The male of Progradungula carraiensis Forster and Gray (Araneae, Gradungulidae) with observations on the web and prey capture

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The male of *Progradungula carraiensis* is described. Notes are given on the structure of the webs of female spiders and of the cribellate silk used in the prey 'catching ladder'. Prey catching and avoidance behaviour are described.

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INTRODUCTION

Progradungula carraiensis Forster and Gray is the only cribellate representative of the hypochiloid family Gradungulidae. A description, based on female and juvenile specimens from Carrai Bat Cave, New South Wales, and a discussion of the phylogenetic significance of the genus was given in Forster and Gray (1979).

Recently, a penultimate male spider was collected from a web in Carrai Bat Cave. The web consisted simply of a sparse network of non-cribellate silk spanning a wall recess. The spider was subsequently reared to maturity in the laboratory.

The basic structure of the *Progradungula* male palp (Figs 3, 4) resembles both that seen in the related ecribellate genus *Gradungula* Forster (Davies, 1969; Forster, 1955) and the Tasmanian hypochiloid genus *Hickmania* Gertsch (Hickmaniidae) in which the conductor and embolus are fused and the bulb is inserted basally on the cymbium. In the other hypochiloid genera a discrete conductor and embolus is present and, in *Hypochilus* Marx and *Ectatosticta* Simon, the bulb is inserted apically upon the cymbium (Gertsch, 1958). However, in *Thaida* Karsch the bulb is basally inserted as it is in the Gradungulidae and *Hickmania*. The presence of a notch on the tibial bothria of *Thaida* and *Hickmania* seems to represent a significant synapomorphy between these genera (Forster and Gray, 1979). The gradungulid bothria are elaborately notched or crenellated, rather more so in the ecribellate species than in *Progradungula*.

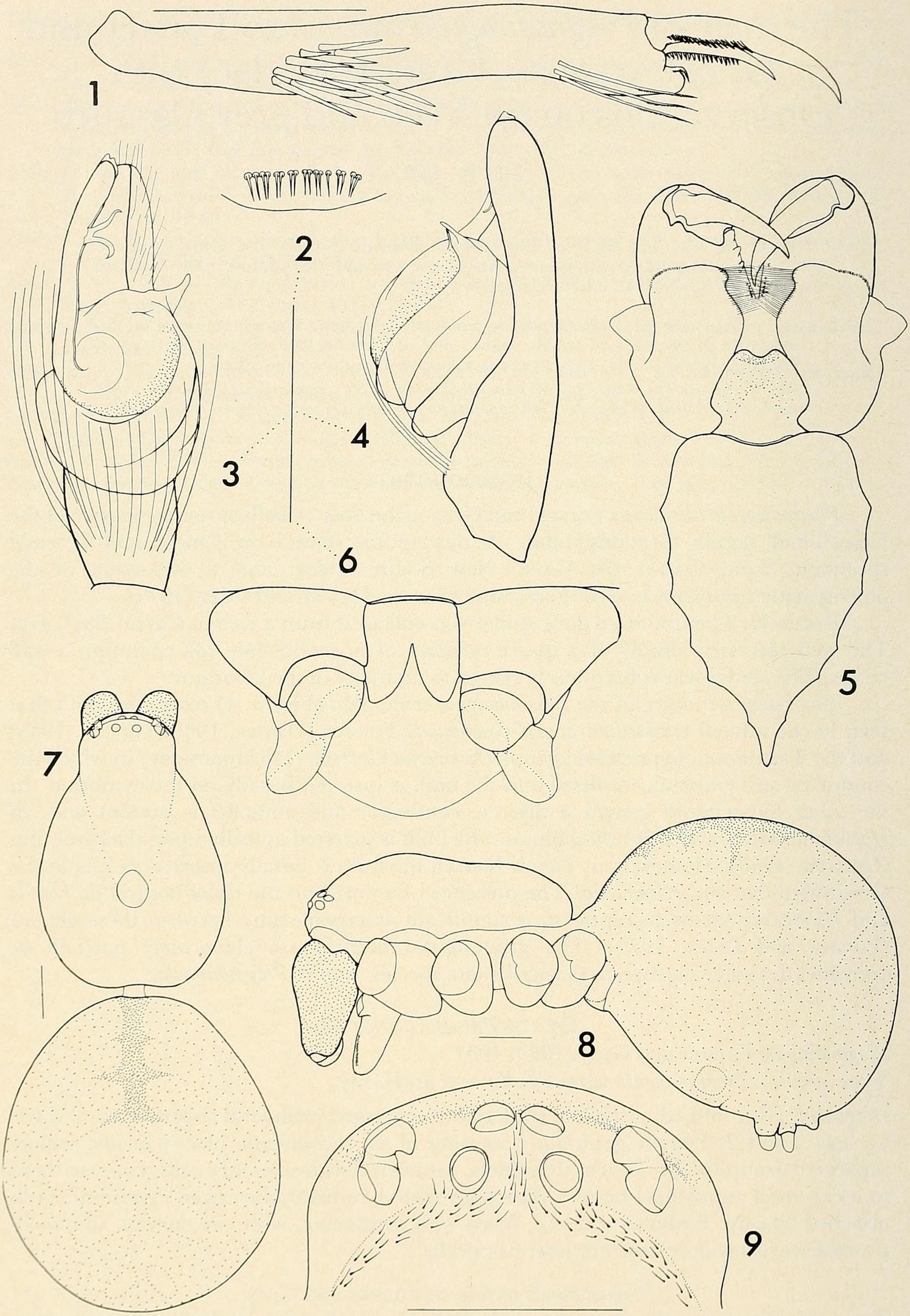
GENUS *PROGRADUNGULA*

Progradungula Forster and Gray, 1979: 1051.
Type species: *Progradungula carraiensis* Forster and Gray.

Diagnosis: Four lunged, cribellate spiders with enlarged prolateral superior tarsal claws on legs 1 and 2. Female genitalia consisting of six receptacula placed in two widely separated groups of three each; thin ducts, associated with secretory cells, connect them to a common copulatory bursa. Male palp with a ventrally furrowed cymbium, bulb attached basally. Embolus rod-like, fused with conductor, with two curved, spine-like processes arising close together near its middle.

Progradungula carraiensis Forster and Gray

Types: Holotype female: New South Wales, Carrai Bat Cave, Carrai State Forest, 19.vii.1971, M. Gray; in Australian Museum, Sydney (KS 1583). Paratypes: 2 females, coll. 24.iv.1974, other data as above; in Otago Museum, Dunedin. 1 juvenile,



Figs 1-9. Progradungula carraiensis, male. **1,** tarsus, first leg, proventral. **2,** epiandrous glands. **3-4,** male palp: 3, ventral; 4, retrolateral. **5,** cephalothorax, ventral. **6,** spinnerets. **7-8,** cephalothorax and abdomen: 7, dorsal; 8, lateral. **9,** eyes, dorsal. Scale lines 1.0 mm.

locality as above, coll. 1.vii.1970, J. A. Harris; in American Museum of Natural History.

Description of male (Figs 1-9)

Measurements (mm) — Carapace length 5.03, width 3.41. Abdomen length 11.0, width 9.5.

Colour pattern (Figs 7, 8) — carapace, sternum and legs light fawn-brown, legs slightly darker. Chelicerae dark brown. Abdomen light brown with an indistinct, greyish, mid-dorsal stripe followed by three pairs of paler dorso-lateral chevron markings.

Carapace (Figs 7, 8) — longer than wide in ratio 1:0.68. Cephalic area prominent, anterior margin strongly recurved; profile domed. Ocular area delimited in front and behind by transverse grooves. Fovea a broad, shallow, rounded pit. Clypeus convex, projecting over the chelicerae; clypeus height 3.5 times the diameter of an AME.

Eyes (Fig. 9) — lateral eyes on a common, low prominence. All eyes with complete tapeta. ALE> PME> PLE> AME in ratio 1:0.85:0.79:0.69. Interdistances (mm): AME-AME 0.10, AME-ALE 0.29, ALE-PLE 0.08, PLE-PME 0.35, PME-PME 0.23. M.O.Q. length 0.38 mm, anterior width 0.36 mm, posterior width 0.58 mm. Posterior eye row slightly longer than anterior eye row in ratio 1:0.95. Eye row curvatures: from above both rows are slightly recurved; from in front the anterior row is straight to slightly procurved, posterior row slightly procurved.

Chelicerae (Fig. 5) — boss absent, fang groove long and narrow with 4 large, evenly-spaced prolateral teeth; and 7 retrolateral denticles in basal half of groove.

Maxillae (Fig. 5) — length 1.56 mm, width 0.86 mm. Linear serrula of 60-70 teeth on antero-ectal border.

Labium (Fig. 5) — length 0.79 mm, width 0.82 mm. Not fused with sternum. Margin rebordered.

Sternum (Fig. 5) — length 2.68 mm, width 1.69 mm. Long, extending to level of posterior margins of coxae 4.

Palp — Spination: femur d 5 (apical third), p 1-3 (apical), r 1-3 (apical), v 100; patella d 11, r 1, p 1, (all weak); tibia d 11, p 010, r 011. Cymbium ventrally furrowed, bulb attached basally (Figs 3, 4). Tegulum with a fixed retrolateral process. Embolus and fused conductor form a gently sinuous rod running below the cymbial furrow. Two slender, spine-like, curved processes arise retrolaterally from the embolus at the junction of its central and distal thirds. Embolus apex blunt, indented, non-sclerotized.

Legs — 1423. Long and slender. Length (mm), legs 1-4: 37.37, 29.91, 24.87, 30.01. Spination: Leg 1, femur p seventeen in single row, r 12121101100, d 102(1111111, all retrolateral) 2, v 121221210; patella p 1, r 1; tibia p 111111, r 101111, d 010001, v 221222; metatarsus p 11101, r 1010101, v 2221; tarsus v fourteen (proximal). Leg 2, femur p thirteen (in single row), r 1120000, d 12(11111, all retrolateral)02, v 222220; patella p 1, r 1; tibia p 111111, r 10111, d 00101, v 22222; metatarsus p 11112, r 110102, v 22121; tarsus v eleven (proximal). Leg 3, femur p ten (in single row, dorsal), r 1111000, d 221111113, v 1222121; patella p 1, r 1; tibia p 11111, r 111111, d 01101, v 21222; metatarsus p 11112, r 11102, v 22121; tarsus v 010. Leg 4, femur p 101111101, r 00011111, d 2111110001, v 212211211; patella p 1; tibia p 11111, r 111111, d 10001, v 221112; metatarsus p 11112, r 10112, v 211221; tarsus v 010. Legs 1 and 2 with short, curved, ventrally concave tarsi, ventral spines bunched proximally and prolateral superior claws enlarged (Fig. 1). Empodium prominent with a slender inferior claw. Teeth on superior tarsal claws (legs 1-4): prolateral 19, 18, 10, 11, retrolateral 25, 19, 11, 11; on inferior tarsal claws, 1-2. Ventral tarsi with several toothed hairs (14-16 pectinations in distal half) arising subdistally. Trichobothria: tarsus, none; metatarsus, 1 distal (legs 1 and 2), 1 subdistal (legs 3 and 4); tibia (legs 1-4), prodorsal, 2 in distal third to fifth, 8-9 in proximal quarter, retrodorsal 9-10 in distal half to two thirds. Bothria crenellated on antero-internal margin. Trochanters shallowly notched. Calamistrum reduced to a short row of weak hairs.

Abdomen (Figs 7, 8) — A broad common spiracle, placed near spinnerets opens into an atrium leading to the posterior lung books. Posterior lung books placed closer to spinnerets than to genital groove. Epiandrous glands present in a single row along the anterior border of the epigastric fold (Fig. 2). Cribellum reduced.

Collection Data: Male, Carrai Bat Cave, Carrai State Forest, N.S.W., M. Gray, 21.2.1980; KS 6740, Australian Museum.

Web Structure

All of the webs so far observed have been found in cave environments. However, it seems reasonable to assume that *Progradungula* may also occur in suitable epigean habitats e.g. within rotting logs or moist rock/soil cavities.

Notes on web structure based upon a vertically elongated web were given in Gray (1973) and Forster and Gray (1979). Further observation of the webs of female spiders at Carrai Bat Cave indicates that webs are generally more compact than this, most ranging from 20 to 50 centimetres overall in both vertical and horizontal extent. The webs are built between adjacent rocks or under rock overhangs, usually near the cave walls. They are not particularly associated with bat roosting areas but occur sporadically throughout the twilight and dark zones.

The structure of the *Progradungula* web (Fig. 10) may be summarized as follows: a narrow, cribellate catching ladder (a) is suspended low down between two semi-vertical lateral support lines (b) which run from an irregular retreat network (d) above to ground attachments below. These attachments may be to soil or rocks on the cave floor or, less commonly, to the cave wall.

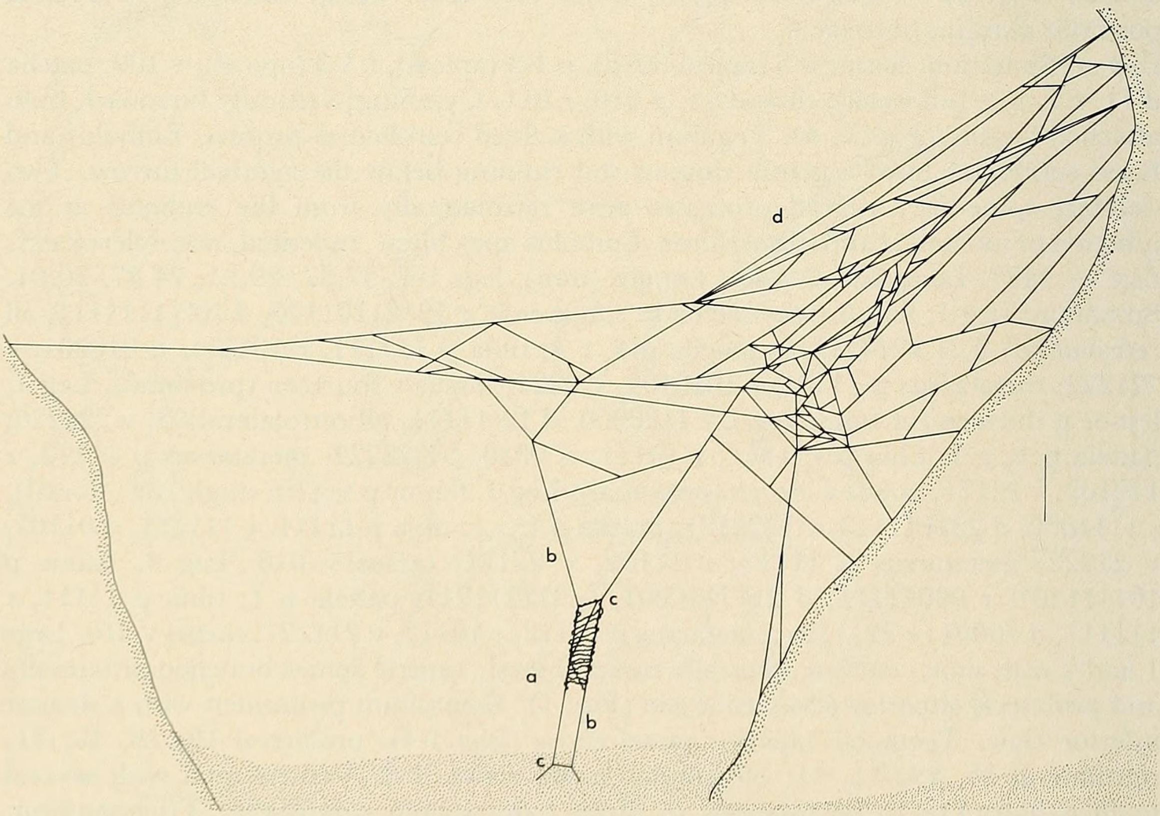
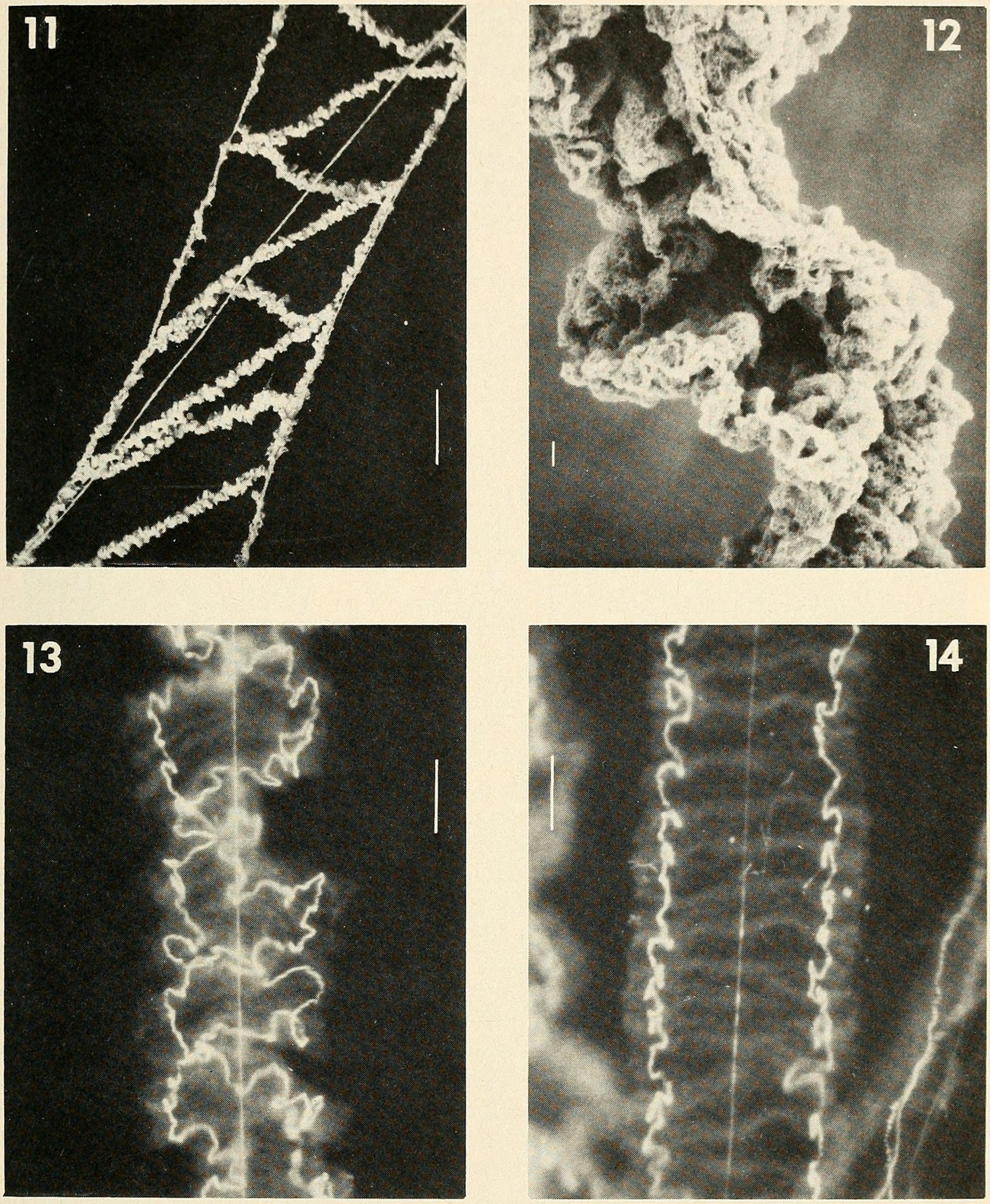


Fig. 10. Web of *Progradungula carraiensis* — (a) prey catching ladder; (b) lateral support lines; (c) bridge lines; (d) retreat network. Scale line 2.5 cm.



Figs 11-14. Progradungula carraiensis, catching ladder. **11,** part of ladder showing non-cribellate support and cribellate catching lines. Scale line 3.0 mm. **12,** cribellate line showing dense, fibrillar surface structure. **13-14,** structure of cribellate silk line. 13, relaxed; 14, stretched. Scale lines 0.15 mm.

The most unusual feature of the web is the subvertical prey-catching ladder (referred to as the catching 'platform' in Forster and Gray, 1979; 'ladder' is more accurately descriptive). The catching ladder is delimited by transverse upper and lower bridge lines (c, Fig. 10) set some 50 to 120 millimetres apart. With one or two diagonal brace/support lines, they hold the main lateral support lines in place at a near parallel separation of 5 to 8 millimetres. An upper diagonal line is always present below the upper bridge line; the lower diagonal line is usually shorter and may be replaced by a secondary cribellate line. The lower bridge line is placed from 5 to 20 millimetres above ground level; rarely there may be two lower bridge lines or none at all.

Only the upper part of the catching ladder receives an application of cribellate silk, the lower part being left open. A continuous line of cribellate silk is applied in a series of loose loops back and forth across the lateral and diagonal support lines, often overlapping the laterals, to form a zig-zag, ladder-like structure (Fig. 11). In adult webs the number of cross loops varies from 14 to 25. Cribellate silk is also applied to the adjacent parts of the lateral support lines and often to the diagonal and upper bridge lines as well.

The webs of other cribellate hypochiloid spiders are very different in structure. For example, *Hypochilus* Marx makes a short, slightly tapered cylindrical web ('lamp-shade'-shaped) while the web of *Hickmania* Gertsch takes the form of a large sheet (Shear, 1969; Hickman, 1967). The cribellate part of the *Progradungula* web, the catching ladder, may be homologous with the simple, zig-zag element which forms the basis of many, more elaborate cribellate webs. The web is probably derivative, resulting from simplification of web structure in association with both space-restricted habitats and specialized feeding behaviour.

CRIBELLATE SILK STRUCTURE

The cribellate silk laid down across the support lines of the catching ladder is only loosely adherent to them. Each cribellate line consists of a thick, irregularly twisted network of fine, curling microfibrils (Fig. 12). The microfibrils are supported by four longitudinal silk lines, two axial and two lateral. The axial lines lie next to each other and appear fused as a single, straight line whereas the lateral lines are well separated and are normally strongly crimped, forming a wave-like interlocking structure (Fig. 13). When the cribellate thread is stretched the lateral lines and the microfibril mass straighten (Fig. 14); these components may move as a unit which slides along the fused axial lines during stretching.

The cribellate silk structure of *Progradungula* differs slightly from that of *Hypochilus* Marx (Comstock, 1940; Shear, 1969). In *Hypochilus* the two straight 'axial' lines are well separated, rather than fused into a single line.

PREY CAPTURE

P. carraiensis adopts a head-down hunting position upon the lower surface of the sub-vertical catching ladder (Fig. 15). The third and fourth legs hold the spider onto the lateral support lines. The tarsi of the fourth legs are placed at or above the junctions of the latter with the upper bridge line. The tarsi of the third legs are placed near the middle of the cribellate platform. They push the lateral support lines away from the body so that the catching ladder is bent at an obtuse angle. This tenses the whole structure and creates a sizeable gap between the ladder and the spider's body. In this position the spider's chelicerae are approximately at the level of the lowest cribellate threads in the catching ladder. The first and second legs, with their enlarged prolateral tarsal claws, do not touch the web but are held poised in a partially outstretched position below and anterior to the ladder. However, the tarsi of the second legs sometimes rest near the junctions of the lower bridge and lateral support lines. The tarsal claws of the first legs are held just above ground level.

The two ground attachments of the catching ladder and the spider's outstretched first and second legs form a semi-circular prey capture zone some 10-15 cm^2 in area.

Prey moving just beyond the capture zone can be sensed by the spider. Air currents affecting the trichobothria or substrate vibrations transmitted via the ladder's

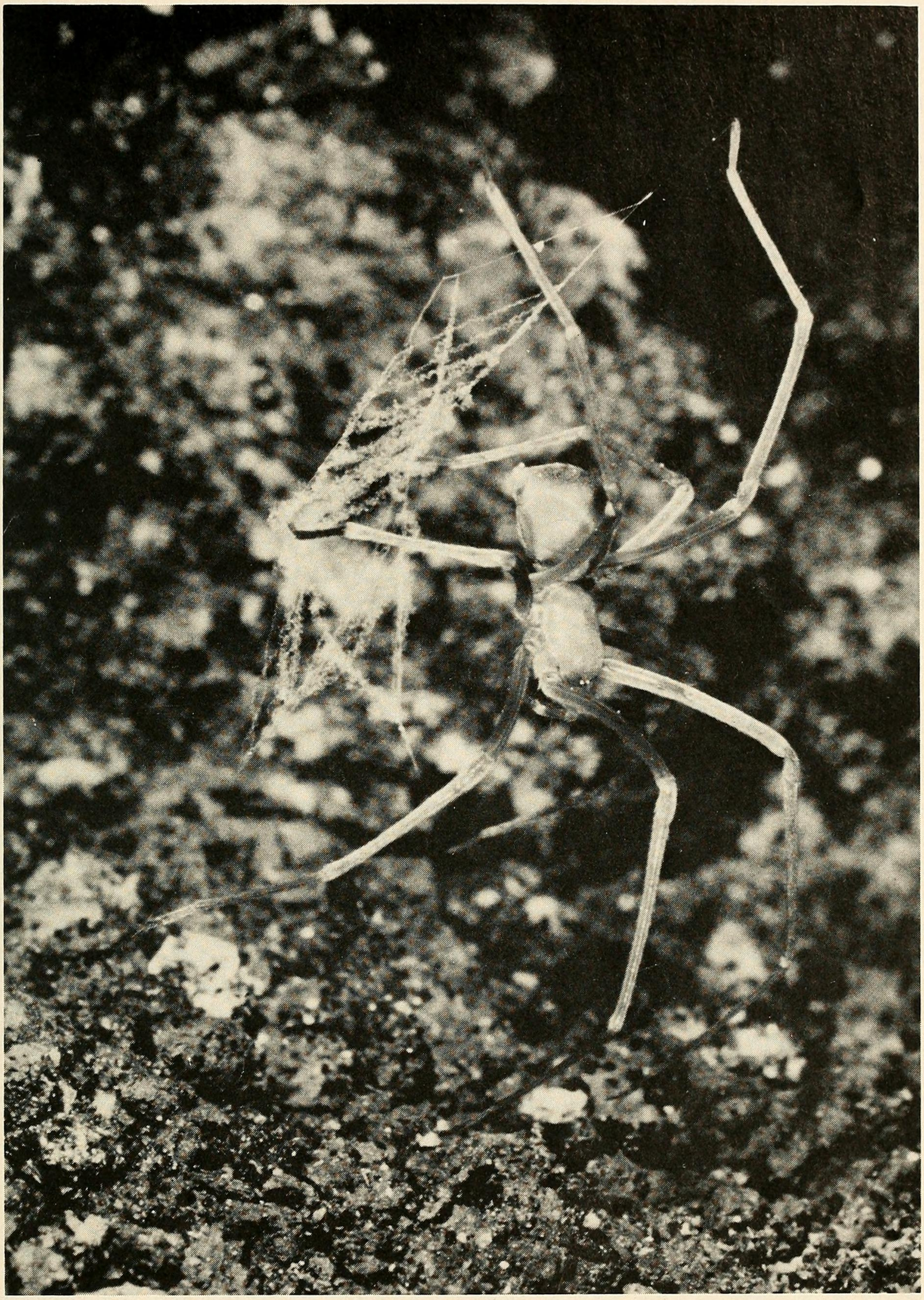


Fig. 15. Female *Progradungula carraiensis* in hunting position on catching ladder.

ground attachments may be the stimuli involved. In response the spider makes probing movements with its first legs toward the disturbance. At the same time the pliable catching ladder is flexed in the direction of probing. As soon as the first legs touch the prey the spider lunges forward and down, and uses the enlarged prolateral claws and ventrally-spined, concave tarsi of the first and second legs to scoop it up. These legs are flexed upwards so that the prey is thrust into the space between the catching ladder and the spider's body and so onto the cribellate silk of the ladder. At the same time the third legs are relaxed allowing the catching ladder to spring in towards the prey. The cribellate silk detaches readily from its supports and thoroughly enfolds the struggling prey. The spider then bites the enmeshed prey while maintaining a 'jack-knifed' embrace of it in its front legs for about ten seconds.

Once the prey is immobilized the spider moves to a head up position above it and begins prey wrapping, the tarsi of the fourth legs being used alternately to draw silk. This continues for several minutes. At this stage the prey is suspended from the tangled support lines of the upper platform; the lower cross bridge and the ground attachments of the lateral support lines remain undisturbed. The wrapped prey may be bitten again for a few seconds. The spider then climbs to the upper part of the web near the side wall holding the prey in its jaws and feeds upon it.

Only tineid moths (6-10 mm long), which are common on the floor of Carrai Bat Cave, have been observed as prey of *P. carraiensis*. Other potential prey includes small beetles, juvenile cave crickets, spiders and flies. Larger prey, such as carabid beetles, seems to be avoided, the spider possibly judging prey size during the probing movements. Avoidance behaviour involves retreat onto the support lines or into the upper web. If further disturbed here the spider will either move out of the web onto the rock wall; or it will drop from the web and lie motionless on the ground with the legs tightly flexed. The latter escape response is typical of that shown by many other araneomorph web builders.

In cave and equivalent epigean environments the invertebrate fauna is mainly substrate dwelling. The web, behaviour and morphology of *P. carraiensis* are well adapted for the capture of such prey. Very little energy has to be expended in web building, only the small cribellate platform requiring regular renewal. During prey capture the spider functions as an active extension of its web. It combines the ambushing tactics of the lie-in-wait hunter, aided in prey grasping by the modifications of the first and second tarsi, with the immobilizing effect of a cribellate snare which provides an 'instant prey wrapping' function. The simultaneous clasping and biting of the enmeshed prey upon the catching ladder precludes prey escape but probably limits the capture ability of *P. carraiensis* to prey of about its own body size or smaller. This contrasts with the net casting spiders (family Dinopidae) whose small cribellate snare represents another type of instant prey-enswathing/immobilization device. The first and second legs of these spiders hold the snare between the spider and its prey and direct its placement onto the latter. This snare is highly elastic and can be stretched to several times its original size, allowing quite large prey (e.g. male trapdoor spiders, crickets) to be successfully attacked.

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