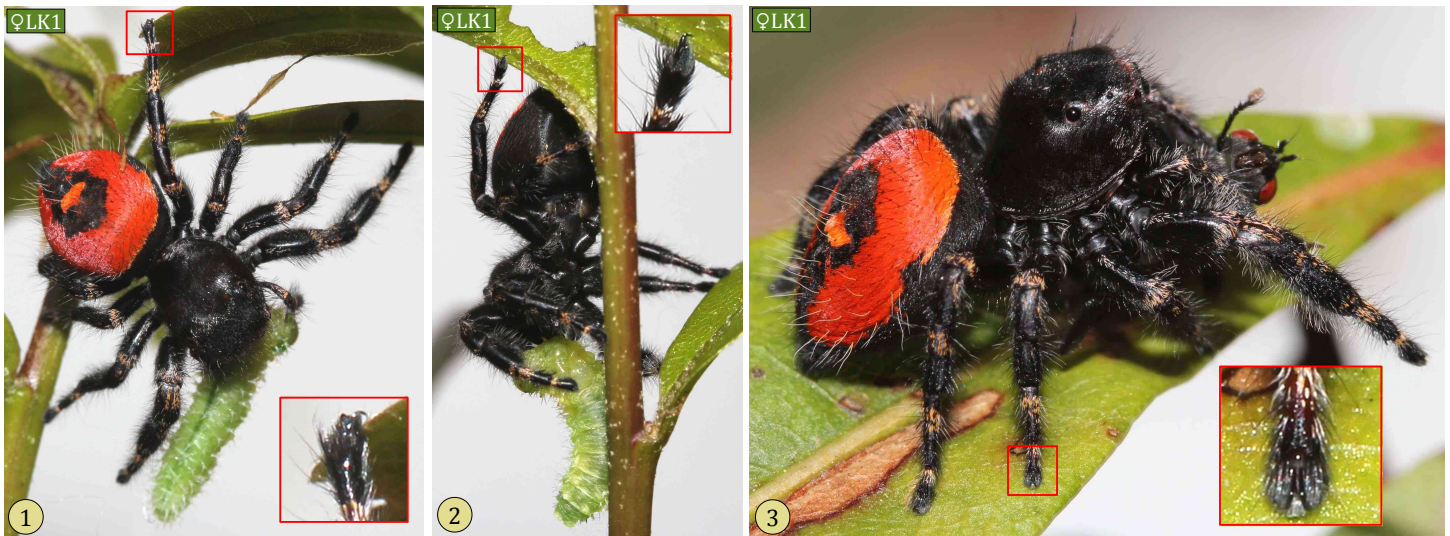


Figure 45. Feeding by an adult female *Phidippus pulcherrimus* from Tavares in Lake County, Florida, after staged encounters. **1-2**, Two views with inset detail showing how the claws of left leg IV were used to suspend this spider from a leaf while feeding on a caterpillar. **3**, On top of a flat surface the claws can be retracted and the footpads extended as shown in the inset detail of right leg III. This spider was feeding on a brachyceran fly.

My field observations in Greenville County, South Carolina, suggest that small moths and conspecific spiders are frequent prey of immature *Phidippus princeps*. Sourakov (2013) staged encounters between the Red-banded Hairstreak (*Calycopis cecrops*) and *P. pulcherrimus*, resulting in unsuccessful attacks by this spider aimed at the tailed hind wings (or false head) of these butterflies (Figure 46), although attacks on moths of comparable size were invariably successful. Like *P. pulcherrimus*, *C. cecrops* is a common inhabitant of the forest understory in the southeastern United States.

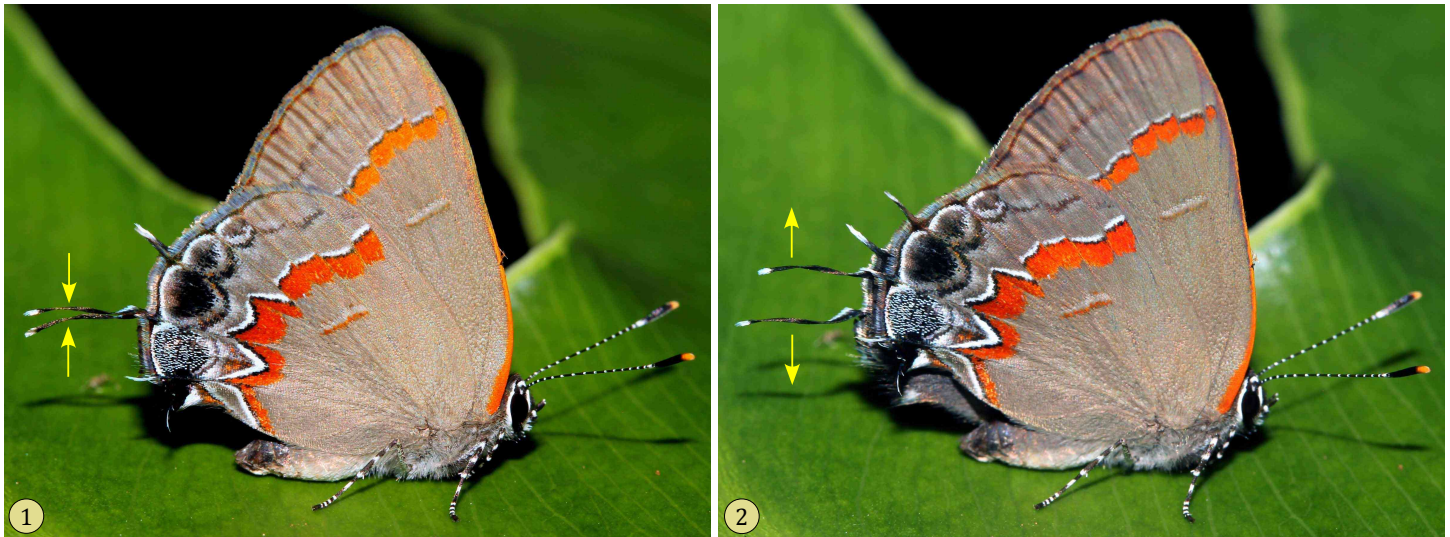


Figure 46. Two views of a *Calycopis cecrops* on a leaf in southern Greenville County, South Carolina (17 August 2017). Alternating up and down movement of the tailed hind wings (arrows) is almost continuous when these lycaenid butterflies are resting on plants, leading salticids like *P. pulcherrimus* to attack the wrong end (Sourakov 2013). These butterflies are often found with damaged hind wings.

In Greenville County, South Carolina, I have observed two instances of predation by *Phidippus princeps* that suggest a much greater predatory versatility for these spiders. In the first instance I found a late immature (instar 5-7) *P. princeps* holding a leafhopper but also trapped in the orb web of a much larger araneid (most likely *Acanthepeira* sp.) on a small tree in an open field. Without dropping the leafhopper, this *P. princeps* fought off several approaches by the resident araneid by batting it with both legs I until able to use its mouthparts to cut itself free of the adhesive silk of the orb web and drop to the ground. In the second instance I found a penultimate *P. princeps* in a clearing along the margin of a mature forest, in the sunshine on top of an upper leaf of an herbaceous plant. This *P. princeps* was alternately macerating a mass of small flies that it had captured and rapidly flicking its pedipalps up and down to flash its iridescent green chelicerae toward the front (See Figure 19:1-4). As I watched, I saw this spider capture two more small flies in succession as they approached, both added to the mass that it was feeding upon.

Courtship and mating (Figures 47-55). Courtship in the *Phidippus princeps* group is relatively simple and follows a pattern seen in many *Phidippus* species. During courtship display a male faces a potential mate, holding each pedipalp to the side to expose the iridescent front surface of the chelicerae in the direction of the female. At a distance legs I are extended to either side, maximizing their width as seen by the female. As a male approaches a female legs I are brought together facing toward the front, curved with the tarsi of the two legs I closer together than the patellae. In the final approach legs I are brought even closer together and extended forward to touch the top of the carapace of the female. As they approach males generally step from side to side but the extent to which they do this, and the duration of courtship activity, appears to depend not only on the ability of vegetation to support lateral movement but also on the response of a female. A responsive female may advance slightly toward a courting male or rotate her opisthosoma to one side. Males seem to advance quickly once females stop turning to follow their side-to-side movement.

The courtship of *P. princeps*, *P. pulcherrimus*, and intermediate forms follows essentially the same course. I have not recorded details of the flicking of legs I or the movement of pedipalps during these courtship displays, but Edwards (1980) described a double flick of legs I and pedipalp movement during each cycle of advancement toward a female. According to Edwards *P. princeps* males hold their legs higher and also flick these with a greater amplitude as they advance than do male *P. pulcherrimus*. In an earlier paper (Hill 1977a) I described the manner in which northern (Hennepin County, Minnesota) male *P. princeps* defended themselves with legs I from attacks by aggressive females, and the general lack of success by male *P. princeps* that displayed during encounters staged in the open. At the same time male *P. princeps* males were almost always successful when they entered the resting sac of a female to cohabit, something that could continue for several days. I have generally considered northern *P. princeps* to be relatively dangerous to conspecific males, but this might relate to the smaller relative size of northern males that may mature earlier than females (Robertson & Stephens 2002), a tendency of *P. princeps* living in dense populations to prey on conspecifics, or simply the fact that a long over-wintering season gives northern *P. princeps* males a greater opportunity to cohabit with females. Any of these factors may have a basis in diverging genes as a result of selective pressures that vary throughout the range of the species.

Agonistic behavior. Agonistic encounters between males in either species resemble those that I have seen in other species of *Phidippus* (e.g., in *P. clarus*, Hill 2014). Staged encounters between males (Figures 56-57) resulted in an initial stage of display in which males reared up and extended their pedipalps even further to either side than they do in courtship, rotating each paturon laterally to expand the width of the chelicerae as viewed from the front. This often escalated to extension of the fangs and a closer approach with legs I extended fully to the sides, or even to dangerous grappling that included leg contact.



Figure 47. Courtship by *Phidippus princeps* from Greenville County, South Carolina. Courtship was staged by placing males and females near each other on plants taken into the laboratory. **1-2, 4,** Males displaying to distant females with outstretched legs I. **3,** Composite image showing three sequential positions (1-3) of a male and female. The female turned in place to follow movement of the male. **5,** Final approach with legs I extended to the front. **6-7,** Sequential positions during courtship. **8-9,** Sequential images of final approach and contact with a receptive female.



Figure 48. Courtship by *Phidippus princeps* from Laurens County, South Carolina. **1**, Composite showing two sequential positions as a male stepped from side to side in front of a female at a distance. The female did not move. **2-5**, Positions assumed by males as they displayed to females at a distance.



Figure 49. Courtship by intermediate *princeps-pulcherrimus* from Orangeburg County, South Carolina. **1-2,** Display by males at a distance. **3-5,** Sequence leading from final approach with legs I extended forward, contact, and the onset of mating.

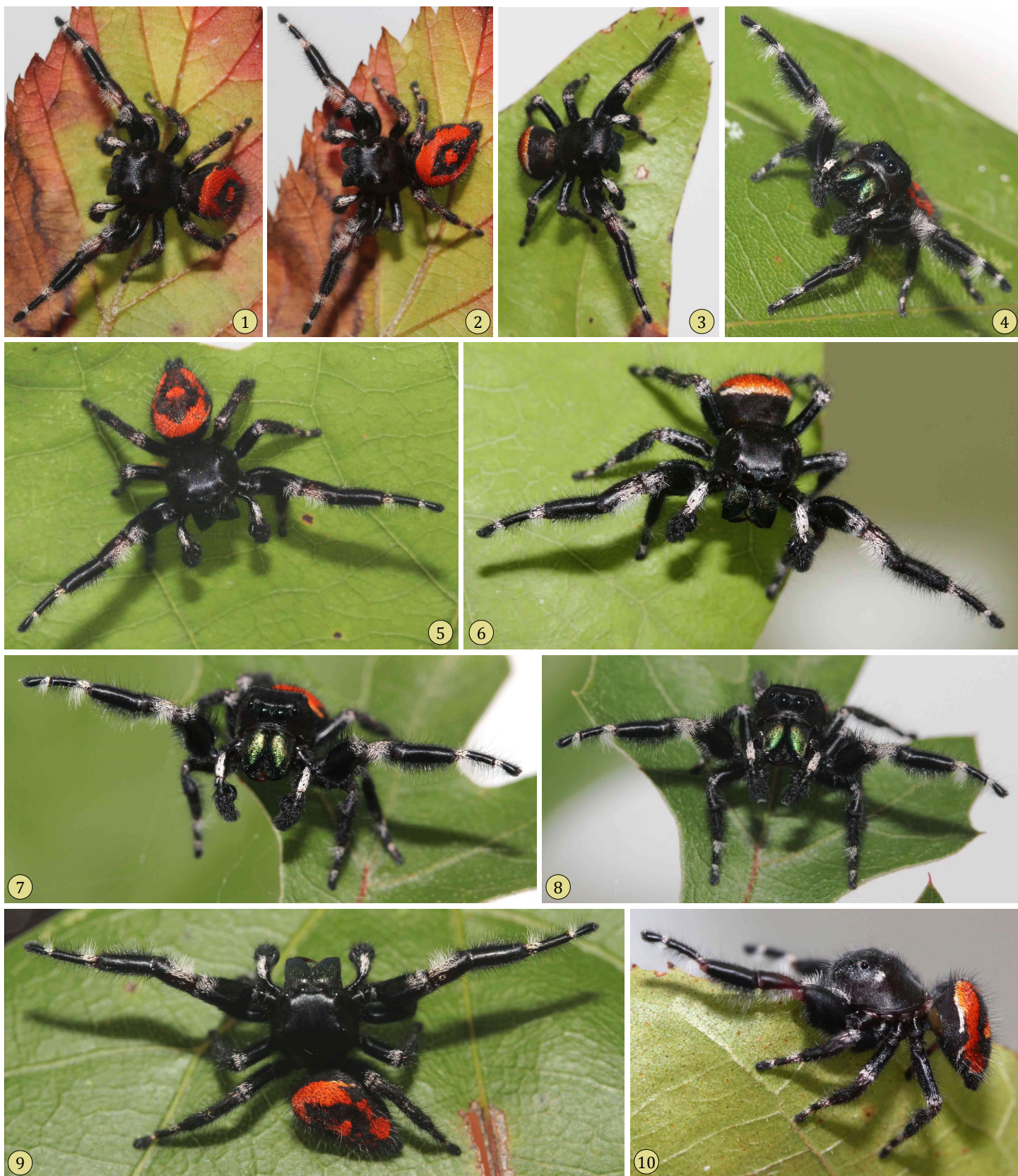


Figure 50. Displays at a distance by courting *Phidippus pulcherrimus*-like males from Screven County, Georgia.

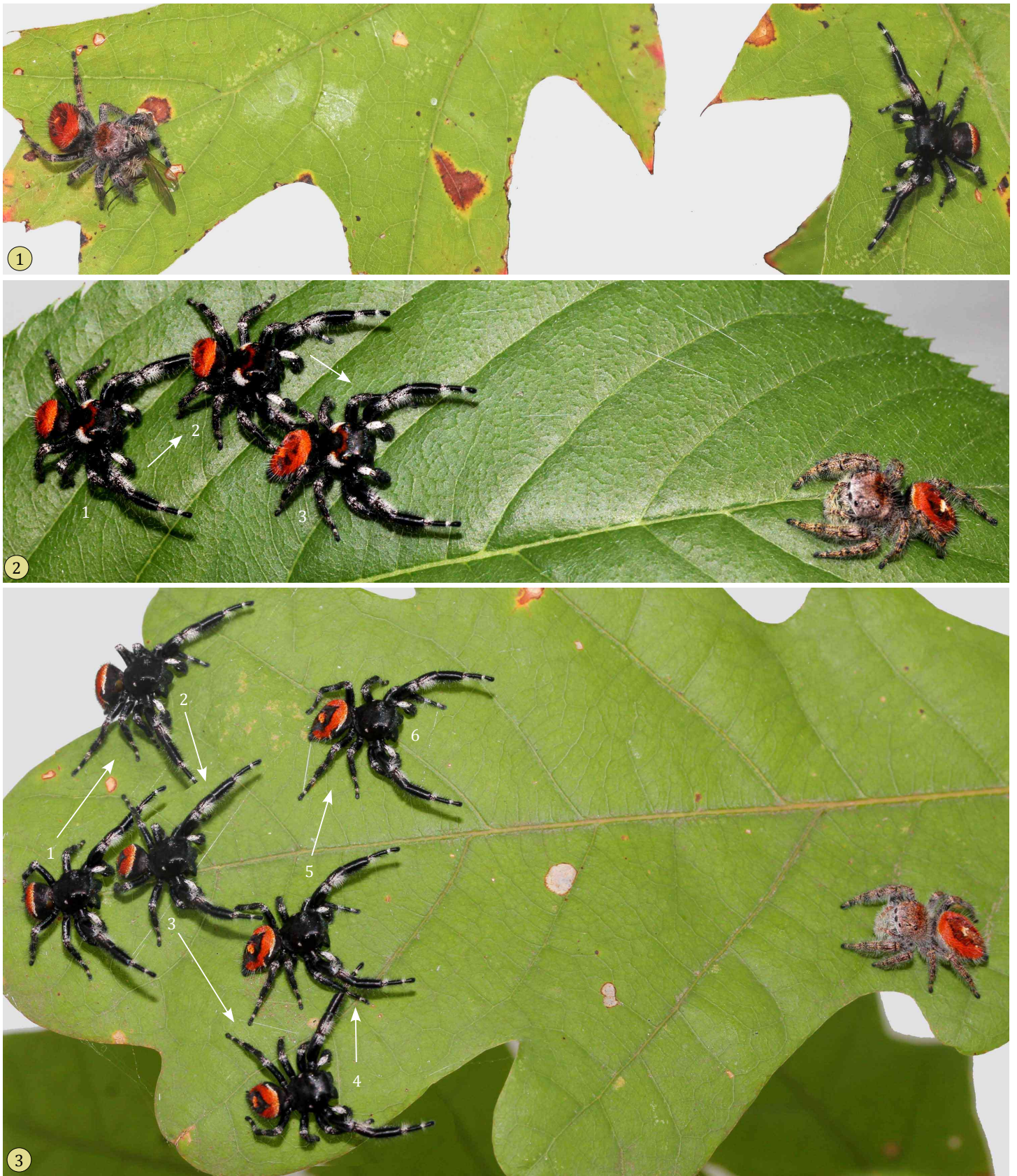


Figure 51. Courtship by *Phidippus pulcherrimus*-like spiders from Screven County, Georgia. **1**, Male displaying to female with prey, at a distance. **2**, Composite image showing three successive positions (1-3) during approach by a male. **3**, Composite images showing six successive positions during approach by a male.



Figure 52. Courtship by *Phidippus pulcherrimus*-like or intermediate spiders from Screven County, Georgia. 1-3, Sequence of approach. 4-5, Sequence showing male stepping to the side of a female that was not moving.



Figure 53. Final stages of courtship and mating by *Phidippus pulcherrimus*-like or intermediate spiders from Screven County, Georgia. 1-6, Sequence from final approach to contact and mating, first on the right side (5), then on the left side (6). 7-10, Four different mating pairs.

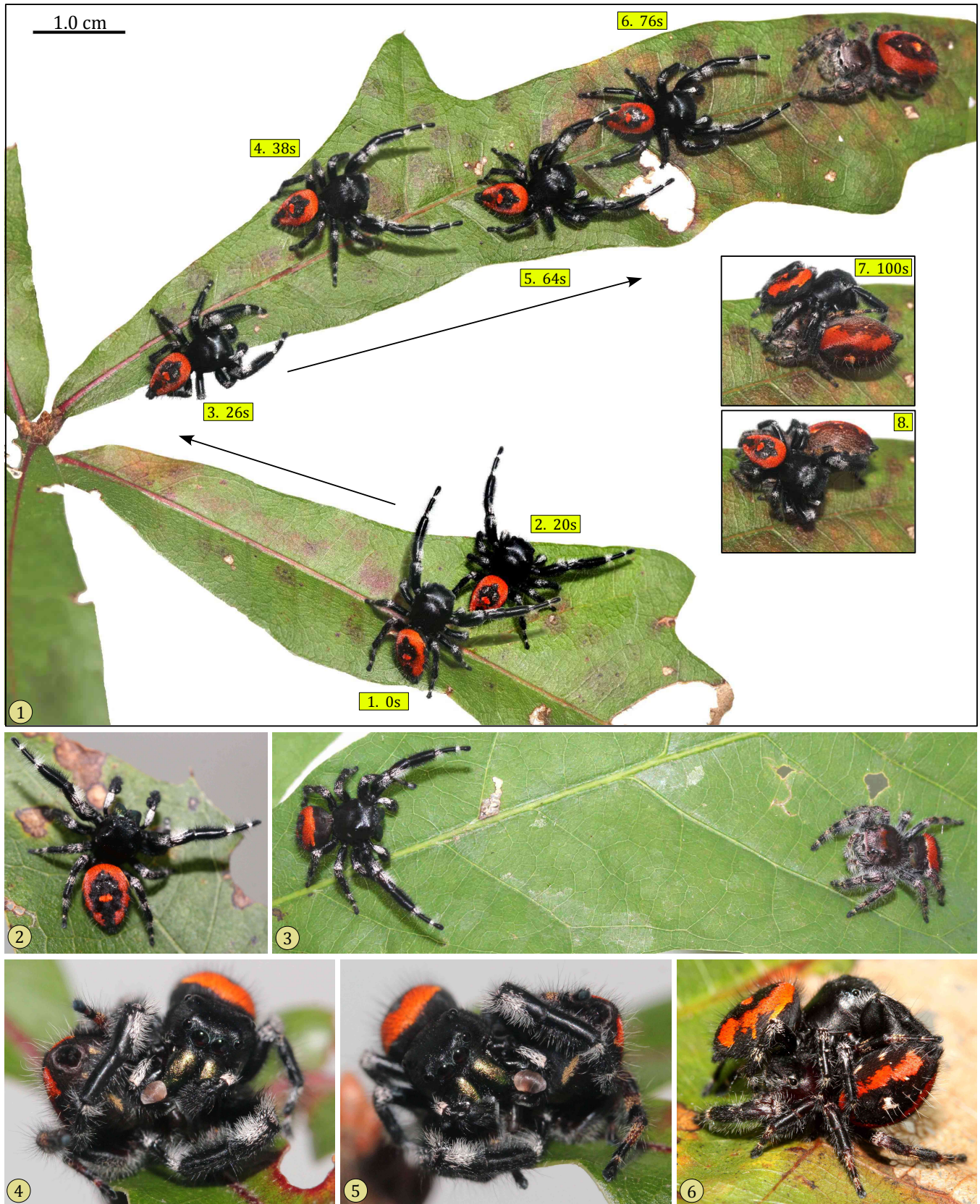


Figure 54. Courtship and mating by *Phidippus pulcherrimus* from Nassau County, Florida. **1**, Composite image showing approach and mating, first on the right side (7), then on the left side (8). **2**, Display by a male at a distance. **3**, Display at an intermediate distance. **4-5**, Sequence showing mating on right side (4) followed by mating on left side (5). **6**, Another mating pair.

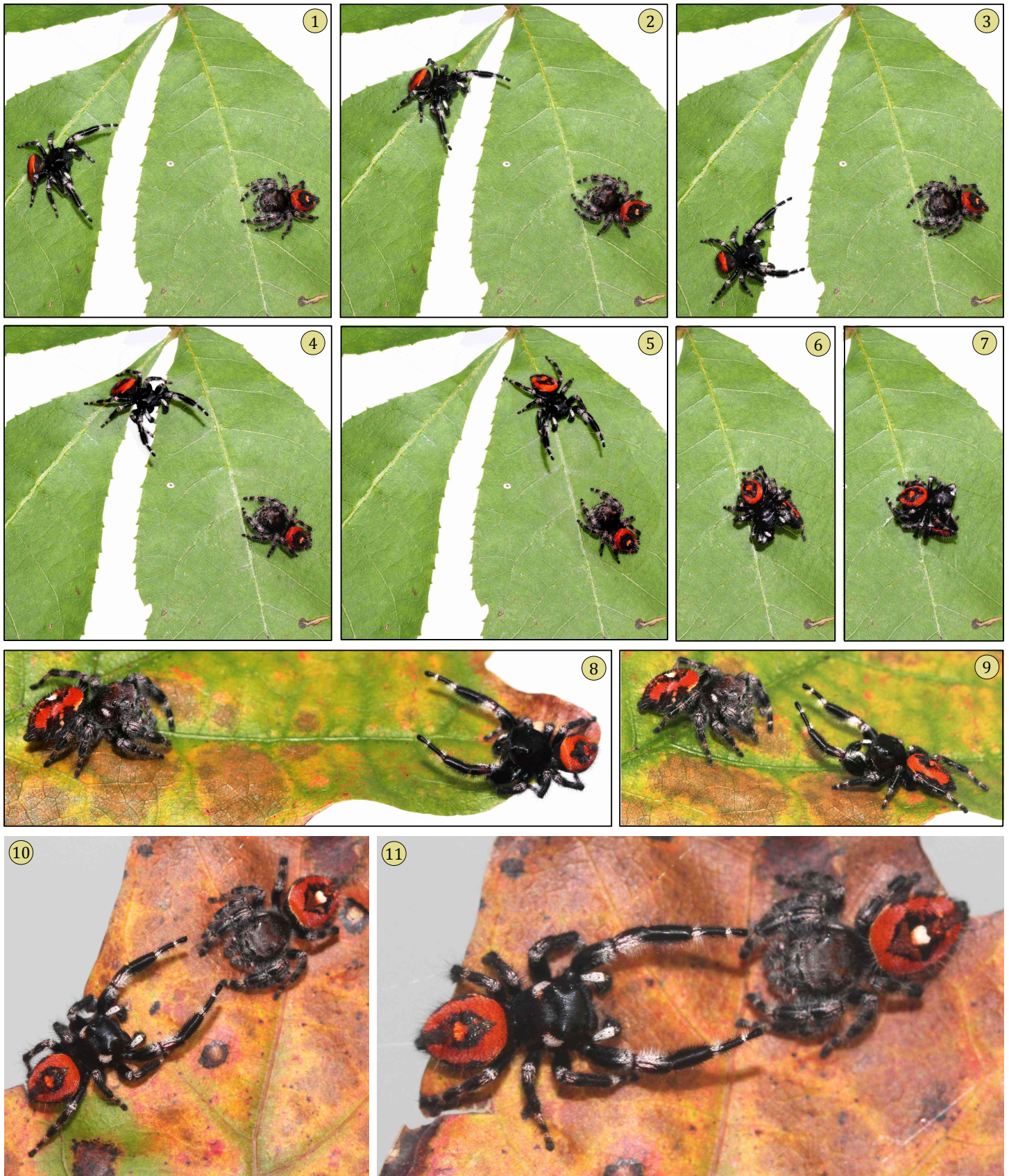


Figure 55. Courtship and mating by *Phidippus pulcherrimus* from Nassau County, Florida. 1-7, Sequence showing approach and mating, first on the left side (6), then on the right side (7). 8-9, Sequence showing final approach. 10-11, Another sequence showing final approach.



Figure 56. Agonistic encounters. All encounters were staged by placing spiders near each other on plants in the laboratory. **1**, Two male *Phidippus princeps* from Laurens County, South Carolina. **2**, *P. pulcherrimus*-like males from Orangeburg County, South Carolina. **3-5**, *P. pulcherrimus* males from Nassau County, Florida. **6**, Aggressive/defensive encounter between male and female from Nassau County, Florida.

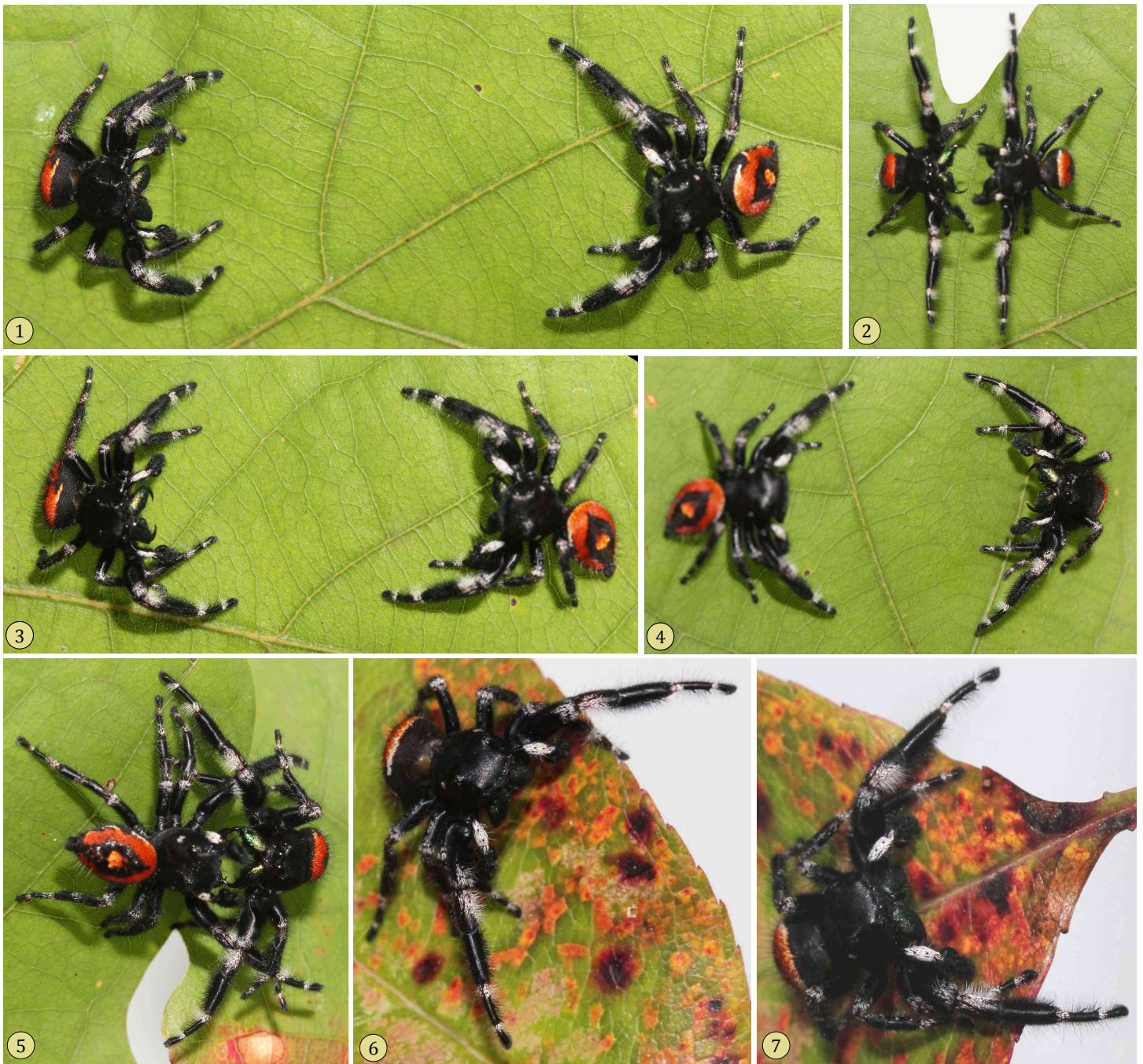


Figure 57. Agonistic encounters between *Phidippus pulcherrimus*-like males from Screven County, Georgia. **1-5**, Sequence showing threat with chelicerae separated (1), close approach with fangs barred and legs I outstretched (2), threat with fangs barred (3-4), and grappling (5). **6-7**, Two threat positions.

Speciation. The evidence for active interbreeding between *Phidippus princeps* and *P. pulcherrimus* can be summarized as follows:

- 1) Many shared characters, including size and detailed structure of genitalia
- 2) Shared dimensions of niche including seasonality and microhabitat
- 3) Absence of localities where both types are found without intermediates
- 4) Acceptance of males or females of either species by the other species
- 5) Presence of many fertile mixed or intermediate forms in a *hybridization zone*
- 6) The *width* of the hybridization zone across the southeastern United States (Figure 1)
- 7) The *depth* of the hybridization zone, or distance at which intermediate characters can be found on either side of this zone

Hill & Edwards (2013) hypothesized the northward migration of *P. princeps* from the western Gulf Coastal Plain and *P. pulcherrimus* from a much wider Florida peninsula since the last glacial maximum (LGM, ~20Ka). The two species may have diverged when isolated during a long period (>100Ky) of continental glaciation. If this is the case, then the presence of a hybridization zone in the southeast indicates that this speciation process was underway but not completed. This corresponds to the suggestion by Hammond (1991) that *secondary intergradation between differentiated populations takes place in hybrid suture zones that often correlate with past geographic isolating barriers*. If true then we are now witness to the convergence of two previously divergent populations. As an alternative hypothesis, differing selection pressures in the temperate eastern forest and the subtropical coastal plain may support an on-going process of divergence or speciation. However, opposing gene flow and divergent selection regimes may also maintain a long-lasting and dynamic equilibrium between two divergent populations. In this case divergence may not result in speciation (Nosil 2008).

Edwards (2004) suggested that the aposematic coloration of a number of *Phidippus* species in the southeastern United States might be associated with *mutillid mimicry*, driven by a greater population of mutillid wasps in that region. Bright orange to red-orange or red forms of *P. audax*, *P. clarus*, *P. otiosus* and *P. regius* can also be found in the southeast (Figure 58). In the temperate northern areas occupied by *P. princeps*, cryptic coloration may be more advantageous. Curiously a single local population of *P. clarus* may include a variety of both cryptic and aposematic female color morphs (Hill 2014).

Species concepts and implications for taxonomy. The *species problem* in biology (*What is a species?*) is related to the use of many different definitions for a *species* (e.g., Mishler & Brandon 1976; Wheeler & Platnick 2000; Wilkins 2002; Hey 2001, 2014; Saikia et al. 2008). In fact, some writers (e.g., De Queiroz 2007) advocate the creative extension of the species concept to even more dimensions and definitions. Nonetheless a number of critical thinkers (Mayr 1942, 1976; Chung 2003; Ghiselin 2004; Haffer 2006) have suggested that we have two basic alternatives when it comes to the definition of *species*:

- 1) Application of the *biological species concept* (BSC) that defines a *species* as a population of all individuals that are capable of interbreeding
- 2) Application of a *typological species definition* (TSD), or any similar approach that uses *species* to delimit a taxon irrespective of speciation

A case can be made for separate biological species when these can coexist without hybridization (Wallace 1865; Wilson & Brown 1953; Thomson 1969; Mallet 2009). Trinomial nomenclature that incorporates the concept of *subspecies* was introduced to describe separate geographic populations where replacement rather than coexistence is the norm (Mallet 2013). Mayr (1982) viewed the subspecies as a useful *sorting device in collections, that is, as an index to populations that differ from each other "taxonomically."* Others have also emphasized the arbitrariness of subspecies designations, particularly since each allele in a population can have its own geographic distribution (Mayr 1942; Wilson & Brown 1953).



Figure 58 (continued on next page). Orange to red forms of *Phidippus* species in the southeastern United States. Representatives in the northern part of the range of each of these species tend to lack this coloration, although most *P. clarus* populations usually contain a variety of color forms. **1-2**, Two adult female *Phidippus audax* (Hentz 1845) from Columbia County in northern Florida. A variety of related color forms have been found in roadside post holes in northern Florida (Hill 1978a). **3-4**, Two adult male *Phidippus audax* from Columbia County in northern Florida. **5-6**, Two adult female *P. clarus* Keyserling 1885 from southern Greenville County, South Carolina (See Hill 2014).



Figure 58 (continued from previous page). Orange to red forms of *Phidippus* species in the southeastern United States. **7-8**, Two adult female *P. otiosus* from Highlands County, Florida. **9**, Adult male *P. otiosus* (Hentz 1846) from Highlands County, Florida. **10**, Adult male *P. otiosus* from Montgomery County, Alabama. **11-12**, Two adult female *P. regius* C. L. Koch 1846 from Tosohatchee Wildlife Management Area in Orange County, Florida.

With respect to the naming of species in the *princeps* group, at least three different resolutions are possible. There are no international standards to determine which of these is a correct approach:

- 1) For those who wish to use *species* in the sense of a *biological species*, but eschew the use of trinomials, the presence of an active hybridization zone indicates that *Phidippus pulcherrimus* should be viewed as a synonym of *Phidippus princeps*. This approach simplifies the formal classification of intermediate forms.
- 2) For those who also accept the use of trinomials to classify geographically distinct forms, *Phidippus princeps* would become the subspecies *Phidippus princeps princeps*, and *Phidippus pulcherrimus* would become the subspecies *Phidippus princeps pulcherrimus*.
- 3) For those who prefer to retain the current separation of two typological species, no change is necessary. However this makes the naming of intermediate forms more difficult (e.g., *Phidippus princeps* x *pulcherrimus* hybrids).

Research (Table 3). Compact in size and easy to rear in the laboratory, spiders of the *Phidippus princeps* group have played an important role in the study of salticid behavior. Both typological species have performed well in experiments related to navigation through the complicated three-dimensional environment that they inhabit. More recent studies have dealt with their movement through vegetation and interactions with a number of potential prey species.

Table 3. Chronological list of research on members of the *Phidippus princeps* group, according to typological species.

reference	species	summary
Hill 1977a	<i>princeps</i>	In laboratory trials 8 of 8 males placed directly near female nests entered those nests and mated successfully. Males were frequently attacked by females outside of nests.
Hill 1977b	<i>princeps</i>	Field observations of nesting, nest-site fidelity and predatory behavior in Hennepin County, Minnesota.
Hill 1978b, 1979b, 2007 2010a	<i>princeps</i> and <i>pulcherrimus</i>	Experimental study of the integrated use of distance and direction information (idiothetic, visual and gravity-referent) during the indirect or detoured pursuit of sighted objectives, including prey and plant positions.
Hill 1979a	<i>princeps</i>	Described scale patterns of typical adult females and the three-shafted red-orange pigmented scales and the flat reflective scales on the opisthosoma of adult males.
Edwards 1980	<i>princeps</i> and <i>pulcherrimus</i>	Described many aspects of taxonomy, behavior, reproduction, phenology and ecology with emphasis on <i>pulcherrimus</i> in northern Florida.
Roach 1988	<i>princeps</i>	Reported three broods of 21-60 young from February-April, dispersal from March-July in South Carolina.
Edwards 1990	<i>pulcherrimus</i>	Described sit-and-wait predation and seasonal nesting in Alachua County, FL.
Anderson 1996	<i>pulcherrimus</i>	Found average metabolic rate (oxygen consumption) of 30 $\mu\text{L O}_2/\text{hr}$ for 156 mg adult live mass. For salticids and thomisids metabolic rate was proportional to live mass.
Robertson & Stephens 2002	<i>princeps</i>	Described development of instars in the laboratory, courtship, mating and fecundity of spiders captured as immatures in Macon County, Illinois.
Hill 2006a, 2010b, 2018	<i>princeps</i>	In trials a spider would jump faster and higher to reach prey or positions at a greater distance or a higher relative elevation. Just before reaching prey spiders braked on the dragline and reversed pitch, pulling the legs together in a "catching basket."
Hill 2006b, 2010c	<i>princeps</i> and <i>pulcherrimus</i>	Described extension and retraction of foot pads and claws associated with each foot, and their respective use for attachment to plant surfaces or for walking on and handling silk lines.
Skow & Jakob 2006	<i>princeps</i>	In trials a change of setting (context) was associated with an increased tendency to attack aposematic prey.
Hill 2009	<i>princeps</i>	Video study of feeding females.
Baker 2007	<i>princeps</i>	In trials spiders preferred movement through vegetated corridors to movement over bare ground.
Jakob et al. 2008	<i>princeps</i>	In trials some spiders became significantly better at associating prey with a red or a blue color after repeated trials.
Baker et al. 2009	<i>princeps</i>	In trials spiders moved preferably toward taller, green, grass-like targets.
Stankowich 2009	<i>princeps</i>	In trials larger spiders fled for a shorter distance before they turned to confront a threat.
Hill 2011	<i>princeps</i>	Described mouth and structures of anterior digestive tract from examination of exuviae.
Long et al. 2012	<i>princeps</i>	In trials learned avoidance of unpalatable fireflies by spiders was facilitated through association with flashing LED
Hill & Edwards 2013	<i>princeps</i> and <i>pulcherrimus</i>	Figured males and females and hypothesized northward migration of <i>princeps</i> from the Gulf Coastal Plain and <i>pulcherrimus</i> from the Florida peninsula since the last glacial maximum.
Sourakov 2013	<i>pulcherrimus</i>	In trials spiders attacked the "false head" at the rear of each butterfly (<i>Calycopis</i>), failing to capture it.
Hill 2016	<i>princeps</i>	In trials found short-term learned avoidance of milkweed bugs (<i>Oncopeltus</i>) reared on milkweed seeds (<i>Asclepias</i>).

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