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Natural History and Systematics of Arthropod Symbionts (Araneae; Hemiptera; Diptera) Inhabiting Webs of the Spider *Tengella radiata* (Araneae, Tenggellidae)

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ABSTRACT

The webs of the Costa Rican tengellid spider *Tengella radiata* (Kulczyński) are regularly inhabited by at least four species of arthropod symbionts: the phorid fly *Megaselia scalaris* Loew; the plokiophilid bug *Lipokophila eberhardi* Schuh, new species; the uloborid spider *Philoponella vicina* (O. P.-Cambridge); and the mysmenid spider *Mysmenopsis tengellacompa* Platnick, new species. Other arthropods found in *Tengella* webs in small-

er numbers include the theridiid spider *Argyrodes bryantae* Exline and Levi, the mysmenid spiders *Mysmenopsis dipluramigo* Platnick and Shadab and *Maymena rica* Platnick, new species, and the plokiophilid bug *Lipokophila tengella* Schuh, new species. The behaviors of the symbionts and hosts, and the interactions among them (which include contest competition, parasitism, predation, and commensalism) are described.

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INTRODUCTION

The webs of large spiders, such as the orb-weavers *Nephila* and *Cyrtophora*, and some diplurids, psechrids, and social theridiids, are known to harbor a number of species of relatively small kleptoparasites such as uloborid, theridiid, pholcid, and mysmenid spiders, chloropid and drosophilid flies, and others (Exline and Levi, 1962; Thornhill, 1975; Vollrath, 1976, 1979a, b, c; Robinson and Robinson, 1977; Robinson and Lubin, 1979; Eberhard, 1980; Nyffeler and Benz, 1980; Rypstra, 1981; Sivinski and Stowe, 1981; Tanaka, 1984; Griswold, 1985; Nentwig, 1985; Sivinski, 1985; Forster and Murphy, 1986; Whitehouse, 1986; Baert and Murphy, 1987; Coyle and Meigs, 1989, 1992; Coyle et al., 1991). In general, these species take advantage of the fact that the large spiders often do not respond to the presence of very small animals in their webs (presumably thus avoiding expenditures of energy that are unlikely to significantly enhance prey intake). Some symbionts capture small prey that fall into the web and are undetected or ignored by the owner, and some feed directly from prey being consumed by the owner.

This paper describes still another situation of this sort, with the unusual complication that four rather than one species of insect and spider regularly inhabit webs of the host, *Tengella radiata* (Kulczyński). These include a phorid fly, a plokiophilid bug, and representatives of two other spider families (Uloboridae and Mysmenidae). The interactions among these species are complex, and include contest competition, parasitism, predation, and commensalism. Two of the species, the mysmenid spider *Mysmenopsis tengellacompa* and the plokiophilid bug *Lipokophila eberhardi*, are described below as new by the second and third authors, respectively.

Fincke (1981) showed that one of the associated species, the uloborid spider *Philoponella vicina* (O. P.-Cambridge), facultatively builds its orb-webs in the mesh of threads above *Tengella* sheet webs, and apparently prefers such websites over alternatives. Those *Philoponella* spiders associated with *Tengella* fed more often and disappeared less often from their websites than did nonassociated conspecifics.

Other arthropod species that inhabit *Tengella* webs but have been collected in smaller numbers include the theridiid spider *Argyrodes bryantae* Exline and Levi, the mysmenid spiders *Mysmenopsis dipluramigo* Platnick and Shadab and *Maymena rica* Platnick, new species, and the plokiophilid bug *Lipokophila tengella* Schuh, new species.

We thank Drs. F. C. Thompson and R. Peterson of the Systematic Entomology Laboratory, United States Department of Agriculture, for identifying the phorid flies. In addition to material in the American Museum of Natural History (AMNH), specimens were supplied by Mr. Darrell Ubick of the California Academy of Sciences (CDU), Mr. John A. Murphy of Hampton, England (JAM), and Dr. H. W. Levi of the Museum of Comparative Zoology, Harvard University (MCZ). Help with illustrations was provided by Dr. Mohammad U. Shadab (AMNH). We thank Drs. Jonathan A. Coddington of the National Museum of Natural History and Frederick A. Coyle of Western Carolina University for helpful comments on a draft of the manuscript.

NATURAL HISTORY

METHODS

Most of the behavioral observations were made on animals kept on *Tengella* webs in 22×30×10 cm plastic containers with glass tops. This permitted observations of details of behavior inside the tubular retreats that would otherwise have been difficult or impossible. Some additional observations were made in the field near San Antonio de Escazu, Costa Rica. Counts of symbionts were made by collecting entire webs, including retreats, and carefully examining their contents.

THE HOST

Tengella radiata is an unusual spider, and the family Tengellidae is of uncertain limits. The association with *Tengella* of such genera as *Calamistrula*, *Lauricius*, *Liocranoides*, and *Zorocrates* proposed by Lehtinen (1967) remains unsupported by synapomorphies, but Griswold (cited in Coddington and Levi,

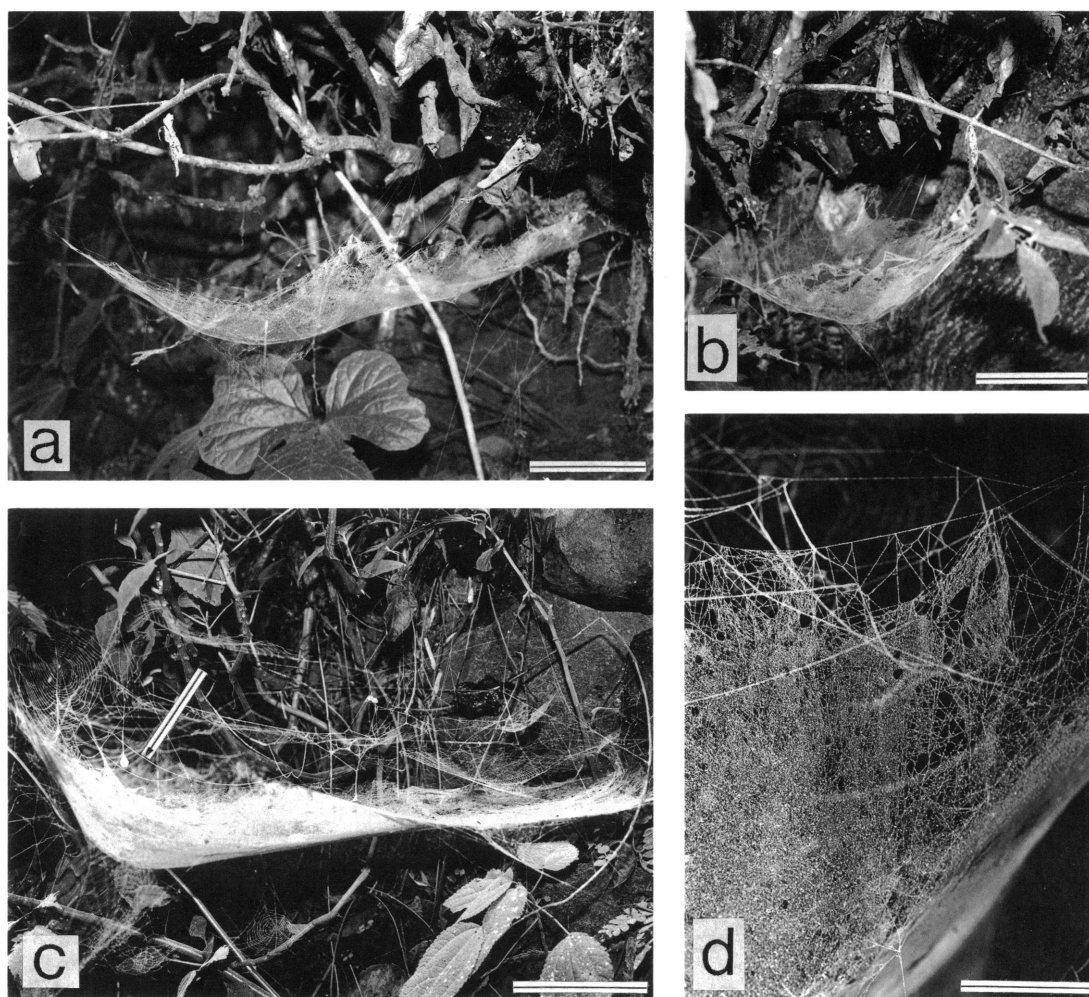


Fig. 1. Webs of mature *Tengella radiata* females. Lateral (a) and end-on (b) views of a newly built web (probably built the preceding evening). Lateral view (c) of an older web, with close-up (d) of outer edge of sheet. The tunnel retreat is at the right in (a) and (c). Arrow in (c) marks long, sagging sticky line. Note also sparse mesh and orbs of *Philoponella vicina* which are present in (c) but nearly completely lacking in (a) and (b). Scale bar = 10 cm in (a), (b), and (c), 2 cm in (d).

1991) has treated tengellids as the sister group of the classical Lycosoidea. Only three species of *Tengella* are known, and two of those are apparently very rare, being represented by a total of four specimens from Mexico, Guatemala, and "South America" (Wolff, 1977). *Tengella radiata*, however, is extremely common in a wide variety of habitats in Costa Rica, ranging from elevations of about 50 m in tropical rain forest up to at least 1500 m in secondary growth in and around coffee fields in the Valle Central

(Wolff, 1977; W. Eberhard and M. Santana, unpublished data). Despite its obvious success in varied habitats, however, *T. radiata* is unknown outside Costa Rica. In Panama and further south, similar webs in similar sites are constructed by mygalomorph spiders of the family Dipluridae. What factors limit the ranges of these apparently ecologically equivalent groups remain unknown.

The web of *T. radiata* is generally a large, flat sheet turned up at the edges, narrowing to a tube at the rear, protected side (fig. 1).

During the day, the spider, which is about 2 cm long, is usually found in the tube, whereas at night it rests at the mouth or on the upper surface of the sheet near the entrance. Contrary to the report of Fincke (1981), spiders will often attack prey during the day. There is a meshwork of threads of variable density and extension above the sheet, and long, sagging lines of cribellum (sticky) silk are often attached to the meshwork near the edges of the sheet (fig. 1). In a newly built web, the mesh above the sheet was reduced, and there were no lines of cribellum silk. When prey falls onto the sheet, the spider usually rushes out, seizes it with its chelicerae, and rushes back to the tube, where it finishes subduing the prey and feeds.

THE SYMBIONTS

Lipokophila, *Mysmenopsis*, and *Philoponella* symbionts were present in appreciable numbers in the webs of larger *Tengella* at both Finca La Selva (elev. 100 m, near Puerto Viejo, in Heredia province) and San Antonio de Escazu (elev. 1300–1400 m, in San José province). The phorid fly *Megaselia scalaris* Loew was uncommon in San Antonio, and not seen at La Selva. At another highland site (Monteverde, elev. approximately 1200 m, in Puntarenas province), an additional symbiont, *Argyrodes bryantae* Exline and Levi, was also common, along with species of *Lipokophila* and *Mysmenopsis* (J. Crawford, unpublished data).

At all sites symbionts were usually absent from the webs of early instar nymphs of *Tengella*. In a collection of 25 webs of adult female and penultimate nymphs of *Tengella* made on 10 Dec. 1982 at La Selva, there were an average of 5.8 ± 6.0 *Lipokophila* bugs (range 0–20) and 2.0 ± 2.2 *Mysmenopsis* spiders (range 0–6); these counts are conservative, since the considerable quantities of detritus in some webs made it difficult to find the symbionts. There was a strong positive correlation between the numbers of bugs and spiders (linear correlation coefficient $r = 0.69$, $p = 0.00013$); possibly this was due to older *Tengella* webs having accumulated larger numbers of symbionts. All behavioral observations reported below were made on specimens from San Antonio de Escazu.

BEHAVIOR AWAY FROM THE *TENGELLA* RETREAT

Both *Mysmenopsis tengellacompa* and *Lipokophila eberhardi* were frequently seen on the sheet of the host's web. Both walked either on top of or under the sheet without apparent difficulty. Most movements were relatively leisurely, but *M. tengellacompa* individuals occasionally made brief, quick runs, especially when fighting among themselves near prey. In both cases, and probably especially in the case of the bug, older individuals (both males and females) were more likely to be found on the sheet away from the tube than were younger ones.

Both of these species attacked small insects (e.g., ants about 2 mm long) dropped onto the web. The spiders usually moved to the prey in a series of short bursts of running or walking that were interspersed with short pauses. They often reoriented and moved more directly toward the prey after such pauses, and in general gave the impression of having only an imprecise ability to orient toward prey struggling on the sheet. Attacks by *M. tengellacompa* were simple, with the spider running or walking toward the prey, usually on the undersurface of the sheet, and biting it through the sheet. When the prey became more or less immobile, the spider pulled it through the sheet by cutting a small hole, and carried it away. The spiders did not usually wrap their prey either before or after immobilizing it, but in one case a spider, after having had a difficult time pulling the prey free from the sheet (due to another spider holding it from the other side of the sheet), wrapped the prey with slow alternate movements of its legs IV.

On one occasion (in the field), a spider attacked and fed on an intermediate-sized nymph of *L. eberhardi* that was feeding with several other bugs on a dead ant that had been killed but then rejected by the *Tengella*. Specimens of *M. tengellacompa* usually either fled from the vicinity of prey trapped in the sheet that were larger than themselves, or approached only part way and then retreated. Both male and female spiders attacked prey, but females that were carrying egg sacs (held with one leg IV on a short line from the spinnerets, in the manner of some theridiids and

neusticids—see, e.g., Bristowe, 1958) did not respond to prey except to move away.

Sometimes more than one *M. tengellacompa* responded to the same prey, and in these cases aggressive interactions often ensued (aggression was also seen once around a drop of water on the web from which one of the spiders had been drinking). When the two spiders were of unequal sizes, the larger one generally chased the smaller one from the vicinity of the prey. When spiders of approximately equal size fought, they met head-to-head and interlocked legs I and perhaps also legs II. In some cases they remained more or less immobile in this position for several seconds before one withdrew a little and the other then chased it away. When the prey was large compared to the spiders, several often fed on it simultaneously, with the smaller ones positioned so that the prey was between themselves and the larger spiders. Most spiders were on the underside of the sheet; those on the other side from an attacker were less susceptible to being chased. On some occasions, a smaller spider on the other side of the sheet fed, despite apparent attempts to chase it away, until the larger one finally made a hole in the sheet to pull the prey through. Once a small prey was freed from the sheet, the spider that carried it always moved away at least a few millimeters, and extended aggressive interactions ceased, as the spider carrying the prey simply moved away when others approached.

On two occasions when a larger prey was dropped onto the sheet, a large *M. tengellacompa* that had been resting near the mouth of the tube retreat ran out under the sheet to wander more or less in the area of the sheet where the *Tengella* had attacked the prey, stopping briefly at pieces of debris it encountered there. On other occasions, the rush of the *Tengella* onto the sheet to attack prey apparently stimulated several *M. tengellacompa* to a burst of less directed movement. In two cases this type of behavior resulted in a meal for the *M. tengellacompa*. In one case the *Tengella* had been feeding on another prey, and when it initiated its attack on the second prey it laid the first on the sheet, where the *M. tengellacompa* began feeding on it from below. In the second case one of the prey's legs became detached from its body during

its struggle with the *Tengella*, and again the *M. tengellacompa* fed on this overlooked food item.

M. tengellacompa also chased *L. eberhardi* bugs that approached when the spiders were attacking or feeding on prey. The bugs usually retreated, but on one occasion the bug returned and inserted its proboscis into the prey for 30–60 sec while the spider chased off a second spider. On another occasion, the bug fed from below the sheet while the spider fed on the prey from above. The bugs often returned persistently, usually each time from a different angle than before, with the eventual result in some cases of having the prey more or less between themselves and the spider. When the prey was large enough, this sometimes resulted in both the spider and bug feeding from the same prey. It appeared from the bugs' behavior that they may have been able to distinguish the general area where a spider and its prey were from a distance, but that they had to touch the prey with an antenna in order to guide the insertion of their probosces. Occasionally an adult bug did not run from an approaching *M. tengellacompa*, but instead flattened itself to the sheet and remained immobile while the spider arrived. In some cases the spider tapped the bug with its legs and pedipalps, and it was clear that the spider could have attacked the bug, but did not.

These were not the only species to squabble over small prey on the sheet. On two occasions the relatively huge *Tengella* came onto the sheet to seize a *Drosophila*-size prey that *M. tengellacompa* spiders were about to attack. And on one occasion, a *Philoponella* that had an orb whose frame lines were close to the edge of the sheet came to the edge of its web and attacked a prey that was near the edge of the sheet, and then carried it back to its hub.

The *L. eberhardi* bugs also attacked prey by themselves. They generally approached slowly, and probed repeatedly with their extended probosces. When a bug was below the sheet, it inserted its proboscis through the sheet to reach the prey. The bugs were quite cautious, and often made repeated approaches without inserting the proboscis. In one case an adult bug made a series of unsuccessful approaches to a struggling prey on the top of

the sheet, then moved through a hole in the sheet to the underside and approached much less cautiously and succeeded in inserting its proboscis, suggesting an ability to take advantage of the protection offered by the sheet.

Both the spiders and the bugs also fed on inanimate objects. On several occasions bugs inserted their probosces into a discarded prey package that had fallen onto the sheet from a *Philoponella* web above; in some of these cases the bug's proboscis remained in the package for a minute or more, suggesting that the bug was actually extracting nourishment rather than just testing. In one case (in captivity), a *Tengella* constructed an egg sac above the web's sheet, but its eggs failed to adhere to the sac and fell onto the sheet in a wet mass, where bugs, *Mysmenopsis*, and the female *Tengella* all fed on it.

BEHAVIOR WITHIN THE *TENGELLA* RETREAT

Three of the symbiont species (all but *Philoponella* and *Argyrodes*) were often found near the tunnel-like retreat of the *Tengella*, and observations in captivity showed that they fed there on prey captured by *Tengella*. The simplest behavior was that of the *L. eberhardi* bugs and *Megaselia* flies. In both cases, the insects walked slowly toward the spider, and climbed directly onto the prey that it held in its chelicerae. Once on the prey, they applied their mouthparts to it, and within several minutes their abdomens were usually distinctly swollen. After obtaining a meal, the insects dropped from the prey onto the floor of the tunnel. The flies usually stayed near the tunnel even when not feeding (they were found in spiders' retreats in the field), but the bugs, as noted above, were also commonly found out on the sheet. When the *Tengella* rushed out, attacked a prey, and then rushed back to its retreat, the bugs on the sheet generally began moving slowly but directly toward the tunnel. The nymphs of *Lipokophila* are bright red, and the "mites" noted by Fincke (1981) on the prey of *Tengella* in the retreat were probably these bugs.

The behavior of the *M. tengellacompa* spiders was more complex. Younger juveniles behaved much as did the flies and bugs, climbing slowly directly onto the prey inside

the tunnel. Their approaches to the prey were clearly cautious, and it appeared that they were stimulated to move by movement on the part of the *Tengella*, a tactic also seen in parasitic wasps attempting to attack eggs defended by female pentatomid bugs (Eberhard, 1975). The larger spiders (all the adults observed) differed in that they never moved inside the retreat. They remained instead on the retreat's outer surface, and attempted to bite the prey that the *Tengella* was feeding on where it contacted the tunnel wall. It was clear on several occasions that an *M. tengellacompa* had been successful in doing this, as when the *Tengella* began to move its prey it came loose with a jerk from the point on the tunnel wall where the *M. tengellacompa* was biting.

No aggressive interactions were observed among symbionts within the retreat. Occasionally large *M. tengellacompa* on the outside surface squabbled over access to a point where the prey contacted the wall of the retreat.

Sometimes it seemed that a *Tengella* sensed the movement of *M. tengellacompa* on the other side of the tunnel wall. It responded by tapping the sheet carefully with its palps where the other spiders were moving, and by repeatedly shifting the prey, setting it down, wrapping it, and picking it up again, and also by moving back and forth within the tunnel. Such movements of the prey often (but not always) caused the bugs that were on it to decamp. Only infrequently did a *Tengella* appear to sense the presence of other species inside the tunnel with it, or on the prey, but on several occasions spiders used a leg or palp in an apparent attempt to brush one of them off the prey. The *Tengella* either quickly withdrew its leg or brushed it with another when a bug or *M. tengellacompa* touched it.

At night *Tengella* fed on prey near the tunnel mouth, and stilted high on its legs as it did so. This stilting may represent a further defense against the kleptoparasites, making it more difficult for them to climb onto the prey and to bite the prey from the other side of the web. The *Tengella* never made any more forceful defensive responses to any of the parasites, despite the fact that they were able to locate and attack such small prey as *Drosophila* flies and small calliphorid larvae on their webs. One observation suggested that

this lack of responsiveness by the *Tengella* may be due to previous unpleasant experiences rather than an inability to sense the presence of the parasites. When a prey that a *Tengella* was holding in its retreat was experimentally poked with a small stick, a *L. eberhardi* nymph that had been feeding there was inadvertently squashed. The spider immediately dropped the prey and rushed to the far edge of the web, where it remained motionless, hanging over the edge, for 10–20 min. A moment after squashing the bug, a pungent odor was apparent; presumably, the spider's flight was caused by the odor of the squashed nymph. This odor may also induce dispersal among the bugs, as the attack on a nymph by an *M. tengellacompa* noted above was immediately followed by the dispersal of all the bugs that had been feeding on the same prey, with only a gradual return later.

OTHER BEHAVIORS

Mating. One pair of *Lipokophila* was seen copulating while they were on a prey held in the chelicerae of a *Tengella*. After several minutes, the spider brushed them off, and they separated. When several adults were in close proximity, as when near a large prey, males made short, quick dashes in apparent attempts to mount other individuals. The other individuals either avoided the dashes or quickly ran out from under the males.

Two mating pairs of *Mysmenopsis* were observed. In both cases, the spiders were facing each other (in mating position I of Gerhardt), and each held the sheet with all its legs. The male's legs were folded quite tightly to his body, whereas the female's legs were somewhat more extended, and partially encircled the male. One palp was inserted at a time in the opposite side of the female (i.e., the male's right palp reached across the female and inserted in her right epigynal opening). Each palp was inflated repeatedly during each insertion, but otherwise the spiders were nearly motionless.

Maternal Care. Several *Mysmenopsis* females carried an egg sac attached to a short line held with one leg IV. One female with an egg sac passed her leg III repeatedly over the surface of the sac while she held it in the normal position dangling from one leg IV.

This movement may serve as a defense against egg parasites; similar movements are made by theridiid spiders defending against scionid wasp egg parasites (Valerio, 1984).

DISCUSSION

The ecological relationships documented here are outlined in figure 2. At least three of the symbionts parasitize the host by feeding on prey (or digestive juices) that would otherwise have been utilized by *Tengella*. There is also direct competition between *M. tengellacompa* and *L. eberhardi* for food, with the spiders attempting to sequester food from other spiders and also from the bugs. The spiders are apparently better able to subdue prey than the bugs, and feeding by the bugs at prey captured by *M. tengellacompa* can be considered parasitism (or, in this case, hyperparasitism). In addition, the *M. tengellacompa* at least occasionally prey on the bugs.

The relationship of *Philoponella* to the other symbionts is not as intimate. The discarded prey packages of these spiders may represent a portion of the diet of the bugs, and the spiders may occasionally take prey that would have been captured by one of the symbionts or by the *Tengella*. It seems very unlikely that the *Philoponella* capture the bugs with any frequency, as Fincke (1981) suggested might happen. In general the biological impact of *Philoponella* on the other species is probably of minor importance.

The puzzling lack of responsiveness by the *Tengella* to the presence of symbionts in its retreat and on its prey may be explained by the defensive odor of the bugs. If this is the case, then both the flies and the *Mysmenopsis* spiders may derive benefit from the presence of the bugs because the bugs' odor makes the host spider less likely to attack them.

The bugs and the *M. tengellacompa* and *Tengella* spiders all show behavioral responses to the presence of other species in the *Tengella* webs. The stilting and frequent changes of feeding site by *Tengella* make it more difficult for the *M. tengellacompa*, particularly the larger ones, to feed on its prey. The change in *M. tengellacompa* feeding sites from inside to outside the tunnel with increased size, their cautious approaches inside the tunnel, and their apparent searches in ar-

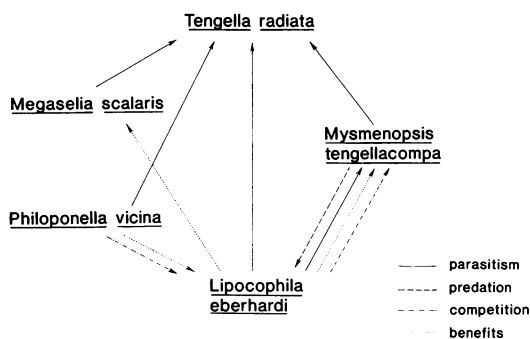


Fig. 2. Possible ecological relationships among the taxa discussed.

eas where the *Tengella* had just attacked prey may all be adaptations to the behavior of *Tengella*. Similarly, the tendency for *L. eberhardi* to reapproach prey defended by *M. tengellacompa* from different directions in successive tries, to crouch when approached by an *M. tengellacompa*, to move from the sheet into the tunnel when *Tengella* captures a prey, and their less cautious attack when the sheet is between them and a potential prey all suggest adaptations to interactions with other species on *Tengella* webs.

SYSTEMATICS

ARANEAE

FAMILY THERIDIIDAE

Argyrodes bryantae Exline and Levi

Figures 3, 4

Argyrodes bryantae Exline and Levi, 1962: 172, figs. 286–288 (male holotype from Boquete,

Chiriquí, Panama, in Museum of Comparative Zoology, not examined).

Exline and Levi (1962) presented a description of both sexes of this species. Unfortunately, the epigynum of their only female specimen was lost before it could be illustrated. A pair of specimens taken from a *Tengella* web at an elevation of 1350 m at Monteverde, Puntarenas, Costa Rica (June 1986; W. G. Eberhard; AMNH) allows us to present here illustrations (figs. 3, 4) of the epigynum. The species has been collected in both Costa Rica and Panama, but because no habitat data accompanied any of the original specimens, it is unknown whether the species is restricted to *Tengella* webs.

FAMILY MYSMENIDAE

Mysmenopsis tengellacompa

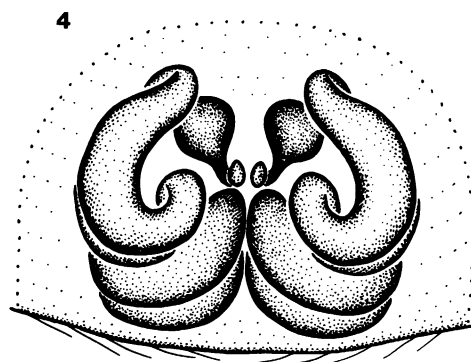
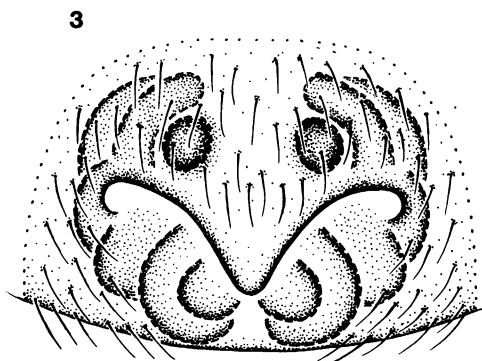
Platnick, new species

Figures 5–9

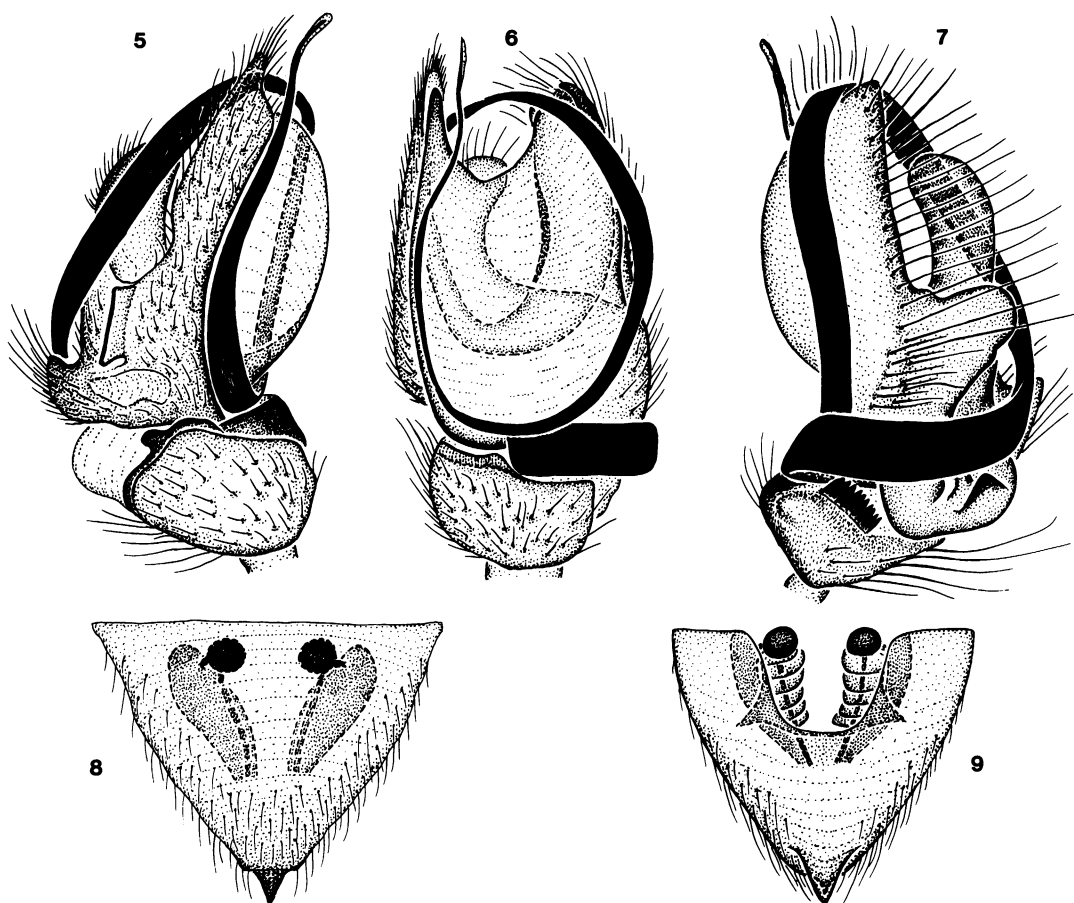
TYPES: Male holotype taken in a web of *Tengella radiata* at an elevation of 100 m at La Selva, near Puerto Viejo, Heredia, Costa Rica (Apr. 1983; W. G. Eberhard), deposited in AMNH.

ETYMOLOGY: The specific name refers to the lifestyle of these spiders as *Tengella* companions.

DIAGNOSIS: This species seems most closely related to *Mysmenopsis cymbia* (Levi), which is known only from Florida. In the cladogram of the genus proposed by Platnick and Shadab (1978: fig. 1), *M. cymbia* represents the sister group of all other known *Mys-*



Figs. 3, 4. *Argyrodes bryantae* Exline and Levi, epigynum, ventral and dorsal views.



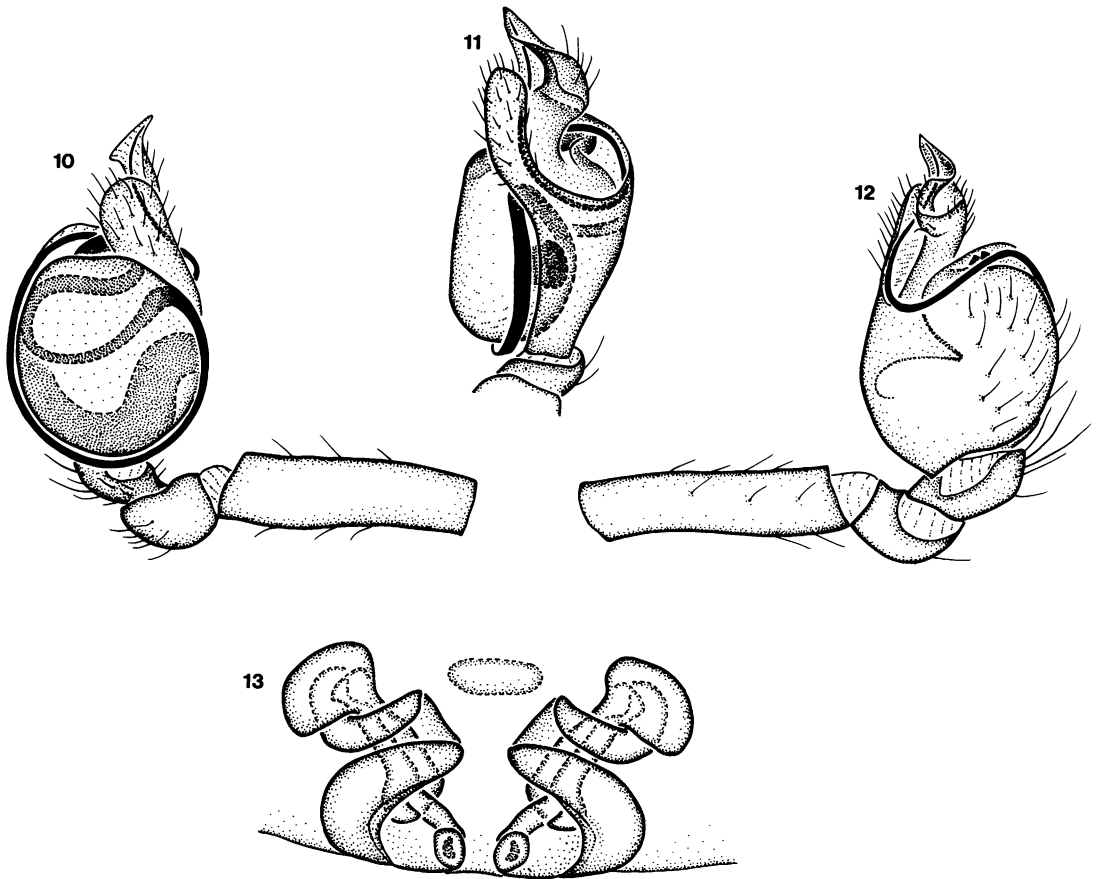
Figs. 5–9. *Mysmenopsis tengellacompa* Platnick, new species. 5. Left male palp, prolateral view. 6. Same, ventral view. 7. Same, retrolateral view. 8. Epigynum, ventral view. 9. Same, dorsal view.

menopsis, and this new species agrees with *M. cymbia* rather than its congeners in having the embolus encircling the palpal bulb, a feature judged plesiomorphic because of its occurrence in *Mysmena* and *Maymena*. The new species is united with *M. cymbia* by the presence of a greatly thickened embolus found only in those two species. Males of *M. tengellacompa* can be distinguished by the transversely oriented embolar origin (figs. 5–7), females by the more complex spermathecal ducts (fig. 9).

MALE: Total length 2.03 mm. Carapace 1.14 mm long, 0.99 mm wide, 0.56 mm high. Structure and coloration typical for genus (see Platnick and Shadab, 1978: 6) except as follows. Pars thoracica paler medially than laterally. Transverse abdominal white bands

outlining six pairs of dark rectangles. Femora without median dark rings; tibiae with proximal dark spots on venter only. Clypeal height about five times anterior median eye diameter; pair of conspicuously lightened oval areas present below those eyes. Femora II, III, and basal one-third of IV with row of stiff setae retroventrally. Tibia I with strong subdistal claspingspines, metatarsus with strong, sinuous subproximal claspingspines. Palp as in figures 5–7.

FEMALE: Total length 2.70 mm. Carapace 1.18 mm long, 1.01 mm wide, 0.38 mm high. As in male, except as follows. Clypeal height only about four times anterior median eye diameter; no pale areas noticeable below those eyes. Claspingspines absent; femur I sinuous but without ventral or prolateral tubercles,



Figs. 10–13. *Maymena rica* Platnick, new species. 10. Left male palp, prolateral view. 11. Same, ventral view. 12. Same, retrolateral view. 13. Epigynum, dorsal view.

with ventral subdistal sclerotized spot. Metatarsus I without spines. Epigynum as in figures 8, 9.

OTHER MATERIAL EXAMINED: Except as noted, all specimens were captured in *Tengella* webs. **COSTA RICA:** **Heredia:** La Selva, near Puerto Viejo, Apr.–June 1982–1983, elev. 50–100 m (W. G. Eberhard, AMNH), 12♂, 15♀. **Limón:** 2 km W Bribri, May 17, 1987, elev. 100 m, moist tropical forest (D. Ubick, CDU), 2♂, 2♀. **Puntarenas:** Monteverde, Feb. 10, 1978, from diplurid web along stream (N. Moran, AMNH), 1♂, 4♀, Aug. 26, 1983, hotel grounds (J. A. Murphy, JAM), 2♂, 1♀, June 1986, elev. 1350 m, near cheese factory (W. G. Eberhard, AMNH), 2♂, 1♀, June 1986, elev. 1350 m, in web of unidentified agelenid near cheese factory (W. G. Eberhard, AMNH), 1♂. **San José:** Parque Nacional Braulio Carillo, Apr. 28–30, 1983, elev.

1100 m, cloud-rainforest transect (D. Ubick, CDU), 2♂, 3♀; San Antonio de Escazu, June 1983, elev. 1300–1400 m (W. G. Eberhard, AMNH), 5♂, 5♀.

DISTRIBUTION: Known only from the webs of *Tengella* and unidentified agelenids and diplurids in Costa Rica.

Mysmenopsis dipluramigo
Platnick and Shadab

Mysmenopsis dipluramigo Platnick and Shadab, 1978: 10, figs. 22–27 (male holotype from Pipeline Road, Canal Area, Panama, in AMNH, examined).

NEW RECORDS: **COSTA RICA:** **Heredia:** La Selva, near Puerto Viejo, Mar.–Apr. 1983, elev. 100 m, in webs of *Tengella* and an unidentified ctenid (W. G. Eberhard, AMNH), 3♂, 1♀. **PANAMA:** **Canal Area:** 4 mi W Gam-

boa, Aug. 7, 1983, lowland rainforest (R. J. Raven, AMNH), 3♂, 1♀; Río Frijolita, July 4, 1976 (L. Kirkendall, AMNH), 1♂. **Panamá:** upper Río Majé, Bayano region, June 13, 1976, in pisaurid web (L. Kirkendall, AMNH), 1♂.

DISTRIBUTION: Known only from the webs of *Tengella* and unidentified pisaurids, ctenids, and diplurids (probably *Linothele* sp.; see Paz, 1988) in Panama and Costa Rica.

***Maymena rica* Platnick,**
new species
Figures 10–13

TYPE: Male holotype and female allotype taken on West River Road at the Organization for Tropical Studies field station at Finca La Selva, near Puerto Viejo, Heredia, Costa Rica (Jan. 13, 1982; J. Coddington), deposited in MCZ.

ETYMOLOGY: The specific name is a noun in apposition taken from the type locality.

DIAGNOSIS: This distinctive species is easily recognized by genitalic characters. The relatively short but complexly twisted cymbium of the male palp (figs. 10–12) is diagnostic; the female epigynum (fig. 13) most closely resembles that of the Mexican species *Maymena cascada* Gertsch, but has the sclerotized ducts straight rather than curved. In both sexes, the abdomen is posteriorly flattened, so that it appears triangular in lateral view, rather than rounded as in typical members of the genus.

MALE: Total length 1.08 mm. Carapace 0.56 mm long, 0.49 wide, 0.21 mm high. Structure typical for genus (see Gertsch, 1960: 30–31) except as follows. Carapace light brown, lightest near margins; tibiae, metatarsi, and tarsi III and IV with distal dark rings; abdomen dark gray anteriorly, with about seven transverse white stripes posteriorly, most anterior stripe thickest. Ocular area protruding strongly forward, clypeal height only twice the anterior median eye diameter; anterior lateral eyes smaller than anterior medians, not on ocular protrusion. Chaetotaxy: femora: I d1-0-0, p0-1-1, r0-0-1; II d1-0-0, p0-0-1, r0-0-1; III d1-0-0; patellae I–IV d0-0-1; tibiae: I p0-1-0, r1-0-0 plus distal prolateroventral clasping spur that overlaps similar sput situated proximally on metatarsus I; II p0-1-1, r1-0-1; III d1-0-0, p0-1-0; IV d1-0-

0; metatarsus III p0-1-0. Palp as in figures 10–12.

FEMALE: Total length 1.24 mm. Carapace 0.59 mm long, 0.53 mm wide, 0.26 mm high. As in male, except as follows. Chaetotaxy: femur IV d1-0-0; tibia I d1-0-0, p0-1-1, r0-0-1, without clasping spur; metatarsus I without clasping spur. Epigynum with only slight posteromedian evagination externally, dorsal view as in figure 13.

OTHER MATERIAL EXAMINED: **COSTA RICA:** **Cartago:** Guyabo, near Turrialba, May 1981, elev. 1300 m (W. G. Eberhard, AMNH), 1♀; Tuis hilltops, Apr. 1, 1979 (J. Coddington, MCZ), 1♀. **Heredia:** West River Road, OTS Station, Finca La Selva, near Puerto Viejo, Nov. 14–Apr. 12, 1979–1982 (J. Coddington, MCZ), 11♂, 13♀, Dec.–Mar. 1978–1983, elev. 50–100 m (W. G. Eberhard, MCZ, AMNH), 1♂ (penultimate), 12♀. **Puntarenas:** Llorona, Corcovado National Park, Aug. 10, 1979 (J. Coddington, MCZ), 1♀. **San José:** Parque Nacional Braulio Carrillo, Apr. 26–30, 1983, elev. 1100 m, cloud-rainforest transect (D. Ubick, CDU), 1♂; Río Hondura, Mar. 1986, elev. 1200 m (W. G. Eberhard, AMNH), 2♀.

DISTRIBUTION: Known only from Costa Rica, where it occasionally inhabits the webs of *Tengella*.

NOTE: The web and web-building behavior of this species were described (as *Maymena* sp.) by Eberhard (1986); because specimens of this species do construct a normal *Maymena* web, their occurrence in *Tengella* webs may be accidental.

HETEROPTERA
FAMILY PLOKIOPHILIDAE

Three species of spider-web dwelling Plokiophilidae have previously been described from the New World: *Plokiophila cubana* (China and Myers, 1929) from Cuba and *Lipokophila chinai* Stys (1967), and *L. stysi* Carayon (1974), from Santa Catarina, Brazil. Two additional species of *Lipokophila* are described below from Costa Rica, both occurring in the webs of *Tengella radiata*, sometimes in the same web. *Lipokophila eberhardi* is the more common of the two species and is also available from nymphs of nearly all instars.

In addition to the Plokiophilinae, representatives of at least three other groups of

Heteroptera appear to live as commensals in spider webs. Some Emesinae (Reduviidae) are regularly found in webs, and many have modifications of the foretarsi that may represent adaptations for such a mode of life (Wygodzensky, 1966).

The genus *Ranzovius* (Miridae: Phylinae) contains seven species (Henry, 1984), all of which are apparently obligate web dwellers. During the course of this study Schuh examined specimens from Costa Rica identifiable as *Ranzovius crinitus* (Distant) and another unidentifiable species represented only by females, all from the webs of *Anelosimus* (family Theridiidae) from Costa Rica. Wheeler and McCafferty (1984; see also Henry, 1985: 1130) reviewed the biology of *Ranzovius clavicornis* (Knight) from eastern North America.

Kerzhner (1990) described two new species of *Arachnocoris* (Nabidae) from the webs of Pholcidae from Costa Rica, along with the recognition of *Arachnocoris panamensis* (Distant), from the same area. Lopez (1989) described a new species of *Arachnocoris* from the Lesser Antilles, also commensal in the webs of Pholcidae, bringing the total number of described species to 12. Members of the genus had previously been keyed by China (1946), and a key to the Costa Rica species was provided by Kerzhner (1990).

The general morphology of *Lipokophila* has been well described by Štys (1967) and amplified by Carayon (1974). The claws are very long, slender, nearly straight, and of unequal length (fig. 18), a feature common to many web-inhabiting Heteroptera (Cobben, 1978; Štys, personal commun.). There is a single setiform parempodium associated with the longer claw. By contrast, the claws of an undescribed *Embiophila* sp. from near Taxco, Mexico, are relatively shorter, stouter, and more strongly curved and both parempodia are lacking.

In the first instar nymph of *Lipokophila eberhardi* the compound eye is composed of five ommatidia with a single central eye seta and a second seta lying outside the ring of ommatidia (fig. 17), conforming in general to the pattern in the Euheteroptera described by Cobben (1978).

The corium in *L. eberhardi* is uniformly covered with what Carayon (1974) referred to as corial glands. Under transmitted light

one sees a large pelucid glandular body (Carayon, 1974: fig. 1B), whereas the SEM reveals an opening with an attenuated structure rising above it and directed posteriorly (fig. 20; Carayon 1974: fig. 13). The corium in the abovementioned *Embiophila* sp. is also completely covered with corial glands but the structure of the openings is somewhat different from that found in *L. eberhardi*.

The male genitalic structures of *Lipokophila* were described in detail by Štys (1967) for *L. chinai* and for *L. stysi* by Carayon (1974). The structure and location of the copulatory tubes for both those species was described by Carayon (1974: figs. 25, 26).

KEY TO SPECIES OF *LIPOKOPHILA*

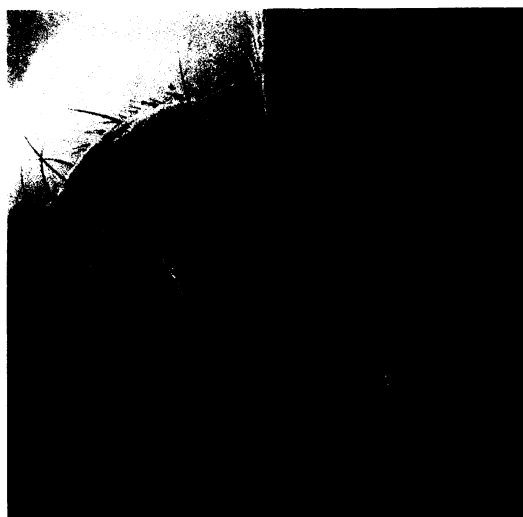
1. Large species, approximate total length from apex of tylus to apex of membrane 2.70–2.90 mm; corium generally brown, pale basally and apically (fig. 14); pygophore elongate, tubular, and somewhat decurved (fig. 21), parameres nearly straight and apically decurved (fig. 22); Costa Rica *eberhardi*
 –Smaller species, approximate total length from apex of tylus to apex of membrane 2.10 mm or less; coloration and structure of pygophore variable 2
2. Hemelytra with a more or less quadrate pattern of pale and brown (fig. 15); pygophore decurved and parameres nearly straight and slightly decurved apically, structurally similar to *eberhardi* (figs. 21, 22); Costa Rica *tengella*
 –Hemelytra largely brown, with some lighter areas on corium basally and apically; pygophore not decurved, parameres never nearly straight and decurved apically 3
3. Pygophore very short, parameres broadened mesially, narrowing and recurved apically (Carayon, 1974: fig. 23); Santa Catarina, Brazil *stysi*
 –Pygophore weakly elongate, parameres slender and of nearly uniform width of entire length, very broadly curving and nearly forming a semicircle (Carayon, 1974: fig. 24); Santa Catarina, Brazil *chinai*

Lipokophila eberhardi Schuh, new species

Figures 14, 16–22

HOLOTYPE: ♂, COSTA RICA: Heredia Prov.: La Selva, nr. Puerto Viejo, ca. 100 m, Apr. 1983, W. Eberhard, on webs of *Tangella radiata*; deposited in AMNH.

DIAGNOSIS: Recognized as a member of *Li-*

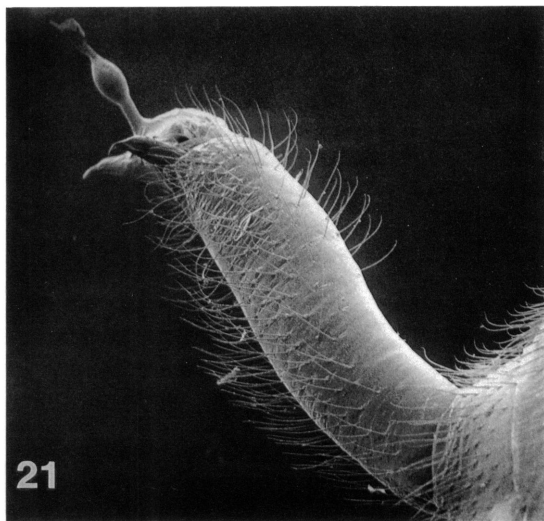
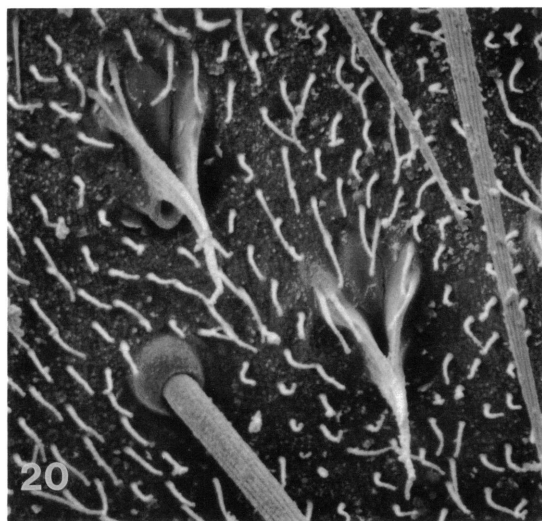
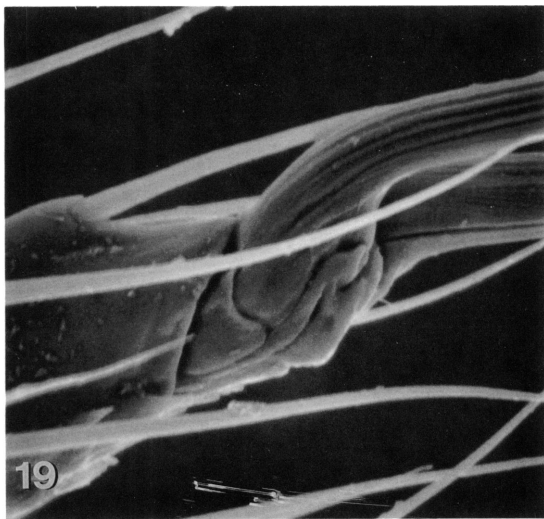
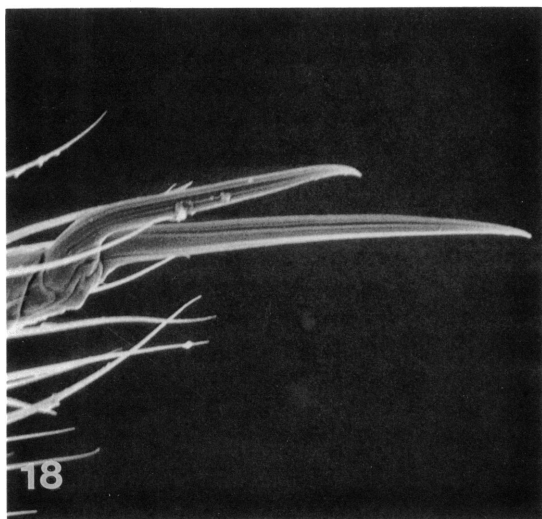


Figs. 14–17. 14. *Lipokophila eberhardi* Schuh, new species, male, habitus. 15. *L. tengella* Schuh, new species, female, habitus. 16. *L. eberhardi*, fifth instar nymph, lateral view of head. 17. *L. eberhardi*, first instar nymph, lateral view of head.

pokophila by the long, three-segmented tarsi and the structure of the male genitalia. Distinguished from its congeners by its large size (total length 2.70–2.90 mm) and largely brown coloration of the hemelytra (fig. 14).

DESCRIPTION: MACROPTEROUS MALE.
Coloration, vestiture, and surface texture.
 General coloration of dorsum, venter, anten-

nae, and coxae deep brown to castaneous; pronotal collar and most of exocorium pale and distinctly contrasted with surrounding areas; legs, including trochanters, light brown. Membrane with a large, round, whitish area laterally and just posterior to cuneus and a smaller, lateral, subapical whitish area. Head and venter polished and shining; pronotum



Figs. 18–21. *Lipokophila eberhardi* Schuh, new species. 18. Pretarsus, foreleg. 19. Detail of pretarsus, foreleg. 20. Corial surface showing corial gland openings. 21. Lateral view of phygophore.

and hemelytra appearing smooth but dull. Entire body clothed with relatively short, reclining, golden, common setae.

General structure. Very similar to that of *Lipokophila chinai* as described by Stys (1967). Antennal segments 3 and 4 subequal in length to segment 2 and somewhat more slender. Dorsal external orifices of corial glands as in figure 20. Pretarsus as in figures 18 and 19, claws nearly straight over most of length, of conspicuously unequal length, a single parempodem present. Genital capsule and parameres as in figures 21 and 22. Length

apex tylus–cuneal fracture 2.70; width head across eyes 0.30; interocular space 0.18; length pronotum 0.52; width pronotum 0.78; length antennal segment 2 0.55.

MACROPTEROUS FEMALE. General coloration, vestiture, and structure as in male. Ovipositor valves completely absent. Length apex tylus–cuneal fracture 2.90; width head across eyes 0.30; interocular space 0.17; length pronotum 0.48; width pronotum 0.80; length antennal segment 2 0.56.

NYMPHS. Compound eye of first instar with five ommatidia and a single centrally

located seta (fig. 17). Compound eye of fifth instar similar to adult (fig. 18).

ETYMOLOGY: Named after the collector, William G. Eberhard.

PARATYPES: Same data as holotype, 41♂, 26♀ (AMNH; Universidad de Costa Rica). **COSTA RICA: Puntarenas:** Monteverde, 1500 m, Jan. 1983, W. Eberhard, on agelenid web, SA1-92A (AMNH), 1♀; Monteverde, 1350 m, nr cheese factory, June 1986, W. Eberhard (AMNH), 1♀ in agelenid web, 1♂, 3♀ in web of *Tengella radiata*. **San José:** San Antonio de Escazu, 1400 m, June 1983, W. Eberhard, in web of *Tengella radiata* (AMNH), 7♂, 7♀.

ADDITIONAL SPECIMENS: **COSTA RICA:** Same data as holotype, approximately 80 nymphs (some of these may belong to *Lipokophila tengella*). **San José:** San Antonio de Escazu, 1400 m, June 1983, W. Eberhard, in web of *Tengella radiata* (AMNH), 6 nymphs.

Lipokophila tengella Schuh,
new species

Figure 15

HOLOTYPE: ♂, **COSTA RICA:** Heredia Prov.: La Selva nr. Puerto Viejo, ca. 100 m, Apr. 1983, W. Eberhard, on webs of *Tengella radiata*; deposited in AMNH.

DIAGNOSIS: General structure similar to that of *L. eberhardi*, but differing as follows: smaller, total length of female approximately 2.07, basal one-third of corium pale, exorium dark across middle one-third, in conjunction with dark cuneus giving appearance of four large, dark maculae on hemelytra (fig. 15).

DESCRIPTION: MACROPTEROUS MALE. Coloration, vestiture, and surface texture. General coloration of dorsum, venter, antennae, and coxae deep brown to castaneous; pronotal collar, and one-third of corium, and antennal segment 4 pale and distinctly con-

22

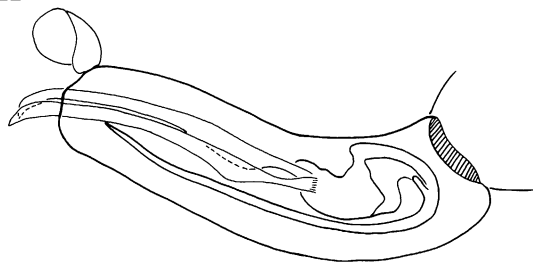


Fig. 22. *Lipokophila eberhardi* Schuh, new species, lateral view of pygophore, showing parameres and phallus.

trasted with surrounding areas; legs, including trochanters, light brown. Membrane with a large, round, whitish area laterally and just posterior to cuneus and a smaller, lateral, subapical whitish area. Head and venter polished and shining; pronotum and hemelytra appearing smooth but dull. Entire body clothed with relatively short, reclining, golden, common setae.

General structure. Very similar to that of *L. eberhardi*, but overall dimensions smaller. Male genitalia similar in structure to those of *L. eberhardi*. Measurable male specimens not available.

MACROPTEROUS FEMALE. General coloration, vestiture, and structure as in male. Ovipositor valves completely absent. Length apex tylus–cuneal fracture 2.07; width head across eyes 0.23; interocular space 0.15; length pronotum 0.65; width pronotum 0.58; length antennal segment 2 0.28.

ETYMOLOGY: Named for its occurrence in the webs of *Tengella*; a noun in apposition.

PARATYPES: Same data as holotype, 1♂, 3♀ (AMNH). **COSTA RICA: San José:** Braulio Carrillo N. P., Send. Nat. cloud-rainforest trans., 1100 m, Apr. 29–30, 1983, D. Ubick, ex *Tengella* web (AMNH), 1♀.

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