**PECKHAMIA 279.1**, 22 October 2022, 1–83

LSID urn:lsid:zoobank.org:pub:8B32C857-C358-450D-8401-E1767D0BC5D6 (registered 19 OCT 2022)

## Jumping spider scales (Araneae: Salticidae)<sup>1</sup>

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**Summary**. The state of our knowledge of salticid scales is reviewed, with emphasis on recent discoveries related to the iridescence of scales associated with either multilayers (*Cosmophasis, Maratus*) or diffraction gratings (*Maratus*). The distinctive scales found in certain genera may be of use in taxonomy, particularly if they can be imaged in detail. In many if not most salticids, however, scales follow common patterns (e.g., setiform, or pinnate) that may represent a transition from the "ordinary" seta to the scale (bent to lie along the surface of the cuticle). This supports the hypothesis that an ancestral toolkit that supports the intracellular assembly of scales persists in many different lineages.

Keywords. iridescence, phylogeny, scalae, setae, structural color, taxonomy

More than 40 years ago I published a paper on the subject of salticid scales (Hill 1979). At the time, scanning electron microscopy (SEM) was still a relatively expensive novelty, and the high resolution associated with this technology gave us a new view of everything that we looked at. Unfortunately, just as macrophotography has opened up new worlds for exploration by field naturalists, SEM nonetheless remains costly and relatively inaccessible to naturalists. We can only anticipate that this will change in the near future.

In my earlier paper I suggested that the comparison of salticid scales would be of great use to taxonomists. Although a relatively small number of papers published since that time have included SEM images or drawings of the scales of salticids and other spiders (e.g., Townsend & Felgenhauer 1998a, 1998b, 1998c, 1999a, 1999b, 2001; Metzner 1999; Benjamin 2004; Zakharov & Ovtsharenko 2015), these have generally been of limited, or no, use with respect to our understanding of spider taxonomy and phylogeny. Instead, the emergence of DNA sequencing and the increasingly sophisticated comparison of these sequences (e.g., Maddison et al. 2014, 2017; Wheeler et al. 2017) have transformed our understanding of spider phylogeny from an inexact science into a much more robust field of inquiry.

Spider scales (or *scalae*, after Hill 2010b) represent a class of specialized setae that are bent at the pedicel so that they lie relatively flat against the underlying cuticle of the spider (Figure 1; Hill 1979; Townsend & Felgenhauer 1998c). Although spiders are usually covered with many other setae, often in regular and dense patterns, those setae are usually elongate, surrounded on all sides by small spines (setules or spinules), and not flattened or elaborately sculpted. Like scales, other setae can be pigmented or even iridescent (Foelix, Erb & Hill 2013).



**Figure 1.** Generalized structure of a keeled, lanceolate (Figure 2: class 8) salticid scale. The sharp, central keel and thick margins represent the three shafts of this scale. Most scales lack small spines (*spinules* or *setules*) on the upper surface but, as shown here, can be elaborately sculpted.

Here (Figure 2) I present a simplified classification of the many, diverse scale types of salticid spiders, based on their external structure. This includes the *lanceolate* and *spatulate* classes recognized by Townsend & Felgenhauer (1998c), but their third class, of *plumose* scales, is divided into a number of new categories.



**Figure 2.** Working classification of salticid scale types (*hypothetical grades*), based on external structure. More *primitive* types (toward the bottom) may be retained in the genetic toolkit of species that have evolved more *advanced* scales. The setiform (class 1) scales look much like "ordinary" setae, with spinules (setules) on all sides. Otherwise these are divided primarily into those that retain these spinules on the upper side (classes 2-4), and those that have a smooth or sculpted dorsal surface (classes 5-13).

The surface structure of scales greatly affects their reflectivity and the saturation of pigment colors, irrespective of how far light penetrates that surface (Figure 3). We usually find that lighter and brighter scales are wider, and darker scales with dark pigments are narrower. The brushy or narrower scales restrict the reflection of light, forcing its interaction with the pigments contained within these scales. In combination with a *microlens* structure of a dark, pigmented cuticle, *Maratus* males have used the tortuosity of brushy scales to produce super black spots (Figure 12; McCoy et al. 2019). Photopigments (biochromes) that may be found in spiders include ommochromes (smaller yellow to red ommatins, larger brown to black ommins, or a combination of the two), bilins (green), carotenoids (yellow to red, but not yet detected in scales), and brown to black eumelanin (Hsiung, Blackledge & Shawkey 2014, 2015; Stavenga, Otto & Wilts 2016; Hsiung et al. 2017a; McCoy et al. 2019). Wider scales without pigment may nonetheless be highly reflective or "shiny" when viewed from certain directions.



**Figure 3.** Transverse sections of keeled scales. **1,** Many salticids, including dendryphantines and *Habronattus*, have bright white, lanceolate (class 8) scales, keeled with thick margins (*three-shafted*), that are highly reflective. The wide, five-shafted scales of *Salticus* species are similar to this, and also bright white. **2,** The deep red scales of *Phidippus* species are much narrower with little surface reflection (also class 8). **3,** Many salticids, including *Platycryptus*, have wide, reflective scales like this with a prominent keel (class 6). **4,** Narrow, keeled scales like these (class 7, bladelike) are usually highly pigmented or dark, with little surface reflection.

*Iridescent scales.* The detailed (*nanoscale*) surface and interior structure of scales can also be associated with their iridescent properties, or structural color. Whereas photopigments work through selective absorbance of light at the level of individual molecules, structural color is the product of constructive or destructive interference between alternative pathways for photons as they are reflected or diffracted by physical structures at the nanoscale level, corresponding to the wavelength of these photons (Figure 4; Ducet & Meadows 2009). The phenomenon of *iridescence* is associated with structures that affect the direction of reflected or diffracted light in a manner that varies according to wavelength. Thus iridescent scales separate colors, and can emit intense "beams" of highly saturated color in specific directions relative to the direction of illumination. Incoherent or less-ordered structural scattering of light also can produce a shiny or metallic appearance, without iridescence.

Of the various kinds of structural interference observed in nature, thin layers or multilayers may be the most common, and diffraction gratings are thought to be uncommon (Kinoshita & Yoshioka 2005). However, many arthropods may use other *biophotonic nanostructures*, to include the use of nanospheres to produce structural color; a hexagonal column has even been reported for a blue scale on the opisthosoma of an unspecified salticid (Saranthan et al. 2015).



Figure 4. Structural color is the result of the constructive or destructive interaction of alternative, multiple pathways for light. 1, Interference through a single layer (*thin layer*) with negligible refraction at the boundary. Arrows show the two different pathways that a photon can take as it is reflected, each of a different length. **2**, Interference through a single layer (*thick layer*), with a higher refractive index (shaded,  $\sim$ 1.5) than air ( $\sim$ 1.0). Both the thickness and refractive index of the layer produce a longer path for light that is not reflected at the upper surface. 3, The many alternate paths that a photon could take through a multilayer reflector, comprised of alternating layers with high (white,  $\sim 1.0$ ) or low (shaded,  $\sim 1.5$ ) refractive index. **4**, Another view of the many pathways that a photon could take through this multilayer (3), showing each pathway separately. With regular spacing and alignment at the nanoscale, this can produce a series of consistent differences (each corresponding to a multiple of the favored wavelength) and a constructive effect as a result. 5, Passage of light through the slits of a transmissive diffraction grating. As with the interference of light through reflection at multiple layers, this produces a series of possible pathways for each photon, each of different length. As shown here, red light, because of its longer wavelength, is favored over blue light at larger angles relative to the incident light. 6. Reflection of light from a reflective diffraction grating. The effect is similar to that seen in a transmissive grating (5), in that the interaction of photons with different points of reflection produces a series of different path lengths, favoring longer wavelengths (red) at lower angles of reflection relative to the incident light. 7-12, Relationship of relative direction of incoming light, wavelength, and spacing of reflectors to interference. When the difference between two alternative pathways is equal to an integer multiple of the wavelength of a photon, interference of light traveling on the two pathways is constructive ("additive"). When it is equal to an integer multiple of half of that wavelength, interference is destructive ("subtractive" as one path cancels out the other). Anything else is somewhere in-between.

Although observed interference patterns are often explained through an analogy with water waves, as the collision of multiple wave fronts, we now know that this interference can be observed when individual photons, one by one, are given the option of multiple pathways. Although this is contrary to our everyday experience, each photon *appears to* pass through all available paths at the same time, interfering with itself to determine the most likely outcome. The same phenomenon (sometimes called *wave-particle*)

*duality*) has been observed not only with photons, but also with electrons as well as some relatively large molecules, to include  $C_{60}$  (Jönsson 1974; Tonomura et al. 1989; Arndt et al. 1999; Nairz, Arndt & Zeilinger 2003; Menzel et al. 2012; Rueckner & Peidle 2013; Aspden, Padgett & Spalding 2016; Kaur & Singh 2020; Nash 2021). The main requirement for this effect is that the respective photon (or particle) is given the option of multiple pathways, and that we do not directly measure the pathway that is taken by that photon (or particle) *in transit. Constructive interference* is greatest when the lengths of the interfering pathways are separated by an integer multiple of the wavelength, and *destructive interference* is greatest when the lengths of these pathways are separated by an integer multiple of the wavelength, and *destructive interference* is greatest.

Although multilayer inference is responsible for much of the iridescence that we observe in nature, it has had little study with respect to salticid coloration. Ingram et al. (2011) observed that the green iridescence of the anterior surface of each paturon of the jumping spider *Phidippus johnsoni* (Peckham & Peckham 1883) was produced by a stack of 86 layers of alternating air and chitin. Land et al. (2007) found that near-UV (~385 nm) and green-orange (540-620 nm) photons were selectively reflected with constructive interference by *corrugated* (wavy or *type 1*) scales aligned across the carapace of a male *Cosmophasis umbratica* Simon 1903, the product of a multilayer comprised of only three layers within those scales (Figure 5). Curiously an earlier study of the iridescent carapace of the male *C. thalassina* C. L. Koch 1846 found evidence of multilayer diffraction, but failed to mention the presence of scales (Parker & Hegedus 2003).



**Figure 5.** Iridescent scales of the male chrysilline *Cosmophasis umbratica*. **1**, Adult male from Bali, showing the two bands of green-orange (or gold) iridescent scales that cross the top of the carapace. Land et al. (2007) called these *type 1* scales. **2**, Model section through the multilayers of a type 1 scale, showing nanoscale photon pathways (after Land et al. 2007). This configuration was thought to produce a peak reflection at 600 nm, but this would vary according to the relative direction of illumination at any position along the length of the scale. *Optical thickness* of each respective layer is depicted here. These scales also reflected near-UV light (~385 nm peak), a color that, according to Li et al. (2008), also plays a role in the recognition of males by female *Phintella vittata* (C. L. Koch 1846). Attribution and ©: 1, normfarmerimages.

The recent discovery of the large and diverse clade of Australian peacock spiders (*Maratus*) has spurred a high level of interest in the unique iridescent scales to be found in this group (Figures 6-12; Foelix, Erb & Hill 2013; Hsiung, Blackledge & Shawkey 2014; Hsiung et al. 2017b; Wilts, Otto & Stavenga 2020). The patterns displayed on the fan of male *Maratus* exhibit a high degree of contrast in both brightness and color, often with tracts of pigmented scales that reflect a highly saturated color, surrounded by a field of brilliantly iridescent scales, with color that varies in wavelength and intensity according to direction.



**Figure 6.** Courtship display by male peacock spiders (Euophyrini: *Maratus*). The fan (dorsal opisthosomal plate) of these spiders bears a distinctive, high color contrast, and high saturation pattern comprised of both pigmented and iridescent scales, in most cases raised and expanded in front of a female as shown here. Each of the species shown here was first described in the last decade. Attribution and ©: 1-14, Jürgen C. Otto.



**Figure 7.** Colorful scales of the male *Maratus volans* (O. Pickard-Cambridge 1874). **1**, Typical courtship display by male, with elevated and extended fan held in front of the long, extended legs III. **2**, Depending on the relative direction of illumination, the brilliance of the blue-green iridescent scales near the center of the fan can be displayed to full effect. 3-4, Under the transmission electron microscope (TEM), thin transverse sections through the iridesent scales of *M. volans* reveal a nanoscale architecture of repeating linear, external and internal, ridges (drawings after Foelix, Erb & Hill 2013). The interval between internal ridges is much shorter and more regular than the interval between external ridges. In this case, the relatively uniform blue-green iridescence of these scales may be the product of both transmissive and reflective diffraction. *M. volans*, widely distributed in eastern Australia, is the best-known member of the genus. Attribution and ©: 1-2, Jürgen C. Otto.



**Figure 8.** Scales of the male *Maratus chrysomelas* (Simon 1909). **1**, Courtship display by male, with fan elevated and extended between the long, extended legs III, as the male moves rapidly from side to side in front of a female. **2**, Field of iridescent blue scales near the rear of the fan (SEM image). At lower right several dark black scales (class 2, brushy) can be seen. Each iridescent scale is keeled and bladelike (class 7), with many more-or-less regular ridges aligned with the long (pedicel-to-apex) axis. **3-4**, Details of iridescent scales, showing the nanoscale separation of ridges that support reflective diffraction at the observed wavelengths. **5**, Thin transverse section through a single iridescent scale, showing the spacing of ridges around the sides and top of the scale. *M. chrysomelas* is widely-distributed in Australia (Otto & Hill 2021), with a number of different color forms, including those with iridescent blue-green scales, represented. Attribution and ©: 1, Jürgen C. Otto; 2-5, Hsiung et al. 2017b.



**Figure 9.** Scales of the male *Maratus splendens* (Rainbow 1896). **1,** Courtship display with extended fan. **2,** Fan retracted. **3,** SEM of eye region. **4-6,** SEM views of brushy (red, pigmented) and smooth (blue, iridescent) scales that cover the fan. **7,** Schematic sections through an iridescent scale showing external ridges and internal filaments thought to enhance diffraction and multilayer interference (after Stavenga, Otto & Wilts 2016). Attribution and ©: 1-2, Jürgen C. Otto; 3-6, Rainer F. Foelix.



**Figure 10.** Scales of the male *Maratus nigromaculatus* (Keyserling 1883). **1**, Courtship display by a male in front of a female. Like the closely related *M. chrysomelas* (Figure 8), the male *M. nigromaculatus*, with fan elevated and extended, steps rapidly from side to side during this display. **2**, Detailed view of fan, showing the large field of relatively uniform iridescent blue scales, interrupted by black spots. **3**, Middorsal part of fan with blue scales as seen under the light microscope. Note the multicolor diffraction that is difficult to observe at a lower magnification. **4-6**, SEM views of these iridescent blue scales, showing cross section in (6). In this species the mostly parallel ridges are not straight, but wind around the surface of each scale. The nanoscale spacing of these ridges accounts for the production of the observed colors through reflective diffraction (Wilts, Otto & Stavenga 2020). These keeled and bladelike (class 7) scales are similar to those of *M. chrysomelas*. Attribution and ©: 1-2, Jürgen C. Otto; 3-6, Wilts, Otto & Stavenga 2020.



**Figure 11.** Scales of the male *Maratus robinsoni* Otto & Hill 2012. **1**, Courtship display by male. **2-5**, Views of the dorsal opisthosoma, showing variation of iridescent color by direction. **6**, **11**, Detailed light views of iridescent scales, from above. **7**, **12-13**, SEM views of attached scales (class 7, bladelike), from above. **8**, SEM view showing regular spacing of the grating on the side of a detached scale. **9**, Separation of parallel ridges on the surface of a scale. **10**, SEM, cross section of scale (sharp top of scale at left). Attribution and ©: 1-4, Jürgen C. Otto; 5-10, Wilts, Otto & Stavenga 2020; 11-13, Hsiung et al. 2017b.



**Figure 12.** Super black spots of male Maratus (7-11 after McCoy et al. 2019). **1-2**, Two male *M. karrie* engaged in courtship display. Variable color of the fan (green to blue) may be due to either individual variation, the relative direction of illumination and observation, or a combination of the two. **3**, *M. speciosus* with fringe of fan retracted, concealing the bright orange coloration of the bicolored setae of that fringe. **4**, *M. speciosus* display with expanded fan. **5-6**, Detailed views of the expanded fan of two male *M. speciosus*. **7**, Dorsal view (SEM) of opisthosoma of *M. karrie*, showing smooth, iridescent blue scales surrounded by brushy scales and dark cuticle (*microlens array*). **8**, Section through (7). **9**, Dorsal view (SEM) of opisthosoma of *M. speciosus*. **10**, Section through (9). **11**, Schematic view of reflection and absorption of light by dark brushy scales above the *microlens* structure of the cuticle. Attribution and ©: 1-6, Jürgen C. Otto; 7-10, McCoy et al. 2019.

The scales of the *Maratus* species that have been studied to date (Figures 7-12) indicate that the reflective diffraction grating, as well as multilayers which may incorporate an internal diffraction grating, represent important approaches to achieve structural color in this group. In *M. volans* (Figure 7; Foelix, Erb & Hill 2013) and *M. splendens* (Figure 9; Stavenga, Otto & Wilts 2016) iridescent scales also have multilayers as well as a regular internal structure or grating at the nanoscale of visible light, a *biophotonic architecture* representing a more elaborate form of diffraction. For *M. splendens*, iridescent blue scales on the carapace differ from those on the fan (dorsal opisthosoma). The iridescent scales of the closely related *M. chrysomelas* (Figure 8; Hsiung et al. 2017b) and *M. nigromaculatus* (Figure 10; Wilts, Otto & Stavenga 2020) are similar, with external, more-or-less regular nanoscale ridges that function as reflective diffraction gratings. The bladelike (class 7) iridescent scales of *M. robinsoni*, a very small (~2 mm) spider, are remarkable with respect to their ability to separate and to reflect the full visible spectrum of colors, corresponding to an extremely regular grating of ridges along the sloping but flat sides of each scale, separated by a sharp ridge at the top (Figure 11; Hsiung, Blackledge & Shawkey 2014; Hsiung et al. 2017b; Wilts, Otto & Stavenga 2020). Similar diffraction gratings have not been found in other salticids.

Alignment and placement of scales. The pedicel-to-apex alignment of scales on the body and appendages of a salticid generally follows the direction in which the cuticle is shed during ecdysis (Figure 13). Thus removal of the old exoskeleton does not push against the expansion or extension of the new set of scales during the molting process. This produces a general anterior-to-posterior alignment of opisthosomal scales, but scales on the posterodorsal opisthosoma may have a transverse orientation, perpendicular to the body axis (Figure 14). Salticids may also exhibit a distinctive, genus-specific, pattern of scale placement that can aid in their identification (Figures 15-18).



**Figure 13.** Adult female *Platycryptus undatus* (De Geer 1778), Greenville County, South Carolina. Green arrows indicate the pedicel-to-apex alignment of body scales.



**Figure 14.** Male *Maratus amabilis* Karsch 1878 from eastern Australia. **1-2**, Courtship display with elevated and expanded fan. **3**, Transverse alignment of pigmented scales near the rear of the fan. Attribution and ©: 1-3, Jürgen C. Otto.



**Figure 15.** Some of the scale patterns found in females of the neotropical freyine genus *Phiale*. These are usually simple, but bright and bold patterns. Attribution and ©: 1, jsirker; 2, 9, Thomas Shahan; 3, Tom Kirschey; 4, Rogerio Dias; 5, jorgearrestre4; 6, davisgunn; 7, Guilherme A. Fischer; 8, Tom Murray.



**Figure 16.** Some of the scale patterns found in females of the Nearctic dendryphantine genus *Phidippus*. In this genus the dorsal opisthosoma typically bears one pair of anterior spots, a central triangle comprised of two fused spots, and two posterior pairs of spots (Edwards 2004). These spots are comprised of pigmented scales on a black background. Surrounding these spots on the black background there are usually many flat, transparent, shiny and sometimes iridescent scales. **3-4**, Note the variation in the color and scale pattern of these female *P. californicus*, from Mexico and Oregon, respectively.



**Figure 17.** Representative chrysillines. Many members of this primarily Afroeurasian group, and particularly those that occur in tropical Asia, have brilliant iridescent scales on both the carapace and opisthosoma, often arranged in transverse bands. African genera, to include *Mexcala* (5) and *Natta* (see Hill 2009a), tend to be more subdued in coloration. Attribution and ©: 1, 11, Roman Prokhorov; 2, Girish Gowda; 3, Daniel Kurek; 4, Felix Riegel; 5, Thomas Shahan; 6, Kit Law; 7, Harshith JV; 8, Richard Ong; 9, hollythefrog; 10, Ben Tsai.



**Figure 18.** Representatives of the cosmopolitan genus *Salticus*. The well-known zebra spiders can often be easily recognized by their transverse to oblique stripes on the opisthosoma. Some species (7-9) have brilliant, iridescent scales, but these have not been studied in detail. *S. scenicus* has a holarctic distribution. **2-4**, Note the variation in scale pattern of these European *S. cingulatus*. **6**, The diagonal stripes on the sides of the opisthosoma are present but less evident in this female *S. mutabilis*. The four dark spots on each side of the carapace in females of this species appear to mimic the face of a salticid spider, perhaps providing some protection against attack from the side (see Hill, Abhijith & Burini 2019; Hill 2022). Attribution and ©: 1, Buddy; 2-3, Roman Providukin; 4, Cédric Mondy; 5, Óscar Mendez; 6, Diego Trillo; 7-8, Jillian Cowles; 9, gwentomologist; 10, faluke; 11, Ryan Kaldari; 12, corndog.

*Development of scales*. With each molt, a spider produces a new set of setae, including scales. With no available studies for the development of scales by spiders, we can assume that this development is similar to that of butterflies and moths. Each lepidopteran scale is the product of a *scale precursor cell* that may divide several times before finally producing a scale-forming (*trichogen*) cell, surrounded at its base by a socket-forming (*tormogen*) cell (Greenstein 1972; Keil 1997; McDougal et al. 2021). Each scale-forming cell projects through a developing socket into the lumen between the old and new cuticle. Once they expand, scales may be filled with air, and they are not innervated as are many other setae (Foelix 2011).

The genes that allow each scale-forming cell to find its position, and to produce often-elaborate scales, should represent enhancement of a more general capability of all trichogen cells. Accordingly, we can view the setiform scales, found in many salticids, as *primitive*.

*Function of scales*. Scales are certainly associated with much of the color that we associate with jumping spiders, but beyond this general observation the function of scales and as well as the color that they produce is not that easy to determine. For perspective, we should note that there are many salticids that are not covered with scales (Figure 19). In addition, scales do not represent the only means of coloration for a spider, as cuticular layers and epidermal pigment, as well as other, "normal," setae may also provide both pigmented and iridescent colors.



**Figure 19.** Some salticids with relatively few scales. Absence of scales can be associated with either transparency or the presence of green bilins in the cuticle. At the same time, scale cover in the eye region may prevent predators from observing movement of the AME. Attribution and ©: 3-4, Thomas Shahan.

In addition to coloration, scales of Lepidoptera have been associated with thermoregulation (including insulation), production of pheromones, protection from spider webs (by the release of scales), and improvement in the aerodyamic efficiency (lift) of the wings (Kevan & Shorthouse 1970; Grodnitsky & Kozlov 1991; Slegers et al. 2017). All of these functions could be considered with respect to the scale of jumping spiders, but, given the limited "flight" of jumping spiders, aerodynamics seems less likely, and we have no demonstration that the scales of any spiders are associated with pheromones. The uses of color are legion (e.g., camouflage, intraspecies communication, mimicry, aposematism or warning), but explanations for the use of colored scales by salticids are few. For example, modified white scales around the anterior eyes may make these eyes more prominent and assist in recognition by conspecifics (Hill 2022). The beetle-like *Coccorchestes* may have few scales, but the few that they do have (on their legs)

almost certainly play a role in their mimicry of weevils (Alan 2022). Recently the role of coloration with respect to intraspecific communication has received much attention (e.g., Taylor 2012; Taylor, Clark & McGraw 2014; Girard, Kasumovic & Elias 2018). When basking, jumping spiders of the genus *Phidippus* orient the dorsal opisthosoma, often bearing numerous flat, transparent scales just above the heart, toward the sun; this is certainly associated with some effect on heat transfer and retention, but that effect has not been measured (Hill 1979). Simon (1901-1903) also suggested that scales play a role in the protection of these spiders, although it seems likely that hard and thick cuticle would be more effective.

*Ancestry of spider scales.* Cuticular scales are also found in other spider families, to include the Anyphaenidae, Araneidae, Corinnidae, Gnaphosidae, Liocranidae, Lycosidae, Oxyopidae, Philodromidae, Pisauridae, Sparassidae, Thomisidae and Uloboridae (Townsend & Felgenhauer 1998a, 1998b, 1999a, 1999b, 2001; Zhakarov & Ovtsharenko 2015). A recent, phylogeny of these entelegyne families, supported by comparison of DNA sequences, is shown in Figure 20.



**Figure 20.** Hypothetical or working phylogeny of the entelegyne spiders, based on Wheeler et al. (2017). Families known to include species with cuticular scales are highlighted in green. Scales are also found in other families in this group.

## jumping spider scales

The oldest fossil record that we have for the Salticidae is that of the Baltic Amber. There is still some disagreement about the age of this amber within the 34-55 Ma range, but dating of the blue earth (*blau Erde*) deposits in which it has been found suggests that it originated during the Lutetian stage of the Middle Eocene,  $44.3 \pm 4$  Ma (Ritzkowski 1997; Engel 2001; Wappler 2003, 2005). We can estimate a minimum age for this amber of ~45 Ma. By that time salticids were already quite diverse, with some species that we now associate with the Hisponinae, and others with large very PME, not recognizable by family but thought to represent a primitive grade. As shown in Figure 21, some of these salticids had both pinnate or keeled (class 5 or 6) scales on the carapace, as well as specialized scales around the front eyes.



**Figure 21.** Fossil salticid (HCBA7 in D. E. Hill collection; see Hill & Edwards 2013) embedded in Baltic Amber collected at Palanga near the Baltic Sea. **1**, Note the large PME on the side of the carapace. **2**, Detail of inset from (1). Note the specialized scales that surround the AME. **3**, Detail of inset from (2), showing long pinnate scales that are keeled (class 6 or 7), much like *Platycryptus* (Figure 33). As shown in Figure 2, these are thought to represent a more primitive grade of pigmented scale, but one that is still found in many species.

*Diversification of salticid scales.* The last sections of this paper include documentation of many of the diverse scales of jumping spiders, following a recent, working version of salticid phylogeny based primarily on the comparison of DNA sequences (Figure 22; Maddison et al. 2014, 2017; Maddison 2015; Maddison & Szűts 2019). Although these scales have been of considerable interest in recent years, we still know very little of them. As more information emerges, we should be able to develop a much better picture of the evolution of scale forms and the many innovations associated with their construction and placement.

							Eupoinae		
Salticidae							Asemoneinae		
								Lyssomaninae	Lyssomanes
								Spartaeina	Portia
							Spartaeini	Holcolaetina	
	Spartaeinae					Spartaeinae		Cocalodini	
								Langijni	
							Onomastinae		
							Uianoninao		
								Conhoini	Colonya
		Salticinae						Gopfioffi	Colonius Attachar
								Sitticini Duadini	Attuius
			Amycoida					Breaini	
								Scopocirini	
								Iniodinini	
								Sarindini	Sarinda
								Simonellini	
								Huriini	
								Amycini	Hypaeus
								Baviini	
				Astioida				Myrmarachnina	Myrmarachne
						Myrmarachnini		Levieina	
								Ligonipedina	
								Neonini	Neon
								Astiini	
								Monsini	
						Viciriini		Viciriina	
								Cimeethine	
								Dallini	
								Tinneihini	
								risanibini Coma nalima	
								Synagelina	
								Itatina	
				Marpissoida		Marpissina		Balmaceda, Maevia, Marpissa, Mendoza, Metacyrba,	
							Dendryphantini		Platycryptus, Psecas
			Salticoida					Bagheera, Beata, Dendryphantes, Eris, Hentzia, Mascaroeris,	
								Dendryphantina	Paraphidippus, Pelegrina, Phidippus, Rhene, Sassacus,
									Tutelina, Zygoballus
				Saltafresia				Nannenini	
								Hasariini	
								Agorini	
								Churcillini	Chrysilla, Cosmophasis, Heliophanus, Menemerus, Mexcala,
								Chiryshinni	Phintella, Phintelloides, Siler
					Simonida				Anasaitis, Antillatus, Athamas, Bathippus, Belliena, Chapoda.
									Coccorchestes, Colvttus, Corvthalia, Cvtaea, Diolenius,
									Ecuadattus, Euophrys, Foliabitus, Illaraus, Iotus, Laufeia,
								Euophryini	Lenidemathis Maeota Maratus Marma Nanhrys Neonella
									Ohilimia Omoedus Pristohaeus Prostheclina Pseudeuonhrys
									Saitis Sanhrys Servaea Talayera Thiania Thoralliola
									Tulogonus
								Lentorchestini	Vilonus
								Aelurilling	Adurillus Dhlagra Stongolurillus
							Achumillini	Frouina	Dhialo
							Plexippini	Thiratac	<i>Fillule</i>
								Thiratoscirtina	
								Plexippina	Brancus, Burmattus, Epeus, Evarcha, Hyllus, Parajotus,
									Piexippoiaes, Plexippus, Ptocasius, Telamonia, Thyene
								Harmochirina	Bianor, Habronattus, Harmochirus, Modunda, Neaetha,
									Pellenes
								Salticini	Salticus

**Figure 22.** Working hypothesis for the phylogeny (from left to right) of salticid spiders, with genera treated here presented in the right column (after Maddison et al. 2014, 2017; Maddison 2015; Maddison & Szűts 2019). Not all branches of this tree have been resolved. Note that many clades, for which scales have not been described, are not covered in this review. Names for the clades shown here follow names proposed by Maddison (2015).

*Lyssomaninae*. The mostly Neotropical lyssomanines have few scales (Figures 19.1-19.2, 23). On the carapace, they have brushy (class 2) pigmented scales, much like setiform (class 1) scales, but with regular rows of thickly set spinules (setules) surrounding the single shaft of each scale.



Figure 23. SEM, brushy scales, carapace of a female Lyssomanes viridis. Attribution and ©: 1-2, Dimitri V. Logunov.

*Spartaeina*. *Portia fimbriata* have regular, pigmented, pinnate (class 5) scales on both the carapace and opisthosoma (Figure 24). *Portia* can be identified by the presence of irregular tufts of longer setae on the body and legs.



**Figure 24.** Female *Portia fimbriata*. **1**, Suspended in her irregular web. **3**, SEM, regular pinnate scales on carapace. **4**, SEM, similar pinnate scales on opisthosoma. Attribution and ©: 1, Bruce Teo; 2, martisma; 3-4, Dimitri V. Logunov.

*Amycoida*. Except for the sitticines, this is a Neotropical clade, sister to the much larger Salticoida (Figure 22). Many have relatively few scales (Figures 19.3-19.4, 25). Some have both wider, pinnate (class 5) and narrow, bladelike (class 7) scales on the opisthosoma (Figure 26), but few amycoids have been studied.



**Figure 25.** Two amycoids with a subtropical distribution in the southeastern United States. **1**, Female *Colonus sylvanus* (Hentz 1846). This species can be distinguished from the related *C. puerperus* (Peckham & Peckham 1909, not Hentz 1846 which is a female *C. sylvanus*) by the presence of red-orange scales around the eyes, and black flecks that are visible through the sides of the carapace. **2**, Female *Sarinda hentzi* (Banks 1913). These have only a few, simple scales (Figure 26.6), some near the eyes, and the others forming a broken band around the opisthosoma. This band has the appearance of a constricted ant abdomen, much like the ants that share the microhabitat of this ant-mimic.



**Figure 26.** Line drawings of the opithosomal scales of some amycoids. These were viewed under an oil immersion lens (x 1000) and drawn with a *camera lucida*. Those shown in white (pinnate, class 5) have white pigment and a granular appearance under transmitted light. Clear or transparent scales (bladelike, class 7) are viewed from the side and shown in their approximate color under transmitted light.

*Astioida*. This is a large and diverse Australasian clade. We presently have little information about astioid scales. The two genera shown here (Figures 27-28) have simple setiform (class 1) scales.



**Figure 27.** *Mymarachne formicaria*. **1-2,** Male and female. **3-4,** SEM, setiform scales on carapace (3) and opisthosoma (4) of female. Attribution and ©: 1, Pierre Bornand; 2, spidereyes, 3-4, Dimitri V. Logunov.



**Figure 28.** *Neon.* **1,** Male *Neon* sp. **2,** SEM, setiform scales on opisthosoma of female *N. minutus* Żabka 1985. **3,** SEM, setiform scales on carapace of female *N. reticulatus* (Blackwall 1853). **4-5,** SEM, setiform scales on carapace (4) and opisthosoma (5) of female *N. sumatranus* Logunov 1998. Attribution and ©: 1, Óscar Mendez; 2-5, Dimitri V. Logunov.

*Ballini*. Benjamin (2004) published SEM images of the pinnate (class 5) scales of *Ballus, Baviola, Colaxes, Cynapes, Indomarengo* and *Philates,* and the lanceolate (class 8) scales of *Afromarengo, Cynapes* and *Sadies.* Several balline genera also have long, flat setae extending below tibia I, but these may not be scales.

*Marpissina* (Figures 29-34). This is a diverse group, with many representatives that are flattened and live under tree bark. The relationship of marpissine to dendryphantine genera needs work. *Marpissa pomatia* have smooth, elongated scales (class 12, Figure 31), and *Mendoza canestrinii* have smooth, flat lanceolate scales (class 11, Figure 32). North American species placed in *Marpissa* by Barnes (1958), e.g. *M. bina* and *M. pikei* (Figure 30), have both three-shafted, lanceolate (class 8) and flat, lanceolate (class 11) scales, like dendryphantines. The variegated colors of *Platycryptus*, on the other hand, are the product of a mixture of wide, pinnate, keeled (class 6) and thin, dark bladelike (class 7) scales (Figure 33).



**Figure 29.** Representative marpissines. Attribution and ©: 1, Ísis Meri Medri; 4, Felix Riegel; 5, Óscar Mendez; 6, spidereyes 2020; 7, Ryzhkov Oleg; 8, giorege1959.



**Figure 30.** Camera lucida drawings of the opisthosomal scales of some marpissines. Bladelike, keeled scales are drawn from the side. The keel of the wide, white scales of *Platycryptus* (11, compare with Figure 33) was not visible in this view.



**Figure 31.** SEM, scales from carapace (1) and opisthosoma (2) of a female *Marpissa pomatia*, from Tuva. Attribution and ©: 1-2, Dimitri V. Logunov.



**Figure 32.** SEM, scales from carapace (1) and opisthosoma (2) of a female *Mendoza canestrinii*. Attribution and ©: 1-2, Dimitri V. Logunov.



**Figure 33.** Scales of female *Platycryptus californicus* (Peckham & Peckham 1888). **1**, Dorsal view of female from Mineral County, Montana (28 JUL 2022). This species, closely related to *P. undatus* (Figure 13), lives under loose bark in nature but is also commonly found on man-made structures. **2-4**, SEM, scales of the dorsal opisthosoma of a female from Corvallis, Oregon, 1974. All scales are keeled, the lighter-colored ones wider (class 6), the darker ones narrow and bladelike (class 7). Attribution and ©: 1, Kristi DuBois.

Neotropical marpissines of the genus *Psecas* are particularly colorful (Figure 34), with wavy iridescent scales that resemble those of *Cosmophasis* from tropical Asia and Australasia, and elongated red to red-orange pigmented scales. The detailed stucture of these scales is not known.



**Figure 34.** Representatives of the neotropical genus *Psecas* C. L. Koch 1850. **4**, Detail of dorsal opisthosoma of the female shown in (3). In this species transverse bands of long, narrow red-orange scales alternate with wide, wavy iridescent light (lower saturation) blue-green scales. Attribution and ©: 1, Philipp Hoenle; 2, César Favacho; 3-4, Thomas Shahan.

*Dendryphantina* (Figures 16, 35-49). This large clade is thought to have its origin with an ancient group of Neotropical marpissoids that crossed the island archepelago that is now Central America to North America, where it diversified greatly (Hill & Edwards 2013). Subsequently the persistent Bering land bridge (Beringia) provided a land bridge for seasonal species to cross into Asia. Some of the South American dendryphantines may also have a North American ancestry, since the Panamanian land bridge has been available for ~2.8My. American dendryphantines that have been studied have fairly consistent scale structure, a combination of three-shafted (class 8, keeled, lanceolate, with thick margins) pigmented scales and flat (class 11, flat, lanceolate) transparent and reflective or iridescent scales.

However, little is known of the Afroeurasian dendryphantines, or their relationship to American genera. Some, like *Dendryphantes* (Figures 35.5, 47,1-47.5, 48) resemble North American species, but the relationship of other Afroeurasian genera is more problematic. Scales of *Macaroeris* (Figures 35.6, 47.6-47.13, 49) resemble the wide and narrow pinnate scales of *Plexippus. Rhene* (Figures 35.8-35.10) has long, thin scales that look more like those of *Marpissa pomatia* (Figure 31).



**Figure 35.** Some of the diverse salticids that are presently placed in the Dendryphantina. Attribution and ©: 1, weisswolf; 2-3, Ashley M. Bradford; 4, Thomas Shahan; 5, Roman Providukhin; 6, Per Hoffman Olsen; 8, Chaturi Jayatissa; 9, Vijay Vanaparthy; 10, Matt Hamer.



**Figure 36.** Carapace scales of *Hentzia* sp., Tolland County, Connecticut (13 OCT 2014). **1**, view of carapace, showing distribution of white and orange pigmented scales. **2**, Detailed view. All scales are three-shafted. The orange scales may be narrower, but some scales are also intermediate in color. Attribution and ©: 1-2, Macroscopic Solutions.



**Figure 37.** Female *Paraphidippus aurantius* (Lucas 1833), Oklahoma. **3-4**, Detail of scales on the carapace (3) and dorsal opisthosoma (4). Both the white, pigmented scales (4) and the iridescent green-to-violet scales are similar in size and shape (lanceolate). Attribution and ©: 1-4, Thomas Shahan.



Figure 38. Camera lucida drawings of opisthosomal scales for some dendryphantine salticids from North America.

jumping spider scales



Figure 39. Camera lucida drawings of opisthosomal scales for species of the genus Phidippus from North America.



**Figure 40.** Adult male *Phidippus audax.* **1-2**, Male from Laurens County, South Carolina. **3-7**, SEM, scales of dorsal opisthosoma, male from Johnson County, Iowa (1975). **3**, Cluster of three-shafted, white scales (toward the bottom) of the left posterior white spot. Above this are flat, smooth, shiny transparent dorsal scales. **4**, Distinctive triangle of white, pigmented scales at the center of the opisthosoma. **5**, Detail from (4). **6**, Detail of three-shafted white scales. **7**, Detail of flat, smooth, shiny transparent scales.



**Figure 41.** SEM, more scales of *Phidippus audax* from Johnson County, Iowa (1975). **1**, Dorsal pedipalp of adult male. Note the metatarsal slit-sense organ. **2**, Femur of left pedipalp, adult male. **3**, Detail from (2), showing pore or *pit organ* behind an "ordinary" seta. **4**, Leg of adult male, with spine and scales. **5-6**, Detail of surface texture of individual scales of an immature. **7**, Underside of scale from adult male, showing ventral spines.



**Figure 42.** Scales of adult male *Phidippus clarus.* **1**, Opisthosoma, male from Greenville County, South Carolina. Broad white marginal scales, narrow red-orange scales, and middorsal flat, shiny transparent scales can be seen. **2-7**, SEM, scales from opisthosoma of male from Benton County, Oregon (1974). **2-4**, Above the marginal band of broad white scales can be seen narrower, red-orange scales. **5**, Detail of narrow, red-orange scales. **6**, Red-orange scales below a group of flat, shiny transparent scales. **7**, Flat, shiny transparent scales.



**Figure 43.** Scales of adult male *Phidippus johnsoni* (Peckham & Peckham 1883). **1**, Male from Puyallup, Washington (7 MAY 2010). **2-3**, SEM, dorsal opisthosoma of male from Corvallis, Benton County, Oregon (1974). The pigmented three-shafted scales are uniform and red in color. Attribution and ©: 1, Lynette Elliot.



**Figure 44.** Scales of adult male *Phidippus pius* Scheffer 1905, from Greenville County, South Carolina. **1**, Dorsal view of male. **2**, Transition from setae and shiny cuticle to transverse tract of red scales across the eye region. **3**, dorsal opisthosoma showing parallel tracts of shiny scales. **4**, SEM, showing detailed surface texture of a red-orange scale. **5-6**, Red and transparent, shiny scales under light-field and dark-field magnification. Attribution and ©: 2-6, Rainer F. Foelix.



**Figure 45.** Scales of *Sassacus papenhoei*. **1-4**, Female from Greenville County, South Carolina (27 JUN 2021). **5**, SEM, scales from anterior margin of opisthosoma of a male from Corvallis, Benton County, Oregon (1974). The smooth scales to the left are transparent and iridescent (yellow to green to violet).



**Figure 46.** Scales of a female *Tutelina* sp. **1**, Dorsal view of female from Lane County, Oregon (17 MAY 2021). **2-3**, SEM, Dorsal views of opisthosoma of female from Benton County, Oregon (1974), showing uniform, tapered scales. Attribution and ©: 1, Noah Strycker.
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**Figure 47.** Line drawings of the scales of some European dendryphantines. Attribution and ©: 1-13, Heiko Metzner.



**Figure 48.** SEM, scales from the carapace (1) and opisthosoma (2) of a female *Dendryphantes rudis*. Attribution and ©: 1-2, Dimitri V. Logunov.



**Figure 49.** SEM, scales from the carapace (1) and opisthosoma (2) of a female *Macaroeris nidicolens*. These resemble the pinnate scales of *Plexippus paykulli*. Attribution and ©: 1-2, Dimitri V. Logunov.

*Chrysillini* (Figures 5, 17, 50-54). This Afroeurasian clade is well-known for brilliant iridescence and color of its tropical Asian members. Available records, which are still limited, suggest that the scales that thickly cover the carapace and opisthosoma of these spiders are predominantly lanceolate and sculpted (Class 8), or lanceolate and flat (class 11), As noted previously (Figure 5; Land et al. 2007), iridescence in *Cosmophasis* can be explained by multilayer interference within hollow lanceolate scales that have a wavy or undulating surface. *Cosmophasis* also have a distinctive cover of overlapping pigmented or transparent scales on the opisthosoma, shaped much like fish scales (Figure 53; class 8-9, lanceolate to rounded; Hill 2009a; Hurni-Cranston & Hill 2021). Similar scales are found on the opisthosoma of the related African genus *Natta* (Hill 2009a).

However members of the well-known, often synanthropic genus *Menemerus* have simpler pinnate, keeled (class 6) scales, or even narrower bladelike (class 7) scales (Figure 50). These scales resemble those of the marpissine *Platycryptus* (Figure 33), which occupy a similar habitat.



**Figure 50.** Scales of *Menemerus bivittatus*. **1**, Adult male. **2**, Adult female. **3**, Camera lucida drawing of the opisthosomal scales of an adult female. **4-5**, SEM, pinnate scales from the carapace of two different females. Attribution and ©: 2, Thilina Hettiarachchi; 4, Dimitri V. Logunov; 5, Bruce E. Felgenhauer.



**Figure 51.** Male *Phinella piatensis* from the Philippines. **1-2**, Two views of an adult male. **3**, SEM, scales from the carapace of an adult male. Attribution and ©: 1-2, Jerian Dale V. Figueroa; 3, Dimitri V. Logunov.



**Figure 52.** Female *Phintelloides versicolor* from east Asia. **1-3**, Three different females, showing variation in scale patterns. Detail of this dense scale cover is shown in the inset (3). **4-5**, SEM, lanceolate, sculpted scales (class 8) from the carapace (4) and opisthosoma (5) of a female. The male of this species is quite different in coloration (Figure 17.8). Attribution and ©: 1, Nikolay Petrov; 2, ag\_nesy; 3, Jimmy Chan; 4-5, Dimitri V. Logunov.



**Figure 53.** Scales of *Cosmophasis* (after Hurni-Cranston & Hill 2021). **1**, Adult female *C. squamata* (Banda Besar, 8 FEB 2016). **2**, Detail of overlapping scales from inset in (1). **3-4**, Camera lucida drawings of opisthosomal scales from a female *Cosmophasis* sp. (Brunei, 1975). **5**, Schematic diagram of overlapping opisthosomal scales (posterior direction at the top). Dorsal opisthosoma of exuvium, male *C. valeriae* (Bali). Attribution and ©: 1-2, 6-7, Tiziano Hurni-Cranston; 3-5, David E. Hill.



**Figure 54.** Adult male *Cosmophasis valeriae* (after Hurni-Cranston & Hill 2021). **6-8,** Lanceolate, wavy, iridescent scales of the carapace. **9-10,** Iridescent and dark, lanceolate-ovate scales of opisthosoma. Attribution and ©: 1-10, Tiziano Hurni-Cranston.

*Euophryini*. In the most current leveling scheme for subfamilies within the Salticidae (Figure 22; Maddison 2015) the euophryines are situated some four levels below the rank of subfamily (*Salticinae*). The group represents a much larger share of salticid diversity than this would suggest. Here the Euophryini is divided into seven hypothetical clades (Figure 55, 1-6, and *Holophyrni*).



**Figure 55.** Simplified working phylogeny for the clade or tribe Euophryini, after Zhang & Maddison (2013, 2015 fig. 1). New names for seven larger clades (numbered 1-6, and *Holophyrni*) have been added here, in bold print. This phylogeny may be revised based on new DNA sequencing data in the future (Junxia Zhang, pers. comm.). Distribution of these species suggests an origin for the Euophryini before or during the Eocene of southern Gondwanaland (South America + Antarctica + Australasia), with isolation of the Australphryni and Papuaphryni in Australasia by the end of the Eocene (~34 Ma; Hill 2009b). Seasonal Holarctic genera (ancestral Holophryni) could move between North America and Asia over the Bering Land Bridge (Beringia; Hill & Edwards 2013).

*Mesophryni* (Figures 56-58). This clade includes many species of *Anasaitis* and *Corythalia*, known primarily from the Caribean and Mesoamerica. Many feed on ants (Jackson & Van Olphen 2009). Scales, often shiny or iridescent, can be elaborate (class 8, lanceolate), or narrow and long (class 7 or 12).



**Figure 56.** Three species representing the large Neotropical genus *Corythalia*. Presently 88 species are described for this genus (WSC 2022), and many remain to be discovered. Attribution and ©: 1, Antonio Tosto; 2, Ísis Meri Medri; 3, Josue Ramos Galdamez.



**Figure 57.** *Anasaitis canosa.* **1-3,** Female from Greenville County, South Carolina (25 JUN 2022). **4-7,** SEM, scales from opisthosoma (4) and carapace (5) of immature, and adult carapace (6-7). Attribution and ©: 4-7, Bruce E. Felgenhauer.



**Figure 58.** Camera lucida drawings of scales from the opisthosoma of two species of *Anasaitis, A. canosa* and *A. venatoria*. Scales of *A. canosa* reflect many metallic colors, including brass, bronze or gold, and brilliant white-silver.

*Palaephryni* (Figures 59-62). This clade includes many small salticids with a primarily Palaearctic ditribution. Many males have colorful, pigmented scales on the face, but these have not been studied. The pigmented scales that have been studied for this clade are relatively simple, some pinnate as viewed under a light microscope, but probably keeled (class 6). The genus *Euophrys* has long been used as a repository for unrelated species, and still contains about 100 species (WSC 2022), most little known.



**Figure 59.** Palaephrynes in the *Euophrys clade* (Zhang & Maddison 2015). Attribution and ©: 1, Alexis; 2, Tituan Roguet; 3-4, 6, Óscar Mendez; 5, Gábor Keresztes.



**Figure 60.** SEM, long and narrow keeled scales from the sculpted carapace (1-3) and opisthosoma (4) of a female *Euophrys frontalis* from Sweden. Note the many ridges along the length of these scales. Attribution and ©: 1-4, Dimitri V. Logunov.



**Figure 61.** SEM, scales of *Talavera* species. **1-2**, Carapace (1) and opisthosoma (2), female *T. aequipes* from Byelorussia. **3**, Carapace of a female *T. esyunini* from Finland. **4-5**, Carapace of a male *T. petrensis* from Kazakhstan. Note the uniformity of prominent keels and oblique ridges on these scales. Attribution and ©: 1-5, Dimitri V. Logunov.



**Figure 62.** Line drawings of the scales of some palaephrynes. Under the light microscope, the keel and lengthwise ridges of these scales can be difficult if not impossible to observe. Attribution and ©: 1-34, Heiko Metzner.

*Antilphryni* (Figures 63-64). This is a diverse, largely Neotropical group with many representatives in the Antilles. Some have iridescent scales, but only the scales of *Naphrys*, small leaf-litter inhabitants in North America, have been studied. At least some of these are leaf litter inhabitants that frequently prey on ants (Clark, Jackson & Cutler 2000).



Figure 63. Some Neotropical antilphrynes. Attribution and ©: 1, Antonio Tosto; 2, Karl Kroeker; 3, Ísis Meri Medri.



**Figure 64.** *Naphrys.* **1,** Male *N. pulex* from Greenville County, South Carolina, 12 MAY 2022. **2,** Female *N. pulex* from Greenville County, South Carolina, 4 JUN 2021. **3-4,** Scales from carapace (3) and opisthosoma (4) of a female *N. pulex.* **5-8,** Camera lucida drawings of scales from the opisthosoma of three *Naphrys* species. Attribution and ©: 3-4, Dimitri V. Logunov.

*Neophryni* (Figure 65). This little-known clade of very small to medium-sized Neotropical euophryines appears to represent the sister group of the diverse and well-known Australphryni, a major part of the Australasian salticid fauna. Many of these are from elevated habitats in the Andes. Some have colorful or even iridescent scales or setae, but the scales of neophrynes have not been studied. Representatives of the group are shown here because of their interesting relationship to the better known Australphryni.



**Figure 65 (continued on next page).** Representative neophrynes, mostly from Ecuador. Attribution and ©: 1-9, Wayne P. Maddison.



**Figure 65 (continued from previous page).** Representative neophrynes, mostly from Ecuador. Attribution and ©: 10-12, 17-18, Wayne P. Maddison; 13, weisswolf; 14-15, Daniel Roueche; 16, Professor Sel.

*Australphryni* (Figures 6-12, 14, 66-68). Scales of the now well-known peacock spiders (*Maratus* species) have already been reviewed in the discussion of iridescence. This is a diverse clade in temperate to subtropical Australia, where it, along with the Astioida, dominates the salticid fauna. At the same time there are many tropical australphrynes (e.g. *Colyttus, Thiania, Thorelliola*) that appear to have ancestors that once travelled from Australasia (*Sahul*) to Southeast Asia (*Sunda*), where they are now established (Hill 2010a). The European distribution of *Saitis*, a close relative of the peacock spiders (Zhang & Maddison 2013, 2015), is more problematic. This may represent the result of a series of introductions to Mediterranean ports from Australasia by early European traders (Otto & Hill 2012).

The scales of australphrynes remain little-known and may be quite diverse. No clear relationship can be seen between the scales of *Maratus* and the other members of this group.



**Figure 66.** Representative australphrynes. Attribution and ©: 1, 11, budak; 2, 5, Nikolai Vladimirov; 3, Richard Ong; 4, Jürgen C. Otto; 6, simon cooper; 7, Jacky Lien; 8, John; 9-10, Tony Iwane; 12, Nikolay Petrov.



**Figure 67.** *Saitis.* **1-2,** The type species for this genus, the synanthropic *S. barbipes*, is well-known in Europe where its range may be growing. **3-5,** Some Australian *Saitis.* Although DNA sequencing supports a close relationship of some Australian *Saitis* to *S. barbipes* (Zahng & Maddison 2013, 2015), the relationship of the species shown here is not known. **6-26,** Line drawings of scales from European *Saitis* species. These appear to range from setiform (class 1) to brushy (class 2) or pinnate (class 5), but no relationship to the scales of *Maratus* can be seen. Some may resemble the scales of *Servaea* or *Thorelliola* (Figures 68.3-68.7). Attribution and ©: 1-2, Cédric Mondy; 3-5, Jürgen C. Otto; 6-26, Heiko Metzner.



**Figure 68 (continued on next page).** SEM, scales of some australphrynes. **1-2**, SEM, rounded scales from carapace (1) and opisthosoma of a female *Laufeia keyserlingi* (Thorell 1890). **3-4**, SEM, sculpted, lanceolate (class 11) scales from the carapace (3) and opisthosoma (4) of a female *Lepidemathis sericea* (Simon 1899). **5**, SEM, flat scales from the opisthosoma of a male *Servaea* sp. **6**, Pinnate (class 5) scales from the eye region of a female *Servaea* sp. **7**, Brushy (class 2) scale beneath the PLE of a female *Servaea* sp. Attribution and ©: 1-7, Dimitri V. Logunov.



**Figure 68 (continued from previous page).** SEM, scales of some australphrynes. **8-9,** SEM, iridescent scales on the carapace (8) and opisthosoma (9) of a male *Thiania bhamoensis* (Figures 66.9-66.10). **10-11,** SEM, carapace (10) and opisthosoma (11) of a female *Thorelliola ensifera* (Figure 66.12). Attribution and ©: 8-11, Dimitri V. Logunov.

*Papuaphryni* (Figures 69-71). This large clade is a major component of the tropical Australasian fauna, with some representatives (e.g., *Cytaea*) that have diversified in southeast Asia. They may have been isolated from South American euophrynes for a longer period of time than have the Australphryini. Many unusual forms are endemic to New Guinea, but scales are only known for *Cytaea* (Figure 70), and these resemble the scales of *Lepidemathis* (Figures 68.1-68.2). *Cytaea* may have shiny or iridescent scales that, like those of certain chrysillines, overlap and cover the opisthosoma like fish scales. *Athamas* have a covering of brushy (class 2) scales on both the carapace and opisthosoma (Figures 71.1-71.2), and *Bathippus* have simple, pinnate (class 5) scales (Figures 71.3-71.4). These deserve much study in the future.



**Figure 69.** Representative papuaphrynes, mostly from New Guinea (Papua). The come in many remarkable forms, but perhaps the most amazing of all are weevil mimics of the genus *Coccorchestes* (5-6; see Allan 2022). Attribution and ©: 1, Felix Fleck; 2-4, Philipp Hoenle; 5-10, Wayne P. Maddison; 11, budak.



**Figure 70.** *Cytaea.* **5,** The opisthosoma of this *Cytaea* is covered with overlapping scales, much like those of *Cosmophasis.* **10-11,** SEM, carapace (10) and opisthosoma (11) of a male *Cytaea oreophila* Simon 1902. **12,** Carapace of female *Cytaea mitellata* (Thorell 1881). Attribution and ©: 1, valryr; 2, Narong Thepphibalsathit; 3, Pasin Maprasop; 4-6, Robert Whyte; 7-9, Tiziano; 9, marcel-silvius; 10-12, Dimitri V. Logunov.



**Figure 71.** Scales of some unusual papuaphrynes. **1-2**, SEM, brushy scales of the opisthosoma of a female *Athamas whitmeei*, a widely distributed inhabitant of islands in the southwest Pacific (Figure 69.1; Hill & Fleck 2018). **3-4**, SEM, pinnate scales from the carapace (3) and opisthosoma (4) of a female *Bathippus* sp. Attribution and ©: 1-4, Dimitri V. Logunov.

*Leptorchestini* (Figures 72-73). The sand-dwelling Eurasian spiders of the genus *Yllenus* have very distinctive scales, although their colors are not remarkable. In recent years some taxonomists have followed Prószyński (2016), transferring some species to either *Marusyllus* or *Pseudomogrus*.



Figure 72. Three views of a Yllenus (Pseudomogrus) univittatus. Attribution and ©: 1-3, Martin Galli.



**Figure 73 (continued on next page).** SEM, scales of *Yllenus* spp. **1-4**, Carapace of female *Y. albocinctus* (Kroneberg 1875). **5**, Metatarsus of female *Y. albocinctus*. **6**, Carapace of female *Y. arenarius* Simon 1868. Attribution and ©: 1-6, Dimitri V. Logunov.



**Figure 73 (continued from previous page).** SEM, scales of *Yllenus* spp. **7-9**, Carapace of female *Y. arenarius*. **10-11**, Carapace of female *Y. coreanus* Prószyński 1968. **12**, Opisthosoma of female *Y. coreanus*. **13-14**, Carapace of female *Y. mongolicus* Prószyński 1968. Scales on the carapace and opisthosoma of these Yllenus (class 8, keeled, lanceolate) are relatively uniform and elaborately sculpted on the upper surface. After Logunov & Marusik 2003. Attribution and ©: 7-14, Dimitri V. Logunov.

*Aelurillina* (Figures 74-77). This is a large, almost entirely Afroeurasian clade. The few aelurilline scales that have been described (Figures 75, 77) appear to be either brushy (class 2) or pinnate (class 5), but a detailed view of the pinnate scales of *Phlegra* (Figure 75) shows that these are remarkably flat, with very regular rows of setules on either side.



**Figure 74.** Representative aelurillines. Attribution and ©: 1-2, Arnold Wijker; 3, Simon Oliver; 4-5, raedwulf68; 6-7, Felix Riegel; 8-9, Bernard Noguès, 10-11, acharya\_mr; 12, Anubhav Agarwal.



**Figure 75.** *Phlegra fasciata.* **4-7,** SEM, regular flat, pinnate scales from the opisthosoma of a male. Until recently, the exclusively North American *P. hentzi* (Figure 76) was thought to represent the same species (Logunov & Kopenen 2002). Attribution and ©: 1, Rasmus Allesoee; 2, Felix Riegel; 3, Pascal Dubois; 4-7, Dmitri V. Logunov.



Figure 76. Male Phlegra hentzi, an aelurilline from eastern North America.



Figure 77. Line drawings of some aelurilline scales. Attribution and ©: 1-25, Heiko Metzner.

*Plexippina* (Figures 78-83). This clade is primarily Afroeurasian, with little representation outside of that vast region except for the cosmotropical *Plexippus paykulli* (Figure 80) and a few *Evarcha* species. The few scales that have been examined in detail are mostly pinnate (class 5; Figures 79-82), but there are also many other scale types to be found here.



**Figure 78.** Representatives of the Plexippina. Attribution and ©: 1, 5-7, 12, Wynand Uys; 2, Narong Thepphibalsathit; 3, C. Sano; 4, 8, Thomas Shahan; 9, Jungle Johnny; 10, budak; 11, Dan Lee.



**Figure 79.** Pinnate scales of two Palaearctic *Evarcha* species. **7-8**, SEM, carapace (7) and opisthosoma (8) of a female *E. arcuata*. **9-10**, SEM, carapace (9) and opisthosoma (10) of a female *E. falcata*. Attribution and ©: 1-4, Felix Riegel; 5, astrobert; 6, Lutautami; 7-10, Dmitri V. Logunov.



**Figure 80 (continued on next page).** *Plexippus* species and their pinnate scales. **5-13,** SEM, scales of an adult male P. paykulli from Georgia, USA (1975). **5,** Dark scales with rounded apices below the left PLE. **6,** Narrower, dark brown scales of the carapace margin below wider white scales. Attribution and ©: 1, Christian Schwartz; 2, 杨小峰 (windywings).



**Figure 80 (continued from previous page).** *Plexippus* species and their pinnate scales. **7,** Scales near left lateral margin of the carapace. Below, wider scales are white to orange (at the transition), above narrower scales are dark brown. **8-10,** Three views of darker scales of the carapace, with narrow shafts. **11-12,** White to off-white scales from the carapace (11) and a leg (12), with wider shafts. **13,** Underside of scales removed from a leg, showing irregular rows of spinules.



Figure 81. SEM, carapace (1) and opisthosoma (2) of a female Burmattus pockocki. Attribution and ©: 1-2, Dmitri V. Logunov.



Figure 82. Female *Telamonia dimidiata*. 2, Detail showing keeled, lanceolate (class 8) scales of the carapace. Attribution and ©: 1-2, Roman Prokhorov.



Figure 83. Line drawings of some plexippine scales Note the diversity of forms in Thyene. Attribution and ©: 10-27, Heiko Metzner.

*Harmochirina* (Figures 84-91). Long known as *pellenines*, this mostly Afroeurasian clade includes the well-known North American paradise spiders of the genus *Habronattus*, characterized by a high degree of ornamentation and the elaborate courtship display of adult males. For many *Habronattus*, male display includes elevation of the ornamented and expanded patellae (*epaulets*) of legs III above the carapace.



**Figure 84.** Some representative harmochirines (pellenines). **4**, Note the decorated patella and tibia of leg III. Attribution and ©: 1, watsaisaeng; 2, 5-6, Thomas Shahan; 3, Luis Stevens; 4, Robby Deans; 7, Anubhav Agarwal; 8-10, Simon Oliver; 11, Denis Doucet; 12, Максим Стефанович.

Although the scales of relatively few species in this group have been examined in detail, the scales that are known are quite variable, even on a single individual. Most scales of *Habronattus* and *Pellenes* species appear to be either wider, lighter, keeled and lanceolate (or three-shafted, class 8), or narrow, darker and elongated (class 12). But some, like male *H. coecatus* (Figure 85), also have red brushy (class 2) scales on the clypeus, producing a highly saturated color. Iridescent scales of *H. hallani* are lanceolate but flat (Foelix, Erb & Hill 2013). Scales of the less-known *Harmochirus* (Figure 87) and *Neaetha* (Figure 88) are also keeled and lanceolate (class 8), but with elaborate and distinctive sculpturing of the upper surface.



**Figure 85.** Male *Habronattus coecatus.* **2**, SEM, brushy (class 2) scales of the clypeus. The surface stucture of these scales reduces reflection and thus contributes to the highly saturated red color of these scales. **3**, SEM, cream-colored scales of the tibia of the pedipalp. **4**, Cream colored scales of the leg I metatarsus. Attribution and ©: 2-4, Rainer F. Foelix.



**Figure 86 (continued on next page).** Male *Habronattus ophrys.* **7-19,** SEM, specimen collected with holotype in Corvallis, Oregon, 4 MAY 1974. **7,** Face. **8,** Upper left corner of carapace. Attribution and ©: 1-6, Thomas Barbin.



**Figure 86 (continued from previous page, continued on next page).** Male *Habronattus ophrys.* **9-10,** Short, three-shafted scales below the left anterior eyes. **11-13,** Lanceolate scales from side of carapace. **14,** Anterodorsal corner of opisthosoma, showing wider, lighter marginal scales grading to narrow, dark scales of the dorsum. **15,** Transitional scales near anterior margin of the opisthosoma (at left).



**Figure 86 (continued from previous page).** Male *Habronattus ophrys.* **16-19,** Detailed views of three-shafted, wider, creamcolored, lanceolate (class 8), and narrow, dark, elongated (class 12) scales of the dorsal opisthosoma.



**Figure 87.** Female *Habronattus pyrrithrix.* **2-3**, SEM, lanceolate scales of carapace (2) and opisthosoma (3). Attribution and ©: 1, Luann Wright; 2-3, Dmitri V. Logunov.



**Figure 88.** *Harmochirus.* **5-7,** SEM, finely sculpted lanceolate scales of carapace margin (5), below the PLE (6), and in the eye region (7) of a female *H. brachiatus* from Sumatra, after Logunov (2000). Attribution and ©: 1, Luke Mackin; 2, Lawrence Hylton; 3-4, Robert Wienand; 5-7, Dmitri V. Logunov.


**Figure 89.** *Neaetha membrosa.* **4-7,** SEM, finely sculpted, keeled, pinnate scales from the carapace of a female behind the AME (4-5), on the clypeus (6), and below the PME (7), after Logunov (1996). The margins of these scales are particularly intricate. Attribution and ©: 1, Claudia Fernández; 2, Óscar Mendez; 3, Antonio J. Pizarro Méndez; 4-7, Dmitri V. Logunov.



**Figure 90.** *Pellenes.* **4-5,** SEM, scales from the carapace (4) and opisthosoma (5) of a female *P. lapponicus.* **6-7,** SEM, scales from the carapace (6) and opisthosoma (7) of a female *P. sibericus* from Tuva. These are similar to the scales of *Habronattus*. Attribution and ©: 1-2, calebcam; 3, Ирина; 4-7, Dmitri V. Logunov.



Figure 91. Camera lucida drawings of the opisthosomal scales of some North American harmochirines.

*Salticini* (Figures 18, 92-93). Many *Salticus* have transverse bands of alternating white and dark brown or black scales. The bright white scales are wide, finely sculpted, keeled, and lanceolate (class 8), with five shafts visible on the dorsal surface. Each shaft corresponds to a regular row of spinules (setules) on the underside of each of these scales (Figure 92:5). The dark scales are long and narrow, and laterally compressed or bladelike (class 7). Scales of other genera presently assigned to the Salticini are not well-known, and may have little relationship to the distinctive white scales of *Salticus*. Carapace scales of *Mogrus larisae* Logunov 1995, as shown in an SEM image by Logunov (1995, fig. 1), are regularly pinnate (class 5) and bear no resemblance to those of *Salticus*.



**Figure 92.** *Salticus scenicus.* **3-7,** SEM, scales from the dorsal opisthosoma of an immature collected in Johnson County, Iowa (1995). **3-4,** A band of narrow bladelike (class 7) scales (at right) contrasts with a band of wide, lanceolate (class 8) scales. **5,** Underside of lanceolate scales. **6-7,** Detailed views of lanceolate scales. Attribution and ©: 1, Kristi DuBois; 2, Frank Hendre.

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jumping spider scales



**Figure 93.** Line drawings of scales from some *Salticus* species. Reflected, not transmitted, light is required to view the five shafts of the wide scales under a light microscope. Attribution and ©: 3-19, 22-25, Heiko Metzner.

### Acknowledgements

I am very grateful for the important contributions of Bruce E. Felgenhauer, Rainer F. Foelix, Frank Hendre, Tiziano Hurni-Cranston, Dmitri V. Logunov, Heiko Metzner and Jürgen C. Otto to this paper, something that has been in the works for a long time. I am also grateful to Wayne Maddison, the authors of a series of published papers, and a long list of dedicated *iNaturalist* contributors, all of whom have made their work accessible through *Creative Commons* licenses. I thank Don Cadle, Bruce Cutler, Glavis B. Edwards, David B. Richman and Patrick Zephyr for their assistance in the collection of spiders, and Christopher J. Bayne, Thomas Eisner, Jon Reiskind and C. Y. Shih for their support with my earlier studies of salticids and salticid scales. Contributions are acknowledged with respective figures, and are also listed in Appendix 1. I have generally followed the identification of spiders as posted at the *iNaturalist* site, and any errors in this department are my own, subject to correction in a later edition of this paper.

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![](_page_79_Figure_23.jpeg)

Figure 94. Pen and ink drawing of the opisthosomal scales of Phidippus audax, from the original PECKHAMIA 1:5 (JUN 1978).

# Appendix 1. Detailed attribution for images by figure.

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## jumping spider scales

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$\begin{array}{c} 57.1-57.3\\ 57.4-57.7\\ 58\\ 59.1\\ 59.2\\ 59.3\\ 59.4\\ 59.5\\ 59.5\\ 59.6\\ 60\\ 61\\ 62\\ 63.1\\ 63.2\\ 63.3\\ 64.1\\ 64.2\\ 64.3-64.4\\ 65.1-65.12\\ 65.13\\ \end{array}$	female Anasaitis canosa, Greenville County, South Caroline, 25 JUN 2022           SEM, scales of Anasaitis canosa           camera lucida drawings of Anasaitis scales           male Euophrys frontalis, Steglitz-Zehlendorf, Berlin, Germany, 3 JUL 2021           male Euophrys herbigrada, Montpellier, France, 19 MAY 2022           male Euophrys nigripalpis, Vacarisses, Barcelona,Spain, 9 JUN 2017           male Euophrys nigripalpis, Vacarisses, Barcelona,Spain, 9 JUN 2017           male Euophrys rufibarbis, Barcelona, Spain, 8 OCT 2017           female Pseudeuophrys erutica, Biatorbágy, Hungary, 19 MAR 2022           male Talavera petrensis, Barcelona, Spain, 27 MAR 2021           SEM, scales of Falovera species           line drawings, scales of Euophrys and Pseudeuophrys respecies           male Antillanus cambridgei, Cambita Garabitos, Domincan Republic, 9 JUN 2015           female Angota giller, Cartago Province, Turrialba, Costa Rica, 6 APR 2019           male Maphrys pulex, Greenville County, South Carolina, 12 MAY 2022           male Naphrys pulex, Greenville County, South Carolina, 12 MAY 2022           male Naphrys pulex, Greenville County, South Carolina, 4 JUN 2021           SEM, scales of Maphrys pulex           camera lucida drawings of Naphrys pulex scales           Neophryn from Ecuador	David E. Hill Bruce E. Felgenhauer David E. Hill Alexis Titouan Roguet Öscar Mendez Öscar Mendez Gåbor Keresztes Öscar Mendez Dimitri V. Logunov Dimitri V. Logunov Heiko Metzner Antonio Tosto Karl Kroeker Isis Meri Medri David E. Hill David E. Hill David E. Hill Wayne P. Maddison Weisewolf	https://www.inaturalist.org/observations/85742704 https://www.inaturalist.org/observations/18672816 https://www.inaturalist.org/observations/18672816 https://www.inaturalist.org/observations/106927128 https://www.inaturalist.org/observations/109093601 https://www.inaturalist.org/observations/109093601 https://www.inaturalist.org/observations/80716500 https://www.inaturalist.org/observations/127016134 https://www.inaturalist.org/observations/36306648 https://www.inaturalist.org/observations/25363184 https://salticidae.org/salticidImages/ https://salticidae.org/salticidImages/	CC BY 4.0 with permission CC BY 4.0 CC BY 4.0 CC BY-NC 4.0 CC BY 4.0 CC B
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#### Peckhamia 279.1

## jumping spider scales

70.1	female Cytaea alburna, Magnetic Island, Oueensland, 18 APR 2016	valrvr	https://www.inaturalist.org/observations/65489527	CC BY-NC 4.0
70.2	male Cytaea dispalans, Bangkok, Thailand, 24 MAR 2013	Narong Thepphibalsathit	https://www.inaturalist.org/observations/120950312	CC BY-NC 4.0
70.3	female <i>Cytaea dispalans</i> , Bangkok, Thailand, 2 MAY 2022	Pasin Manrason	https://www.inaturalist.org/observations/114656818	CC BY-NC 4.0
704-706	male Cytage expectans Bainhow Beach Queensland 18 MAY 2019	Robert Whyte (robertwhyte)	https://www.inaturalist.org/observations/25587499	CC BY-NC 4.0
70.7-70.9	male dytage appetancy and presize NOV 2019	Tiziano	https://www.inaturalist.org/observations/2000/199	CC BV-NC 4.0
70.7-70.0	famelo Cutaca haematica, Tunik Visik Tombula, Poli 16 SED 2021	marcal ciluius	https://www.inaturalist.org/observations/4220011/	CC BV NC 4.0
70.9	remare cyliceu nuemianau, rurak Krisik, remouk, ban, 10 SEF 2021	Dimitri V Lemmer	https://www.maturanscorg/observations/95149920	CC DI-INC 4.0
70.10	SEM, scales of female cycled interface car pace	Dimitri V. Logunov		with permission
/0.11-/0.12	SEM, scales of male <i>Cytaea oreophila</i> carapace and opisthosoma	Dimitri V. Logunov		with permission
71.1-71.2	SEM, scales from opisthosoma of female Athamas whitmeei	Dimitri V. Logunov		with permission
71.3-71.4	SEM, Bathippus sp, scales from carapace and opisthosoma	Dimitri V. Logunov		with permission
72.1-72.3	Yllenus (Pseudomoarus) univittatus, Le Grau-du-Roi, France, 13 APR 2022	Martin Galli	https://www.inaturalist.org/observations/112134499	CC BY-NC 4.0
73.1-73.14	SEM. Yllenus species	Dimitri V. Logunov		with permission
741-742	male <i>Aelurillus concolor</i> Digor /Kars Turkey 7 MAY 2009	Arnold Wijker	https://www.inaturalist.org/observations/35979881	CC BY-NC 4.0
74.2				CC DI-INC 4.0
/4.3	male Aelurinus luctuosus, Granada, Spain, 28 JAN 2015	Simon Oliver	nttps://www.inaturalist.org/observations//0933626	CC BY-NC 4.0
74.4-74.5	male and female Aelurillus v-insignitis, Junglinster, Luxembourg	raedwulf68	https://www.inaturalist.org/observations/75452837	CC BY-NC 4.0
74.6-74.7	female Asianellus festivus, Passau, Bayern, Deutschland, 14 JUL 2020	Felix Riegel	https://www.inaturalist.org/observations/65477976	CC BY-NC 4.0
74.8-74.9	female Phlegra cinereofasciata, near Toulon, France, 28 MAY 2021	Bernard Noguès	https://www.inaturalist.org/observations/80638201	CC BY-NC 4.0
74.10	female Stengelurillus albus, Dakshina Kannada, Karnataka, 24 OCT 2021	acharva mr	https://www.inaturalist.org/observations/99196711	CC BY-NC 4.0
7411	male Stengelurillus lesserti Bangalore Karnataka 14 IIIN 2020	acharva mr	https://www.inaturalist.org/observations/49618432	CC BY-NC 4.0
74.12	male Stangelurillus metalligus Kanglore, annam Tamil Nedu 9 IAN 2017	Anubhay Agamual	https://www.inaturalist.org/observations/17010102	CC BV NC 4.0
74.12	hale Stenderur mus metamcus, Kancheepuram, Family Naud, o JAN 2017	Allubliav Agai wai	https://www.inaturalist.org/observations/47739932	CC DI-INC 4.0
/5.1	male Phiegra fasciata, Fanø, Danmark, 29 MAY 2022	Rasmus Allesoee	nttps://www.inaturalist.org/observations/119334303	CC BY-NC 4.0
/5.2	female Phiegra fasciata, Freiham, Munchen, Bayern, Germany, 25 MAY 2021	Felix Riegel	https://www.inaturalist.org/observations/91409702	CC BY-NC 4.0
75.3	female Phlegra fasciata, Chuyer, France, 21 MAY 2017	Pascal Dubois	https://www.inaturalist.org/observations/19121924	CC BY-NC 4.0
75.4-75.7	SEM, scales of opisthosoma of male <i>Phlegra fasciata</i>	Dimitri V. Logunov		with permission
76	male Phlegra hentzi. Wheeler County, Georgia, USA	David E. Hill		CC BY 4.0
771-7725	line drawings of scales of Adurillus species	Heiko Metzner		with permission
77.1-77.23	nine urawings of scales of Aetal mas species	Devid F Hill		
70.1	camera nuciua ul awings of scales of a female PhileyPu field21	Manand Ibre	https://www.instandist.org/sharp.stic.co/0026002	CC DV NC 4.0
/8.1	remaie <i>bruncus mustelus</i> , Basnee, South Africa, 18 NOV 2017	wynand Uys	https://www.inaturalist.org/observations/8926902	UL BY-NU 4.0
78.2	male Burmattus pococki, Phetchaburi, Thailand, 1 NOV 2020	Narong Thepphibalsathit	https://www.inaturalist.org/observations/99854899	CC BY-NC 4.0
78.3	male Epeus glorius, New Taipei City, Taiwan, 31 AUG 2019	C. Sano	https://www.inaturalist.org/observations/31842099	CC BY-NC 4.0
78.4	male Evarcha ignea, Sofala, Mozambique, MAY 2018	Thomas Shahan	https://www.inaturalist.org/observations/70289135	CC BY-NC 4.0
78.5	male Evarcha striolata, Mopani, Limpono, South Africa, 15 MAY 2018	Wynand Uys	https://www.inaturalist.org/observations/12508006	CC BY 4.0
78.6	female Hullus arayrotoxus Rlyde River near Hoodenruit South Africa 20 DEC 2017	Wynand Ilys	https://www.insturalist.org/observations/0204001	CC RV 4.0
70.0	fomale <i>Darajetus rafulação</i> , Divide River near Unitedaria (C. 1), ACAN 2012	Wimand Here	https://www.inaturalist.org/00servations/7504081	CC BV 4.0
/8./	remaie <i>rurujotus refuigens</i> , Biyde Kiver near Hoedspruit, South Africa, 16 JAN 2019	wynand Uys	nups://www.inaturalist.org/observations/196/5854	LL BY 4.0
78.8	male Plexippoides doenitzi, Kyoto, Japan, NOV 2018	Thomas Shahan	https://www.inaturalist.org/observations/98306213	CC BY-NC 4.0
78.9	female Ptocasius weyersi, Liang, Brunei, 13 AUG 2022	Jungle Johnny	https://www.inaturalist.org/observations/130621039	CC BY-NC 4.0
78.10	male <i>Telamonia festiva</i> , Yio Chu Kang, Singapore, 18 MAR 2022	budak	https://www.inaturalist.org/observations/108911514	CC BY-NC 4.0
78.11	female Thyene inflata Makoni Zimbabwe 16 OCT 2021	Dan Lee	https://www.inaturalist.org/observations/98474142	CC BY-NC 4.0
70.11	formale Thyone and an Mononi South Africa 9 MAY 2019	Wimand Hug	https://www.inaturalist.org/observations/30171112	CC PV 4.0
70.12	renaie <i>Hyene ogueni</i> , Mopani, South Anica, o Mar 2010	Falix Diagal	https://www.inaturalist.org/observations/1220/140	CC DV NC 4.0
/9.1	male Evarcha arcuata, Munchen, Bayern, Deutschland, 25 AUG 2020	Felix Riegel	nttps://www.inaturalist.org/observations/68063622	CC BY-NC 4.0
79.2-79.3	female Evarcha arcuata, München, Bayern, Deutschland, 14 JUL 2021	Felix Riegel	https://www.inaturalist.org/observations/102802415	CC BY-NC 4.0
79.4	female Evarcha arcuata, Garmisch-Partenkirchen, Bayern, Germany, 10 AUG 2021	Felix Riegel	https://www.inaturalist.org/observations/108882883	CC BY-NC 4.0
79.5	male Evarcha falcata, Lilienfeld, Austria, 2 AUG 2020	astrobert	https://www.inaturalist.org/observations/55472122	CC BY-NC 4.0
79.6	female Evarcha falcata Dzyarzhynsk District Belarus 31 IIII. 2022	Lutautami	https://www.inaturalist.org/observations/131225420	CC BY-NC 4.0
79.7-79.9	SEM scales of caranas and onisthering for all a surger a ground	Dimitri V Logunov		with permission
70.0 70.10	SEM, scales of carapace and opisthosoma, female Evaluation areau	Dimitri V. Logunov		with permission
79.9-79.10	SEM, scales of carapace and opistiosonia, female Evarcha functua	Dimitri V. Logunov		
80.1	male <i>Plexippus petersi</i> , Ubud, Gianyar, Bali, Indonesia, 31 JUL 2015	Christian Schwarz	https://www.inaturalist.org/observations/12999166	CC BY-NC 4.0
80.2	male Plexippus setipes, Lishui, Zhejiang, China, 7 JUL 2022	杨小峰 (windywings)	https://www.inaturalist.org/observations/136997376	CC BY-NC 4.0
80.3-80.4	male Plexippus paykulli, Chattahochee County, Georgia, USA, 8 JUN 2020	David E. Hill		CC BY 4.0
80.5-80.13	SEM, scales of male Plexinnus navkulli, Georgia, USA, 1975	David E. Hill		CC BY 4.0
911-912	SEM scales from caranace and enisting on a female Burmattus neckecki	Dimitri V Logunov		with permission
021022	formale Telemonia dimidiata Colombo Sri Lanka, 7 EEP 2022	Doman Brokhorow	https://www.insturalist.org/obcomations/106272212	CC PV NC 4.0
82.1-82.2	iemaie <i>Telamonia alimiatata</i> , Colombo, Sri Lanka, 7 FEB 2022	Roman Proknorov	https://www.inaturalist.org/observations/1065/2215	CUBI-INC 4.0
83.1-83.9	camera lucida drawings of plexippine scales	David E. Hill		CC BY 4.0
83.10-83.27	line drawings of Thyene scales	Heiko Metzner		with permission
84.1	male Bianor angulosus, Pathum Thani, Thailand, 21 SEP 2017	watsaisaeng	https://www.inaturalist.org/observations/100317868	CC BY-NC 4.0
84.2	male Habronattus americanus, Montana, JUL 2022	Thomas Shahan	https://www.inaturalist.org/observations/126158549	CC BY-NC 4.0
84.3	male Habronattus aztecanus Puerto Vallarta Jalisco Mexico 26 IIII. 2021	Luis Stevens	https://www.inaturalist.org/observations/89135400	CC BY-NC 4.0
94.4	male Habronattus anteriadus, Austin Tayas 24 MAP 2020	Pobby Deans	https://www.inaturalist.org/observations/09100100	CC BV-NC 4.0
04.5	male Hubbonattus forticulas, Rustin, Texas, 24 MAR 2020	Themas Chahan	https://www.inaturalist.org/observations/40730730	CC DV NC 4.0
84.5	male Habronattus nanani, Arizona, JON 2012	i nomas snanan	https://www.inaturalist.org/observations/74578749	CC B1-INC 4.0
84.6	maie Habronattus virgulatus, Arizona, JUN 2012	i nomas Shahan	nttps://www.inaturalist.org/observations/74589152	CC BY-NC 4.0
84.7	male Modunda staintoni, Kodaikanal, Tamil Nadu, India, 13 AUG 2021	Anubhav Agarwal	https://www.inaturalist.org/observations/92214986	CC BY-NC 4.0
84.8	male Napoca constanzeae, Granada, Spain, 10 JUN 2019	Simon Oliver	https://www.inaturalist.org/observations/71066591	CC BY-NC 4.0
84.9	female Pellenes arciger, Granada, Spain, 3 APR 2017	Simon Oliver	https://www.inaturalist.org/observations/70935023	CC BY-NC 4.0
84.10	female Pellenes geniculatus, Granada, Spain, 3 MAY 2015	Simon Oliver	https://www.inaturalist.org/observations/70934806	CC BY-NC 4.0
84.11	female Pellenes neninsularis Riverside-Albert New Brunswick 30 APR 2020	Denis Doucet	https://www.inaturalist.org/observations/44422480	CC BV-NC 4.0
94.12	male Pallanas cariatus Savastonol Crimon 26 ADD 2010	Максим Стофанории	https://www.insturalist.org/observations/12/262276	CC BV NC 4.0
07.12	male i eneres seriutus, sevastopoi, orinnea, 20 APK 2019	David F UII	https://www.indturalist.org/observations/124302370	CC DY 4.0
05.1	male nutronallus coeculus, Greenville County, South Carolina	David E. Hill		UL BY 4.0
05.2-85.4	DEM, male Habronattus coecatus scales	Kainer F. Poelix		with permission
86.1-86.2	male Habronattus ophrys, Capital, British Columbia, 8 JUL 2019	Thomas Barbin	https://www.inaturalist.org/observations/28482707	CC BY-NC 4.0
86.3-86.4	male Habronattus ophrys, Vancouver Island, 3 AUG 2017	Thomas Barbin	https://www.inaturalist.org/observations/7341069	CC BY-NC 4.0
86.5-86.6	female Habronattus ophrys, Capital, British Columbia, 15 MAY 2020	Thomas Barbin	https://www.inaturalist.org/observations/46200580	CC BY-NC 4.0
86.7-86.19	SEM, male Habronattus ophrys, Corvallis, Oregon, 4 MAY 1974, collected with holotype	David E. Hill		CC BY 4.0
87.1	female Hahronattus pyrrithrix San Carlos San Diego 30 IIII 2022	Luann Wright	https://www.inaturalist.org/observations/129602497	CC RV-NC 4.0
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0/.2-8/.3	Scales from carapace and opistnosoma of a female Habronattus pyrrithrix	Dimitri v. Logunov		with permission
88.1	male Harmochirus brachiatus, Sungai Penuh City, Jambi, Indonesia, 11 DEC 2021	Luke Mackin	https://www.inaturalist.org/observations/102982320	CC BY-NC 4.0
88.2	male Harmochirus insulanus, Hong Kong, JUN 2022	Lawrence Hylton	https://www.inaturalist.org/observations/123194884	CC BY-NC 4.0
88.3-88.4	female Harmochirus luculentus, Ehlanzeni, Zaire, OCT 2021	Robert Wienand	https://www.inaturalist.org/observations/99221647	CC BY-NC 4.0
88.5-887	SEM, scales of female Harmochirus brachiatus	Dimitri V. Logunov	, , , , , , , , , , , , , , , , ,	with permission
89.1	male Negetha membrosa Olesa de Montserrat Barcelona España 2 MAV 2021	Claudia Fernándoz	https://www.inaturalist.org/observations/105376015	CC RV_NC 4.0
00.2	fomale Negatha membrosa Darcelona Egnaña 20 MAD 2010	Óagar Mandag	https://www.inaturalist.org/observations/1003/0013	CC DV NC 4.0
07.2	remaie ivedeura memorosa, barcelona, Espana, 29 MAR 2018	A design of the state of the st	https://www.indturalist.org/observations/80/69414	CC D1-NC 4.0
89.3	temale Neaetha membrosa, Rota, España, 16 APR 2017	Antonio J. Pizarro Méndez	https://www.inaturalist.org/observations/8791879	CC BY-NC 4.0
89.4-89.7	SEM, scales of female Neaetha membrosa	Dimitri V. Logunov		with permission
90.1-90.2	female Pellenes lapponicus, Colorado, JUN 2022	calebcam	https://www.inaturalist.org/observations/122945303	CC BY-NC 4.0
90.3	female Pellenes sibericus, Kamchatka. Russia. 4 AUG 2020	Ирина	https://www.inaturalist.org/observations/71285350	CC BY-NC 4.0
90 4-90 5	SEM scales of female Pellenes Jannonicus	Dimitri V Logunov	, , , , , , , , , , , , , , , , , , ,	with nermission
90.6.00.7	SEM scales of female Pollones sibering	Dimitri V Logunov		with permission
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91.1-91.8	camera juciua drawings of narmochirine scales	David E. Hill		LL BY 4.0
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92.1	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021	KI ISU DUBUIS		-
92.1 92.2	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus	Frank Hendre		with permission
92.1 92.2 92.3-92.7	female <i>Salticus scenicus</i> , Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male <i>Salticus scenicus</i> SEM, scales of an immature <i>Salticus scenicus</i> , Johnson County, Iowa, 1975	Frank Hendre David E. Hill		CC BY 4.0
92.1 92.2 92.3-92.7 93.1-93.2	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus SEM, scales of an immature Salticus scenicus, Johnson County, Iowa, 1975 camera lucida drawings of scales. male Salticus austinensis. Pavne County. Oklahoma, 1970	Frank Hendre David E. Hill David E. Hill		CC BY 4.0
92.1 92.2 92.3-92.7 93.1-93.2 93.3-93.19	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus SEM, scales of an immature Salticus scenicus, Johnson County, Iowa, 1975 camera lucida drawings of scales, male Salticus austinensis, Payne County, Oklahoma, 1970 line drawings of scales, Salticus son	Frank Hendre David E. Hill David E. Hill Heiko Metzner		with permission CC BY 4.0 CC BY 4.0 with permission
92.1 92.2 92.3-92.7 93.1-93.2 93.3-93.19 92.20.02.21	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus SEM, scales of an immature Salticus scenicus, Johnson County, Iowa, 1975 camera lucida drawings of scales, male Salticus austinensis, Payne County, Oklahoma, 1970 Jine drawings of scales, Salticus spp.	Frank Hendre David E. Hill David E. Hill Heiko Metzner		with permission CC BY 4.0 CC BY 4.0 with permission
92.1 92.2 92.3-92.7 93.1-93.2 93.3-93.19 93.20-93.21	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus SEM, scales of an immature Salticus scenicus, Johnson County, Iowa, 1975 camera lucida drawings of scales, male Salticus austinensis, Payne County, Oklahoma, 1970 line drawings of scales, Salticus spp. camera lucida drawings of scales, female Salticus scenicus, Cook County, Illinois, 1951	Frank Hendre David E. Hill David E. Hill Heiko Metzner David E. Hill		with permission CC BY 4.0 CC BY 4.0 with permission CC BY 4.0
92.1 92.2 92.3-92.7 93.1-93.2 93.3-93.19 93.20-93.21 93.22-93.25	female Salticus scenicus, Grant Creek, Missoula, Montana, 3 JUN 2021 penultimate male Salticus scenicus SEM, scales of an immature Salticus scenicus, Johnson County, Iowa, 1975 camera lucida drawings of scales, male Salticus austinensis, Payne County, Oklahoma, 1970 line drawings of scales, Salticus spp. camera lucida drawings of scales, female Salticus scenicus, Cook County, Illinois, 1951 line drawings of scales, Salticus zebraneus	Frank Hendre David E. Hill David E. Hill Heiko Metzner David E. Hill Heiko Metzner		with permission CC BY 4.0 CC BY 4.0 with permission CC BY 4.0 with permission