Marchena and other jumping spiders with an apparent leg-carapace stridulatory mechanism (Araneae: Salticidae: Heliophaninae and Thiodininae)

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Summary

The western North American jumping spider *Marchena minuta* (Peckham & Peckham) is redescribed; *Marchena sissonii* Peckham & Peckham and *Sitticus synopticus* Chamberlin are synonymised with *M. minuta*. *Marchena* and the neotropical genus *Helvetia* are here considered to belong in the subfamily Heliophaninae, otherwise known only from the Old World, for they share with the heliophanines a row of setae-bearing tubercles on the first leg, and rugose carapace sides. These two structures are well placed to function as a leg-carapace stridulatory mechanism. Stridulation may function in social communication in these possibly-communal jumping spiders. The thiodinine *Cotinusa* has a similar leg-carapace stridulatory mechanism.

Introduction

This paper began as a review of the little-known jumping spider genus *Marchena* of western North America, and indeed much of the paper still consists of a redescription of the single species, *Marchena minuta*. However, the discovery of peculiar tubercles on the femora of the first legs led me to expand the study to include a search for close relatives of *Marchena*. I found the tubercles in the neotropical *Helvetia*, a genus studied by Galiano (1963, 1965, 1976), and in many of the primarily Old World Heliophaninae, a subfamily recently studied by Prószyński (1983a, b, 1985), Andreeva *et al.* (1984) and their co-workers. These tubercles not only suggest a subfamilial placement for *Marchena* and *Helvetia*, but they also appear to be part of a stridulatory mechanism. Previous reports of sound production by salticids (Edwards, 1981; Maddison, 1982; Gwynne & Dadour, 1985), have described stridulation during courtship, but in the heliophanines stridulation is probably used outside of courtship and may help maintain a social organisation, as discussed below.

Materials and Methods

Drawings of external genitalia were made with a camera lucida on an Olympus compound microscope using incident fibre-optics light. The epigynum was placed in warm trypsin solution to digest tissues and mounted in clove oil for dorsal view drawing with transmitted light. Measurements were obtained using an ocular reticle on an American Optical stereoscope for a sample of five ♂ and five ♀; they are presented in mm or as ratios. The smallest, median and largest values in the sample are presented as smallest(median) largest. Carapace length is the maximum length measured from the side, including anterior eyes; height measured at posterior eyes; length of ocular quadrangle measured from above. Specimens were identified by me except the *Festucula, Carrhotus, Heliophanus, Icius,* and the European and African *Pseudicius,* which were in the Museum of Comparative Zoology (MCZ) Peckham collection and presumably identified by the Peckhams or by Simon. I have confirmed that they were correctly identified at least to genus. I have followed Prószyński's (1983b, 1985) interpretation of the correct use of the names *Phintella* and *Siler*.

Marchena minuta (Peckham & Peckham, 1888) (Figs. 1-6, 9-10)

Cytaea (?) minuta Peckham & Peckham, 1888: 73, pl. 1 fig. 55 ♀, pl. 5 figs. 55 ♂, 55a ♀. Syntypes in MCZ 1♂ 1♀ with labels "Cytaea (?) minuta Pkm. 1888. California. Type. ♂♀" and "G. W. Peckham Coll.", examined.

Marchena sissonii Peckham & Peckham, 1909: 513, pl. 40 figs. 9, 9a ♂, pl. 42 fig. 5 ♂ (labelled as ♀). Holotype in MCZ 1♂ with label "570 Marchena sissonii Peck. Type. 41=32 G. W. & E. G. Peckham Coll.", from Sisson [= Mt. Shasta; Gudde, 1962], California (Peckham, 1909), examined. NEW SYNONYMY.

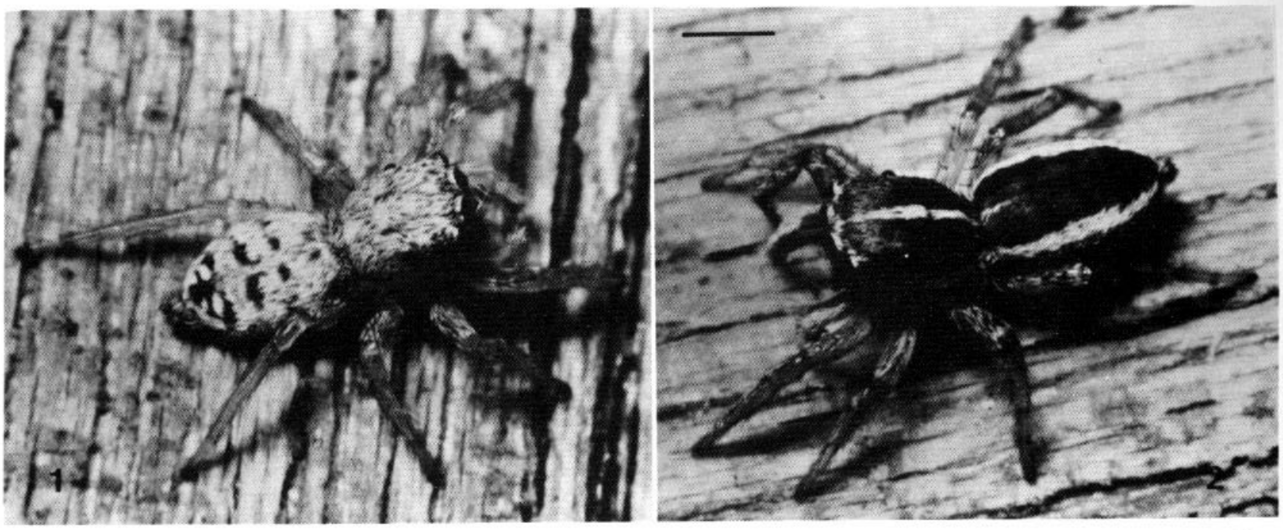
Marchena minuta: Peckham & Peckham, 1909: 514, pl. 40 fig. 10 ♀, pl. 42 figs. 4 ♀, 4a ♂.

Sitticus synopticus Chamberlin, 1925: 130, fig. 44. Holotype in MCZ 1♀ with label "*Sitticus synopticus* Chamb., ♀ holotype, Cal.: Sausalito, R. V. Chamberlin Coll., 1057", examined. NEW SYNONYMY.

Remarks on synonymy: Marchena was erected by the Peckhams in 1909 for three specimens in two species: *M. sissonii,* the type species by original designation, and *M. minuta,* both from California. I have synonymised these, for I have not found consistent differences among the specimens that would indicate two species. The Peckhams reported a difference in relative leg lengths (*M. minuta* male said to have a short fourth leg) but in fact there is none (the left fourth leg in the male type of *M. minuta* is regenerated). They also report differences in first leg spination, but these seem to be only intraspecific variation (see description below). Depending upon this spination, different specimens key out in Richman & Cutler's (1978) key to salticid genera to *Marchena, Metaphidippus, Bredana, Ballus, Chalcoscirtus* or get stuck at couplet 31. This illustrates the frequent difficulties in using spination to differentiate salticids. With the synonymy of *minuta* and *sissonii,* only one species remains in the genus.

Diagnosis: The row of seta-bearing tubercles (Fig. 9) on the first femur of adults and immatures is distinctive among North American salticids.

Male: Body brown above with three longitudinal white bands, the medial band extending back only to base of abdomen (Fig. 2). Clypeus brown. Legs tan, first pair with darker brown stripe on anterior lateral face of femur, patella, tibia, and on both sides of tarsus and metatarsus. *Chelicera:* One retromarginal and two promarginal teeth. *Palp:* Embolus a broad curved blade, fused to tegulum (Fig. 3). Tegulum bearing bump slightly proximal and retrolateral to base of embolus (Fig. 3), as in other heliophanines. Two males from Idaho have a second prong on the tibial apophysis, possibly the same as second tibial apophysis common in heliophanines. Dorsal to main apophysis the tibia has toothed bump projecting towards cymbium. *Legs:*



Figs. 1-2: *Marchena minuta*. **1** Adult female (Austin, Nevada); **2** Adult male (Humboldt County, California). Scale line (1 mm) applies to both figures.

Number of anterior lateral: anterior ventral: posterior ventral spines on first tibia varies from 0:0:0 (Austin) to 1:0:0 (Mt Shasta) to 1:1:0 (Washington) to 1:1:2 (Cazadero) to 1:2:2 (type ♂ of *M. minuta*). *Measurements* (5♂): Body length 4.1(4.2)4.8; carapace length 1.8(2.1)2.2; carapace width/length 0.64(0.67) 0.68; carapace height/length 0.35(0.39)0.42; length of ocular quadrangle/carapace length 0.41(0.44)0.47. Males measured from California: (no specific locality, type ♂ of *M. minuta*), Mt Shasta (type ♂ of *M. sissonii*), Salmon Creek (1♂) and Cazadero (1♂), and Nevada: Austin (1♂).

Female: Carapace including clypeus clothed with white scales except for barren strip on sides and two reddish spots between posterior eyes. Abdomen clothed with white except more or less extensive dorsal patch of reddish and dark brown, containing paired white spots (Fig. 1). Palps and legs beige to pale yellow-brown. *Chelicera:* One retromarginal and two promarginal teeth. *Legs:* Number of ant.lat.: ant.vent.: post.vent. spines on first tibia varies from 1:0:1 to 0:0:2 to 1:0:2; in 3 of 5 females the left and right legs differed. *Epigynum:* A central septum divides two large openings leading to deep pockets, from which the ducts proceed anteriorly (Figs. 4-5). *Measurements* (5♀): Body length 3.5(3.9)5.1; carapace length 1.9(2.0)2.3; carapace width/length 0.66(0.69)0.70; carapace height/ length 0.36(0.40)0.40; length of ocular quadrangle/ carapace length 0.41(0.45)0.47. Females measured from California (type ♀ of *M. minuta*) and Nevada: Austin (4♀).

Distribution (Fig. 6): Most records are from northern California and Oregon, but others are from Washington, western Montana, Idaho, Nevada and as far south as Tulare County, California (based on 15♂, 18♀ and 21 immatures in the Museum of Comparative Zoology, American Museum of Natural History and my personal collection).

Habitat: All but one specimen of the *Marchena* I collected were found in retreats under loose bark of conifers (*Sequoia sempervirens* in California, pine in Washington, and *Pinus monophylla* in Nevada). In each of these areas *Marchena* was found on only one or a few trees, but on those trees the presence of the species was made obvious by the many empty retreats. Still, no dense aggregations were found, at most three or four retreats under one piece of bark. A. Moldenke and B. Fichter collected a total of 8 immatures from *Pinus ponderosa* in Oregon and California, and 12 immatures from *Pinus lambertiana,* by beating limbs, in Jackson County, Oregon.

Courtship behaviour: A fragment of courtship display was observed when a male and female from Austin, Nevada were placed together in a petri dish with a paper floor. The male held the first legs up and apart and the palps, down and apart. The chelicerae were pushed forwards somewhat. The abdomen vibrated. No leg motion was noted.

Relationships

Marchena was placed in the Itatinae by Petrunkevitch (1928) and retained there by Roewer (1954). In 1974 Prószyński listed *Marchena* in the *Icius* group of genera, but in 1976 suggested its placement in the Euophryinae. Euophryines are characterised by a coiled embolus joined to the tegulum via a haematodocha. However, *Marchena*'s palpus is like that of the heliophanines (*sensu* Prószyński, 1976), in having a simple blade-like embolus fused immovably to a tegulum bearing a retrolateral bump, and I consider *Marchena* best placed in this subfamily. As noted below, the placement of *Marchena* in the Heliophaninae is especially well supported by the row of femoral tubercles and rugose carapace.

Within the Heliophaninae, the first femur and the side of the carapace may take one of three forms:

(1) with unmodified seta bases on anterior lateral face of first femur, and side of carapace smooth except for scales (♂ and ♀ of *Epocilla* cf. *rufa* Wesolowska, *Siler cupreus* (Simon), *Carrhotus viduus* (C. L. Koch) and *C. bicolor* (Walckenaer));

(2) with an irregular patch of seta-bearing tubercles (Fig. 7) on the anterior lateral distal surface of first

femur, and side of carapace with patch of small bumps (Fig. 8) (♀ of *Phintella,* including *P. castresiana* (Grube) and *P. versicolor* (C. L. Koch); ♂ with tubercles and bumps poorly developed); and

(3) with a regular row of seta-bearing tubercles (Figs. 9, 11) on the anterior lateral distal surface of first femur, and side of carapace with a patch of small bumps (♂ and ♀ of *Heliophanus, Helvetia, Icius, Marchena, Festucula, Pseudicius*; immatures, seen only in latter three genera, have tubercles and bumps like adults).

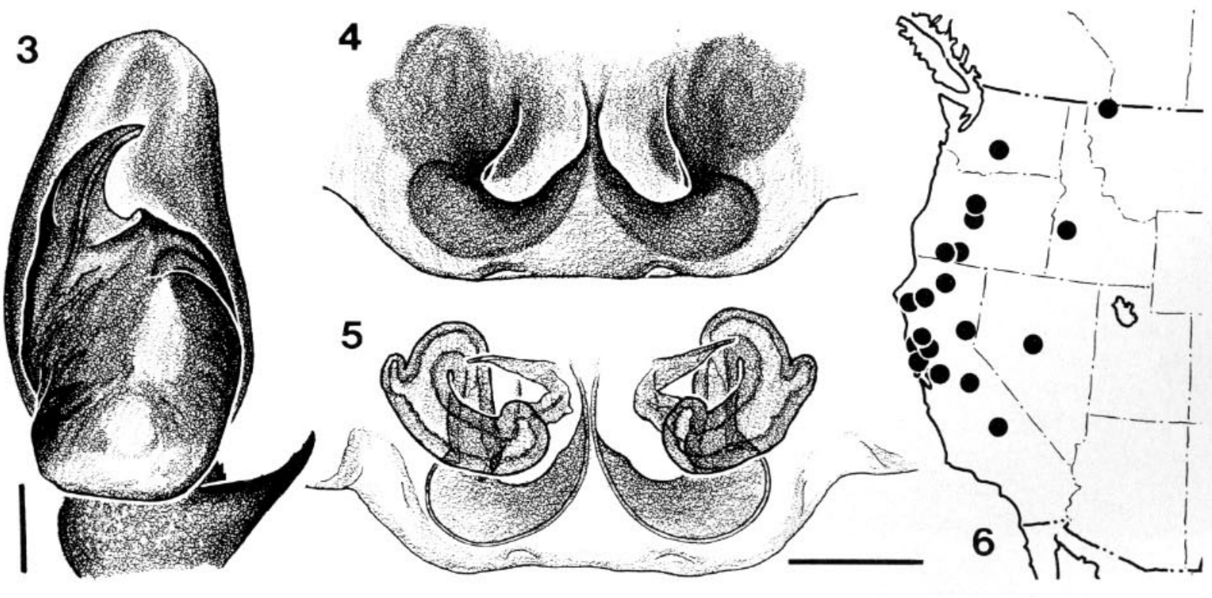
I have not seen *Helicius*, also placed in the Heliophaninae by Prószyński (1976).

The seta-bearing tubercles on the anterior face of the femur and bumps on the side of the carapace are unusual if not unique in salticids and indicate that groups 2 and 3 combined probably form a monophyletic group. Further, the arrangement of these tubercles into a row suggests the monophyly of group 3, for the row is probably a further derivation from the scattered arrangement of tubercles (usual for setae in salticids) seen in group 2. The genera of group 3 also have a similar body form with a striped pattern in males and a chevroned pattern in females, which may also support monophyly, but these characters are not consistent within the group (*Heliophanus* is often shiny and dark) and other subfamilies such as the dendryphantines have rather similar markings. Derived characters unique to groups 1 and 2 have not yet been found, and these groups may be paraphyletic.

Within the group bearing a regular row of femoral tubercles (group 3), there are two subgroups, differing in the form of the femoral tubercle row and the side of the carapace. In the first subgroup, including *Marchena, Icius, Heliophanus* and *Helvetia,* there are 3-6 femoral tubercles in a single row that rises dorsally distally (Fig. 9). The tubercles are spaced fairly far apart. The side of the carapace below the eyes is barren of scales and finely rugose (Fig. 10). Species examined in this subgroup are: *Heliophanus aeneus* (Hahn) ♂♀, *H. cambridgei* Simon ♂♀, *H. cupreus* (Walckenaer) ♂♀, *Helvetia santarema* Peckham & Peckham ♂♀, *H.* cf. *otiosa* Galiano ♂, *H.* sp. (from Chiapas, México) ♀, *Icius hamatus* (C. L. Koch) ♂♀, *Marchena minuta* ♂♀ and immatures. This subgroup may be paraphyletic, for no derived characters have been found to define it.

In the second subgroup, including *Pseudicius* and *Festucula,* there are 4-6 femoral tubercles in a row approximately parallel to the leg axis, plus one or occasionally two additional tubercles just dorsal to the row (Fig. 11). The femoral tubercles in these genera are closely placed and form an almost continuous ridge. They were recently discovered independently by F. R. Wanless (pers. comm.). The side of the carapace is finely rugose as in the first subgroup, but retains scales and, in addition, bears a row of 6-15 seta-bearing tubercles just below the eyes (Fig. 12). This row of carapace tubercles has been previously reported by Berland & Millot (1941: 329) in *Afraflacilla.* Specimens examined in this subgroup are: *Pseudicius encarpatus* (Walckenaer) ♂♀, *P. histrionicus* Simon ♀, *P. unicus* (Peckham & Peckham) ♂, *Pseudicius* spp. (from Australia, India, Marshall Is., Okinawa, Philippines, Solomon Is.) ♂♀ and immatures, *Festucula vermiformis* Simon ♂♀ and immatures. This subgroup is probably monophyletic, for the row of seta-bearing tubercles on the carapace seems unique to this group. Peculiar curled setae on the first legs and an elongate body may also support the group.

Not only does *Marchena* belong in group 3, but it may eventually be synonymised with *Icius*, for it resembles the type species *Icius hamatus*. However, the resemblances may be primitive similarities, and it is possible that *Icius* is cladistically closer to *Heliophanus* and *Marchena* to *Pseudicius*. There are many unanswered questions of heliophanine phylogeny, such as whether the recent synonymy by Andreeva *et al.* (1984) of *Pseudicius* with *Icius* is based on their having synapomorphies or on their lacking the autapomorphies of *Heliophanus*. It seems best to let

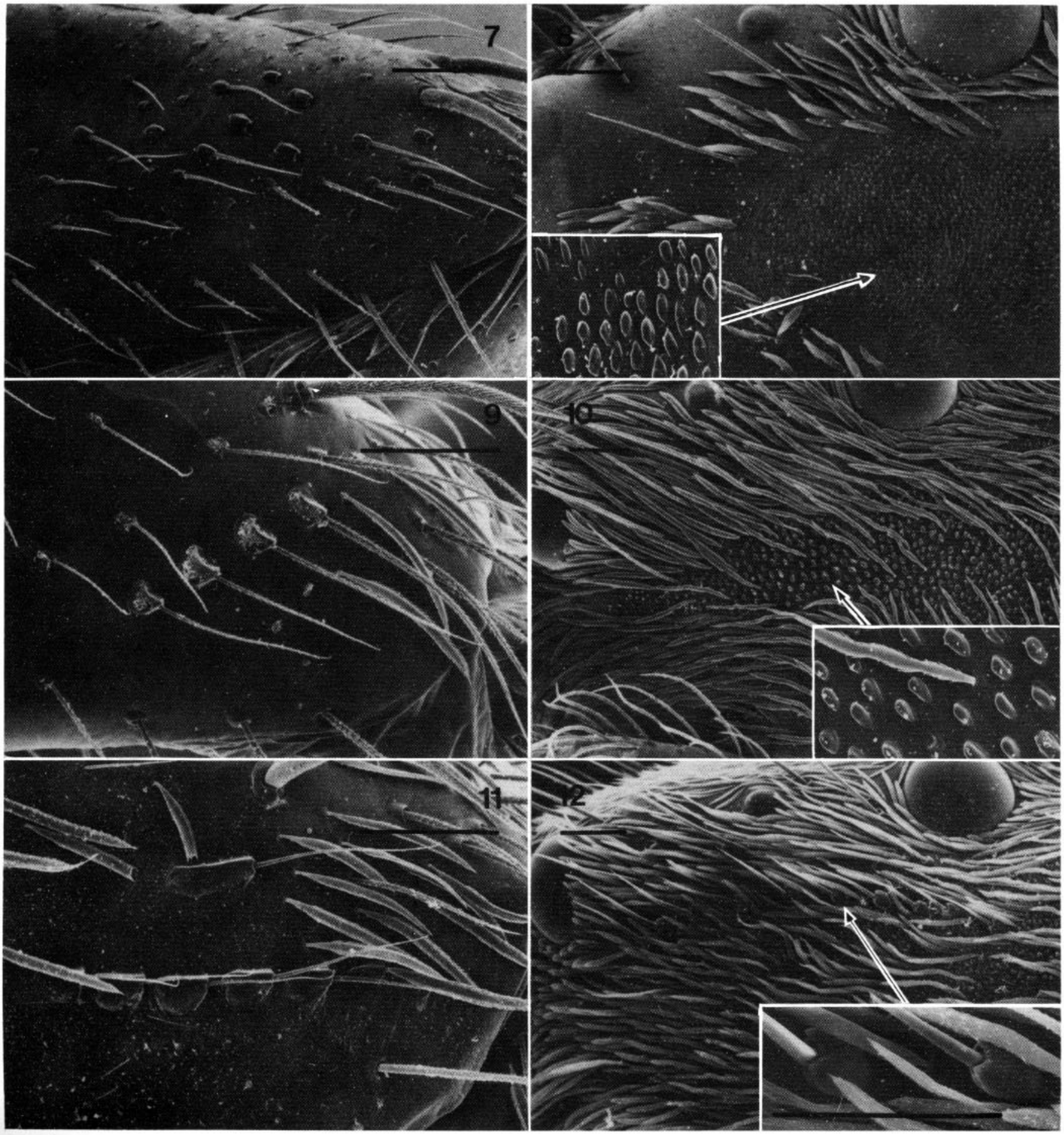


Figs. 3-6: *Marchena minuta.* **3** Left male palpus, ventral view (Humboldt Co., Calif.); **4** Epigynum, ventral view (Austin, Nev.); **5** Cleared epigynum, dorsal view; **6** Distribution in western United States. Scale lines = 0.1 mm.

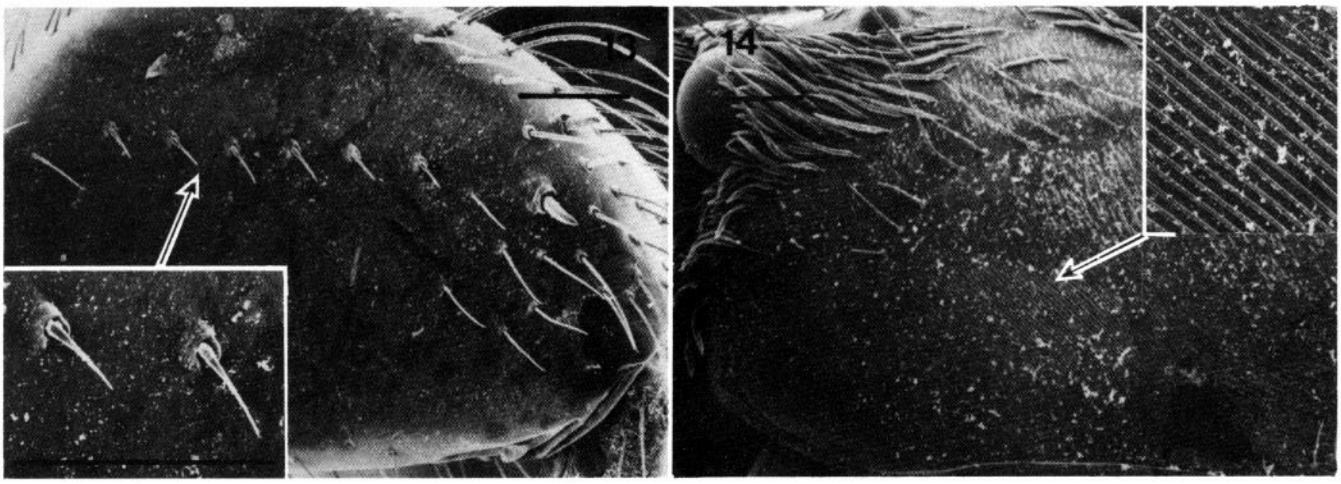
the genus *Marchena* stand until more evidence is available. *Marchena* and *Helvetia* appear to be the only New World heliophanines: I have looked without success for other New World salticids with heliophanine-like genitalia or femoral tubercles.

None of the North American species that have been placed in *Icius* and *Pseudicius* have femoral tubercles, nor do they have heliophanine genitalia. As suggested by Prószyński (1974) and Andreeva *et al.* (1984), they belong elsewhere. Most of the "*Icius*" have already been redistributed to their proper genera such as *Tutelina*. "*Pseudicius*" *piraticus* (Peckham & Peckham) and the closely related *Paramarpissa tibialis* F. O. P.-Cambridge are of uncertain subfamily but apparently not heliophanines (having a haematodocha between the embolus and tegulum). "*Pseudicius*" *monticola* (Banks) is a dendryphantine apparently related to *Metaphidippus neomexicanus* (Banks) and *M. harfordi* (Peckham & Peckham), while "*P.*" *siticulosus* Peckham & Peckham is likewise a dendryphantine, possibly near *Eris* or *Metaphidippus*.

While the femoral tubercle row and carapace rugosity of heliophanines are unique among salticids, they are not without analogues. The small neotropical



Figs. 7-12: Seta-bearing tubercles on female first leg femur, anterior lateral distal surface (7, 9, 11) and side of carapace below eyes (8, 10, 12); insets in Figs. 8, 10, 12 show carapace bumps and tubercles at higher magnification. **7, 8** *Phintella versicolor* (S.W. Fukien, China); **9, 10** *Marchena minuta* (Austin, Nevada); **11, 12** *Pseudicius* sp. (Mindanao, Philippines). Scale lines = 0.1 mm; insets in Figs. 8, 10, 12 all to same scale.



Figs. 13-14: *Cotinusa distincta,* female (Chiapas, Mexico). **13** Anterior lateral distal surface of first leg femur; inset shows stout setae at higher magnification; **14** Side view of carapace; inset shows file at high magnification. Scale lines = 0.1 mm; insets in both figures to same scale.

thiodinine genus *Cotinusa* Simon has a very regular row of 6-8 setae on the central part of the front face of the first femur, running parallel to the axis of the femur (Fig. 13). These setae are differently placed than in the heliophanines, and instead of standing on tubercles, the bases of the setae themselves are swollen. These thiodinines also have a rough patch on the side of carapace, but instead of bearing small bumps, the surface is finely ridged (Fig. 14). Because of the difference in form and the lack of recognised close relationship between *Cotinusa* and the heliophanines, these characters are probably independently derived in these two groups. The following thiodinines were examined and have the setal row and carapace file: *Banksetosa dubia* Chickering (probably belongs in *Cotinusa*), *Cotinusa distincta* (Peckham & Peckham) and *Carabella banksi* Chickering (belongs in *Cotinusa*). Three thiodinine species examined lack both the setal row and the file: *Nilakantha cockerelli* Peckham & Peckham, *Thiodina peurpera* (Hentz) and *T. sylvana* (Hentz).

Stridulation?

In the heliophanines and thiodinines the correlation between a modified femur and a modified carapace is without exception: those species with seta-bearing tubercles or a row of stout setae on the anterior lateral face of the first femur *also* have either a patch of bumps, a row of tubercles, or a patch of ridges on the side of the carapace below the eyes. This correlation suggests a functional relationship between the femur and carapace, the obvious hypothesis being that they act together in stridulation. Raising the femur against the carapace would bring the femoral tubercles in contact with the head rugosity or tubercles. In *Pseudicius* and *Festucula*, where the femoral tubercles would oppose only a narrow band of tubercles on the head, it makes sense (lest the femoral and head tubercles miss each other) that the femoral tubercles are large and almost confluent to form a ridge. In *Heliophanus, Helvetia, Icius* and *Marchena* the femoral tubercles are relatively widely spaced, but the head is rugose over a broad region. The swollen setae on the femur of *Cotinusa,* which are more basally placed than the femoral tubercles in heliophanines, would likewise contact the fine ridged surface on the side of the carapace, which is more ventrally placed than the rough surfaces in heliophanines. It must be emphasised however that stridulation has yet to be observed in these genera.

Many other spider stridulatory mechanisms have been described (Legendre, 1963), but the dysderid *Ariadna fidicina* (Chamberlin) appears to be the only other spider known with a leg-carapace stridulatory mechanism. It has ridges on the sides of the carapace (Chamberlin, 1924; Beatty, 1970) and, at least in the paratype female, one seta-bearing tubercle on the anterior face of the first leg femur. M. J. Moody (pers. comm.) has heard a penultimate male make a loud buzzing sound by vigorously rubbing the carapace ridges.

Sociality?

The behavioural context in which stridulation would occur can only be a matter of speculation. However, there are hints that stridulation may be involved in social communication. In other salticids, sound production has been associated with courting males (Edwards, 1981; Maddison, 1982; Gwynne & Dadour, 1985). It seems unlikely that the sole use of stridulation in heliophanines is in courtship, for the apparatus is present in males, females and immatures (sometimes better developed in females and immatures), unless the apparatus is unused in the latter. An alternative function for stridulation, namely for social communication, is suggested by reports of heliophanines living in aggregations. Jackson (in press) reports that two *Pseudicius* species from Kenya live in nest aggregations in a communal-territorial social structure, but makes no mention of stridulation. Simon (1876: 155) states of *Heliophanus auratus* "il paraît presque vivre en société, car les coques, placées sous de petite écorces, sont nombreuses à côté les une des autres" ("it seems almost to live in a society, for the nests, placed under small pieces of bark, are numerous beside one another"). Tullgren (1949: 21) mentions that *Heliophanus* nests are often aggregated. Prószyński (pers. comm.) has found aggregated nests of a *Heliophanus* species between rocks, in Switzerland. Nests of *Marchena minuta* are somewhat aggregated as mentioned above, but I have made no observations of living *Marchena* since the stridulatory apparatus was discovered. Bellmann (1984: 128) reports winter nest aggregations of *Heliophanus aeneus* under rocks, but does not comment on summer retreats. Fuhn & Gherasim (1984) describe habits and habitat of *Pseudicius* but do not discuss nest aggregation. If stridulation is used in social communication in the heliophanines, then the presence of the stridulatory apparatus in most heliophanines would suggest that most species in this subfamily are communal. Clearly, more natural history studies of this subfamily are needed.

The function of stridulation in the thiodinine *Cotinusa* is even more a matter of speculation. The thiodinines are peculiar in a number of respects, though whether any relate to stridulation is unclear. Most species (including *Thiodina* and *Cotinusa*) have one to four bulbous setae on the underside of the first tibia. At least some species of *Cotinusa* have a concave sternum. A species of *Cotinusa* builds nests associated with the arboreal dolichoderine ant *Tapinoma melanocephalum* (Shepard & Gibson, 1972), suggesting *Cotinusa* might use stridulation in communicating with the ant, although dolichoderine ants apparently do not use stridulation for intraspecific communication (Markl, 1973).

Acknowledgements

Thanks are due to H. W. Levi for many things, including a well-run laboratory in which to work; R. R. Jackson for his manuscript on *Pseudicius* before publication; J. Prószyński and F. R. Wanless for information on Old World heliophanines; M. J. Moody for information on *Ariadna*; D. E. Wheeler for information on ants; L. Avilés, H. W. Levi, D. R. Maddison, and J. Prószyński for useful comments on the paper; N. I. Platnick for lending the AMNH *Marchena* and Ed Seling for operating the SEM.

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Note added in proof

Two references to Simon were overlooked; he discovered the femoral tubercles in *Icius* and *Pseudicius* and used them in his "dendryphantine" key (1937, *Les Arachnides de France* **6**(5): 1213). Regarding sociality, Simon notes "On recontre souvent de nombreuses coque d'*Icius* à côté les unes des autres" (1876: 55).