

## The scales of salticid spiders

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The form and location of the scales of salticid spiders, as revealed by light and scanning electron microscopy, provide useful diagnostic characters for the separation of species, the assignment of species to genera, and a further understanding of the relationships between salticid genera. Partly on the basis of distinctions provided by scale structure, the new genus *Platycryptus*, type-species *Aranea undata* De Geer, 1778, is defined. *Metaphidippus vitis* Cockerell, 1894, is placed in the genus *Sassacus* Peckham, 1895, and *Paramaevia michelsoni* (Barnes), 1955, is returned to the genus *Maevia*. The placement of *Eris*, *Hentzia*, *Icius*, *Metaphidippus*, *Phidippus*, and *Sassacus* in the subfamily Dendryphantinae is substantiated; *Tutelina* and *Zygoballus* are added to this group. On the basis of common scale structure, *Evarcha*, *Habrocestum*, *Menemerus*, *Phlegra*, *Platycryptus*, and *Sitticus* are tentatively assigned to the subfamily Habrocestinae. Scales of *Anasaitis*, *Corythalia*, *Cosmophasis*, *Hyllus*, *Marpissa*, *Metacryba*, *Pellenes*, *Plexippus*, *Salticus*, *Sarinda*, and *Thiodina* are also described.

KEY WORDS:— *Phidippus* — phylogeny — *Platycryptus* gen. nov. — Salticidae — scales — setae — spiders — structure — subfamilies.

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### INTRODUCTION

Most, but not all, species of jumping spiders (Araneae: Salticidae) possess modified setae which may be termed scales. In some cases only a few scales are present, either scattered over the entire body of the spider, or restricted to small,

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well-defined areas. For example, the green *Lyssomanes viridis* is virtually devoid of scales, except for several limited groups of white and red scales near the eyes. In contrast, many salticids, including the well-known *Salticus scenicus*, are almost completely covered by an array of overlapping scales.

Although the characteristics of scale coloration, shape, size, and placement upon the body of the spider may vary greatly between genera and species, these characteristics have very rarely been employed, apart from general statements of coloration, in the systematics of jumping spiders. Lawrence (1942: fig 32a) illustrated scales of *Cylobelus rufopictus*, and Kaston (1948) figured the outline of several white opisthosomal scales from *Phidippus audax*; more recently, Galiano (1975), using scanning electron microscopy, produced a series of pictures of the scales of *P. birabeni*. Apart from these limited presentations, there are virtually no illustrations of the scales of the Salticidae, or those of any spider family, in the literature.

As noted by Prószyński (1971a, b) our current appraisal of the extent of salticid genera, and the relationship between these genera, is far from satisfactory. Indeed, the task of conscientious appraisal has scarcely begun. Prószyński recently (1976) began an ambitious analysis of the relationship of Nearctic to Palearctic genera, based almost exclusively upon male and female genitalia. Unfortunately, the genitalia of salticids are rather simple when compared with those of other spiders. Thus, any conclusions with regard to phylogeny based solely upon the study of genitalia should be supported by additional evidence.

Since scales are universally neglected in species descriptions, this study is essentially an initial effort to establish the relevance of scale characteristics to salticid systematics.

#### MATERIALS AND METHODS

The scales from a variety of primarily Nearctic salticids (Table 1), preserved in 75% ethanol or 70% isopropanol, were examined.

Table 1. Salticid spiders included in this study

Species	Place and date of collection (County, State)	Illustration
♂ <i>Anasaitis venatoria</i> Bryant, 1950	Jamaica, 1969	Fig. 11I
♂ <i>Corythalia aurata</i> (Hentz, 1846)	Marion, Florida, 1976	Fig. 11J
♂ <i>Cosmophasis</i> sp.	Brunei, 1975	Fig. 15P
♀ <i>Eris aurantia</i> (Lucas, 1833)	Cochise, Arizona, 1972	Fig. 10E
♂♀ <i>E. marginata</i> (Walckenaer, 1837)	Benton, Oregon, 1974	Fig. 10F, G
♂ <i>Evarcha hoyi</i> ((Peckham, 1883)	Poverty Bay, Ontario Canada, 1957	Fig. 13G
♀ <i>E. hoyi</i>	Giles, Virginia, 1950	Fig. 13N
♂♀ <i>Habrocestum acerbum</i> Peckham, 1909	Travis, Texas, 1967	Fig. 13J, K
♂ <i>H. pulex</i> (Hentz, 1846)	Alachua, Florida, 1974	Fig. 13H
♂ <i>Habrocestum</i> sp. (not described)	Putnam, Florida, 1975	Fig. 13I
♂♀ <i>Hentzia palmarum</i> (Hentz, 1846)	Levy, Florida, 1975	Fig. 10J, K
♂ <i>Hyllus moestus</i> Pocock, 1903	Kruger National Park, South Africa, 1975	Fig. 15F
♀ <i>Icius harti</i> Peckham (in Emerton, 1891)	Washington, Minnesota, 1970	Fig. 10A
<i>Icius</i> sp. (probably not described)	Benton, Oregon, 1974	Fig. 10B
♂♀ <i>Maevia inclemens</i> (Walckenaer, 1837)	Alachua, Florida, 1974	Fig. 15M, N
<i>Maevia michelsoni</i> (Barnes, 1955)	Alachua, Florida, 1975	Fig. 15O

Table I—continued

Species	Place and date of collection (County, State)	Illustration
♂♀ <i>Marpissa bina</i> (Hentz, 1846)	Levy, Florida, 1975	Fig. 15C, D
♂♀ <i>M. pikei</i> (Peckham, 1888)	Marion, Florida, 1969	Fig. 15A, B
♂ <i>M. sulcosa</i> Barnes, 1958	Alachua, Florida, 1975	Fig. 15E
♀ <i>Menemerus bivittatus</i> (Dufour, 1831)	Alachua, Florida, 1976	Figs 3H, 13B
♂♀ <i>Metacryba taeniola</i> (Hentz, 1845)	Yuma, Arizona, 1961	Fig. 15K, L
♂♀ <i>Metaphidippus galathea</i> (Walckenaer, 1837)	Marion, Florida, 1976	Fig. 10B, C
♂♀ <i>Pellenes arizonensis</i> Banks, 1904	Yuma, Arizona, 1967, 1971	Fig. 11A, B
♀ <i>P. calcaratus</i> Banks, 1904	Marion, Florida, 1976	Fig. 11C
♂ <i>P. hirsutus</i> (Peckham, 1888)	Yuma, Arizona, 1966	Fig. 11F
♂ <i>P. tarsalis</i> Banks, 1904	Yuma, Arizona, 1972	Fig. 11G
♀ <i>P. wrighti</i> Lowrie & Gertsch, 1955	Renville, Minnesota, 1976	Fig. 11H
♀♂ <i>P. cf. coecatus</i> (not described)	Pima, Arizona, 1971	Fig. 11D, E
♂ <i>Pellenes sp.</i> (not described)	Benton, Oregon, 1974	Fig. 12A-C
♀ <i>Phidippus apacheanus</i> Chamberlin & Gertsch, 1929	Daugherty, Georgia, 1953	Fig. 5A
♀ <i>P. audax</i> (Hentz, 1845)	Jackson, Florida, 1954	Fig. 5D
♂♀ <i>P. audax</i>	Johnson, Iowa, 1975	Figs 3E, 5B, C, 6A, B, 7A-C
♂ <i>P. cardinalis</i> (Hentz, 1845)	Putnam, Florida, 1940	Fig. 5H
♀ <i>P. cardinalis</i>	St. Johns, Florida, 1934	Fig. 5I
♂♀ <i>P. clarus</i> Keyserling, 1884	Benton, Oregon, 1974	Figs 3F, 5E, F, 8A, B
♂ <i>P. johnsoni</i> (Peckham, 1883)	Benton, Oregon, 1974	Fig. 9A
♂ <i>P. opifex</i> (McCook, 1883)	Cananea, Sonora, Mexico, 1970	Fig. 5N
♀ <i>P. otiosus</i> (Hentz, 1846)	Duval, Florida, 1948	Fig. 5G
♂♀ <i>P. princeps</i> (Peckham, 1883)	Hennepin, Minnesota, 1976	Figs 2, 3A, C, 5J, K
♂ <i>P. putnami</i> (Peckham, 1883)	Marion, Florida, 1957	Fig. 5O
♂ <i>P. regius</i> C. L. Koch, 1846	Alachua, Florida, 1954	Fig. 5M
♂ <i>P. whitmani</i> Peckham, 1904	Alachua, Florida, 1951	Fig. 5L
♀ <i>Phlegra fasciata</i> (Hahn, 1826)	Giles, Virginia, 1950	Fig. 13C
♀ <i>Platycryptus californica</i> (Peckham, 1888)	Benton, Oregon, 1974	Fig. 13B
♀ <i>P. undata</i> (DeGeer, 1778)	Alachua, Florida, 1976	Fig. 3G, 13A
♂ <i>Plexippus paykulli</i> (Sav. & Aud., 1825)	Georgia, 1975	Fig. 16A-C
♂ <i>P. paykulli</i>	Alachua, Florida, 1976	Figs 3D, 15G
♂ <i>Sassacus vitis</i> (Cockerell, 1894)	Yuma, Arizona, 1961	Fig. 10D
♂ <i>Salticus austinensis</i> Gertsch, 1936	Payne, Oklahoma, 1970	Fig. 15I
♂ <i>S. scenicus</i> (Clerck, 1758)	Johnson, Iowa, 1975	Figs 6C, D, 14A
♀ <i>S. scenicus</i>	Cook, Illinois, 1951	Fig. 15J
♂ <i>Sarinda hentzi</i> (Banks)	Alachua, Florida, 1975	Fig. 15H
♂♀ <i>Sassacus papenhoei</i> Peckham, 1895	Benton, Oregon, 1974	Fig. 10L, N
♂ <i>S. papenhoei</i>	Yuma, Arizona, 1963	Fig. 10M
♂♀ <i>Sitticus fasciger</i> (Simon, 1880)	Ramsey, Minnesota, 1965, 1964	Fig. 13L, M
♂ <i>Thiodina puerpera</i> (Hentz, 1846)	Marion, Florida, 1976	Fig. 13D
♂♀ <i>T. sylvana</i> (Hentz, 1846)	Alachua, Florida, 1974	Fig. 13E, F
♂♀ <i>Tutelina similis</i> (Banks, 1895)	Pipestone, Minnesota, 1967	Fig. 10O, P
♂ <i>Zygoballus bettini</i> Peckham, 1888	Alachua, Florida, 1974	Fig. 10H
♀ <i>Z. nervosus</i> (Peckham, 1888)	Alachua, Florida, 1974	Fig. 10I

For scanning electron microscopy (SEM, Figs 6–9, 12, 14, 16), the detached prosoma, opisthosoma, or leg of the spider was carefully rinsed and dehydrated with 95–100% ethanol prior to critical-point drying. This careful drying procedure is required if one desires to maintain a relatively undistorted opisthosomal cuticle in the specimen. To minimize shrinkage, it is important that storage times in the higher concentrations of alcohol be kept to a minimum. Subsequently the dried specimens were coated with 10–30 nm of gold, prior to examination with a Cambridge Stereoscan S4.

Alternatively, air-dried scales were placed directly onto copper tape on a specimen stub and coated with gold for examination. Although this method does not reveal the position of the scales with respect to the intact cuticle, it does provide better electrical earthing for individual scales, thereby allowing a higher resolution of structure.

Since virtually no salticid systematists are provided with ready access to SEM facilities, simple methods utilizing standard light microscopy were also developed (Figs 5, 10, 11, 13, 15).

For these methods to succeed, it is imperative that specimens are preserved in a dilute alcohol (70%) prepared with distilled or de-ionized water, without chemical impurities which otherwise precipitate upon the specimen with time. Care should also be taken to replace this alcohol at regular intervals to minimize the accumulation of corrosive organic acids. The value of a specimen is vastly increased if these simple precautions are observed.

Specimens are removed from alcohol, rinsed briefly, and placed under a warm lamp until only the cuticle (not the entire specimen) is dry. Scales are gently scraped from the spider with a fine insect pin, which is subsequently *rolled* across the surface of a glass slide to release scales accumulated by electrostatic attraction. The specimen, only slightly altered, is returned to alcohol immediately, and the slide is covered with a *dry* glass cover slip. This air-mount may be made more permanent by the addition of tape or sealant around the edges.

In this study, scales were examined and drawn at  $\times 1000$  with a standard light-microscope fitted with a *camera lucida*. Transmitted light was utilized for examination of scale outlines, as well as the details of the more transparent scales. Strong reflected light was also required to determine the presence of multiple shafts on heavily pigmented (granular) scales. Alternate use of transmitted and reflected light was particularly useful in establishing the types of scales present in a particular specimen.

The appearance of scales varies greatly with the type of illumination employed. Reflected light shows what the observer generally sees in the colour of the living spider. Thus, scales termed *white granular* in this study are white with reflected light, but grey and granular (occluded) in appearance with transmitted light. Clear (transparent) scales are generally dark and shiny with reflected light, and are best described by their transmitted colour, for example, as *light brown clear*. In the latter, ventral spination is readily observed. The lack of such details as ventral spination in drawings of granular scales does not imply that these are not present, but merely that the spines are not readily observed.

For the presentation of representative scale types from the opisthosoma of a variety of salticid spiders (Figs 5, 10, 11, 13, 15), hundreds of individual scales were examined for each species. Although intergrade scales were encountered on

occasion, the scales, as a rule, fall into discrete categories as indicated. It should be noted that, given the technique indicated above, laterally-compressed scales are observed from the side, while dorso-ventrally flattened scales are observed from the top or bottom, as they fall. One must exercise some caution in categorizing scales of intermediate width, which may appear in several orientations.

The absolute length of scales within each category is often quite variable, particularly in the *habrocestine* types, but this does not affect the validity of the process of categorization.

#### THE FORM OF SALTICID SCALES

Salticid scales are modified setae (Fig. 6 A, B), similarly composed of fused cuticular filaments. Unlike all other setae, however, the pedicel or stalk (Fig. 1) of the scale is bent at an obtuse angle where it emerges from its integumental sockets, with the result that the axis of the scale lies adjacent to and parallel with the surface plane of the integument.

Terminology useful in the description of salticid scales is indicated in Fig. 1, a composite diagram based on certain scales of *Corythalia* (Fig. 11J). Certain of these terms are consistent with nomenclature developed for the description of butterfly scales (Downey & Allyn, 1975). Nonetheless, the relatively solid scales of salticid spiders have little in common with the elaborately latticed, hollow scales of higher Lepidoptera.

Inferior spines (Fig. 1: InSp, also Fig. 6B, D), which bring each scale into physical contact with the underlying integument, are generally present. Regular, pointed marginal spines (MSp) often occur adpressed to the lateral margins of the scale (Figs 8B, 12C); these may also be greatly enlarged, in the form of blunt projections (Fig. 16). An apical spine, or pointed apex (Ap), is always present.

Sculpturing of the superior surface, or the lack of such sculpturing, is distinctive for each scale type. Definitive ridges, or ribs, which extend for the

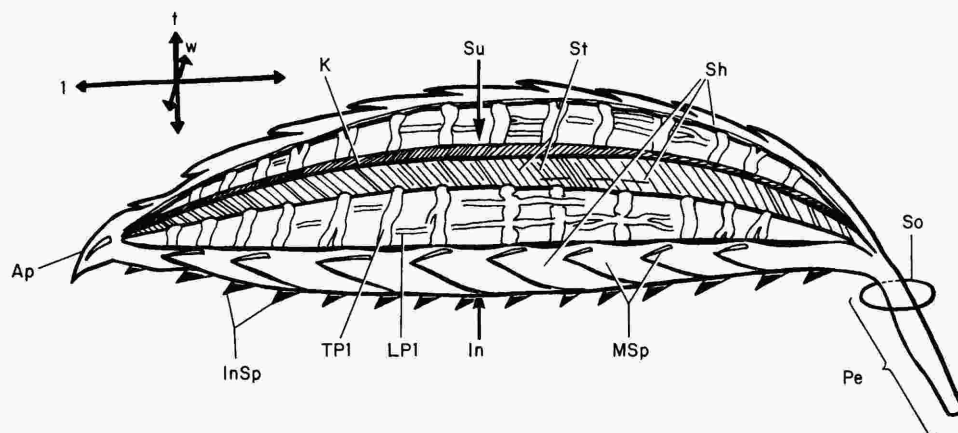


Figure 1. Composite diagram to illustrate the basic external features of salticid scales. The small figure at upper left specifies the axes of length (l), width (w) and thickness (t) for the larger diagram: Ap, apex; In, inferior surface; InSp, inferior spines; K, keel of central shaft; LPI, longitudinal plica; MSp, marginal spines; Pe, pedicel; Sh, shafts; So, socket; St, oblique striae; Su, superior surface; TPI, transverse plica.

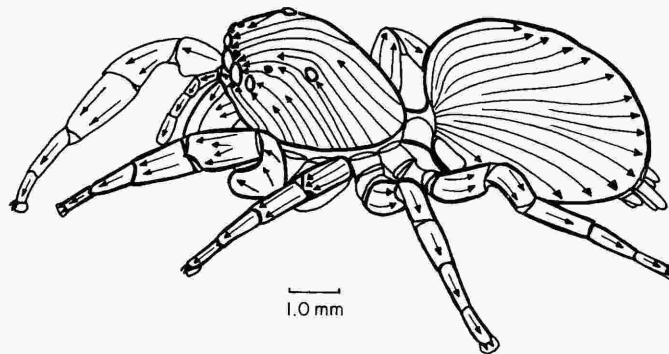


Figure 2. Proximal to distal (pedicel to apex) orientation of scales on the body of an adult female *Phidippus princeps*. This orientation is consistent with the direction in which the old cuticle (exuvium) is removed as the spider molts.

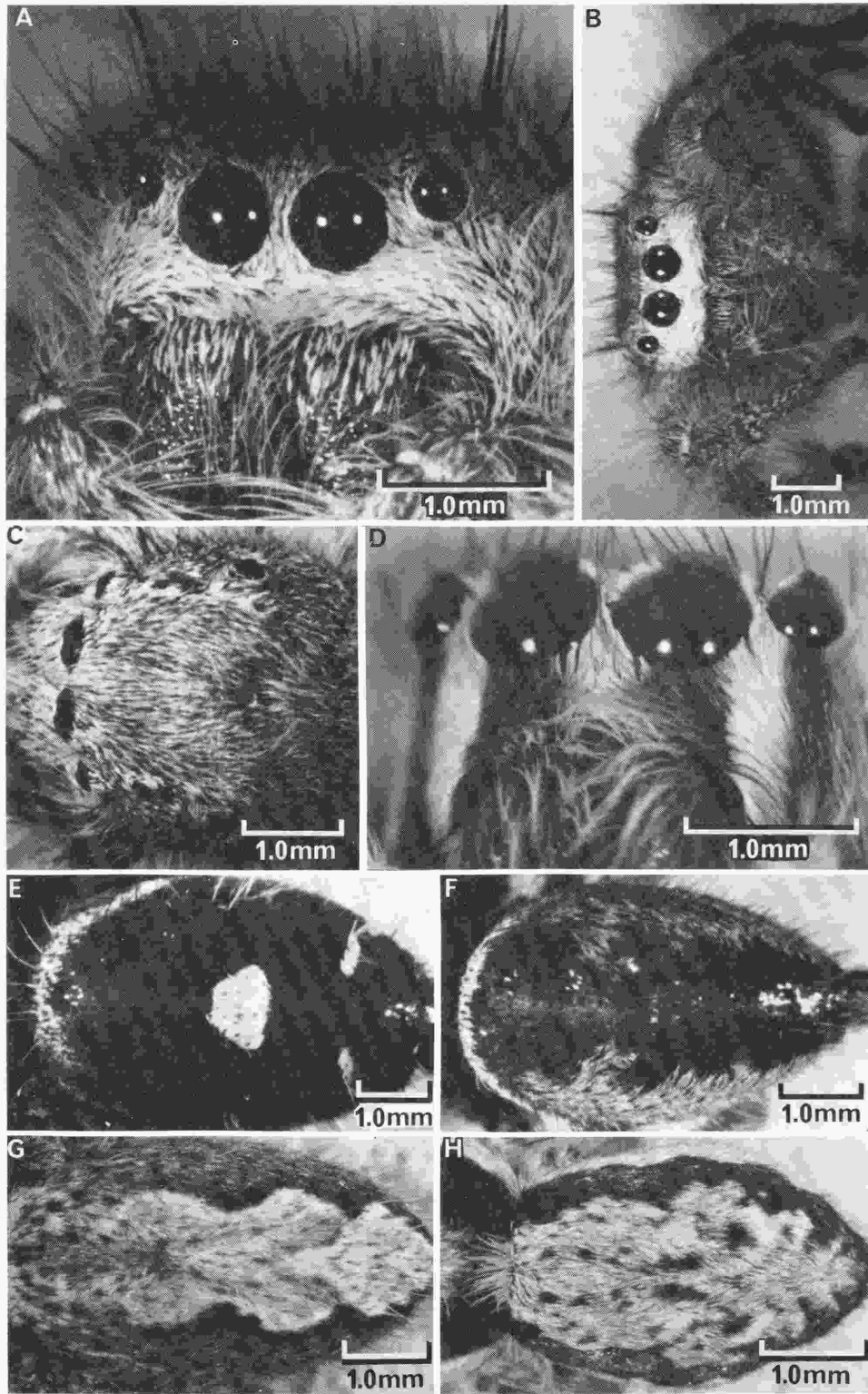
length of the scale are termed *shafts* (Sh). Thus Figs 6A and 8B illustrate three-shafted scales. A sharp ridge is termed a *keel* (K, see also Fig. 14B). Lesser, or subordinate, ridges are termed *plicae*, or folds. Finally, distinct oblique lines, or *striae* (St, also Fig. 14B) may be present on a relatively smooth superior surface.

Scales are generally *clear* or *granular* in appearance when viewed with transmitted light. Clear (transparent) scales are dark and shiny when viewed with reflected light. If they are black to olive-green (transmitted light), then they are quite dark (reflected light), and function as a sink for visible wave-lengths of light. The shape of these dark scales is quite variable, with regard to relative width.

Scales which are highly granular when viewed with transmitted light are, in general, highly reflective. Light-coloured (white or ivory, reflected light), granular scales tend to be broad (wide), while darker granular scales tend to be narrow.

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Figure 3. Distribution of the body scales of various salticids. A ( $\times 25$ ), B. Anterior view of prosoma, adult female *Phidippus princeps* ( $\times 10$ ). In this species the entire clypeal region, as well as contiguous areas of the chelicerae, is covered with a distinctive group of white scales. C. Dorsal view of the prosoma of adult female *P. princeps* ( $\times 15$ ). The entire body of this spider is carpeted with rather uniform, light brown scales. D. Anterior view of prosoma, adult male *Plexippus paykulli* ( $\times 25$ ). The light and dark bands of scales continue along the entire length of this cosmopolitan species, including the opisthosoma. Notice that the pedicel-to-apex orientation of scales and setae in this region agrees with that of *Phidippus* (A, above), despite the difference in colour pattern. E. Dorsal view of opisthosoma with anterior to the left, adult male *Phidippus audax* ( $\times 11$ ). The pattern formed by groups of white scales is distinctive; similar patterns occur in other *Phidippus* species, including *P. putnami* and *P. regius*. Light reflected from a few of the many dark, transparent scales is also visible, along the mid-line. F. Dorsal view of the opisthosoma, adult male *P. clarus* ( $\times 12$ ). The white scales of the anterior margin (left) and two broad lateral bands of orange scales surround a mid-dorsal region containing many dark and transparent scales. This is a typical pattern for *Phidippus*, with distinct segregation of scale types. G. Dorsal view of opisthosoma, adult female *Platycryptus undatus* (comb. nov.) ( $\times 13$ ). A broad mid-dorsal region of distinctive pattern, dominated by broad, ivory scales, is sharply bordered by narrow, dark scales. Laterally brown scales of intermediate width and coloration are most abundant. The overall pattern is more variegated, with greater mixing of scale types than is found in the dendryphantines as a rule, as exemplified by *Phidippus*. H. Dorsal view of opisthosoma, adult female *Menemerus bivittatus* ( $\times 16$ ). Scale types and pattern of distribution are comparable to those of *Platycryptus*.



## THE PLACEMENT OF SCALES

Where they are present, the pedicel-to-apex (proximal to distal) orientation of scales, and other setae as well, is generally consistent with the vector presentation of Fig. 2. This orientation agrees with the direction in which the old cuticle is shed during a molt, for each position on the integument. The physical significance of this pattern with respect to the process of molting is apparently self-evident; with any other arrangement the scales would be pulled off the surface as the exuvium is removed.

As shown in Fig. 3, scales, accompanied by setae, may be present over most of the surface of the salticid body, including all appendages.

## THE FUNCTION OF SCALES

No specific function of the salticid scale, or any spider scale, has yet been verified experimentally, with regard to the behavior and ecology of these animals. Nonetheless certain functions are rather plausible.

The most obvious effect (proximate function) of scales is the creation of a distinctive light and colour pattern on the surface of the spider (Fig. 4). Often highly reflective scales occur upon the dorsal surface of the pedipalps of mature males. The pedipalps are moved in a distinctive pattern during the visual courtship display (Crane, 1949). This role of colour or light pattern in intra-specific communication is strongly suggested by the physiological demonstration of two to four different colour receptors (including ultraviolet) in the anterior medial eyes of salticid spiders (DeVoe, 1975; Yamashita & Takeda, 1976).

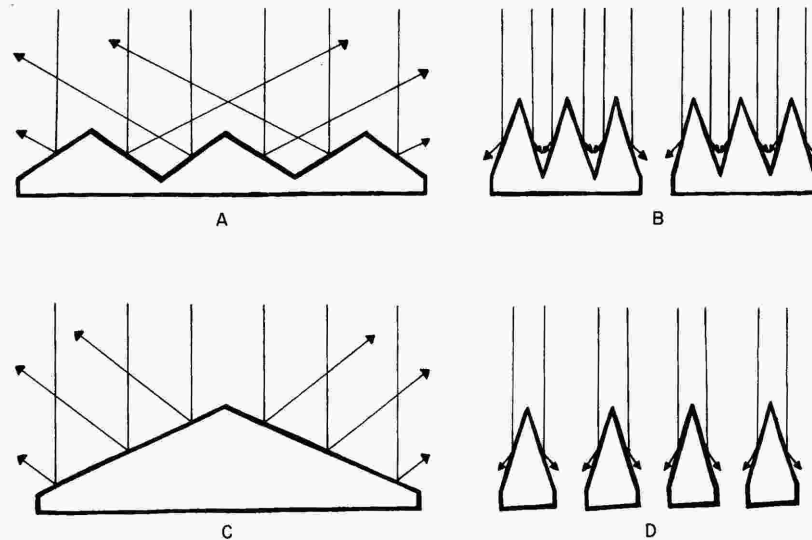


Figure 4. Scattering of light by the superior surfaces of scales. Schematic transverse sections of the light (A) and dark (B) pigmented scales of *Phidippus* are compared with corresponding transverse sections of the light (C) and dark (D) pigmented scales of *Platycryptus* (gen. nov.). The surface geometry of the broad, flattened scales in each case (A, C) enhances the reflection of incident light. In contrast, the shape of the narrow scales (B, D) minimizes surface glare, thus placing a premium upon the interaction of incident light with pigment within the scale (filtering). Figure 14 illustrates the comparable effect of this surface geometry upon the scattering of electrons.



Other patterns, particularly those of the dorsal opisthosoma, may be cryptic, or they may effect an advantageous “startle” reaction in a potential predator. In the case of the zebra spider, *Salticus scenicus*, the alternation of highly reflective white *transverse* bands with highly absorptive black bands may effectively break up the outline of these spiders, which move about on exposed surfaces. In this regard it is significant that other, unrelated salticids which similarly live on exposed surfaces (walls of buildings) exhibit highly contrasting *longitudinal* stripes (*Plexippus*, Fig. 3D), which might have a similar effect.

As with dabbling ducks, male salticids frequently (for example, *Phidippus clarus*) exhibit highly conspicuous (scale) patterns, presumably linked to sexual selection, while the females appear to be relatively cryptic in coloration.

It should be noted that scales are not the only means available to salticids, or other spiders, for the production of body colour. The black of *Phidippus* and *Salticus* species, the vivid green of *Lyssomanes*, and the reddish forelegs of *Metaphidippus castaneus* are all examples of colour produced by pigment contained in the cuticle and hypodermis.

Simon (1901–1903) suggested a protective function for salticid setae in general. *Cosmophasis* (Fig. 15P) is covered by a regular array of broad, overlapping scales, comparable to the scales of a fish or reptile. The potential of this armour to fend off the attack of a spider or insect of comparable size is not difficult to imagine. The scales of a salticid may also detach to facilitate the escape of the spider from the web of an araneid spider, much as do the scales of Lepidoptera in a similar situation (Robinson, Mirick & Turner, 1969).

Finally, there can be little doubt that salticid scales are operational in heat transfer between the organism and its environment, although the actual significance of this role has not been established in spiders. The scales of Lepidoptera appear to have an important role with regard to the absorption of radiation, and in insulation (Clench, 1966; Chapman, 1969; Kevan & Shorthouse, 1970).

The sun-loving salticids must frequently operate at temperatures well above ambient. *Eris marginata* will emerge from a resting sac in the morning to maintain a position with the opisthosoma oriented directly toward the sun. Extensive field observations of *E. marginata* and *Phidippus princeps* indicate that those spiders are often exposed to direct solar radiation for long periods of time.

Nonetheless, the extent of the effect of the structure and placement of spider scales upon heat transfer has never been measured.

#### VARIATION IN THE FORM AND PLACEMENT OF SCALES

As shown in Figs 5–16, a great deal of variation exists with regard to the form of salticid scales. Transparent (clear) scales may be broad and flat (*Phidippus*), or elongate and narrow (*Salticus*, *Pellenes*). White or ivory pigmented (granular) scales are generally broad, but they may be single-shafted (*Plexippus*) or three-shafted (*Phidippus*), and yet maintain the same physical characteristics in each case (Fig. 4).

Figures 5, 7, 8, 9A illustrate the extent of variation in the form of opisthosomal scales within a single well-defined genus, *Phidippus*. In general, the scales of the larger species within this genus, such as the southern form of *P. audax* (Fig. 5D), and *P. otiosus* (Fig. 5G), are larger than are those of the smaller species. The scales

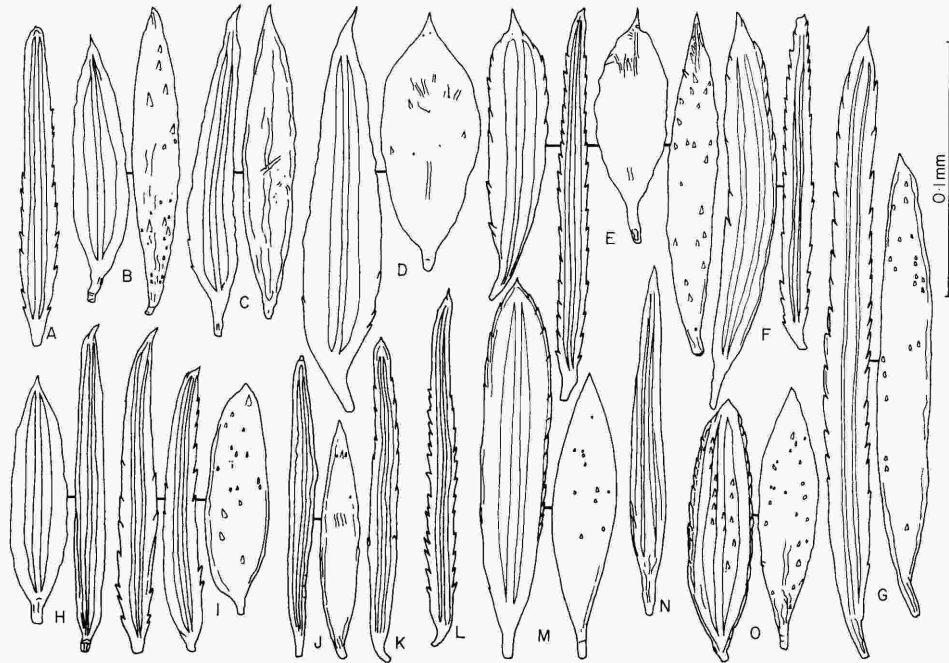
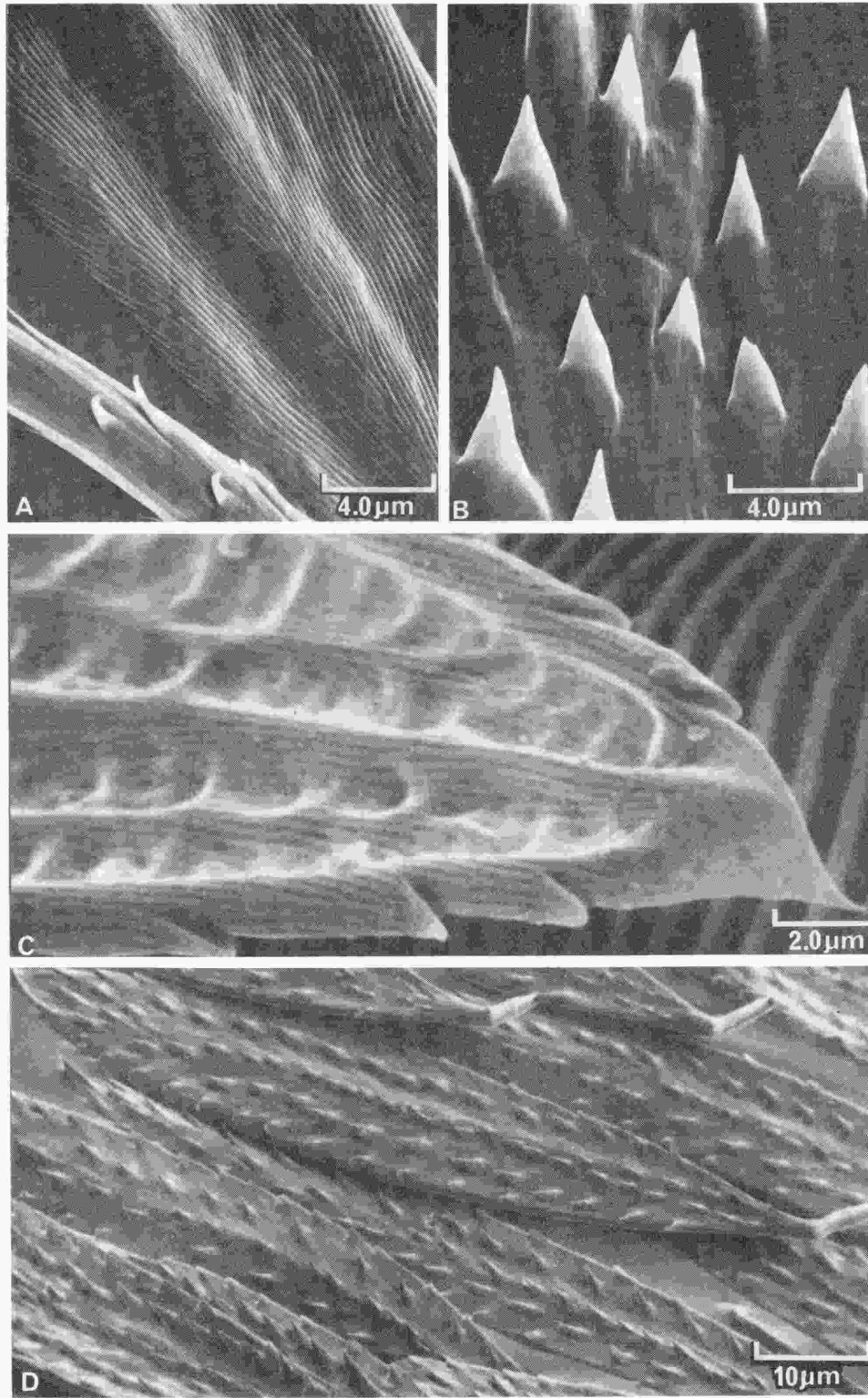


Figure 5. Representative scales of adult *Phidippus* species. A. ♀ *P. apacheanus*: orange granular. B. ♂ *P. audax*: white granular, grey clear. C. ♀ *P. audax*: orange granular, grey clear. D. ♀ *P. audax*: white granular, light brown clear. E. ♂ *P. clarus*: white granular, red-orange granular, olive clear, olive clear. F. ♀ *P. clarus*: ivory granular, orange granular. G. ♀ *P. otiosus*: ivory granular, light-orange clear. H. ♂ *P. cardinalis*: ivory granular, red-orange granular. I. ♀ *P. cardinalis*: ivory granular, red-orange granular, light brown clear. J. ♂ *P. princeps*: red-orange granular, olive clear. K. ♂ *P. princeps*: ivory granular. L. ♂ *P. whitmani*: red-orange granular. M. ♂ *P. regius*: white granular, light brown clear. N. ♂ *P. opifex*: white granular. O. ♂ *P. putnami*: white granular, light brown clear.

within this genus fall into two basic categories: three-shafted granular, and broad-flat clear. Three-shafted scales may be further subdivided into white, and brown-to-orange granular categories. The latter are invariably narrower than are the white scales. This generalization even applies within a species: Compare the three-shafted white scale of a *P. audax* (Fig. 5B) with a three-shafted orange scale from another individual of the same species (Fig. 5C). The broad-flat clear scales are generally smoky-grey in a fresh specimen.

Figure 6. Surface structure of salticid scales. A. Superior view of three-shafted scale from the leg of an immature *Phidippus audax* ( $\times 4080$ ). The fused-filament composition of both scale and ordinary seta (lower left) is evident. In life, this scale is iridescent gold in reflected light. B. Inferior view of white scale from the pedipalp of an adult male *P. audax* ( $\times 4850$ ). The presence of inferior spines oriented in a distal direction is characteristic of all salticid scales, although the size, number, and arrangement of these spines is subject to variation. C. Superior view of the distal portion of a distinctive five-shafted white opisthosomal scale of *Salticus scenicus* ( $\times 7400$ ). Transverse plicae join the shafts. Marginal spines and a distinctive apex are evident. D. Inferior view of a group of white prosomal scales of *S. scenicus* ( $\times 1640$ ). The group of scales was removed without disturbing their respective overlapping positions by direct application of the intact prosoma to copper tape. The angle formed between the pedicel and the blade of the scale is typical of the scales of all salticids, c.  $135^\circ$ . In this case the longitudinal rows of inferior spines correspond closely to the five shafts visible in a superior view.



Within the context of generic characters given above, one can ascertain a substantial amount of species-specific pattern within the genus *Phidippus*. This variation is particularly evident in the SEM pictures (Figs 7, 8, 9A). In some species, the three-shafted scales bear many marginal spines; in others, these are virtually devoid of marginal spines. The three-shafted scales of *P. audax* (Figs 4A, B, C, 7A) taper along most of the length of the scale; in *P. otiosus* these scales are of uniform transverse section for virtually their entire length. The scales of *P. clarus* (Figs 5E, F, 8) exhibit a distinctive apical structure, in addition to a regular series of adpressed, marginal spines. In *P. johnsoni* (Fig. 9A), one finds lateral *plicae* in the place of lateral spines.

Figure 10 presents a series of species which agree with *Phidippus* in the presence of three-shafted white granular scales in combination with broad-flat clear scales. Most of these have been associated with the genus *Phidippus* in the past, within the subfamily Dendryphantinae. The scales of the *Icius* (undescribed) of Fig. 9B agree closely in structure with those of the *P. johnsoni* shown in Fig. 9A. Thus this pattern of scale types may be extended to the entire subfamily Dendryphantinae.

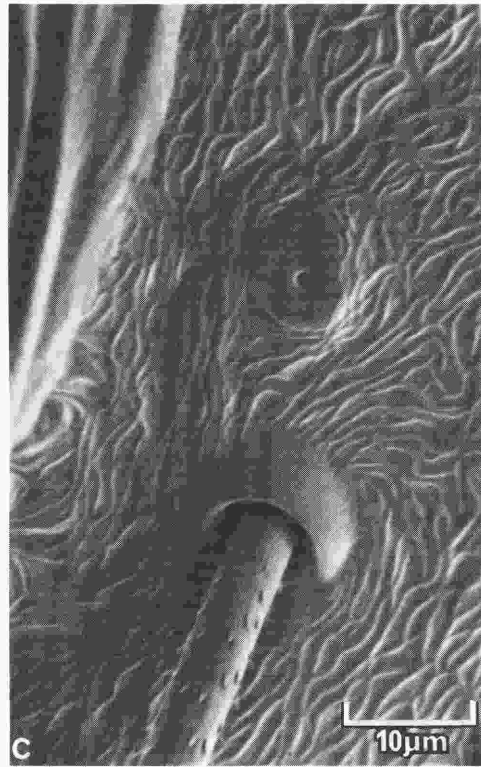
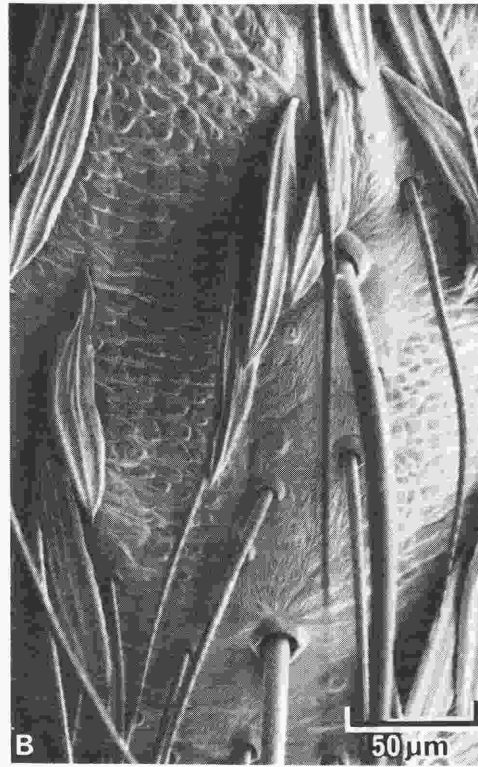
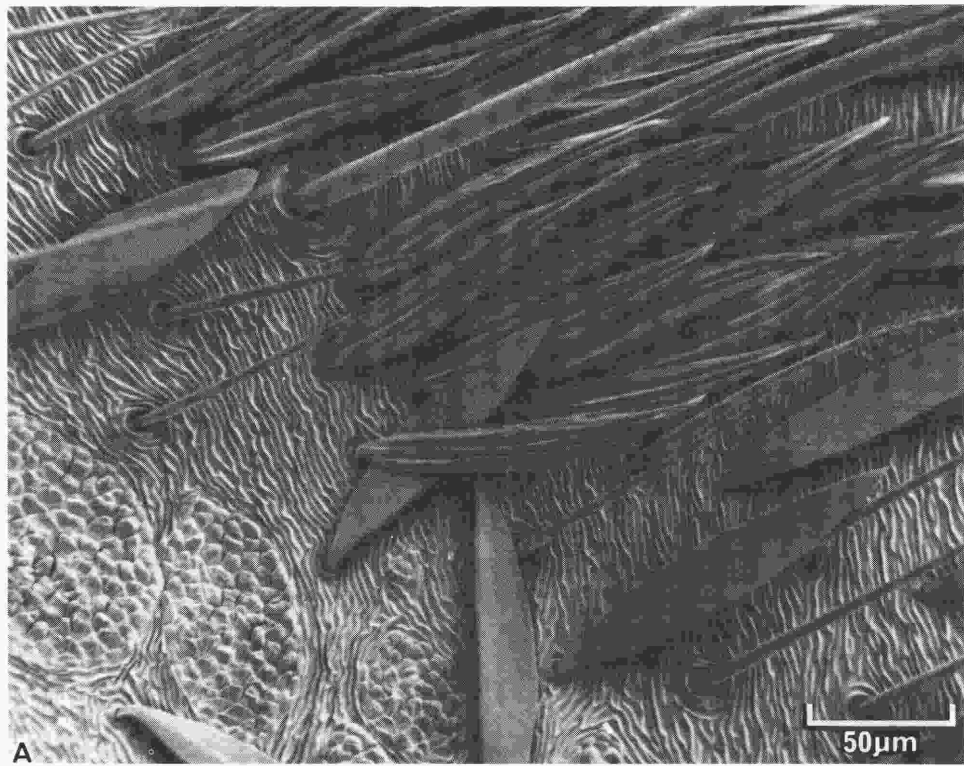
In *Pellenes* (Figs 11A-H, 12), a three-shafted white granular scale type is also present, but this scale is more commonly bordered by an extensive series of lateral spines. More definitively, the central shaft is not *keeled* as in the Dendryphantinae, but rounded (Fig. 12B). The clear scales of *Pellenes* are variable, from the broad, flat form typical of the dendryphantines to that narrow, laterally-compressed form typical of the habrocestines (see below).

The tropical spiders *Anasaitis* (Fig. 11I) and *Corythalia* (Fig. 11J) both exhibit a similar combination of broad-flat three-shafted scales with narrow, laterally-compressed scales. Those of *Corythalia* exhibit particularly large spines, and a remarkable variety of colour and iridescence. The inclusion of these species in this study should serve to emphasize the fact that the primary diversity of the Salticidae, with regard to scales as well as other features, resides in the tropics, and still awaits the beginning of an adequate analysis.

Figure 13 includes a number of Nearctic species which share a set of scale characteristics which may, for the present, be termed *habrocestine*. In this group, broad white granular scales are single-shafted, with regular, and relatively long, lateral spines. Dark, clear scales are similarly single-shafted; these are narrow, laterally-compressed. Brown scales are intermediate in form (see also Fig. 14B). Most of these species possess a dark, clear scale which is uniformly olive-green to

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Figure 7. Scales of adult male *Phidippus audax*. A. Three-shafted white scales and smooth dark scales of the dorsal opisthosoma ( $\times 390$ ). Anterior is to the left; this is the left lateral portion of the large central white spot of Fig. 3 E. Two distinct size classes of ordinary setae are evident. The distribution of the large white setae coincides with the distribution of white scales. The flexible cuticle of the opisthosoma allows for considerable expansion of surface area. At the lower left are sites of muscle attachment to the cuticle. B. Dorsal surface of the femur, left pedipalp ( $\times 350$ ). As on all appendages, the broad white three-shafted scales are oriented in a distal direction. As on the opisthosoma, the bumps on the cuticle correspond to positions of muscular attachment. Two size classes of ordinary setae are similarly evident. C. Detail of relatively smooth cuticle from centre of B ( $\times 1730$ ). The function of the *pit organ* of the salticid cuticle, one of which is shown here, is not known. These typically appear as a perfectly round  $1\ \mu\text{m}$  aperture centered upon a circular to elliptical (depending upon species) smooth elevated region of about  $10\ \mu\text{m}$  in diameter. These have been observed on the opisthosoma, legs, and pedipalps of both immature and adult dendryphantines.





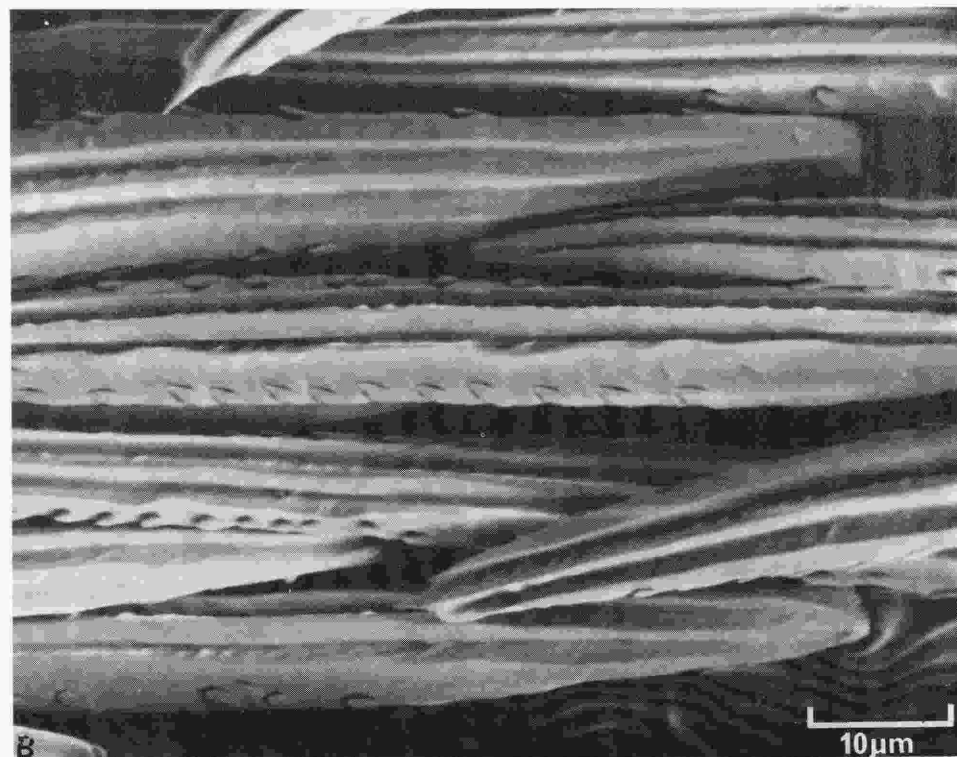
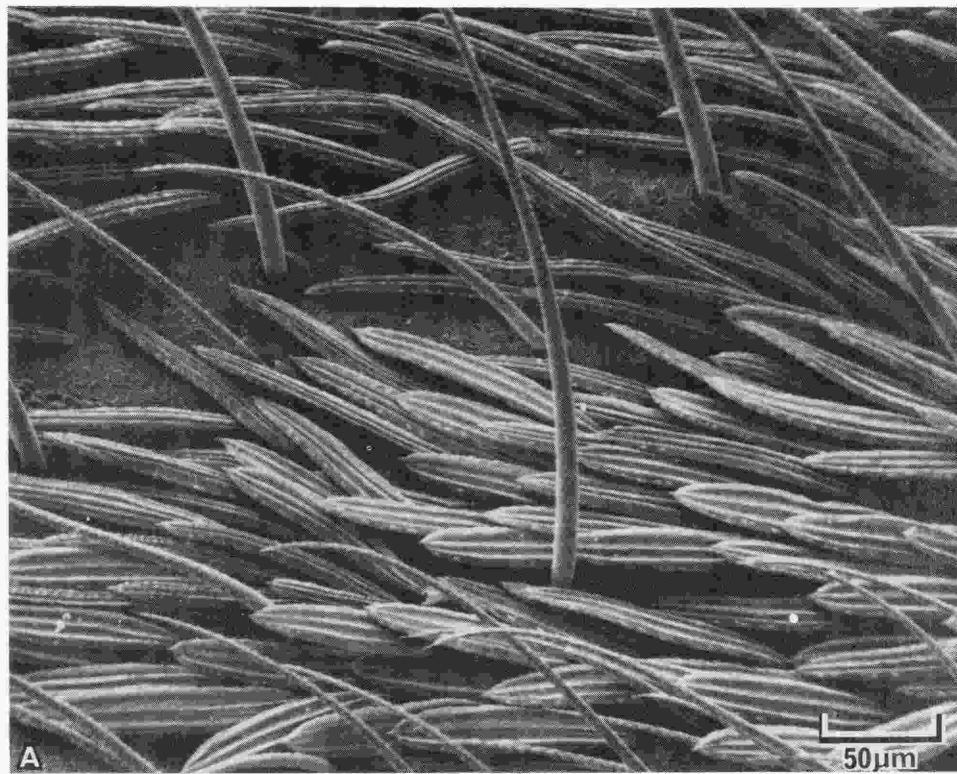


Figure 8. Opisthosomal scales of *Phidippus clarus*. A. Right antero-lateral margin of opisthosoma ( $\times 320$ ). The white marginal band of the opisthosoma is formed of broad white scales (below), while the dorsum is bordered by longitudinal bands of narrow orange scales. All of these scales are three-shafted. Compare with Fig 3 F. B. Detail of the three-shafted orange scales ( $\times 1900$ ). Fairly regular adpressed, marginal spines are characteristic of the three-shafted scales of this species. The shafts are strongly keeled, and the intervening furrows are deep.

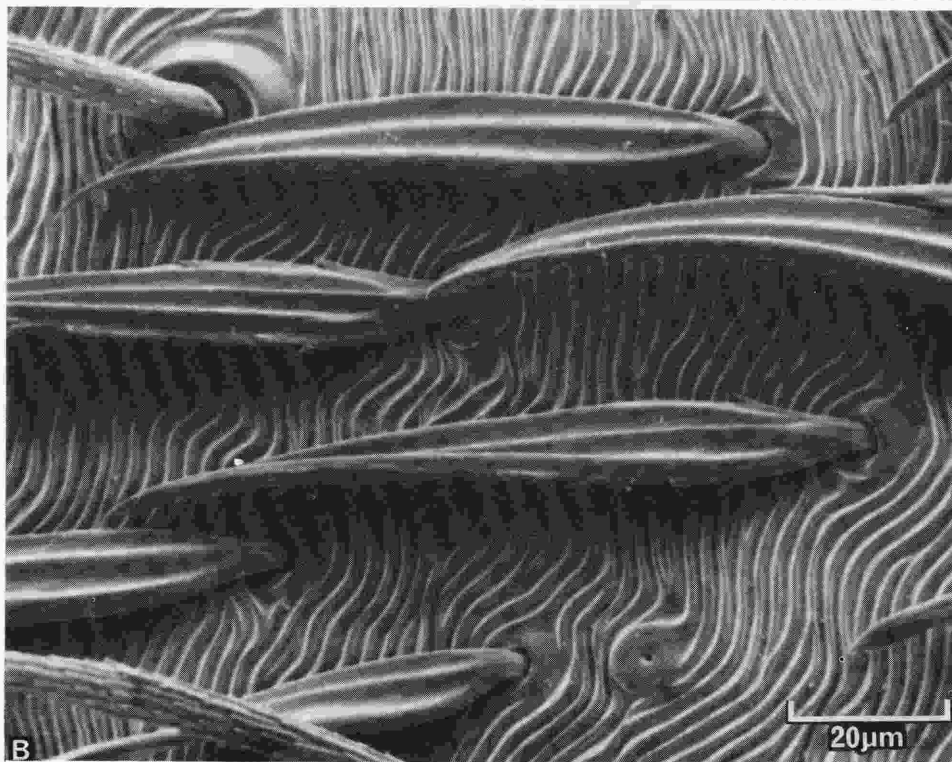
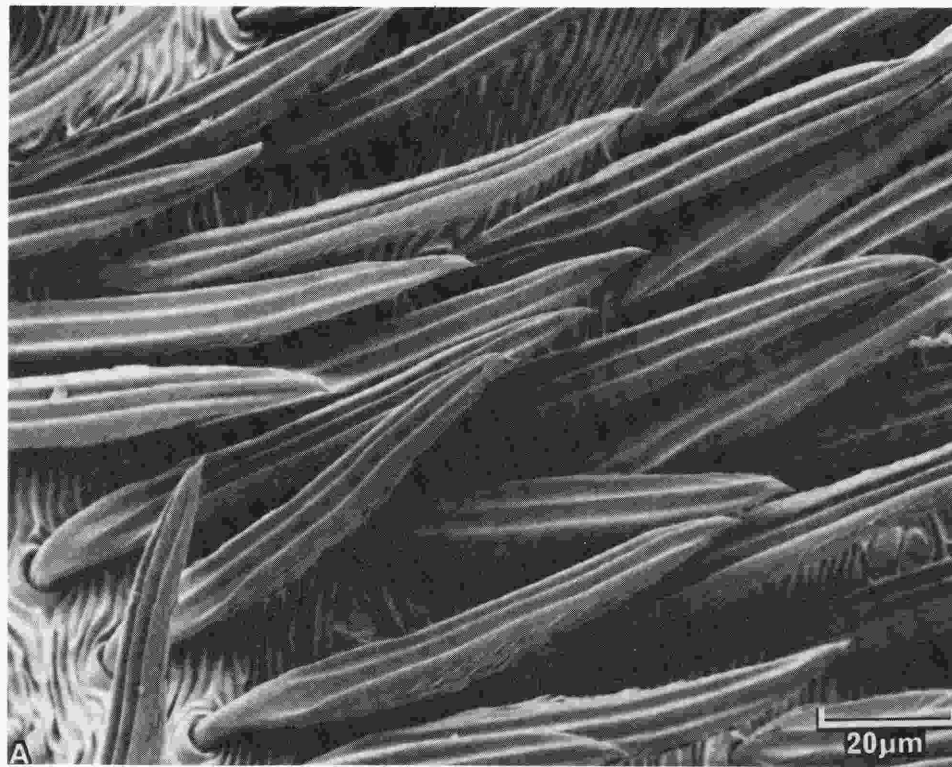


Figure 9. A. Red opisthosomal scales of adult male *Phidippus johnsoni* ( $\times 910$ ). Oblique plicae occur on the lateral margins of these scales, in the absence of marginal spines. B. Opisthosomal scales of immature *Icius* sp. ( $\times 1100$ ). The entire body of this spider is covered with light blue scales of this type; the three-shafted form is characteristic of light, pigmented dendryphantine scales. A typical *pit organ* may be seen at lower right (cf. Fig. 7C).

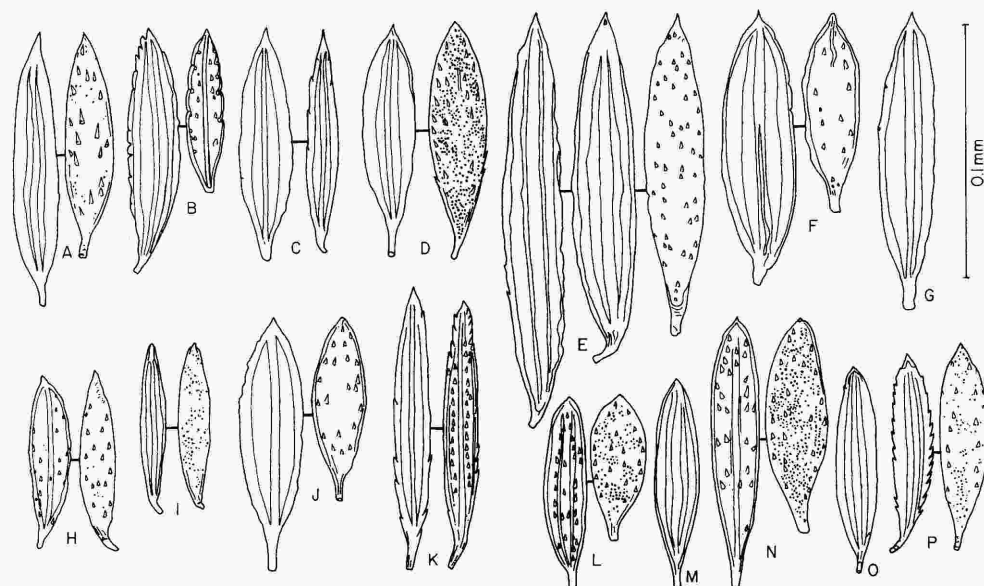


Figure 10. Representative scales from the dorsal opisthosoma of adult dendryphantine salticids. A. ♀ *Icius hartii*: white granular, light brown clear. B. ♂ *Metaphidippus galatheo*: white granular, light brown clear. C. ♀ *Metaphidippus galatheo*: white granular, light brown glandular. D. ♂ *Sassacus vitis* (comb. nov.) white granular, light brown speckled (gold iridescent). E. ♀ *Eris aurantia*: orange granular, white granular, orange clear (gold iridescent). F. ♂ *E. marginata*: white granular, grey clear. G. ♀ *E. marginata*: white granular. H. ♂ *Zygoballus bettini*: white granular, light olive clear. I. ♂ *Z. nervosus*: ivory granular, light brown clear. J. ♂ *Hentzia palmarum*: white granular, light brown clear. K. ♀ *H. palmarum*: ivory granular, light brown clear. L. ♂ *Sassacus papenhoei*: white granular, light brown speckled (gold iridescent). M. ♂ *S. papenhoei*: ivory granular. N. ♀ *S. papenhoei*: white granular, light brown speckled (gold iridescent). O. ♂ *Tutelina similis*: white granular. P. ♀ *T. similis*: white granular, light yellow-brown clear.

brown in colour. This scale is very dark under reflected light, i.e., it reflects very little light.

Apart from the scales of *Marpissa* (Fig. 15A-E), which bear a certain resemblance to those of *Pellenes*, none of the scales shown in Fig. 15 can be definitively related to any of the earlier groups. Each genus illustrated in this figure (also *Plexippus*, Fig. 16) exhibits distinctive characters which isolate it from the earlier (dendryphantine, habrocestine, pellenine) patterns. As more becomes known of the variety of salticid scales, it should be possible to place these in relation to other genera. At present, they stand as representatives of but a small fraction of the diversity in scale form which exists within the family Salticidae.

Although it was not the intention of this study to deal with the arrangement of scales in a rigorous manner, certain aspects of scale placement deserve mention.

In many genera, such as *Salticus*, *Phidippus*, and *Pellenes*, each type of scale occurs in rather well-defined positions, or tracts. For instance, the three-shafted white granular scales of *Pellenes* (Fig. 12B) are situated either along the anterior and lateral margins of the opisthosoma, or in a mid-dorsal band upon the opisthosoma. The narrow, dark scales (Fig. 12C) occur between the bands of broad, white scales upon the dorsal opisthosoma. In *Phidippus audax* (Figs 3E, 7A) the white scales occur in distinct tracts, and the dark, shiny scales occur



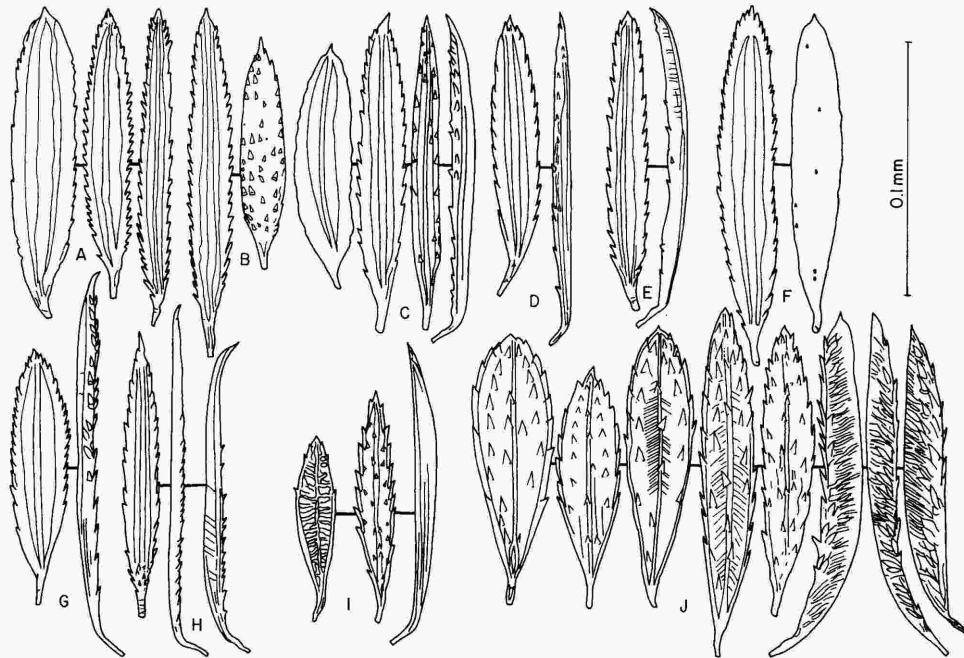


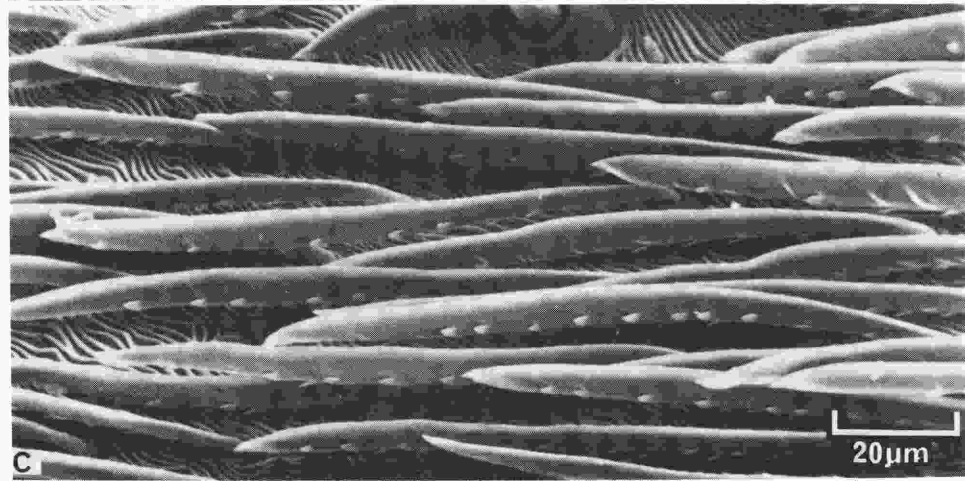
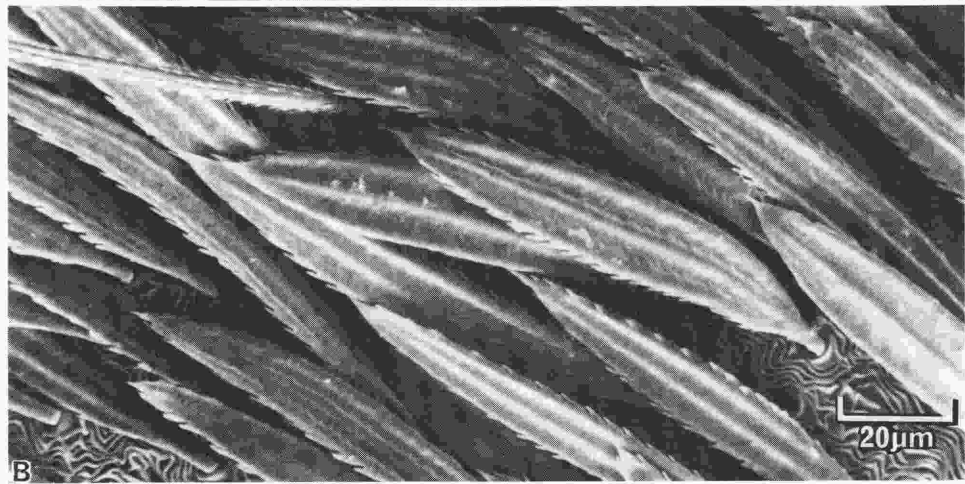
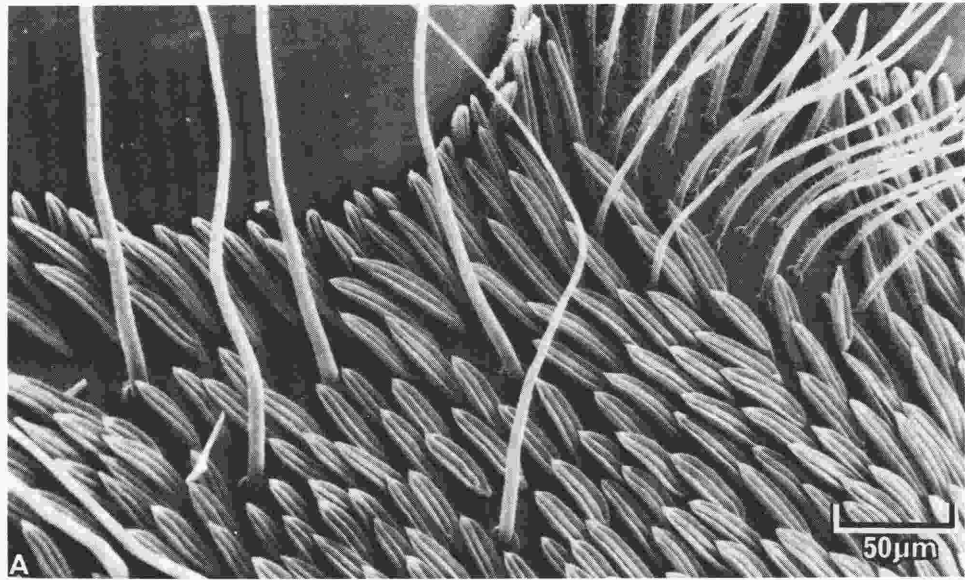
Figure 11. Representative scales from the dorsal opisthosoma of *Pellenes*, *Anasaitis* and *Corythalia*. A. ♂ *Pellenes arizonensis*: white granular, ivory granular, red-brown clear. B. ♀ *P. arizonensis*: white granular, brown clear. C. ♀ *P. calcaratus*: white granular, light brown granular, light yellow-brown clear, olive clear. D. ♂ *P. cf. coecatus*: white granular, olive clear. E. ♀ *P. cf. coecatus*: ivory granular, light brown clear. F. ♂ *P. hirsutus*: white granular, light yellow-brown clear (gold iridescent). G. ♂ *P. tarsalis*: white granular, brown clear. H. ♀ *P. wrighti*: white granular, light brown granular, light brown clear. I. ♂ *Anasaitis venatoria*: light brown clear, colorless clear, light brown clear. J. ♀ *Corythalia aurata*: white to silver to copper granular, light brown granular (gold iridescent), red-brown clear (gold iridescent), yellow-green clear, olive clear, olive clear, colorless clear (silver), red-brown clear.

elsewhere upon the dorsal opisthosoma. The three scale types of *P. clarus* (Figs 3F, 8) are similarly segregated. The same segregation of scale types into homogeneous tracts occurs in *Plexippus* (Figs 3D, 16).

In contrast, the scale categories persist in many of the habrocestine forms, including *Platycryptus* (new genus, Fig. 3G) and *Menemerus* (Fig. 3H), but complete segregation of scale types into tracts does not occur. This is most evident for *P. californicus* (Fig. 14B) where the different scale types are mixed within any given field of the integument.

The developmental significance of this distinction between segregated and integrated tracts is not known.

Scale pattern, but not type, may vary greatly in different populations of the same species. Figure 10L shows the dendryphantine scales of a typical male *Sassacus papenhoei* from Oregon. In this species the three-shafted scales are generally restricted to the anterior margin of the opisthosoma. Figure 10M is typical of the three-shafted scales which covered the entire prosoma and opisthosoma of males from a population of *S. papenhoei* in Arizona. The clear scales (iridescent gold) which cover the dorsal opisthosoma of most *S. papenhoei* throughout North America were entirely lacking in this population.



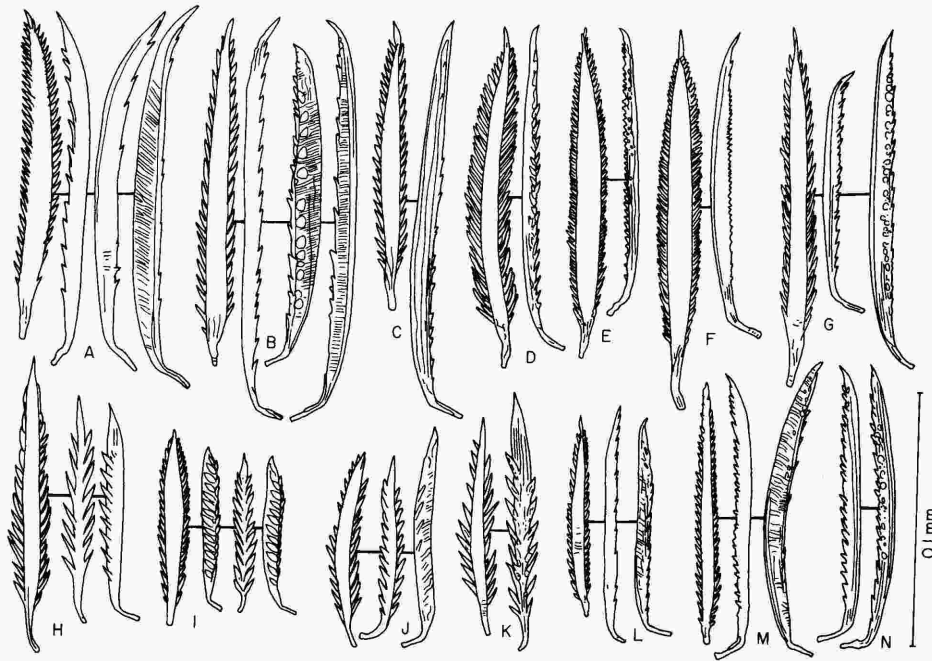


Figure 13. Representative single-shafted scales from the opisthosoma of salticid spiders (Habrocestinae). A. ♀ *Platycryptus undatus* (comb. nov.): white granular, light brown granular, red-brown semi-clear, olive clear. B. ♀ *Menemerus bivittatus*: white granular, light red-brown granular, olive clear, gold clear. C. ♀ *Phlegra fasciata*: white granular, brown clear. D. ♂ *Thiodina puerpera*: white granular, light yellow clear. E. ♂ *T. sylvana*: white granular, brown to orange clear. F. ♀ *T. sylvana*: white granular, brown granular. G. ♂ *Evarcha falcata*: white granular, light brown granular, olive clear. H. ♂ *Habrocestum pulex*: ivory granular, two views of dark orange granular. I. ♂ *Habrocestum* sp. (not described): white granular, orange granular, two views of olive clear. J. ♂ *H. acerbum*: white granular, brown granular, olive clear. K. ♀ *H. acerbum*: white to brown granular, olive clear. L. ♂ *Sitticus fasciger*: white granular, light brown granular, olive-brown clear. M. ♀ *S. fasciger*: ivory granular, light brown granular, olive-brown clear. N. ♀ *Evarcha falcata*: light brown granular, brown clear.

#### EVOLUTIONARY RELATIONSHIPS AMONG SALTICID GENERA

An outline of the historical assignment of the salticids considered here to subfamilies, including the generalities advanced in the preceding section, is given in Table 2.

Although the device of assignment of genera to subfamilies can only be employed with a great deal of subjectivity, it provides a method for the development of hypotheses with regard to evolutionary relationship of genera. It also addresses a simple question, for each pair of genera: are these genera really closely related at all?

Figure 12. Scales of adult male *Pellenes* (*Habronattus*) sp. (not described). A. Iridescent blue-green scales below the anterior eye row ( $\times 320$ ) (anterior medial eye at upper left, anterior lateral eye at upper right). B. Broad ivory granular scales of the mid-dorsal longitudinal tract of the opisthosoma ( $\times 800$ ). In *Pellenes* these are characterized by three rounded shafts and a regular series of marginal spines. C. Single-shafted scales of the dorsal opisthosoma ( $\times 860$ ). In life these are dark, shiny, and transparent. These are typically more rounded than are the single-shafted scales of *Platycryptus* (Fig. 14).

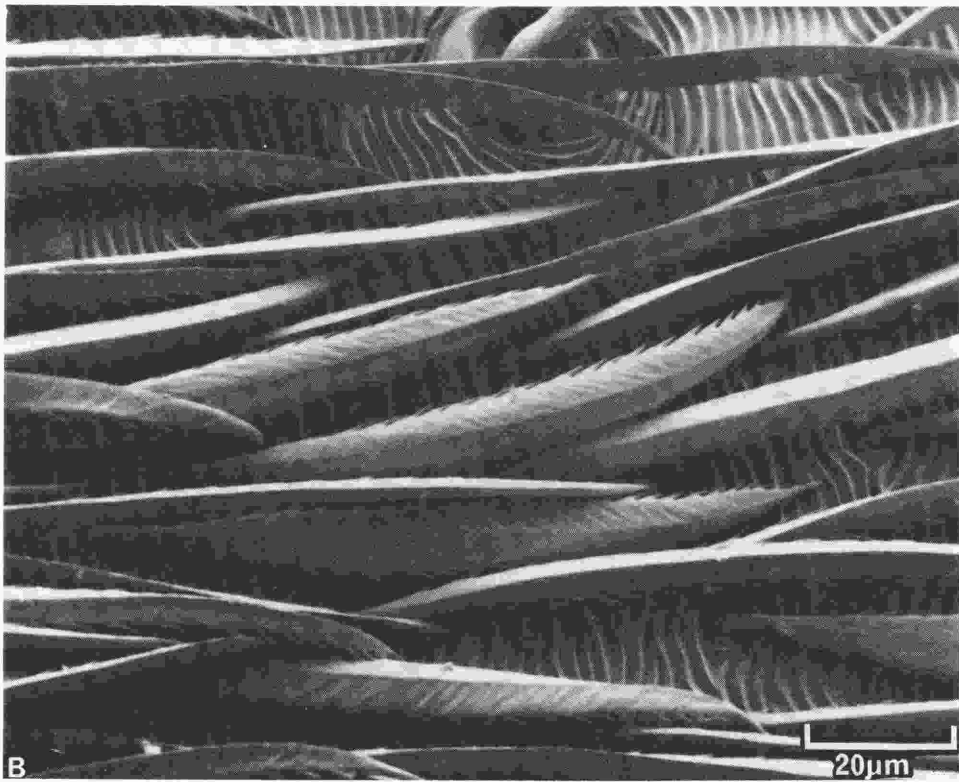
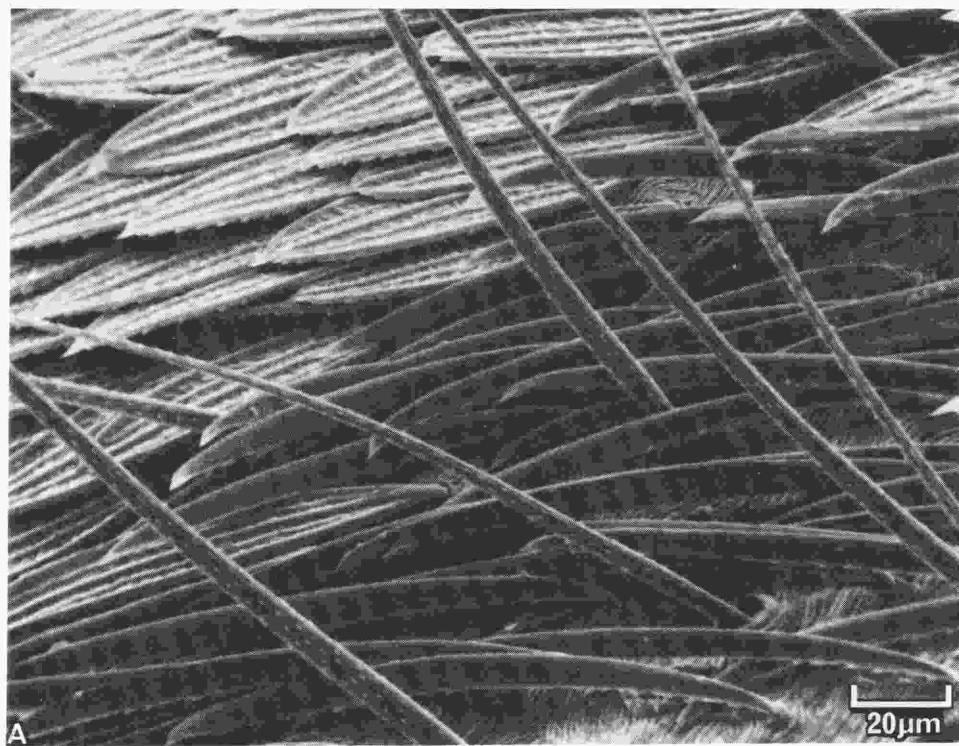


Figure 14. A. Tracts of broad white (above, left), and single-shafted dark (below) scales arranged in transverse bands form the distinctive opisthosomal pattern of the zebra spider, *Salticus scenicus* ( $\times 700$ ). B. Broad ivory, narrow dark, and intermediate brown scales occur together to create this cryptic variegated pattern of the dorsal opisthosoma of *Platycryptus californicus* (comb. nov.) ( $\times 1000$ ). The sharply-keeled single-shafts with oblique striae and regular marginal spines are distinctive.

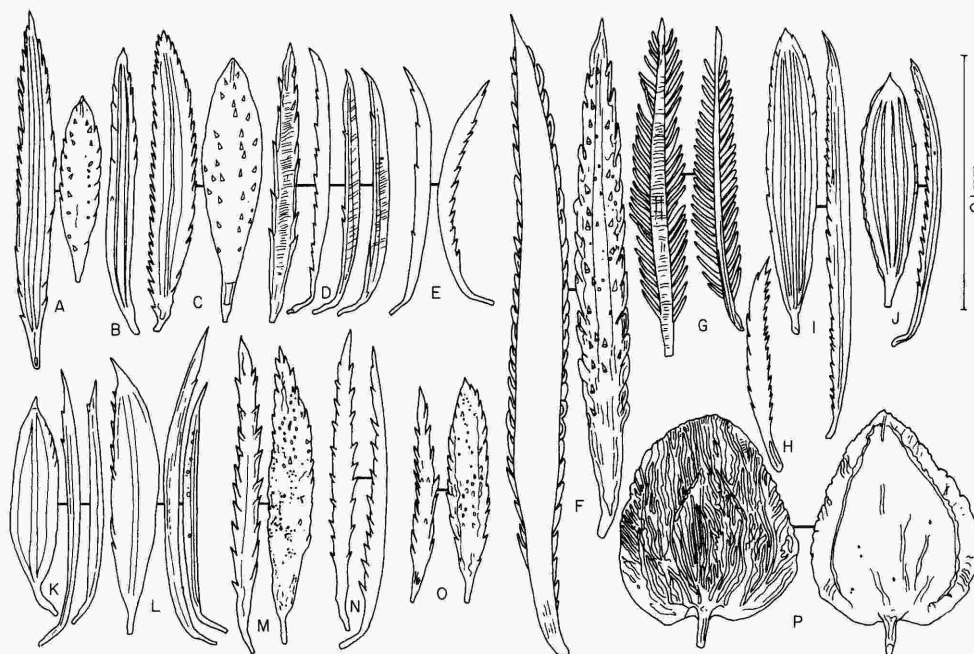


Figure 15. Scales from the dorsal opisthosoma of various salticids. A. ♂ *Marpissa pikei*: white granular, light brown clear. B. ♀ *M. pikei*: white granular. C. ♂ *M. bina*: white granular, light brown clear. D. ♀ *M. bina*: ivory granular, brown granular, orange clear, olive clear. E. ♂ *M. sulcosa*: light brown to orange granular, white granular. F. ♂ *Hyllus moestus*: white granular, light brown clear. G. ♂ *Plexippus paykulli*: white to red-brown granular, black clear. H. ♂ *Sarinda hentzi*: white granular. I. ♂ *Salticus austinensis*: white granular, light brown clear. J. ♀ *S. scenicus*: white granular, brown clear. K. ♂ *Metacyrba taeniola*: white granular, light brown granular, dark brown clear. L. ♀ *M. taeniola*: white granular, light brown granular, colorless clear. M. ♂ *Maevia inclemens*: red-orange or ivory granular, ivory or grey semi-clear. N. ♀ *M. inclemens*: two views of ivory semi-clear or red-orange granular. O. ♂ *Maevia michelsoni* (comb. rev.): ivory or orange granular, grey or colorless clear or semi-clear. P. ♂ *Cosmophasis* sp.: white granular, olive clear. Other categories of similar size and shape include: light brown clear, light violet to purple clear (blue-green iridescent).

The evidence provided by this preliminary examination of scale structure suggests that certain proposals, such as the close relationship of *Thiodina* to the dendryphantines suggested by Prószyński (1976), are untenable. Similarly, the relationship of *Salticus* to *Marpissa*, suggested by earlier workers, is unlikely.

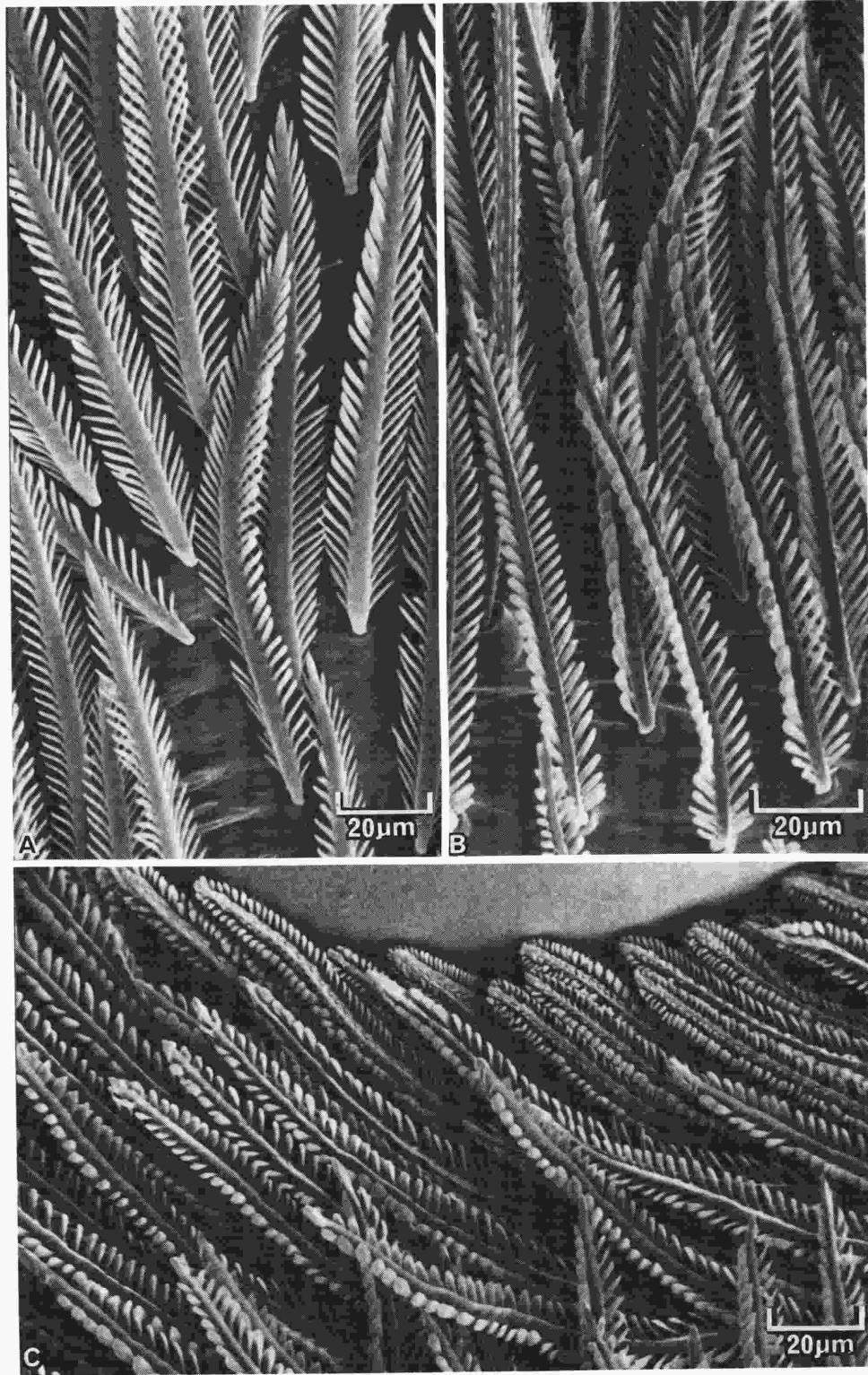
On the other hand, the close relationship of most of the presumed dendryphantines is further substantiated by the common structure of scales in this group.

#### CHANGES IN THE CLASSIFICATION OF SOME SALTICIDS

Table 3 presents four recommended changes in the generic placement of salticids subject to this study.

Barnes (1958) correctly separated the American "*Marpissa*" (Peckham, 1909) from the true European *Marpissa* on the basis of genitalia. Although he acknowledged the great difference between the American "*Marpissa*" and *Metacyrba*, again on the basis of genitalia, Barnes nonetheless incorporated these "*Marpissa*" into the genus *Metacyrba*.





The extreme difference in the form of the three-shafted granular opisthosomal scales of the type-species for the genus *Metacyrba* Pickard-Cambridge 1901, *M. taeniola* (Fig. 15K, L), from the single-shafted granular opisthosomal scales of "*Metacyrba*" *undata* (Fig. 13A) and the similar scales of "*Metacyrba*" *californica* (Fig. 14B) necessitates the separation of the latter two species from the genus *Metacyrba*. Since there is at present no genus to accommodate these well-known American species, it is necessary to describe a new genus:

*PLATYCRYPTUS* GEN. NOV.

"*Platycriptus*" is a combination of Greek words for "broad, flat" and "hidden". The combined term refers to the cryptic appearance and behaviour of these flattened spiders, which frequently wedge themselves into crevices.

These are relatively large (8–13 mm), flattened salticids, common throughout North America. The body of these spiders is covered by a more-or-less variegated pattern of scales of the keeled, single-shafted types indicated in Fig. 13A and Figs 3G and 14B. For additional definitive characters refer to the lengthy descriptions of the included species, *P. undata* and *P. californica*, provided by Barnes (1958), who dealt with these species under the genus *Metacyrba*, as well as the general description of American "*Marpissa*" given by Peckham & Peckham (1909). *Type-species*: *Aranea undata* DeGeer, 1778.

It is recommended that "*Metaphidippus*" *vitis* be included in the genus *Sassacus*, as *Sassacus vitis* (Cockerell), *comb. nov.* The scale types of this species (Fig. 10D) are almost identical to those of *S. papenhoei*. A comparative analysis of courtship completed recently by D. B. Richman (1977) also suggests this change.

The scale types of *Maevia inclemens* (Fig. 15M, N) and "*Paramaevia*" *michelsoni* (Barnes) (Fig. 15 O) are virtually identical in shape and coloration. *P. michelsoni* should be returned to the genus *Maevia*, as originally designated. Note: the genus *Paramaevia* was originally described by Barnes in 1955 as a subgenus of *Maevia*, with type-species *Maevia poultoni* Peckham & Peckham; *michelsoni* was described in the subgenus *Paramaevia*. Barnes (1958) elevated *Paramaevia* to generic rank.

CONCLUSIONS

Lehtinen (1967) proposed a phylogeny for the order Araneae which was, in part, based upon a superficial, hence unreliable, examination of setae. Considering the existence of more than 400 genera of salticids throughout the world, most of which have not been adequately described, this study is also necessarily superficial.

As noted by Prószyński (1971b), the development of a comprehensive understanding of the evolutionary relationships within the Salticidae is an enormous task. Hopefully the present study, with all of its limitations, will lead

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Figure 16. Scales of *Plexippus paykulli*: adult male. A. Ivory coloured scales from the leg ( $\times 680$ ). These are typical of the light-coloured scales of the entire body of this spider, with a relatively broad central shaft and a regular series of broad marginal spines with blunt apices. B. Dark scales of the prosoma ( $\times 800$ ). Although these are similar to the ivory scales, the central shaft is much narrower. C. Dark scales below the left posterior lateral eye ( $\times 690$ ). The scales which border the eyes of salticids are modified, with blunt apices and an increased number of smaller spines where they come into contact with the eye. The same sort of modification may be discerned for *Pellenes* in Fig. 12A.

Table 2. The assignment of genera to subfamilies

	Simon 1901–1903	Petrunkevitch 1928	Prószyński 1976	This study
<i>Anasaitis</i> Bryant, 1950	—	—	—	—
<i>Corythalia</i> C. L. Koch, 1851	Zendoreae	Plexippinae	Euophrydinae	—
<i>Cosmophasis</i> Simon, 1901	Chrysilleae	Heliophaninae	—	—
<i>Eris</i> C. L. Koch, 1846	Dendryphanteae	Dendryphantinae	Dendryphantinae	Dendryphantinae
<i>Evarcha</i> Simon, 1903	Hylleae	Hyllinae	Pelleninae	Habrocestinae
<i>Habrocestum</i> Simon, 1876	Aelurilleae	Pelleninae	Euophrydinae	Habrocestinae
<i>Hentzia</i> Marx, 1883	Dendryphanteae	—	Dendryphantinae	Dendryphantinae
<i>Hyllus</i> C. L. Koch, 1846	Hylleae	Hyllinae	Hyllinae	—
<i>Icius</i> Simon, 1876	Dendryphanteae	Dendryphantinae	Heliophantinae	Dendryphantinae
<i>Maevia</i> C. L. Koch, 1848	Maeveiae	Maeviinae	Pelleninae	Maeviinae
<i>Marpissa</i> C. L. Koch, 1848	Marpisseae	Marpissinae	Marpissinae	—
<i>Menemerus</i> Simon, 1901	Marpisseae	Marpissinae	Aelurillinae	Habrocestinae
<i>Metacyrba</i> Pickard-Cambridge, 1901	Maeveiae	Maeviinae	—	—
<i>Metaphidippus</i> Pickard-Cambridge, 1901	Dendryphanteae	Dendryphantinae	Dendryphantinae	Dendryphantinae
<i>Paramaevia</i> Barnes, 1958	—	—	—	Maeviinae
<i>Pellenes</i> Simon, 1876	Aelurilleae	Pelleninae	Pelleninae	Pelleninae
<i>Phidippus</i> C. L. Koch, 1846	Dendryphanteae	Dendryphantinae	Dendryphantinae	Dendryphantinae
<i>Phlegra</i> Simon, 1876	Aelurilleae	Pelleninae	Aelurillinae	Habrocestinae
<i>Platycryptus</i> ( <b>gen. nov.</b> )	—	—	—	Habrocestinae
<i>Plexippus</i> C. L. Koch, 1846	Plexippeae	Plexippinae	Plexippinae	Plexippinae
<i>Salticus</i> Latreille, 1846	Marpisseae	Marpissinae	Salticinae	Salticinae
<i>Sarinda</i> Peckham, 1892	Sarindeae	Myrmyrarachinae	Synemosyninae	—
<i>Sassacus</i> Peckham, 1895	Dendryphanteae	Dendryphantinae	Dendryphantinae	Dendryphantinae
<i>Sitticus</i> Simon, 1901	Sitticeae	Sitticinae	Sitticinae	Habrocestinae
<i>Thiodina</i> Simon, 1900	Thiodineae	Thiodininae	Dendryphantinae	—
<i>Tutelina</i> Simon, 1901	Chrysilleae	Heliophaninae	—	Dendryphantinae
<i>Zygoballus</i> Peckham, 1885	Zygoballeae	Zygoballinae	—	Dendryphantinae



Table 3. Some changes in generic placement suggested by scale structure

Previous assignment	New assignment
<i>Metacryba californica</i> (Peckham, 1888)	<i>Platycryptus californicus</i> (Peckham, 1888) <b>comb. nov.</b>
<i>Metacryba undata</i> (DeGeer, 1778)	<i>Platycryptus undatus</i> (DeGeer, 1778) <b>comb. nov. gen. nov.</b> [type-species of <i>Platycryptus</i> <b>gen. nov.</b> ]
<i>Metaphidippus vitis</i> (Cockerell, 1894)	<i>Sassacus vitis</i> (Cockerell, 1894) <b>comb. nov.</b>
<i>Paramaevia michelsoni</i> (Barnes, 1955)	<i>Maevia michelsoni</i> Barnes, 1955 <b>comb. rev.</b>

others to examine the scales of salticids, in addition to the genitalia and other distinguishing features, with greater interest.

Galiano (1975), virtually alone among recent workers, considered the diagnostic value of salticid scales, with reference to *Phidippus birabeni*. It is here recommended that salticid systematists include as complete a description as possible of the structure, colour, and placement of scales as they describe new species, or revise the classification of known species. Since certain features of scale structure and placement appear to be rather conservative, such data should provide not only a sound basis for distinctions between species, but also a means for the evaluation of the validity of genera and groups of genera as well.

Certainly the comparative morphology of scales cannot, by itself, decipher the evolution of such a successful and diverse group as the Salticidae. Nonetheless, considering the relative simplicity of genitalia in these spiders, it is likely that scales will provide some of the most reliable characters in the future study of salticid phylogeny.

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