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SPECIALISTS AND GENERALISTS: THE ECOLOGY AND BEHAVIOR OF SOME WEB-BUILDING SPIDERS FROM PAPUA NEW GUINEA

II. *Psechrus argentatus* and *Fecenia* sp. (Araneae: Psechridae)

By **Michael H. Robinson and Yael D. Lubin**[1]

Abstract. This is Part II of a 3-part series. Two genera of the little-known spider family Psechridae were studied at Wau, Papua New Guinea. *Psechrus argentatus* builds a horizontal sheet web that it operates from beneath. Juvenile stages of *Fecenia* sp. build a conical web with a central detritus-covered retreat; at a later stage in the development of the spider, the conical web is replaced by a planar pseudo-orb. The structure and siting of the webs of both species is described and illustrated. Both psechrids immobilize all prey by biting and are not capable of prey-wrapping behavior comparable to that of araneids. The sequences of behaviors involved in the capture of flies, moths and orthopterans were studied and are described herein, along with descriptions of the units of predatory behavior. Courtship and mating is described for *Fecenia* sp. Comparisons between the predatory behavior of the 2 psechrid genera and between psechrids and araneids provide a basis for advancing functional and evolutionary interpretations of the correlation between web structure and predatory repertories in both families. It is suggested that the web is not merely a trap, but a platform for predatory activities, a protection against predators and a device enhancing the range of prey-detecting sense organs. Differences in the efficiency with which webs of different types fulfill these diverse functions are reflected in many aspects of the biology of the spiders concerned.

A general introduction to this series of papers on the biology of some New Guinea web-building spiders is given in Part I (Robinson & Lubin 1979). Part II deals entirely with the biology of 2 psechrid species studied at Wau, Morobe Province, Papua New Guinea. The existing literature on psechrids is scant indeed. There are very brief references to the family in the standard arachnological texts (e.g., Berland 1932, Gerhardt & Kastner 1938) and many records in faunal lists (see Bonnet 1958, Roewer 1954 for bibliographies). Simon saw the 2 principal genera in the field and, as is frequently the case, gave useful summaries of the web structure and web sites of the spiders (1892: 223–26). He correctly noted that the web of *Fecenia* is orblike "les toiles qu'ils filent sont toujours grandes et de deux sortes: celle des *Fecenia,* que j'ai observée à Singapore, rapelle encore celle des Uloborides orbiteles" (Simon 1892: 225). Despite this, Lehtinen (1967: 382–83), who restricts the family to the genera *Fecenia* and *Psechrus,* stated that "psechrids spin a large sheet web and live on its lower surface, not on the upper surface as do agelenids." Forster & Wilton (1973) described 2 new genera of psechrids from New Zealand and stated (p. 297) that they "are both hunters which as far as we have noted do not construct snares." Their genus *Hauroka* has a fairly strong superficial resemblance to *Fecenia,* which the authors noted, but they stated (p. 299) that "The habits seem quite different as these

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spiders hunt on low foliage while *Fecenia* constructs a large sheetweb."

Our own studies revealed that the situation is not quite as simple as that described by Simon (1892). The web of the *Fecenia* sp. that we studied undergoes a profound change during the development of the spider. Initially it is conical in shape with a central acutely conical retreat built of silk, detritus and prey remains. Eventually the web becomes a more or less planar orblike structure with a curled leaf as a retreat. This web was the reason for our interest in the species, and we extended our study to include *Psechrus argentatus* primarily so that we could compare the behavior of a sheet-web psechrid with that of the *Fecenia* sp. found at Wau.

STUDIES OF PSECHRID SPECIES

Fecenia sp.[2]

NATURAL HISTORY AND ECOLOGY

Distribution

Twelve species of *Fecenia* were recognized by Roewer (1954: 1376–77), of which only 1 was recorded from New Guinea: *F. cinerea.* Bonnet (1956: 1896–97) ascribed *F. angustata* and *F. cinerea* to "Malasie, Papouasie." Lehtinen (1967: 382, Fig. 524) restricted the family to "the Oriental region and adjacent parts of the Palearctic and Australian regions." At Wau we found a *Fecenia* sp. at many localities, in forest and at forest edge. This was identified by Fr. Chrysanthus as *Fecenia* sp., close to *angustata.* It is sporadic in the arboretum of Wau Ecology Institute, fairly common on the lower slope of Mt Kaindi and rare on the slopes of Mt Missim. Robinson et al. (1974) recorded the species on all 3 of their transects.

Web location

The species is found in shaded areas within forest and on forest edge wherever there are small shrubs and tall herbs. Shade is not the only factor influencing distribution. In the census of Robinson et al. (1974), the species was rare on their transect I (roadside within a wooded coffee plantation), more common on their transect II (grassy open roadside with embankments and forest edge) and common on their transect III (steeply sloping forest edge roadside with rocky outcrops). Transects I and II were at the same altitude, while transect III was 220 m higher than the others. The respective figures for adult *Fecenia* at the 3 sites (total occurrences based on 52 weekly censuses) are 5, 34, and 512 (1:6.8:102.4). Simon (1892: 225) found the webs of a *Fecenia* sp. in Asia suspended between trees on frames of strong threads. Juvenile webs occur in the same habitats as the adult webs but are often close to the ground within the herb layer. Their siting is reminiscent of the webs of *Cyrtophora munulfi* and particularly of the immatures of that species (Lubin 1974), except that the latter is a grassland species.

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[2] The *Fecenia* sp. has now been identified as *Fecenia angustata* (Thorell) by Dr Herbert W. Levi (in litt.). All references to "*Fecenia* sp." that we studied at Wau and report on in this paper should be read as *Fecenia angustata.*

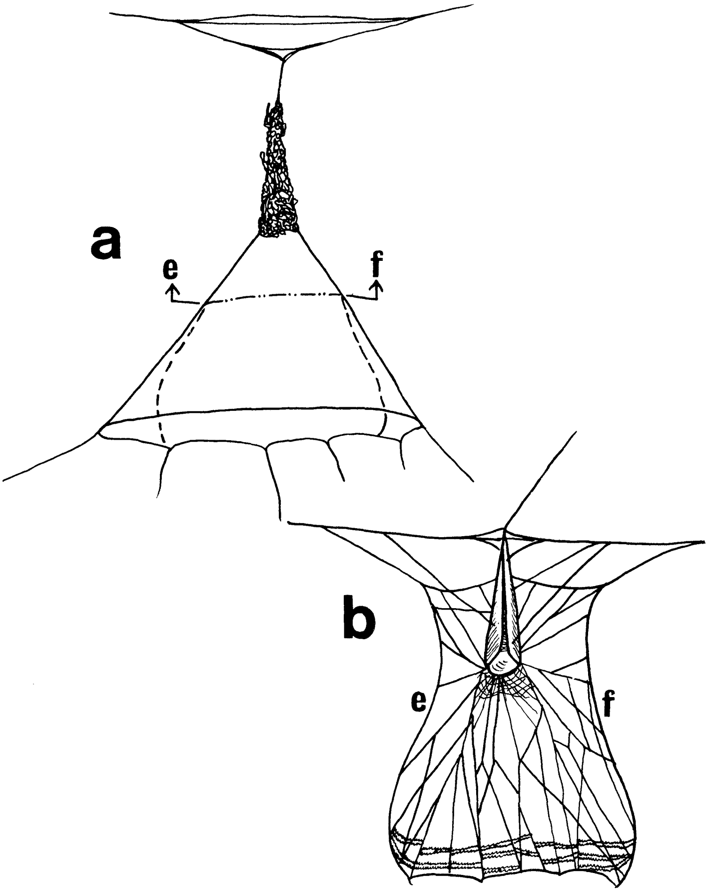

FIG. 1. Diagrams showing (a) juvenile conical web of *Fecenia* with detritus-adorned retreat and (b) possible mode of derivation of adult planar pseudo-orb. It is suggested that the curved surface of the cone below line e-f becomes the principal part of the pseudo-orb, while the small, back portion of the cone (above e-f) comes to lie in the same plane and incorporates the leaf retreat. Double bands of hackled silk are shown only in the lower part of the pseudo-orb; they extend throughout the entire orb (compare FIG. 3).

Web structure

The juvenile web is conical or tented and has an acutely conical retreat at the center of the web cone. This retreat is built even by 2nd-instar spiderlings (assuming that there is a 1st instar within the egg-cocoon as in most spiders; see Valerio 1974). In captivity such spiderlings build the retreat entirely of opaque sheet-silk to which they attach prey debris. Our laboratory raised *Fecenia* that were fed on *Drosophila,* in clean vials, had only *Drosophila* with which to adorn their retreats, whereas wild specimens use a wide variety of small particles: plant debris, soil particles, rock fragments and so on. They never use entire leaves (see adult behavior below). The method of obtaining the debris is unknown. It could be garnered from material falling into the web or collected from the ground and carried to the retreat; adult spiders obtain leaves for their retreats in both ways. The juvenile web-cone is very tough and consists of frame elements of dry silk with hackled silk bands laid down on top of the frame in a crudely (concentrically) circular arrangement. The adhesiveness of the web appears to be high, judging by the ease with which the early instars can be fed in captivity. (MHR has raised several species of araneids from the egg and found *Fecenia* to be much easier to rear than any of these.) Captive specimens used a web for long periods before replacing it (several weeks in some cases). Web renewal could be equally infrequent in the wild, since the hackled silk threads may be much more durable than the viscid elements used by araneids.

The adult web is a planar pseudo-orb with a single leaf suspended in it (FIG. 1b). We do not know at what stage the change is made from the juvenile 3-dimensional web to the adult planar web. The change may be coincident with the change from the particle-covered retreat, but this is not known. MHR has data on the life history of the species, suggesting that it has at least 10 instars. However, he raised only 7 spiders to maturity so these data must be regarded with caution. The spiders built more or less planar webs for at least 3 instars before the final molt. Exact elucidation of this problem must await precise determination of the life history stages and a subsequent examination of a large sample of webs.

The transformation from a conical web to a planar web could occur as a result of the "hypertrophy" of one side of the cone, as shown in FIG. 1. Transitional webs do occur in captivity. Planar webs are never so clearly organized as the webs of araneids, tetragnathids or orb-building uloborids. There is a framework of plain (nonhackled) silk, but the elements radiating from the retreat are never so regular as the radii in a veritable orb web (see FIG. 2). The hackled silk bands are laid down on top of the plain silk, but do not form a complete spiral. YDL saw 1 adult female laying down sticky cribellar silk on an irregular framework of radii that were already in place. The spider moved slowly across the web, combing out silk with legs IV and attaching it to the radii with dabs of the abdomen. Two distinct hackled threads were produced simultaneously (FIG. 3). The hackled bands were laid down in such a way that the spider never made a complete spiral. Further analysis of web structure must await more detailed observations on web construction.

The ontogenetic changes in the web form of *Fecenia,* from cone to pseudo-orb, suggest an evolutionary pathway by which a sheet web could give rise to a primordial orb.

In captive conditions, spiders will collect leaves for retreat building off the cage floor. Flat leaves are curled into a retreat over a period of several days. The spider covers the inner surface of the retreat with silk and this could enhance the curling effect of turgor changes as the leaf dries out. The spider builds an extensive silk suture along the apposed edges of the leaf and presumably replaces this as the edges

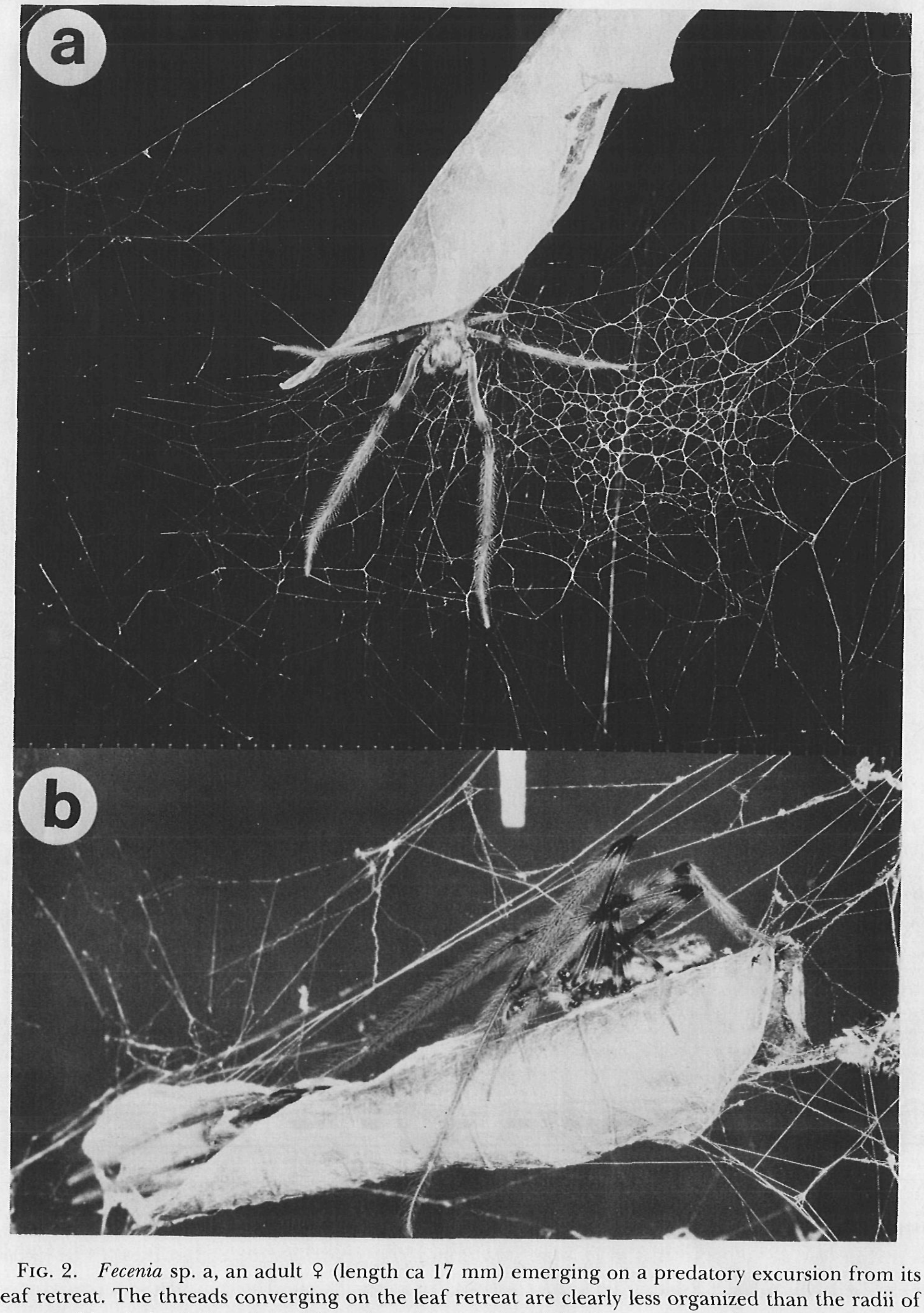

FIG. 2. *Fecenia* sp. a, an adult ♀ (length ca 17 mm) emerging on a predatory excursion from its leaf retreat. The threads converging on the leaf retreat are clearly less organized than the radii of an araneid orb. b, ♂ (length ca 16 mm) on the outside of the ♀ retreat stroking her with one 1st leg. Note the strong guy threads supporting the retreat.

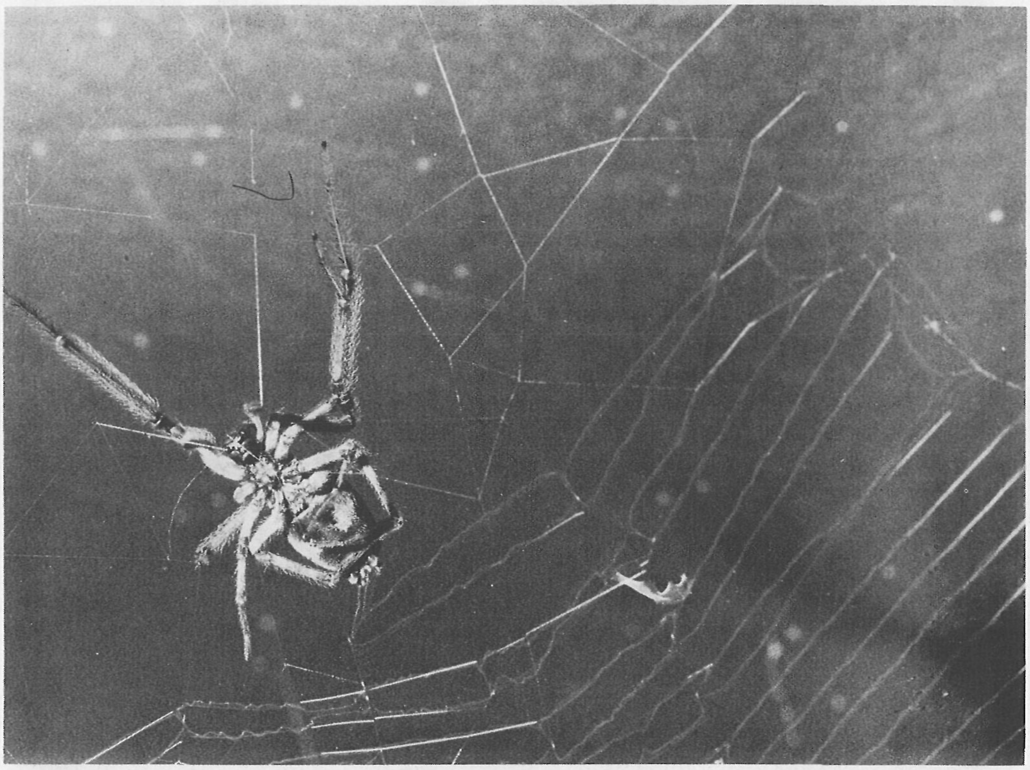

FIG. 3. A ♀ *Fecenia* sp. laying down the sticky hackled silk in 2 distinct bands. The spider's 4th legs are in typical "combing" positions, as seen when cribellate spiders use the calamistrum to produce the hackled effect. In the web section shown, the hackled bands are quite regularly disposed and are superficially similar to an araneid viscid spiral.

move closer and closer together. At first the retreat may be simply a slightly convex leaf in which the spider is plainly visible; in 3 or 4 days it becomes a tightly curled cylinder out of which the spider protrudes its long 1st legs (FIG. 2). The retreat is slung from particularly strong (multistrand) foundation lines, and may be braced at other points by further supporting guys (see FIG. 2b). The egg-cocoons are produced inside the retreat. The retreat may serve not only to conceal the spider but to protect it from exposure to insolation and rainfall. (For details of the responses of some New Guinea araneids to insolation and rainfall see Robinson & Robinson 1973, 1976.) The Australian leaf-curling spider *Phonognatha graeffei* (Keyserling) also has a curled-leaf retreat at the hub. It places its egg-cocoon in a curled leaf suspended near the web (Mascord 1970: 70). Clyne (1969: 150) illustrates the leaf curling involved in forming the egg-sac "retreat." The eggs are closely attached to the leaf surfaces, as in the case of *Fecenia*.

Defenses

As suggested above, the retreat may serve to conceal the spider from visually-hunting predators. MHR saw a pompilid wasp alight on the leaf retreat of an adult *Fecenia.* As the wasp moved over the lip of the retreat to enter, the spider dropped from the retreat to land in the grass a meter or so below the web. The spider was clearly belayed on a dragline and remained motionless in the grass. The wasp entered the retreat and spent some time inside before emerging and flying off. The wasp apparently identified the leaf as the part of the web containing its potential prey; it did not investigate the surrounding web or vegetation after failing to find the spider inside the retreat. The dropping response of the spider, possible on a web of this type or an inclined orb, is one of the common defensive responses of araneids.

Egg-cocoons

The egg-cocoons are constructed on the lower surface of the retreat cylinder close to the entrance. They are covered in dense off-white silk and are of low profile. The spider rests near the cocoon when in its normal predatory posture, i.e., in a position where the cocoon may be close to the abdomen of the spider. This proximity is interesting, since *Psechrus argentatus* actually carries its egg-cocoon. If there is more than 1 cocoon in a retreat, the most recent cocoon overlaps the older cocoon. The eggs are laid onto a thin layer of silk, covering the leaf surface. This does not seem to be a "cushion" of silk as found in the egg-cases of, for example, *Argiope* and *Cyrtophora* spp. A sample of 3 cocoons from widely scattered localities contained 85, 187 and 223 eggs, respectively.

Males

Adult males are approximately equal to females in size, but differ in leg proportions. Exaggeration of the length of the 1st legs of the male also occurs in the *Fecenia*-like psechrid *Hauroka filicola* described by Forster & Wilton (1973: 299–300). In captivity, adult males remained in the webs of the penultimate instar until removed by us. Thus, in nature they may be found in functional webs whether they build and operate webs as adults or not. MHR found that raising males to maturity was extremely difficult since they had problems in molting for at least the last 2 molts before maturity. In 2 cases, penultimate instars were unable to free the long adult pedipalps from the old exoskeleton at the final molt; others had difficulty in freeing legs I. (These problems could have been caused by conditions in captivity.)

Prey

We have only the most fragmentary knowledge of the natural prey of this species. The web is an effective trap for both jumping and flying insects. The hackled silk seems to hold lepidopterans extremely well, and the web is operated both day and night (see below). Prey recorded from webs on Mt Kaindi included a wide range of grasshoppers and tettigoniids, several phasmid nymphs, hemipterans, dipterans, lepidopterans (including a geometrid larva), beetles (particularly the ubiquitous weevils) and 1 large thysanuran.

PREDATORY BEHAVIOR

In describing the predatory behavior of any spider species, it is useful to consider overall patterns, individual behavior units and the sequences of behavior given in response to particular classes of prey. The predatory behavior of araneid spiders has been the subject of numerous studies, both descriptive and analytical/comparative (see review in Robinson 1975). The comparative studies have stressed the key role of prey-wrapping behavior in the evolution of araneid predatory behavior. Eberhard (1967) examined the role of prey-wrapping in the attack behavior of several families of spiders and concluded that attack-wrapping was an evolutionarily advanced behavior. Detailed studies within the family Araneidae suggest that this conclusion is correct (Robinson 1975). *Fecenia* has no attack-wrapping behavior in its predatory repertory and attacks all kinds of prey by biting. In fact, at no stage in the predatory process does *Fecenia* enswathe prey in silk in the manner of araneid or uloborid spiders. The nearest equivalent to the prey-wrapping of araneids and uloborids is a process that could be called "binding" behavior. *Fecenia* binds prey by circling around the insect, attaching silk directly from the spinnerets to the prey surface and/or to the substrate. The result is that the prey is secured to the web, or to the retreat, by a few strands of silk line. This process occurs in 2 contexts: at the capture site after biting (i.e., at the stage when araneids carry out post-immobilization wrapping at the capture site type 1; see Robinson et al. 1969: 491) and in the retreat after prey transportation (when it is functionally equivalent to post-immobilization wrapping at the feeding site; see Robinson et al. 1969: 490). These behaviors are described in detail below, and their presumptive function is compared with araneid "equivalents" in the discussion section. In summary, it can be said that *Fecenia* is comparatively inefficient in the use of silk during predatory sequences and this means that its predatory behavior differs markedly in several respects from that of other spiders that operate orblike webs.

Description of behavior units

Behavior at the retreat at the start of an attack. The first response to impact of the prey on the web is usually the protrusion of the long 1st legs. These may appear slowly if the prey is relatively inactive or rapidly if the prey is buzzing or fluttering. In the latter case, the spider frequently runs straight out to the prey, whereas if the prey is inactive, very small, or struggling weakly, the spider may move out to the attack in a slow, stealthy manner. (In our field notes we remark "the spider glides out of its retreat.") Such slow movements may be inconspicuous and reduce the danger of alerting potential predators. In circumstances in which araneid spiders would pluck from the hub (see, for instance, Robinson & Olazarri 1971: 6–7), *Fecenia* strongly flexes legs I without removing the tarsi from the web. This slow movement results in the web being slowly tensed; it is just as slowly allowed to slip back to its former state as the legs are relaxed and the elasticity of the silk takes over. We assume that this is a prey-detection movement, since it occurs following the impact of difficult-to-detect insects. If the insect arriving in the web is large and struggling vigorously, the spider may protrude the 1st legs after impact and then withdraw them and back further into the retreat, remaining inactive while the insect struggles free. (Ignoring large and potentially dangerous insects may be a necessity imposed on spiders that lack attack-wrapping.)

Approach behavior. A number of features of approach behavior are of considerable interest. If the approach is by running (e.g., towards a rapidly vibrating insect), the spider may overshoot the prey and have to turn back to find it. The same kind of overshoots occur in the same circumstances (rapidly vibrating prey) in the case of araneid attacks. *Fecenia* does something that we have only rarely seen in araneid approaches to prey. It may start an approach in a straight-line (radial) direction that is off the correct bearing leading to the prey, and then sidestep to bring itself on the correct heading. (We assume that either the *Fecenia* web transmits directional information less efficiently than the more organized orb webs, or that the spider is less efficient at determining position; see Discussion.) During a slow approach to a slowly moving insect, the spider may pause and pull on the web with its 1st legs, bunching the web above the prey item. This act may be the functional equivalent of approach-plucking in araneids. When the prey item is relatively heavy, the spider may approach with its long 1st legs off the web and flexed back over the cephalothorax. Such "cautious" approaches have been described for *Nephila clavipes, Nephila maculata,* and *Herennia ornatissima* (Robinson & Mirick 1971; Robinson & Robinson 1973; Robinson & Lubin 1979).

Behavior at the prey before the attack. On reaching a highly stimulating prey (one that is buzzing or flapping), the spider usually attacks immediately; it may not necessarily attack the nearest point, but may move sideways to deliver a lateral attack or seize an appendage. Such sideways attacks are, in our experience, most unusual in araneid spiders but occur fairly commonly in *Fecenia.* We have not been able to isolate a common factor from the incidents that we have recorded. We have, therefore, not been able to define the precise circumstances in which they occur. Before attacking large prey that are struggling sporadically, the spider may cut web elements above the insect, causing it to fall through further layers of silk and become more securely enmeshed.

If the prey is not immediately attacked, it may be tapped, from a distance with the long 1st legs. After a variable period of tapping, the spider may return to the retreat or may touch it with the pedipalps and attack. At the instant before an attack lunge, the spider often attaches its dragline to the web with a conspicuous dabbing movement of its spinnerets.

Attack behavior. As mentioned above, all attacks are by biting. However, the bite

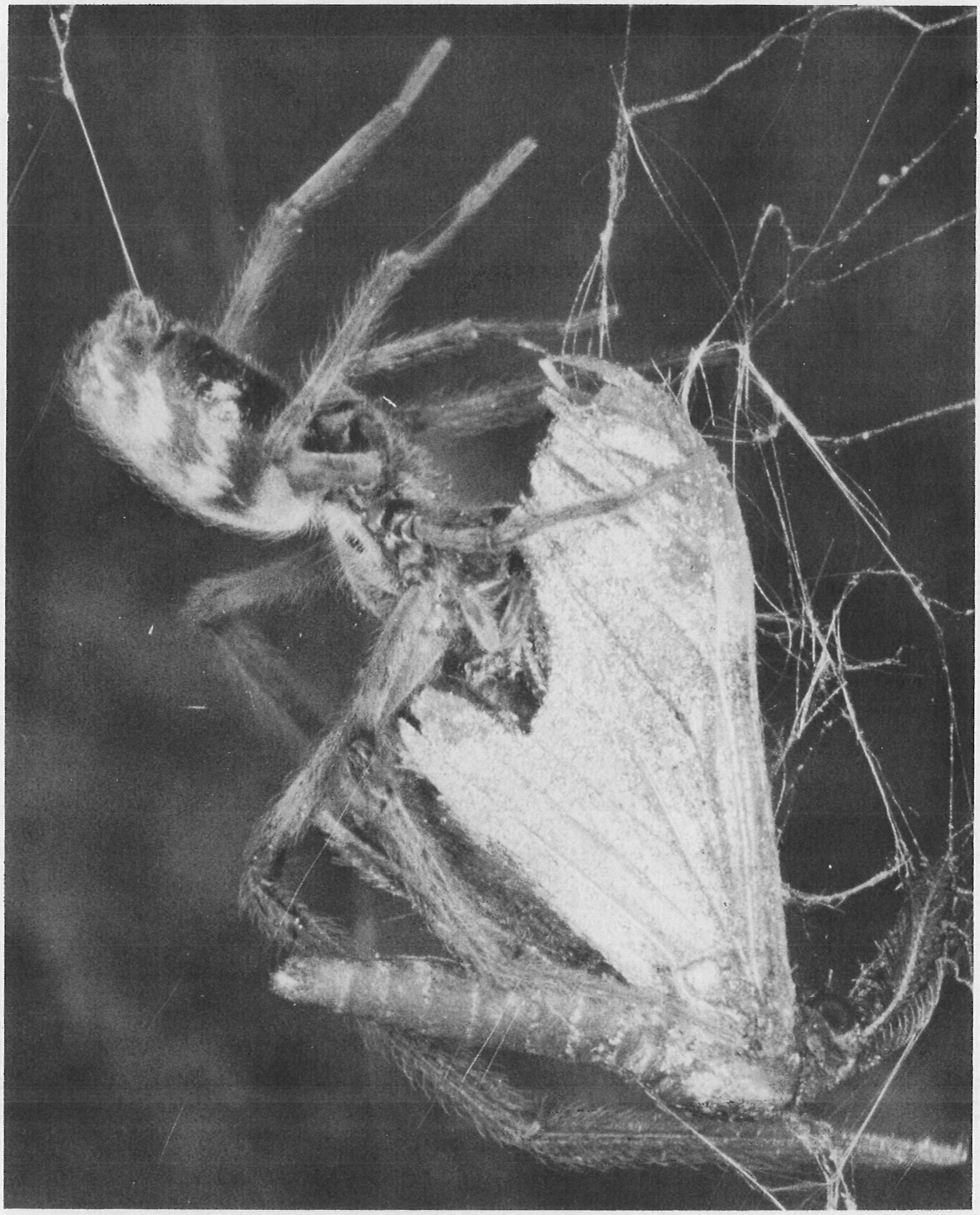

FIG. 4. *Fecenia* making a bite/clasp attack on a moth. At this early stage in the attack, the spider has not yet contacted the body and is biting the wing edge. Of the legs visible above the moth, right legs I, II and III clearly surround the insect.

differs in form according to the kind of prey. Struggling moths evoke a bite/clasp response in which the insect is simultaneously bitten and seized (FIG. 4) [see our description of bite/clasp in section I of this series (Robinson & Lubin 1979)]. Large orthopterans are not, at first, given a sustained bite but subjected to the bite/back-off attack. The spider lunges forward, gives the prey a short-duration bite and then steps back out of contact distance. This process may be repeated several times before the bite is sustained. Before each lunge the spider spreads its chelicerae ready for the attack and this intention movement is very conspicuous. Even the sustained bite is not maintained continuously at one site; on the contrary, the spider moves the cheliceral insertion little by little so that most of the prey body is "nibbled."

Behaviors occurring after biting. After the biting attack, *Fecenia* may interrupt the predatory sequence and return to the retreat for a variable period of time, or it may complete the predatory sequence by removing the prey from the web and transporting it to the retreat, where feeding occurs. An interruption may last as long as 3 hr. An interrupted sequence may or may not involve binding behavior, and this is also true of continuous sequences. Thus, 3 behaviors can immediately follow biting (see later descriptions of behavior sequences for correlations with types of prey): (1) binding behavior, (2) removal of prey from the web, and (3) interruption of the sequence. Both prey removal and interruption can follow binding or occur independently. Binding behavior is totally unlike prey-wrapping behavior so far described for any araneid. It does not involve movements of the 4th legs casting swathes of silk onto the prey from the spinnerets, it does not involve swathes of multistrand silk being laid down while the prey item is rotated by the spider, and the prey item is never held in the 3rd legs of the spider during binding. All 3 of these behaviors are highly characteristic of araneid prey-wrapping. *Fecenia* simply circles around the prey, on the surface of the web, sidestepping and making a number of silk attachments during the movement. While attaching silk and sidestepping, the spider may maintain a jaw-hold on the prey; alternatively it may release the prey altogether. Most of the circlings that we saw were through 1 revolution of 360°, although some involved 1½ or even 2 turns. The silk is attached both to the surface of the insect and to the nearby web. (The movement is clearly derivable from the behavior whereby the spider attaches prey to its retreat, and is similar to the behavior of *Psechrus argentatus*; see below.) We assume that the silk used in binding is ordinary dragline silk and not, as in araneids, distinct swathing silk. FIG. 5 is a reconstruction of this binding behavior based on a composite of field notes and analysis of movie sequences. Quite clearly the effect is to secure the prey to the web with a small number of silk strands and not to immobilize or "package" the prey. Prey is removed in 2 ways. The spider may simply pull the insect from the adhering hackled silk, or it may cut the prey free by severing entanglements with its chelicerae. Pulling-out is reserved for small prey and most lepidopterans; it leaves the web comparatively undamaged. (This technique is also used by araneids in similar circumstances and is widely used by *Psechrus argentatus.*) Essentially, the spider pulls up on the prey held in its jaws by

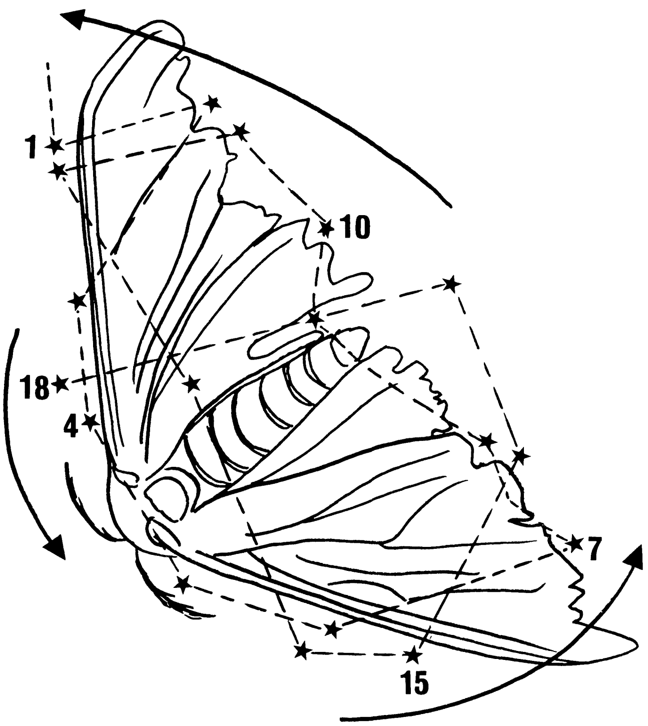

FIG. 5. Binding movements as recorded in an attack on a large moth by *Fecenia* sp. The stars represent successive attachments of the binding silk, either to the web or the insect, as the spider circles the prey twice and makes one zig-zag. Further attachments may have been made to the surface of the moth as the spider spanned the insect with its abdominal apex, but we cannot be certain of this.

straightening its formerly flexed legs. If the prey remains attached at one part, the spider may use a leg to tease away the entanglement. When the spider cuts prey from the web, it circles around very much in the same way as when binding. In the process of freeing the prey, the spider makes dragline attachments to the edge of the hole (FIG. 6), which prevent some tearing of the web due to the contraction of stretched web elements. During prey removal by cutting, the spider usually "bends down" to apply its jaws to the silk but may lift the silk to its jaws by using its legs. At the end of the cutting process, the prey item is usually hanging by a small piece of intact web in the middle of a fairly large hole. The spider holds the prey in its legs, severs the last attachment and then picks the prey up in the chelicerae for transportation. Frequently, however, the spider does not stop to sever the last connection but "blunders" back to the retreat, either tearing away this connection or tearing a large hole in the web. This kind of behavior is very frequently found in the prey transportation of several *Gasteracantha* species (araneids: see part III of this series).

Prey transportation. *Fecenia* never carries prey suspended on a silk line from the

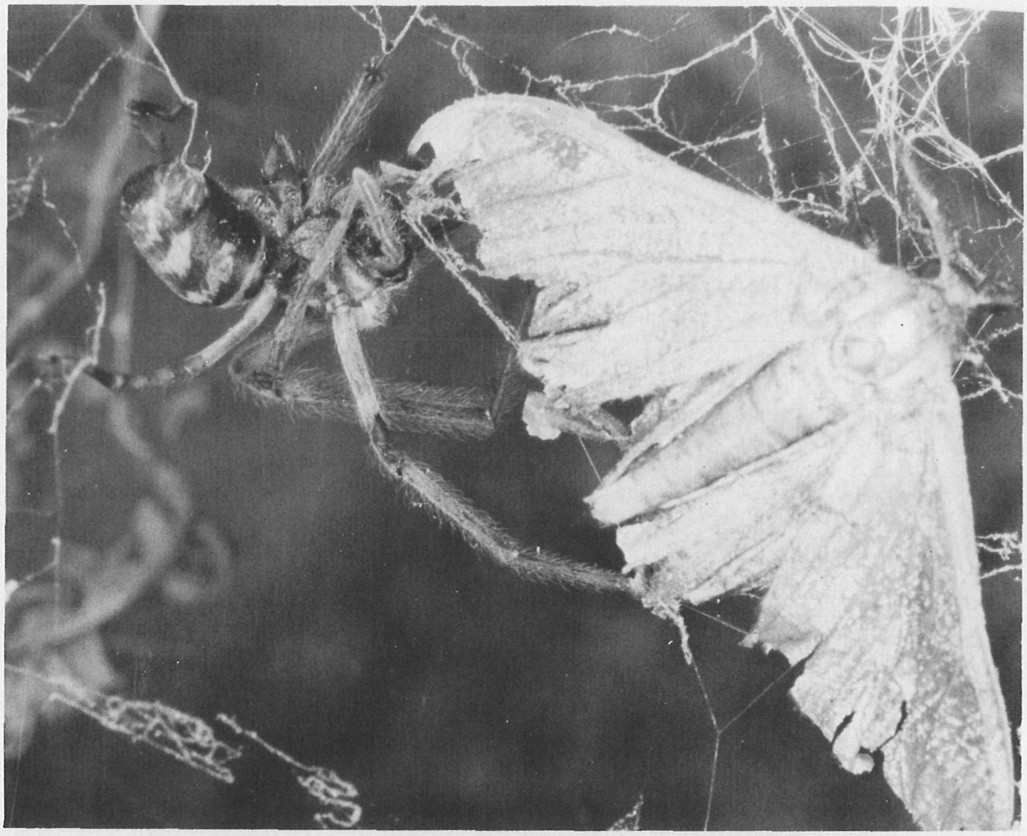

FIG. 6. *Fecenia* "darning" the edge of a hole in the web caused by prey-removal behavior (cutting). Note the strong silk emerging from the spinnerets; this will be attached, in the next move, close to the left tarsus IV, and then to the lower edge of the hole.

spinnerets, although this kind of transportation is commonly used by araneids for carrying large and cumbersome prey items. *Fecenia,* on the contrary, carries all prey items in its chelicerae. Since the prey are not tightly packaged in silk, they may have projecting wings or other appendages and be bulky and difficult to carry. If the spider seizes the prey conveniently it will fall back over the dorsal surface of the spider as it walks forward, up the web to the retreat. Otherwise the prey may (and frequently does) swing below the spider's body and become snagged in the web during transportation. The spider responds to such transportation problems by walking sideways and even backwards. Changing direction often frees the prey, but if it does not, the spider may stop, bind the prey and cut it loose again. The spider can also carry the prey by backing up the web, a device used consistently by *Nephila maculata* to reduce the risk of entangling prey during cheliceral transportation (see Robinson & Robinson 1973: 48–50).

Behavior on arrival at the retreat. The spider always backs into the retreat, pulling the prey in behind it, irrespective of the direction of approach. Once in the retreat, the spider ultimately attaches the prey to the floor of the leaf. It does this by turning around several times within the retreat, dabbing silk attachments against the substrate and, presumably, on the prey itself. If the retreat is tightly coiled, all that can be seen of this process is the appearance of the spider's abdominal apex as it turns. *Psechrus argentatus* carries out the same process in its retreat tunnel where the details are more visible. The end effect is to fasten the prey to the substrate in a loose net formed by several crossing strands of silk. This construction of a tie-down device may be delayed until several minutes after the spider has entered the retreat with its prey.

Predatory sequences

We presented adult *Fecenia* females with live acridids, tettigoniids, flies and moths. We presented 44 orthopterans estimated to weigh between 100–300 mg each. The 16 flies presented were muscids or calliphorids and were estimated to weigh between 30–60 mg each. The 45 moths were a mixed assortment of families (none were aposematic) and ranged from 80–250 mg in weight.

Prey-capture sequences with flies as prey. All the flies were given a simple bite; none were subjected to the bite and back-off attack. No fly was bitten more than twice. The average bite duration was 1.54 min (range 2 sec to 6 min 9 sec). Despite the low weight of these insects and the simple attack sequence, exactly ½ of the sequences were interrupted by the spider returning to the retreat and leaving the prey in situ. In 3 out of 8 interrupted sequences, the spider bound the fly at the capture site. The flies were pulled or cut from the web and carried back to the retreat in the jaws. In all cases the spider ran to the retreat headfirst. At the retreat, the spider turned through 180° and backed into the retreat with the fly held in its jaws. All the flies were wrap-attached to the retreat floor.

Prey-capture sequences with orthopterans as prey. Of the orthopterans (acridids and tettigoniids) presented to *Fecenia,* 22 were equal to the spider in size or slightly larger, and 22 were smaller (100–180 mg) than the spider. Hereafter, we call these 2 categories large orthopterans and small orthopterans. The large orthopterans were attacked preponderantly by the bite and back-off technique, with up to 6 repetitions of the brief bite before the development of a sustained bite. The initial brief bites were directed towards an appendage rather than the body proper. The spiders bit antennae, wings and legs, starting at the distal end and slowly approaching the body. After biting, the spiders frequently interrupted the sequence and returned to the retreat (11 out of 22 sequences). Binding occurred in only 4 instances, 1 during transport of the prey when it became tangled in the web and 3 times prior to returning to the retreat (interrupted sequences). All the large orthopterans were cut out of the web and, in most cases, carried to the hub by a spider that backed up the web. All large orthopterans were wrap-attached to the retreat floor.

The small orthopterans were subjected to substantially fewer bite and back-off attacks (3 out of 22). The spiders interrupted the predatory sequences to retire to the retreat in 12 out of 22 cases. Of these, there were 8 cases in which the spider ran back to the retreat immediately after the bite, that is, without any binding behavior. Four spiders bound the prey at the capture site. Two spiders that retired to the hub without binding the prey returned to the prey and did so (apparently in response to violent struggles by the insect) before again retiring to the retreat. The continuous sequences were relatively simple. The spider attacked by biting, shifting the bite locations several times, and then proceeded to cut the prey from the web and carry it to the hub in the chelicerae, walking or running headfirst. All spiders backed into the retreat and wrap-attached the prey to the retreat floor.

For large and small orthopterans, there is a correlation between size and the occurrence of bite/back-off attacks and also between size and transportation by backing up the web. There appears to be no correlation between size and the tendency to interrupt predatory sequences. Even when presented with small orthopterans, 2 spiders (not included in the sample of 22) ran to the prey, touched it and immediately retired to the retreat without attacking. In addition, 5 spiders cut the web above the prey, further entangling it (see above), during attacks on small orthopterans.

Prey-capture sequences with moths as prey. Unlike the orthopterans, moths were attacked with little delay (low attack latency). In over ¾ of the cases the delay was so short that we were unable to measure it. Forty-four out of 45 moths were bitten by the spider; 1 was touched but not attacked. Bite and back-off attacks did not occur; a proportion of the bites involved the simultaneous clasping of the prey against the spider in a "cage of legs." We have complete notes on the detailed form of the bite for 33 out of the 44 biting attacks. In 23 of these, the bite was a bite/clasp. In more than ½ the cases (23 out of 45), the spider pulled the prey free of the web (orthopterans were all cut free). Interrupted sequences occurred in only 14 out of 45 sequences, in marked contrast to the sequences involving orthopterans as prey. Binding behavior occurred in 16 sequences, of which 6 were interrupted. Slightly less than ½ the moths were carried to the hub by spiders backing up the web; this contrasts with the behavior of the spiders when carrying orthopterans of similar length. Presumably the bulkiness of the moths necessitates a form of transportation that minimizes the risk of entanglement. Six moths, not included in the sample of 45 analyzed above, were put in the web and fluttered free before the spider reached them.

Is Fecenia nocturnal? We suspect that *Fecenia* may attack certain types of prey more readily at night than during the day, but we did not have the opportunity to test this. MHR found that specimens raised in captivity would not attack crickets and ants by day but would attack them at night. However, these individuals had been fed at night since early in their development and their behavior could certainly have been influenced by this. The facility with which wild *Fecenia* attacked buzzing flies and flapping, fluttering moths suggests that if there is a differential diel responsiveness to prey, it may only affect responses to suboptimal prey organisms. On the whole, we would expect that a well-camouflaged (by virtue of its retreat) spider that operated a web

24 hr a day would show enhanced responsiveness by night. This interruption of predatory sequences (described in the section on predatory behavior) can be explained in 2 ways (see below), one of which is that it acts as an antipredator strategy by minimizing the continuous time spent away from the protection of the retreat. If this is so, this behavior should perhaps be suppressed at night when the spider that is out of the retreat is not visible to predators. We do not know whether this is the case, but do know that at night the spider rests with its legs protruding from the retreat rather than remaining inside the retreat, which is its normal diurnal posture.

Other behavior patterns

Defecation. Araneids defecate by moving the abdomen so that it is pointing away from the web and squirting the feces from the anus (Robinson & Olazarri 1971: 14). *Fecenia* has this behavior as well.

Courtship and mating. We did not see sperm induction, but introduced a number of sperm-laden males to adult females. Some of the females were raised in isolation and virgins. Courtship and mating were observed once. A wild female was given a katydid as prey, which she bit, bound with silk and then interrupted the predatory sequence to return to her leaf retreat. A male was sitting on the frame threads above the web of the female and, after the female returned to the retreat, he moved down toward the katydid on the web of the female and cut the web above the prey. The sequence is described in our field notes as follows: "The male, on the female's web just below the retreat, pulls on the radii of the web, goes down to the prey and cuts the web just above the prey. This sequence was repeated four times, during a period of 12.5 minutes. The male then assumed a position just above the katydid, *with one strand of silk connecting the lower, cut portion of the web with the retreat,* cleaned his mouthparts and forelegs and brushed one palp with the other. The male then vibrated the thread leading up to the retreat, using the second pair of legs, and the female emerged with the anterior part of her body out of the retreat. The male moved up to the retreat and mated, orienting his body at right angles to that of the female, and rapidly alternating the palps. Mating lasted about 1 min; the male then dropped on a dragline to the bottom of the web, cleaned the palps and again repeated the process. The second mating lasted less than 1 minute."

In other cases, we saw males approach the female's retreat (FIG. 2b) and spend long periods tapping it with their long 1st legs; the females would respond by moving partly out of the retreat and then remaining motionless while the male tapped them directly. Most of these approaches terminated when the females chased off the male; none led to further courtship as described above and no matings occurred. In one case, a male that was left overnight with a female was found next morning to be in residence with her in the retreat. This case is interesting, since in *Psechrus argentatus* males and females can frequently be found occupying the same long tunnel retreat, in close proximity for several days at a time.

The absence of tactile courtship in the one successful mating that we saw could be because tactile courtship is the first (approach, habituation to the male's presence) phase of courtship and had already taken place before our observations started. There is another explanation, namely that the female had prey in the web and its presence allowed the male to suppress the approach phase of courtship. Certainly male *Nephila maculata* will initiate copulation approaches more readily if the female has food at the hub (Robinson & Robinson 1973: 36).

Psechrus argentatus

NATURAL HISTORY AND ECOLOGY

Distribution

Roewer (1954: 1378) gave the distribution of *Psechrus argentatus* as Malacca, Sulawesi (Celebes), New Guinea, Kei I, and New Pommerania (New Britain). Bonnet (1958: 3803) quoted records from Sri Lanka (Ceylon), China, Malacca, Malay Arch., Sulawesi (Celebes), Amboina (Ambon I, in part), New Guinea and the Bismarck Arch. In the Wau Valley the spider is conspicuous and abundant at many localities. We encountered it widely in the Bulolo area. We also found a psechrid with a similar web in the vicinity of Lae, and at Morobe and Madang (north coast of New Guinea). We found a psechrid with a similar web and appearance at Port Moresby, along the Brown River and abundantly on the Sogeri Plateau, N of Port Moresby. We did not collect the species outside the Wau/Bulolo area but believe that the psechrids encountered at all these localities were probably *P. argentatus.* At least 2 other species, however, are recorded from New Guinea: *Psechrus castaneus* and *P. curvipalpis* (Bonnet 1958: 3804). If these spiders encountered outside of the Wau/Bulolo area were not *P. argentatus,* at least their habitat preferences and webs were very similar.

Web location

We found *P. argentatus* webs in a wide variety of habitats, but would certainly regard the existence of tunnel-retreat sites as an important requisite of web sites. Embankments and rocky outcrops were favored web sites, particularly where shade was available. The tunnel retreat is located in crevices and fissures in such sites; within forest, the spider builds against tree trunks and locates the retreat in cracks and under bark flakes. The species was present on all 3 transects of Robinson et al. (1974).

Web structure

The basic web structure is shown in FIG. 7. The web is a roughly rectangular sheet that may be many times longer than wide and it is highly variable in size. At one end the sheet terminates in a tunnel of dense silk that ends against an earth embankment, rock fissure, tree trunk, or fern clump. The tunnel is roofed by the end of the sheet and is always below it. Both sheet and tunnel may be curved or straight, depending on the exigencies of a particular site. The tunnel retreat tapers towards its apex and is quite wide at the mouth (FIG. 7). The sheet consists of frame members of plain silk to which the spider adds, from below, numerous bands of hackled silk. The resultant texture of the adult web is comparable to muslin (FIG. 8). The sheet is braced at the

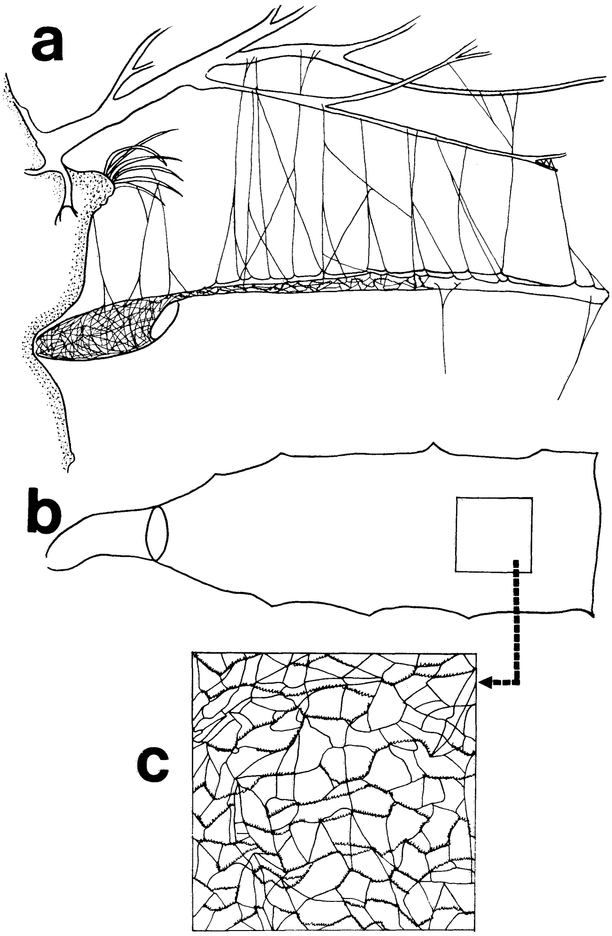

FIG. 7. Diagram of a *Psechrus argentatus* web seen (a) in elevation; (b) in plan view; and (c) as an enlarged section of the plan. The retreat tunnel is to the left in a and b. In c, the hackled bands are represented by zig-zag lines. The enlargement is traced from a photograph.

sides and the end by a large number of irregularly disposed "guy" threads; but these form a loose maze of threads, rather than a dense knock-down snare. The lower surface of the sheet is completely unobstructed and it is on this that the spider operates.

Numerous immatures were present throughout the year on our Kunai Creek study site (near transect III of Robinson et al. 1974). These built webs that were perfect miniatures of the adult web. Webs were extremely durable structures and web sites were in continuous occupation for several months at a time. In areas close to dusty roads, we were able to distinguish between old sections of dusty web and renewed web. Web renewal was certainly a piecemeal operation and we suspect that the whole

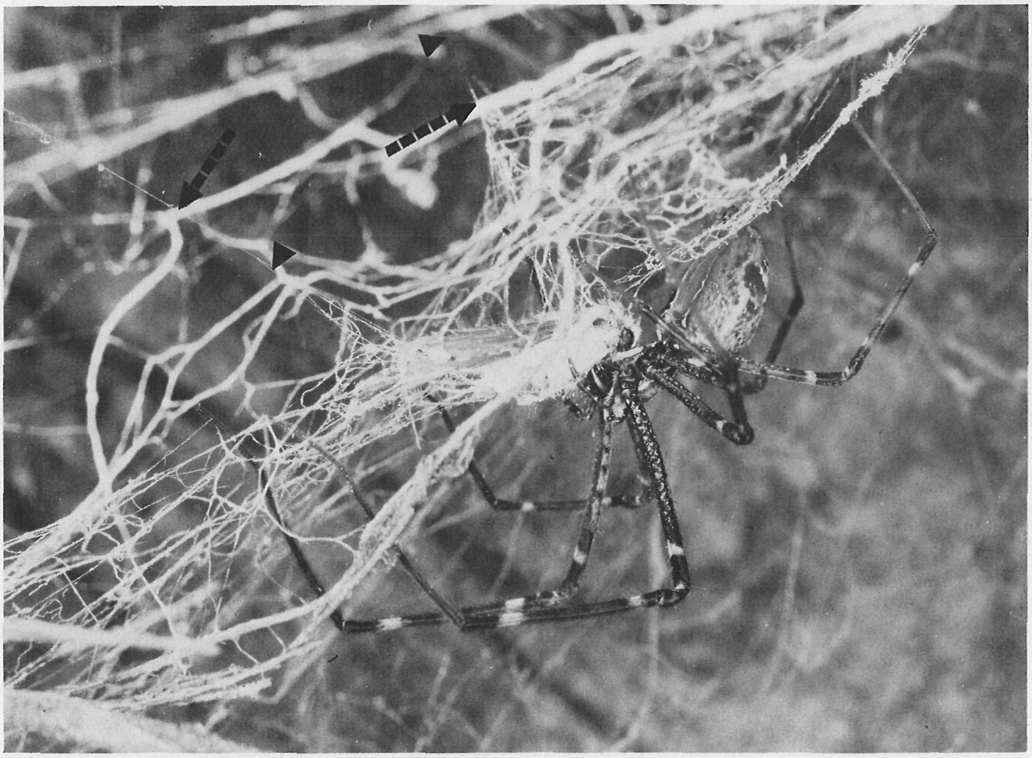

FIG. 8. Adult ♀ *Psechrus argentatus* (length ca 38 mm) biting a moth. The photograph shows the texture of the web relative to the size of the spider. The lines of the upper snare that brace this section of the sheet are arrowed.

web is probably totally rebuilt only if it is destroyed by landslips and similar disasters. The hackled silk may retain its "stickiness" for long periods (even dusty webs seemed to work). We often detected the presence of a few new bands of hackled silk laid down in an apparently unorganized manner on top of old ones. We expected that the spider might produce more hackled bands around the edges of the trap to prevent insects struggling off the sheet; however, we were never able to convince ourselves that this was the case, nor do our photographs show any marked edge banding. Some webs had transverse lines separating sheet material of different ages, suggesting that the length of a sheet might be extended outwards by addition to the "lip." (One web on Mt Missim, the longest we have ever seen, extended over 2 m out from a vertical rockface and was only 38 cm wide at its widest point. This showed signs of several extensions.) Because the "runwaylike" sheet has to be slung from above and braced along its sides, the height above the substrate varies according to the availability of supports. At Wau the ubiquitous waterraces (relics of gold-mining days) provide strange web sites where *Psechrus* builds under aquaducts many feet above ground level. The web can thus be adapted to exploit a surprising range of situations.

Prey

We know nothing of the natural prey of this species. The web is sited in such a way that it could clearly trap ambulatory insects that fall from above onto the sheet, either from vegetation or from the embankment or rockface. (Spiders building from embankments and rockfaces are in reality building at the bottom of a virtual pitfall trap. They also probably capture insects that fall out of vegetation above the ground.) The spiders within forest must catch insects falling from the trees. (Robinson, in prep., has details of the catches of horizontal sticky traps placed beneath trees that suggest this is an important potential resource.) Flying insects may also be trapped in the maze or may alight on the web surface.

Egg-cocoons

The cocoons of *P. argentatus* are roughly spherical and covered with brownish-yellow silk in a dense, papery layer. A typical cocoon is ca 1–1.5 cm in diameter and is carried by the female in her jaws. When egg-carrying females attack prey, they first secure the egg-cocoon to the retreat roof as though it were a prey item (see below).

Males

Males are similar in size to females but have much narrower abdomens.

Defenses

A spider alerted to prey stands beneath the sheet facing outwards from the mouth of the tunnel retreat. At the slightest disturbance the spider rushes into the retreat at great speed. This is also the reaction of the spider to any disturbance of the sheet during an approach to prey or an actual attack; the spider is surprisingly fast. Such escape runs may also be elicited by ground-transmitted vibrations, but in the field situation it is difficult (if not impossible) to control for other variables. Thus the escape runs that we saw that were not triggered by web disturbance could have been responses to air currents, movements of vegetation or noises (to name but a few possibilities). Certainly we saw apparent responses to loud thunder and have seen these in araneids too. It is difficult to guess at the sensory modality involved and tempting to hypothesize a response to air-borne sound (see Lubin 1974: 329–30 for apparent responses by *Cyrtophora moluccensis* to the flight sounds of parasitic flies).

Kleptoparasites and symbionts

The web of *P. argentatus* is a large, complex, semipermanent structure and provides conditions conducive to the evolution of kleptoparasitic and other symbiotic relationships (for examples of associations between spiders and other arthropods, see Brignoli 1966; Exline 1945; Robinson & Olazarri 1971; Vollrath 1976; Robinson 1977, 1978; Lubin 1973). In fact, we found what could be a situation of incipient kleptoparasitism that sheds some light on how such a relationship could evolve. In web sites under rocky overhangs, man-made aquaducts, and in rocky caves, *P. argentatus* often coexists with an abundant New Guinea pholcid (Robinson et al. 1974: 131), which builds typical pholcid webs that often span the upper guy threads of *Psechrus* webs. On several occasions, we have seen the pholcids respond to the struggles of prey caught in *Psechrus* webs long before the web-owner had started an approach (perhaps long before it had detected the prey). The item was well entangled in the psechrid web and safely caught. The following is an extract from our field notes on one such incident: "pholcid is alerted by katydid struggles and goes down, ca. 4″ [10 cm], from web close to rock roof, to *Psechrus* prey, at prey wraps fast and furious, goes back up to its own web laying down line AB (sketched), goes back and forth, seems to be somehow shortening AB. Prey raised slowly above psechrus sheet, then stands on AB motionless above prey, stop observation as *Psechrus* attacks moth in web." We noted 2 hr later, "pholcid feeding on large katydid close to rock-roof, stolen psechrus prey?" Such prey stealing by otherwise independent spiders that are fortuitously associated with the webs of larger spiders, could be a situation favorable to the evolution of specialized symbioses.

We also found tipulids hanging from the webs of *P. argentatus,* as described by Robinson & Robinson (1977).

PREDATORY BEHAVIOR

Psechrus argentatus as an adult is a large and powerful spider. Superficially it resembles a *Nephila* and is about the same size as *Nephila clavipes* (Robinson et al. 1969). It is fast-moving, long-legged, and has powerful chelicerae. Its predatory behavior, as far as we could determine, is simple and effective. The spider operates from below the sheet and never, in our experience, goes onto its upper surface during an attack. All prey are attacked by biting, and post-immobilization wrapping at the capture site is extremely rare. Predatory sequences may be interrupted after the initial attack while the spider retires to the retreat tunnel, but such interruptions are infrequent. All prey are wrap-attached to the roof of the tunnel retreat following transportation in the jaws. The spider runs into the tunnel retreat, carrying prey, headfirst. We presented adult *P. argentatus* with 20 tettigoniids and 30 moths. These insects were similar in size to those presented to *Fecenia.*

Behavior units

It is difficult to see into the retreat, which often has a bend in it, to determine what the spider does at the moment of prey impact or when it starts an attack. Usually our first indication that the spider was alerted by the prey was the appearance of the spider at the mouth of the tunnel retreat. From such a position we could see the slow web-tensioning pull that we have described as part of the behavior of *Fecenia.*

Approach behavior. The spider may (rarely) run straight to the prey location, but generally an approach is made in stages along a far-from-straight course. The first leg of such a course may veer to the right of a direct intersection course, the second course to the left, and so on. At each halt, the spider may tense the web in the general direction of the prey. Interestingly, the speed of approach may decrease from stage to stage. Thus, the last few centimetres may involve a very slow walk with legs I raised off the web and held back over the spider's body. This is essentially similar to what we have called a cautious approach in *Fecenia.* Approaches may take a very considerable time (see below), but insects that walk or kick seem unable to escape from the web. If the insect is buzzing or flapping, approaches are quick and unstaged; in these circumstances the spider may overshoot its prey. If prey items are stuck in the thread maze above the sheet, the spider stops below them and vigorously shakes the web. This is comparable to the behavior of *Cyrtophora moluccensis* (Lubin 1973).

Behaviors occurring before the attack. When an approach is made but an attack is not immediate, the spider may halt in contact distance and touch the insect through the web. This touching is in the nature of a slow "feeling" rather than the tapping seen in *Fecenia.* Distinct pedipalpal contacts occur during slow preattack investigations of prey.

Attack behaviors. After a slow approach to a relatively unstimulating prey, the spider may move from contact distance to biting in a rapid forward lunge. Such *lunge bites* are similar to the 1st phase of a bite and back-off attack in *Fecenia* and *Nephila,* except that they are followed by a sustained bite. *Psechrus,* like *Fecenia,* may bite at appendages first and then slowly move the bite site towards the body. The bite/clasp attack is used on flapping moths. The long legs of the spider are protruded through the sheet, folding over the prey and holding it sandwiched against the sheet and the spider's ventral surface. A most interesting behavior occurs in attacks on sporadically struggling ambulatory insects (grasshoppers, ants, beetles, i.e., insects that do not flap their wings when trapped). When the spider is about to bite such an insect it may gather up the web on each side of the prey, using legs I and II, thereby allowing the insect to drop below the main plane of the sheet, in a loose pocket of silk, towards the spider's chelicerae below. Presumably this behavior not only facilitates biting, but also partly simulates the effect of enswathement by wrapping in araneid attacks. The spider clearly exerts downward tension on the prey during biting so that it is pulled part way through the net, thereby enhancing the entrapment of the prey (the insect is then caught like a herring in a gill net; see FIG. 9).

Behaviors occurring after biting. Interruptions of predatory sequences after biting are rare and most may be responses to disturbances. In most cases, biting is followed by removal of prey from the web. This is done, preponderantly, by pull-out movements. These are strikingly similar to those made by large *Nephila* spp. The spider is biting through the web from below with its legs in a strongly flexed attitude to allow it to reach the prey. As it straightens the legs, it effectively pushes up on the web and pulls down on the prey. This complex of movements may be repeated, and tarsal stances, jaw hold, and body posture changed as the prey is being freed. We noticed *Psechrus* pulling and twisting sideways to release some prey from entanglement. We have not seen such twisting in araneid pull-out behavior; we presume that (as in dentistry) it enhances extraction. Sometimes the spider extends its legs, thereby

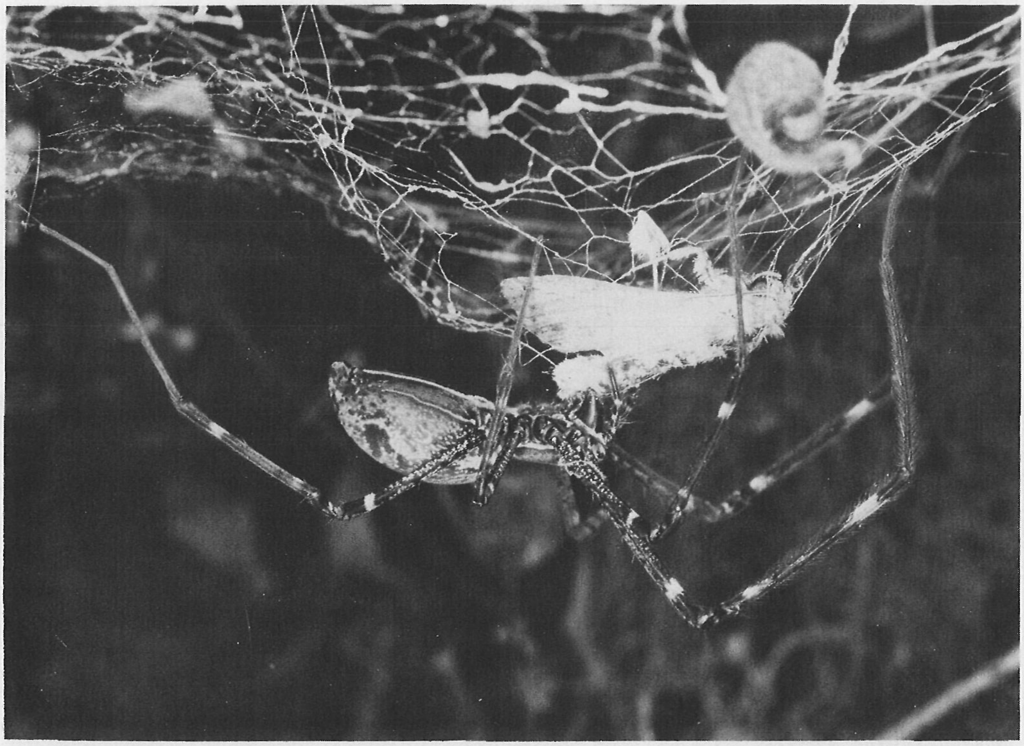

FIG. 9. *Psechrus argentatus* attack-biting a moth; note the downward pressure of the insect that results in its further enmeshment.

pulling the prey away from the web, and then simply walks backwards. This combines a backward pull with a downward one and is frequently effective. However, it may produce a long tear in the web. Cutting, in the manner of *Fecenia,* is extremely rare, as is binding before or after a cut (see below). On the other hand, the spider frequently combines pulling-out behavior with the cutting of entanglements. This occurs as a sequence: pull, cut thread, pull, pull, cut thread, pull free, carry. The number of cutting bouts is variable; the spider may stoop to bring its jaws to the entanglement or may bring down the entangling thread on one tarsus and bring the thread to the jaws. The tarsi are also used to tease away entangling threads from the surface of a prey item. We saw binding behavior only twice in 50 prey presentations and it was a simple circling of the insect as described for *Fecenia.* On one of these two occasions, the light was just right to detect the fact that the binding silk consisted of more than one strand. Pulling-out movements sometimes dismember the prey. On one occasion the spider pulled the head off a katydid and carefully carried it to the retreat tunnel where it was wrap-attached. The spider returned later and removed the body of the orthopteran. Since the body was still twitching spasmodically, it may have been treated as a new prey item.

Prey transportation. All prey items are carried in the chelicerae. Since the spider operates inverted under the web, most items hang dorsal to the spider's cephalothorax and do not risk entanglement as the spider runs back to its retreat. Some items are carried, perhaps by chance, ventral to the spider and may become entangled during transportation; usually the spider frees these by pulling. Only the most cumbersome prey are dragged backwards; usually, after freeing the prey, a spider turns to run forwards towards the retreat. Spiders always enter the retreat headfirst.

Behaviors occurring in the retreat. On arrival at the inner part of the retreat tunnel, the spider appeared to feed for some time, facing inwards, before attachment-wrapping the prey to the tunnel roof and facing outwards. Attachment-wrapping is performed by circling and making spinneret dabs (attachment points) to the web and the insect. It is easy to count the number of slow circlings made by the spider, but difficult to see the location of the attachments, except in the rare cases where we could look right up the tunnel at the spider.

Psechrus argentatus does not always attach prey to the retreat immediately on arrival; in fact, a considerable delay of several minutes may occur. This behavior contrasts strongly with that of most araneids which attach prey to the hub/retreat immediately on arrival. This permits them to make subsequent attacks without the danger of dropping the first prey or the delay of stopping to attach it. Perhaps the kinds of prey falling into a *Psechrus* web have a lower escape potential than the prey of most araneids.

Predatory sequences

Prey-capture sequences with moths as prey. We presented 30 moths and found that predatory sequences occurring in the treatment of these insects were very simple indeed. One escaped during the initial biting attack. All were approached much more rapidly than the katydids (mean 6.6 sec, range 0–100, compared with 78.85 sec, range 0–360, for katydids). Two moths were bitten and left in situ while the spider retired to the hub; all the rest were pulled from the web and carried forwards to the retreat in the jaws. In only 1 case out of 29 did substantial amounts of cutting occur interspersed with pulling. In 5 cases out of 29, the spider rested on the prey during the initial attack phase (i.e., interrupted its bite) for periods of over 30 sec.

Prey-capture sequences with tettigoniids (katydids) as prey. Twenty katydids were presented and the sequences with katydids were found to be slightly more complicated than those with moths. Two spiders (not included in the total of 20 recorded sequences) approached the prey, touched it and ran back to the hub without attacking. All 20 prey were bitten and biting was followed by pull-out attempts in 12 cases. Two prey were bound first and then cut out and 6 spiders interrupted the predatory sequence and retired to the hub after biting (1 of these was disturbed by our efforts to photograph the attack bite). In 9 cases out of 20, the spider rested on the prey, during the attack phase, for more than 30 sec.

In an attempt to elicit binding behavior, we presented a small number of other insects as prey. These included ants, weevils and homopterans. We saw no sequences that departed from the katydid pattern, as outlined above. We failed to elicit binding behavior (see Discussion).

Other behaviors

We have no systematic observations on other behaviors. However, it is noteworthy that we frequently found males living side by side with females in female-built webs. We assume from this that mated pairs may remain together for sufficient time to allow multiple insemination by the same male. Some degree of tolerance between them is clearly operative since they stand in close proximity for long periods.

DISCUSSION AND CONCLUSIONS

Comparative studies of the ecology and behavior of spiders were surprisingly late in developing, considering the predominant role of such studies in organismic biology as a whole. Certain fields of spider biology attracted comparisons before others. Courtship and mating behavior were subjected to the comparative method at an early date, the researches of Gerhardt (1911–1933, full bibliography in Bonnet 1945) being a case in point. However, most of these investigations were interfamilial, with the notable exception of Peckham & Peckham (1889, 1890). Crane's (1949a, b) researches on salticid courtship behavior probably represent the first really detailed comparisons made within a family of spiders. Although the predatory behavior of araneids was an early subject of experimental analysis (for example, the elegant investigations of Peters 1931, 1933a, b), little attention was paid to the evolution of behavior. Probably for this reason their functional analyses lack a comparative base. Eberhard (1967), on the basis of his own research and a literature review, made the first broad treatment of the predatory behavior of web-building spiders of several families. Since then a considerable literature of detailed intrafamilial comparisons has accumulated for both web builders and hunting spiders. A large number of genera and species of araneids have been studied (see e.g., Robinson et al. 1969; Lubin 1973, 1974; Robinson & Robinson 1973; Robinson 1975). Interestingly enough, such a broad approach has not yet been made to web-building behavior, although striking differences exist within, for instance, the araneids. Eberhard (pers. commun.) has accumulated a mass of comparative data on this subject.

We have a broad experience of research into the behavior of araneids (see bibliography for details), and this has enabled us to make comparisons between the psechrids and araneids on the basis of personal experience rather than a literature review. Although the psechrid researches were not conducted in the same experimental/analytical depth as many of our araneid studies, we think that we can make important and informative comparisons. The observations reported in this paper cast light on the functional interpretation of araneid behavior and vice versa.

COMPARISONS WITHIN THE FAMILY PSECHRIDAE

The psechrids are divisible into web builders (*Psechrus* spp. and *Fecenia* spp., total 24 spp.) and hunters (the New Zealand species in 2 genera). The existence of the hunters could be a basis for potentially illuminating further comparisons. Among the web-building species there is a clear distinction, recognized by Simon (1892), between the builders of horizontal sheets and the builders of perpendicular pseudo-orbs. Our discovery of the ontogenetic transformation of the conical (3-dimensional) juvenile web of *Fecenia* into the adult planar pseudo-orb adds a complication to this relatively simple division into 2 web types. It raises the possibility that there may have been a 3rd group of psechrid species that built conical space-webs. Such a group could be ancestral to both *Fecenia* and *Psechrus,* or intermediate between them. If intermediate, what was the direction of change? We are inclined to believe that *Fecenia* is more specialized than *Psechrus,* so that the juvenile *Fecenia* web can be viewed as suggestive of a possible stage in the evolution of the *Fecenia* web from a horizontal sheet web.

The egg-sac of *Fecenia* is distinctly different from that of *Psechrus,* which is similar to that of many hunting spiders (lycosids, pisaurids) that carry the cocoon around with them. Carrying the egg-sac in the jaws may be a primitive feature associated with the hunting habit (it would be nice to know what the New Zealand psechrids do). On the other hand, it may be a response to egg-predators and parasitoids [compare the close association of *Cyrtophora moluccensis* females with egg-sacs (Lubin 1974)]. *Fecenia* rests above her egg-sac within the retreat and is in a good position to defend it. The complex retreat-building behavior of later-stage *Fecenia* (subadults and adults) is more complex and specialized than the silk-retreat building of *Psechrus* and early juvenile *Fecenia*. The "adorned" juvenile retreat of *Fecenia* itself is more complex than the tunnel of *Psechrus.* Associated with the perpendicular web, *Fecenia* has a dropping response in its defensive repertoire, in addition to the simple escape-to-the-retreat response found in *Psechrus.*

Comparisons of the predatory behaviors yield differences that can be largely correlated with differences in web structure. In this respect, it is worth stressing the fact that nearly all spiders' webs are multifunctional artifacts and are not simply traps. Webs function as platforms on which the spider performs its predatory behavior, as antipredator screens, and, at times, as protective devices interposed between the spider and its perhaps dangerous prey. They also clearly function to enhance the efficiency of the spider's prey-detection senses. Since webs serve all these functions, they can be compared with regard to each of them. The *Psechrus* web differs from the *Fecenia* web in being effectively one-sided; the prey must, with rare exceptions, fall from above and be attacked through the web from below. This is not the case with the *Fecenia* web. The respective predatory behaviors of the 2 spiders can be compared on the assumption that *Psechrus* is better protected against dangerous prey. Also, since *Psechrus* operates beneath a dense web, it is better concealed from the eyes of most predators than is *Fecenia,* which operates on either side of a perpendicular, less dense, web. The fact that *Psechrus* attacks through the web may account for the virtual absence of the bite and back-off attack strategy and the comparative absence of prey tapping.

Sudden rapid movements may be much more attention-eliciting than slow deliberate movements. There is little hard evidence for this point of view, but a wide range of cryptic animals seem to make slow deliberate movements by day in contexts suggestive of antipredator function (Robinson 1969). The extra concealment offered by the *Psechrus* web may permit the spider to use an otherwise conspicuous movement with low risk of detection. Conversely, the fact that *Fecenia* is relatively exposed when on the web probably led to selection for the less attention-eliciting slow movements. This slow movement is abandoned if insects struggle vigorously; there must be a balancing of risks. Interrupting a predatory sequence by returning to the retreat could also be an antipredator adaptation, since it splits up the time spent away from the protection of the retreat. *Psechrus* does not do this; it is not conspicuously exposed to view at the capture site and may not be at much greater risk there than in its retreat tunnel. (At the capture site, it is concealed beneath a dense sheet of silk and protected by the upper maze of threads.) It is possible that *Fecenia* interrupts its prey-capture sequences so as to reduce the time spent away from the optimal web-monitoring location and thereby reduces the risk of missing other prey arriving in the web. (This implies that the *Fecenia* web is more highly organized for the directional transmission of vibrations than is the *Psechrus* web. This hypothesis should be testable.) Such a function could coexist with an antipredator function.

Working on a vertical surface necessitates adaptations (and provides opportunities) that are unique. In particular, the spider can enmesh prey by cutting web supports above a struggling insect, causing prey to slip down into sticky areas. This behavior is also seen in some araneids. It is functionally similar to web-bunching in *Psechrus,* but the behaviors involved are very different. Carrying prey up a vertical web imposes problems not encountered by *Psechrus,* which carries prey on the underside of a horizontal web. Backing up the web is clearly an adaptation to this problem. It could have evolved from the behavior of backing (for a short distance) to tear prey free of entanglements that is found in *Psechrus.* Pulling out is gravity-aided in a horizontal web if the spider works from below. It is the predominant prey-freeing behavior in *Psechrus.* On the other hand, freeing prey in a vertical web is less susceptible to such a solution, which may account for the frequent use of cutting-out behavior. Cutting prey from any web raises its own problems; if the jaws are used for cutting, they cannot simultaneously hold the prey and the risk of the prey being dropped thus increases. Binding behavior may function simply to secure the prey safely to the web while it is being cut free. It may have evolved in the sheet-web context to allow large unwieldy prey to be freed from the web. Binding is presumably more advantageous to *Fecenia* with its more-or-less vertical web than it would be to *Psechrus*; prey is more likely to fall onto the body of *Psechrus* as it works below its horizontal web. On the vertical web, prey falling from the spider's jaws is likely to fall out of reach. Since the *Psechrus* web has a maze or loose snare above, insects can be trapped in this and, not surprisingly, the spider has a web-shaking behavior not found in *Fecenia.*

COMPARISONS BETWEEN PSECHRIDS AND ARANEIDS

We are in a position not only to compare the psechrids with conventional orb-weavers, concentrating on *Fecenia,* but also to compare them with *Cyrtophora* and *Mecynogea* spp., whose webs are similar to those of *Psechrus* in that they have a dome-like sheet with a knock-down snare (barrier web) above. Conventional orbs vary considerably in mesh size, shape and conspicuousness, but all are more regularly organized into radial and spiral elements than is the *Fecenia* web. The *Fecenia* web resembles the conventional orb in being roughly planar and orbicular and in consisting of a compound of adhesive and nonadhesive elements. It seems reasonable to first compare araneids that build vertical webs with *Fecenia.* We would judge that even the finest-meshed orb web is less conspicuous than the *Fecenia* web, and this is also true of the cribellate orbs of *Uloborus* spp. *Fecenia* may not bite the insect at its nearest part but step sideways to bite an appendage. Araneids attack the point nearest to their radial approach path. We suspect that side-stepping for an indirect attack may be possible only on a dense platform such as the *Fecenia* web, and that araneids are channelled into attacking the nearest point of a prey by the radial lines of advance. (*Cyrtophora,* however, generally attacks at the first point of contact with the prey, although it does not necessarily run out to the prey along a single radius.) *Fecenia* (and *Psechrus*) often starts a prey-capture run on a wrong bearing, correcting it as it gets nearer the prey. Araneids in conventional orbs hardly ever make such "mistakes," although some *Cyrtophora* species do so in approaching nonvibrating prey. (The very fine-meshed "plankton net" of *Cyrtophora* is more like the sheet of a psechrid than is a conventional orb.) The difference seems likely to be due to the inferior vibration transmission properties of the sheet, rather than due to poorly developed vibration receptors in the spider. The high attack latencies of *Fecenia* for nonvibrating prey may also be a consequence of the relatively poor vibration-transmitting properties of the web; certainly we know of no araneids that are as slow off the mark.

Of course, the major difference between the psechrids and the araneids lies in the development of wrapping behavior. The only absolutely consistent use of silk-wrapping in both families is in attach-wrapping at the retreat. It is this kind of wrapping that Eberhard (1967) suggested to be the most primitive. If the spider did not attach its prey to the web immediately after transportation, it would either have to do so before subsequent attacks or make such attacks with the first prey in its jaws. Either course would greatly reduce its attack efficiency. (In this respect, *Psechrus*'s treatment of its jaw-held egg-cocoon is significant; it attaches it to the retreat roof, like a prey item, before attacking prey.) Robinson et al. (1969) were able to show that when araneids are prevented from wrapping prey at the hub, by a rapid succession of prey, they become increasingly inefficient and lose more and more prey. The post-attack binding behavior at a prey-capture site seen in both psechrid species, but predominantly in *Fecenia,* is very different from that seen in araneids and uloborids. The fact that the hind legs are not involved means that all the silk has to be deposited directly from the spinnerets by movements of the spider's entire body. This has important consequences, most important of which is that the spider must perform wrapping from a position of close proximity to the prey. For this reason it seems probable that such wrapping must always follow the immobilization of the prey by other means; it would be too dangerous to crawl repeatedly over the surface of a potentially dangerous prey before it had been subdued. The method of wrapping used by psechrids is not one capable of rapidly restraining or immediately immobilizing an active prey.

The involvement of the hind legs in wrapping was undoubtedly a key step in the evolution of spider predatory behavior. It was not only essential for the evolution of attack-wrapping, but also permitted the process of prey-packaging to develop. [Wrapping movements in which the hind legs pick up silk from the spinnerets occur in araneids, uloborids, pholcids, theridiids, nesticids and linyphiids. The functional equivalent, involving restraint by silk from a distance, occurs in scytodids which spit a quick-drying, adhesive swathe over the prey. On the other hand, some spiders that lay silk down onto prey directly from the spinnerets have evolved rapid restraints (diplurids, hersilids) but only in highly specialized contexts.] The form of binding behavior in *Fecenia* and *Psechrus* seems to preclude the trussing/packaging function which Robinson et al. (1969) ascribed to some forms of post-immobilizing wrapping. These spiders cannot transport prey on a thread, hanging from the spinnerets, and silk is not used to reduce the bulk of prey items. With respect to wrapping behavior, the psechrids are at the stage 2a, as described by Robinson et al. (1969: 500): "All prey overcome by biting. Post-immobilization wrapping occurs at the capture site when the prey cannot be pulled from the web in the jaws . . . . Function of wrapping enmeshed prey at the capture site: to permit the spider to remove its chelicerae from the prey for use in cutting it from the web. All prey stored at the hub." This (then) hypothetical stage seems to fit the *Fecenia/Psechrus* situation where hub = retreat.

Of the araneids, only the *Nephila*-group spiders (see Robinson 1975: 296–97) have not advanced much beyond this stage. They at least are capable of prey-packaging and may on occasion use wrapping solely for this purpose (stage 2b, Robinson et al. 1969: 500). Despite this advance, some *Nephila*-group spiders rely heavily on backing up the web during prey transportation, almost certainly an adaptation to prevent prey entanglement and, perhaps, a compensation for inefficient prey packaging (Robinson & Robinson 1973: 48, 50; Robinson & Lubin 1979). *Cyrtophora* and *Mecynogea* have impressive web-shaking behaviors used to tumble insects free of the upper snare and onto the sheet (Lubin 1972); *Psechrus* has a closely similar behavior. It might be expected that, since the araneids of this group almost always attack prey through a sheet of fine-meshed webbing, they would use attack-biting more frequently than attack-wrapping (see above). They certainly use biting to attack a wider range of insects than other advanced araneids (Lubin 1973; Blanke 1972; Robinson & Lubin, unpubl. on *Mecynogea* sp.; Robinson, unpubl. on *Cytrophora nympha*). Like *Psechrus,* these araneids do not store prey in the web, but only at the hub (same references).

Our studies of *Fecenia* sp. and *Psechrus argentatus* thus seem particularly helpful in advancing the functional understanding of the role of prey-wrapping in the predatory behavior of web builders. In addition, they provide insights into the effect of web structure on predatory behavior. From the ecological point of view, we feel that there is much to be learned by extending these studies to investigate the prey-trapping efficiency and selectivity of the 2 types of psechrid web. It is a striking fact that the 2 most successful web-builders (in terms of numbers, over a wide range of habitats) at Wau seem to be *Psechrus argentatus* and the araneid *Leucauge papuana.* It would be interesting to know the reasons for the success of these 2 very different spiders operating such different traps.

THE COURTSHIP BEHAVIOR OF *FECENIA* COMPARED WITH ARANEID COURTSHIP

Robinson & Robinson (1980, in press) have studied the courtship and mating behavior of over 50 species of tropical and subtropical araneids. Their study provides a substantial amount of new information on araneid courtship, from which they have developed generalizations about the function and evolution of courtship within the araneids, that differ from previous viewpoints (see Robinson & Robinson 1978 for bibliography). In particular, they have drawn attention to the existence of intermediates between the contact courtship found in the genera *Nephila, Herennia, Nephilengys* and *Argiope* and the largely vibratory courtship, conducted on a male-derived mating thread, found in most other araneid genera. They regard the contact courtship, conducted at the hub or retreat of the female web, as primitive (Robinson & Robinson 1978). In the intermediate situation (found in 11 species of *Argiope* studied so far), the male approaches the female across her web and, after a variable period of contact courtship, cuts a hole in the web across which he makes a mating thread. On this thread the male conducts vibratory courtship and, if he is successful, mating occurs. Robinson (1977: 554) has argued that the construction of a mating thread greatly increases the male's control over the courtship situation: "If the female approaches brusquely, in a manner perhaps indicative of attack rather than sexual response, the male can cut the line ahead of himself and eliminate the danger. At any stage during the approach the male has the cut-off option. Even at the last moment when he prepares for insemination he retains the option . . . ."

It is interesting to compare this type of courtship [called type "B" by Robinson & Robinson (1978)] with our observations on *Fecenia* courtship. *Fecenia* males approach the female across her web. This contrasts markedly with courtship in the advanced araneids (in the sense of Robinson & Robinson 1978) which attach a mating thread to the outside of the female web and do not contact the female at her hub/retreat. In addition, *Fecenia* constructs a mating thread close to the retreat by cutting away the bulk of the web and leaving a single thread in situ. This situation may well be analogous to the construction of a mating thread, in a hole in the web, as described for

11 species of *Argiope* (see above). Our few observations on *Fecenia* courtship are tantalizingly suggestive of widespread similarities. It would be interesting to know whether direct contact precedes mating thread construction, as MHR's fragmentary observations suggest, and whether the male cuts the mating thread if the female's approach is suggestive of a predatory excursion. A study of the courtship of *Psechrus argentatus* should help in elucidating not only the functional questions relating to psechrid courtship, but also permit broader comparisons with the araneids.

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