

## SPIDERS OF THE FAMILY ARANEIDAE IN SINGAPORE MANGROVES

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*ABSTRACT.* - A new species of araneid found in the mangroves of Singapore, *Argiope mangal*, is described. Notes are given on its biology, and on four other araneids found in the mangroves, viz., *Cyclosa mulmeinensis*, *Cyrtophora beccarii*, *C. moluccensis* and *C. cicatrosa*.

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### INTRODUCTION

Records of Southeast Asian spiders contain only isolated references to the spiders associated with mangrove swamps. These include three species whose type localities are in Singapore, viz., *Idioctis littoralis* Abraham, 1924 (Barychelidae), *Lampropelma violaceopedes* Abraham, 1924 (Theraphosidae) and *Tetragnatha josephi* Okuma, 1988 (Tetragnathidae). The presence of *Cyrtophora beccarii* (Thorell) (Araneidae) in the mangrove has been noted by both Workman (1896) and Koh (1989). Koh also refers to two pisaurids, *Thalassius* and *Hygropoda* spp. and four salticids, *Epeus flavobilineatus* (Doleschall), *Hyllus diardi* (Walckenaer), *Ligurra latidens* (Doleschall) and *Phaeacius malayensis* Wanless, which have been collected from mangrove habitat. Murphy (1990) adds his observations on some of these spiders and draws attention to the fact that although spiders are abundant in the mangroves, their presence has been poorly documented.

This paper constitutes an effort to begin to record the spiders in Singapore mangroves, and provide those mangrove ecologists unfamiliar with spider taxonomy with a less formidable working guide. Unless otherwise stated, all specimens examined are in the author's private collection.

### FAMILY ARANEIDAE

Although several araneid subfamilies and many araneid genera are easy to recognize, it is more difficult to characterize this diverse family, which comprises at least 2500-3000 known species, for the benefit of those requiring a quick and simple introduction. Most araneids build

orb webs, or modified orb webs, but this is a character shared by seven other families of spiders. Among these non-araneid orb-weavers are two families of spiders possessing a cribellum, a plate-like spinning organ in front of the spinnerets, viz., Uloboridae (whose web may be an orb, a segment of an orb, or simply a single line of silk) and Deinopidae (which construct an orb-shaped net which can be “thrown” at the prey). Araneids do not have a cribellum. They are generally larger than members of four families of tiny orb-weavers (Theridiosomatidae, Mysmenidae, Symphytognathidae and Anapidae), all less than 2.0 mm in length. The dividing line between Araneidae and Tetragnathidae, the remaining family of non-araneid orb-weavers, has shifted over the last 50 years. Recent studies by Levi (1983) and Coddington (1986, 1990) suggest that on the basis of structural and behavioural characteristics, the nephilines (e.g., *Nephila*, *Nephilengys*, *Herennia*) should be regarded as a monophyletic group and removed from the Araneidae. Coddington (1990) points out that without the nephilines, tetragnathines (e.g., *Tetragnatha*) and metines (e.g., *Leucauge*, *Tylorida*), Araneidae becomes more compact and homogenous, with the apparent reduction of the tapetum of the posterior median eyes (Levi, 1983: fig. 10) as the best synapomorphy distinguishing it from the non-araneids. Other diagnostic features of the redefined Araneidae are shown in the male palp: they include, among other things, the central location of the median apophysis and the presence of a radix (Coddington, 1990 : fig. 56-67). For the non-taxonomists, two other features may help to separate the araneids from the nephilines : the labium of the araneids is wider than long, whereas that of the nephilines is longer than wide; the paracymbium of the araneids is typically hook-shaped, and not a flat lobe as in the nephilines.

Five species of araneids have been collected from the mangroves of Singapore. They represent three easily recognized genera, viz., *Argiope*, *Cyclosa* and *Cyrtophora*. In line with the observations of Levi and Coddington cited above, and in keeping with the listing provided in the catalogue by Platnick (1989), this paper will exclude the nephilines from the Araneidae, and will therefore not discuss *Herennia ornatissima* (Doleschall) and *Nephila antipodiana* (Walckenaer), both of which, particularly the latter, are common in Singapore mangroves. To avoid further confusion, this paper will also omit another orb-weaver collected in Singapore mangroves, *Zygiella nadleri* Heimer, since the genus is also listed under Tetragnathidae by Platnick after Levi (1980), although Coddington (1990) suggests that based on the male palps, *Zygiella* appears to belong to the araneine complex.

### ***Argiope* Audouin, 1825**

The orb webs of *Argiope* females are easily recognized in the field by the presence of a stabilimentum of two or four silken zig-zag bands radiating from a closed hub. The stabilimentum of webs of juveniles is a lacey disk-like platform on the hub. Morphologically, *Argiope* species can be separated from other araneids by their eye arrangement. Like *Gea* and *Neogea*, the posterior eye row is procurved when seen from above (Fig. 1). Unlike *Gea* and *Neogea*, the posterior median eyes are closer to each other than the posterior lateral eyes. Detailed descriptions of other generic characters and keys to the males and females in the Western Pacific area (including Indian species) are given by Levi (1983). Four species have been collected in Singapore: *A. aemula* (Walckenaer), *A. versicolor* Thorell, *A. pulchella* (Doleschall), and the new species described below.

*Argiope mangal*, new species

(Figs. 1-8)

**Diagnosis.** - This species resembles *A. ocula* Fox from Southwest China, Taiwan and Japan, and *A. macrochoera* Thorell from Nicobar Islands in having an epigyne with a well-developed scape but differs from them by its unusually thick and angular rim (which is evident in lateral view, Fig. 4). The male palp is similar to those of *A. picta* and *A. aetherea* in showing an obvious kink on the outer surface of the embolus, but unlike them, *A. mangal* has an inconspicuous angular process on the inner margin of the embolus instead of a long, filamentous pendant (Fig. 8).

**Materials examined** - Holotype - female, mangrove vegetation in intertidal zone, northern end of Lim Chu Kang Road, Singapore, coll. J.K.H. Koh, 8.iii.1991; Allotype - male, wasteland fringing mangrove swamp, northern end of Lim Chu Kang Road, Singapore, coll. J.K.H. Koh, 28.i.1991. Both specimens are deposited at the Zoological Reference Collection, National University of Singapore.

Paratypes. - 3 males and 3 females from mangrove vegetation in intertidal zone, northern end of Lim Chu Kang Road, Singapore, coll. J.K.H. Koh, 8 .iii. 1991. A pair of male and female are deposited at the British Natural History Museum, London and another pair at the Museum of Comparative Zoology, Harvard University, Massachusetts.

**Description.** - Female : Carapace beige, with irregular dark brown patches near the edge, covered with white velvety hair. 4.8 mm long, 4.1 mm wide. Ratio of AME:ALE:PME:PLE = 20:11:25:25. AME 1.0 distance apart, 2.5 diameter from ALE. PLE 1.4 diameter apart, 2.6 diameter from PLE. Sternum whitish yellow. Abdomen pentagonal, 8.5 mm long. Anterior edge black and armed laterally with a pair of low conical protuberances. Dorsum yellow, transverse lines and posterior reticulation black. In live specimens, some of the areas enclosed in the posterior reticulation are yellow, others yellowish orange. Ventrally, the areas surrounding the three pairs of white circles are yellowish orange. A pair of yellow brackets enclose the black area anterior of the spinnerets. Legs banded with white hairs, distinctly at the basal ends of all tibia. Distal half of tibia IV with a thick brush of black spines. Tarsi and distal parts of the metatarsi black. Measurements (in mm):

| Leg | Femur | Patella | Tibia | Metatarsus | Tarsus |
|-----|-------|---------|-------|------------|--------|
| I   | 8.8   | 2.5     | 6.8   | 9.0        | 1.9    |
| II  | 8.2   | 2.4     | 6.6   | 8.4        | 1.7    |
| III | 5.3   | 1.7     | 3.1   | 4.5        | 1.4    |
| IV  | 9.1   | 2.4     | 5.4   | 8.1        | 1.4    |

Male : Carapace light brown, with dark antero-lateral margins near first coxae, 2.0 mm long, 1.8 mm wide. Ratio of AME:ALE:PME:PLE = 10:6:11:10. AME 1.0 diameter apart, 0.7 diameter from ALE. PME 1.2 diameter apart, 1.8 diameter from the PLE. Sternum light brown with a narrow longitudinal white median line, and when alive, red laterally. Coxae yellowish brown. Abdomen 21.0 mm long, white with dorsal greyish brown folium, lower half of the venter black bracketed by a pair of white lines. Legs with distal segments banded, ventral side of the first, second and third femur dark brown. A straight black line runs on the ventral surface of metatarsi and tarsi III and IV. Measurements (in mm):

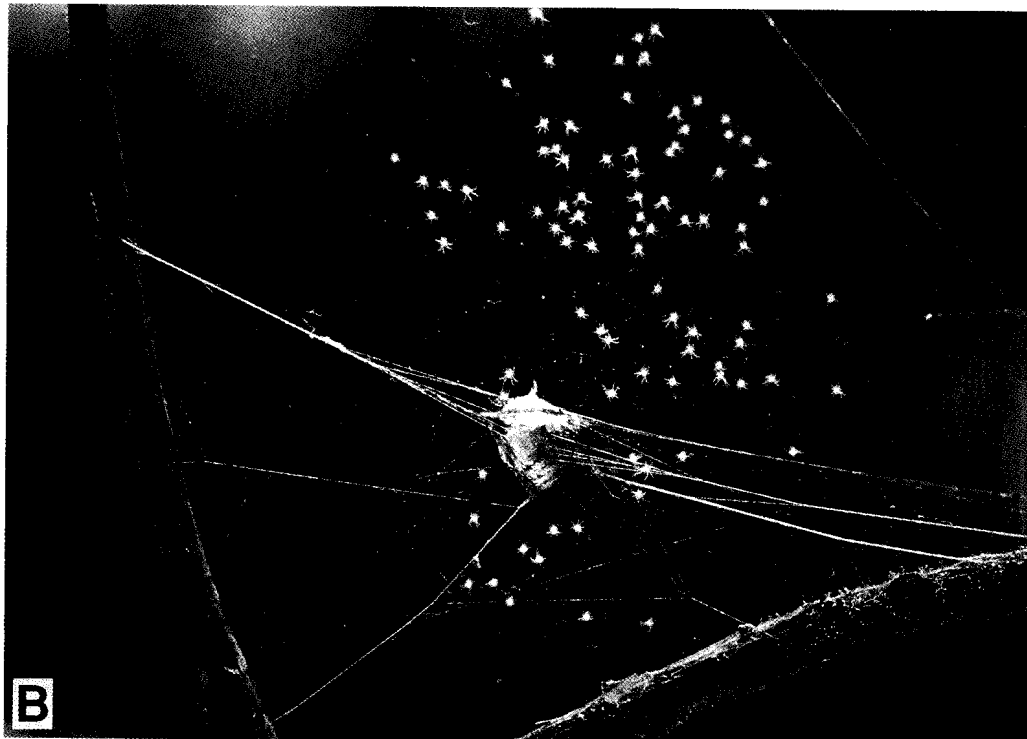
| Leg | Femur | Patella | Tibia | Metatarsus | Tarsus |
|-----|-------|---------|-------|------------|--------|
| I   | 2.9   | 0.9     | 2.1   | 2.5        | 1.0    |
| II  | 2.9   | 0.9     | 2.1   | 2.6        | 1.0    |
| III | 1.8   | 0.6     | 1.0   | 1.2        | 0.7    |
| IV  | 2.7   | 0.7     | 1.6   | 2.1        | 0.9    |

**Variations.** - While the abdomen of live specimens shows a clear pentagonal shape, preserved specimens may undergo shrinkage and may appear oval and/or lobed. Female carapace length can range from 4.3 - 5.4 mm, width from 3.7 - 4.9 mm (8 specimens). Female abdomen from 5.1 - 9.7 mm. The black band on the antero-lateral margin of the male carapace may extend to the posterior edge of the carapace. Male carapace length varies from 1.9 - 2.3 mm, width from 1.9 - 2.2 mm. Male abdomen ranges from 1.9 - 2.5 mm in length (4 specimens).

**Natural History.** - This species appears confined to mangrove swamps, occurring sometimes in large numbers among the foliage and branches in the intertidal zone, but occasionally living among *Acanthus ilicifolius* and *Hibiscus tiliaceus* bushes in the dry and sunny areas fringing the swamp. Males can be found living at a corner of the female's web.

Suspended approximately 70 cm to 2.7 meters from the water or ground, the web of a mature female (recognizable in the field by the prominently protruding scape in lateral view) can span from 38-50 cm in diameter (N = 8). The stabilimentum of a typical web does not show the familiar "St. Andrew's Cross" arrangement, being made up of only two zig-zag bands, one above and the other below the hub (Pl. 1). The bands do not extend into the hub. While precise figures are not available, there appears to be considerable variation in the stabilimentum. In some webs, the zig-zag webbing above the hub seems less distinct than the band below. The stabilimentum of some webs is made of only one zig-zag band, invariably below the hub; others (mainly of immature females) have no stabilimentum at all, while one has been observed with four arms as in the web of *Argiope versicolor* (Doleschall). Another web (of an immature female) has on one side what appears to be a barrier web constructed with several strands of silk. While most webs are free of alien spiders, some are infested by kleptoparasitic theridiid spiders of the genus *Argyrodes*, viz., *A. miniacus* (Doleschall) and, more rarely, *A. argentatus* Cambridge.

When threatened, the spider displays a array of secondary defensive mechanisms seen also in some other *Argiope* (Edmunds & Edmunds, 1986). First, the spider may run up the web and lie motionless on a branch or leaf nearby (but often on the upper surface of the leaf in full view of the potential predator!) Second, *A. mangal* may remain at the hub and vibrate the web by flexing its first two pairs of legs vigorously. This produces a blurring effect in the eyes of the potential predator. Based on observations made on a West African *Argiope*, Edmunds (1986) has suggested that an *Argiope* with well-developed stabilimentum may project a large blurred image of itself when the stabilimentum is seen vibrating with it. However, since the stabilimentum is not always present in the webs of *A. mangal*, and since *A. mangal* has the habit of vibrating the web at the edge after moving away from the hub, far from the stabilimentum, it is probable that the stabilimentum does not serve the function of producing an enlarged illusion of the spider when the web is shaken. Third, the spider may speedily switch itself to the opposite side of the web through a gap near the hub as a result of broken lines, or through the "free zone", a circular zone with relatively large mesh, between the hub and the sticky spirals. (Local *Gasteracantha* spp. also switch from one side of the web to another when threatened, but through an open hub (pers. comm. D.H. Murphy, based on his discussions with the late W.S.



Pl 1. *Argiope mangal*, new species. A. Web of mature female; B. Egg sac with newly hatched spiderlings on a sheet of silk.

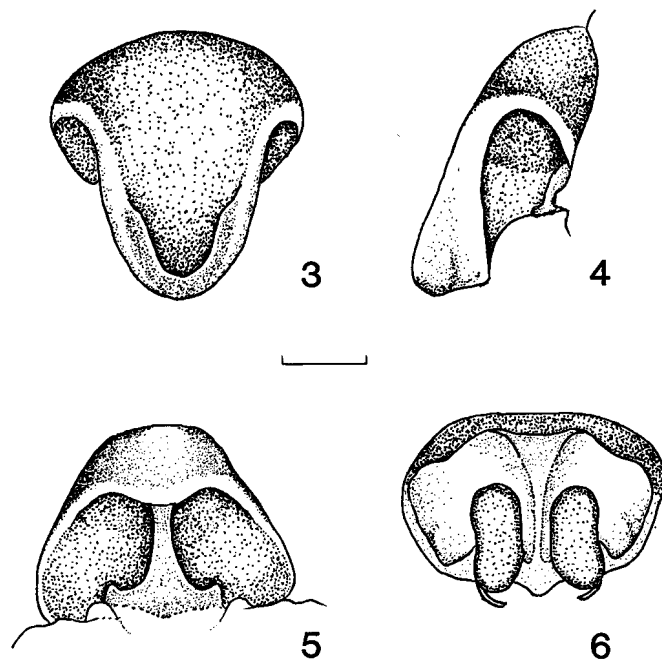
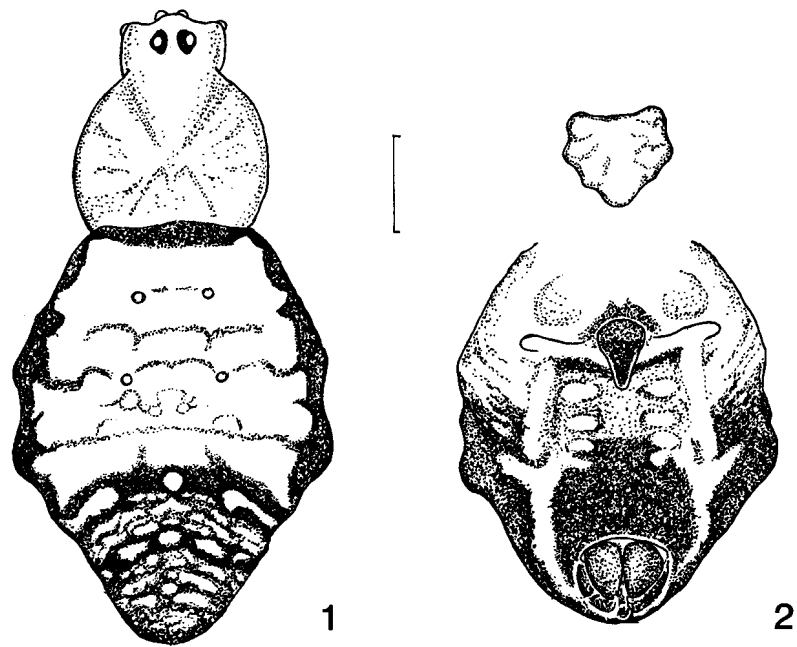


Fig. 1-2. *Argiope mangal*, new species, female : 1. Dorsal view. 2. Ventral view. Scale line: 2.0 mm.  
Fig. 3-6. *Argiope mangal*, new species, Epigyne : 3. Ventral view. 4. Lateral view. 5. Posterior view. 6. Dorsal view. Scale line : 0.5 mm.

Bristowe.) Fourth, the spider may jump off the web. If it manages to land on the ground instead of water, the spider may withdraw its legs and “play dead” for a few seconds before scuttling to another location. This movement is repeated till the spider reaches a fairly sheltered spot. The yellow parts of the dorsum may acquire a light brown tone during such movement, but the colour change does not appear significant enough to help the spider to blend with its immediate surroundings. Fifth, the spider may choose to retaliate by trying to bite the simulated “enemy” (e.g., an approaching pencil), but this happens only very rarely.

*Argiope mangal* also displays a peculiar behaviour when threatened. It lifts the body on its legs and at the same time raises the posterior end of the abdomen. The movement may not be a prelude to web-shaking, as some spiders have been seen shaking without a raised abdomen. In fact, after raising the abdomen, the spider may adopt one of the other defensive movements (except biting) described above — dropping off, running away, or switching side, or simply doing nothing. It is tempting to speculate that raising the abdomen is a threat posture, perhaps simulating the raised tail of a scorpion, but any resemblance between the two does require considerable amount of imagination!

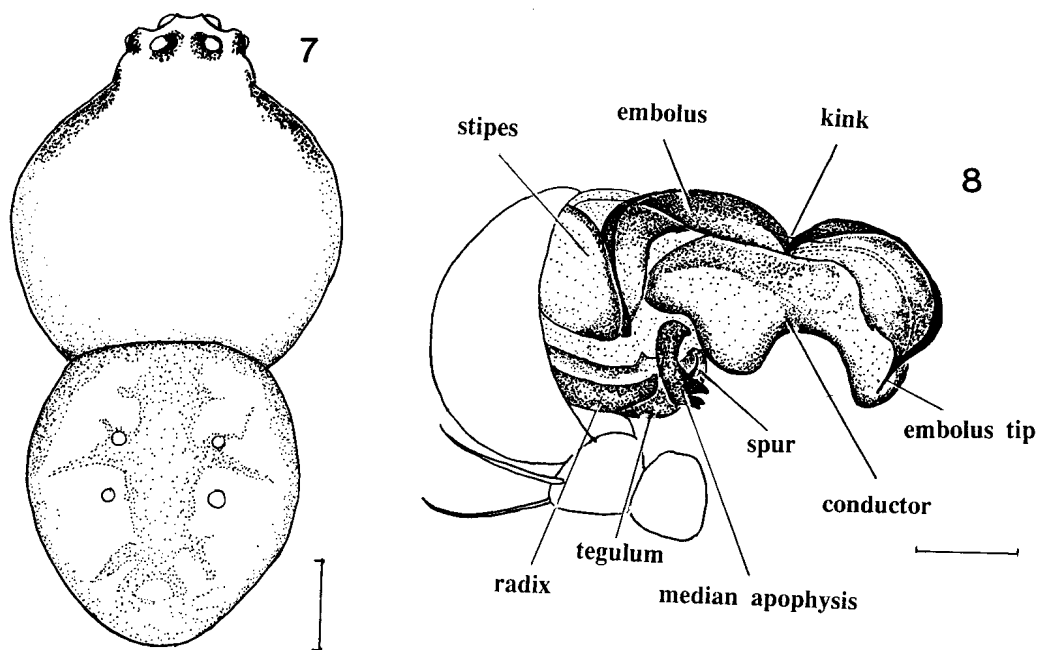


Fig. 7-8. *Argiope mangal*, new species, male : 7. Dorsal view. 8. Left palp, mesal view. Scale line : 0.5 mm.

The egg sac (Pl.1 ) approximates a polygonal (usually pentagonal) cushion with the longest side measuring 9.5-15.0 mm and the narrowest side measuring 4.0-7.0 mm (N = 6). In lateral view, it is flat on one side and bulging on the other, measuring 4.5-5.5 mm in thickness. It is papery in texture, the flat side is uniformly greenish while the bulging side is white, but heavily laced with green silk. The egg sac is fastened on 3-5 strong threads and numerous finer strands of silk stretched between branches or over a single leaf. Some egg sacs are fastened by numerous fine threads under overhanging twigs or leaves. The flat side of the egg sac is invariably vertical. The distance between an egg sac and the nearest edge of a web occupied by a mature female may range from 6-23 cm (N = 4), but it remains to be ascertained whether the nearest female is indeed the mother. One to three egg sacs may be located within the immediate vicinity of a mature female. In some cases, egg sacs may be found with no mature females in sight. Newly hatched spiderlings are greyish, white anteriorly at the abdomen and with two broken transverse bands in the middle. Upon hatching, they collectively spin either a sheet or a tangle of "nursery" web above the egg sac before they eventually disperse. (Duration in "nursery" web not observed.)

**Distribution.** - The spider is not known outside Singapore.

**Etymology.** - The specific name is a noun used in apposition, derived from the technical term for the mangrove ecosystem.

### ***Cyclosa Menge, 1866***

*Cyclosa* species characteristically decorate their orb webs with debris arranged linearly or in clumps on the web. A string of egg sacs arranged on a radius or along the diameter may also be added to the web. In some cases, the web may be further decorated with a stabilimentum of thickened silky lines or concentric loops. The most obvious structural characteristic of *Cyclosa* is the U-shaped groove demarcating the swollen cephalic region from the rest of the carapace (Fig. 9). The posterior median eyes are close to each other. Other distinguishing features of the genus are given by Levi (1977). Eight species occur in Singapore - *C. bifida* (Doleschall), *C. confraga* (Thorell), *C. insulana* (Costa), *C. micula* (Thorell), *C. mulmeinensis* (Thorell) and three undetermined *Cyclosa* species.

### ***Cyclosa mulmeinensis* (Thorell, 1887)**

(Figs. 9-12)

**Materials examined.** - Singapore - 1 female, tree foliage 5 m from water edge, Upper Peirce Reservoir, (22.v.1983); 1 female, Bukit Timah Hill, (17.iv.1987); 1 female, landward edge of mangrove, Lim Chu Kang Road, (22.ii.1988); 1 female, same locality, (10.xi.1990); 2 females, same locality, (8.iii.1991). Malaysia - 1 female, garden hedges, Pulau, Johor, (18.i.1986). Thailand - 1 imm. female, vegetation near rocky beach, Coral Island near Phuket, Southern Thailand; 1 female, wasteland near beach, Koh Mun Khlang Island, Gulf of Siam, (28.xii.1989).

**Diagnosis.** - This species is similar to *C. quavasea* Roberts from Aldabra and *C. quinqueguttata* from Burma in having a pair of conical humps on the dorsum of a globose abdomen. However, only *C. mulmeinensis* has a flat scape which almost covers the entire epigyne. Diagnostic drawings are available in Chrysanthus (1961:203, fig. 34-36, female), Tikader (1982: 187, fig. 356-360, female) and Roberts (1983: 260, fig. 155-157, male, female). Illustrations in colour



are provided by Yaginuma (1986: 121, fig. 64.5, female) and Chikuni (1989: 219, pl. 85, fig. 71, female).

**Natural History.** - Although the spider can be found inland, and some have even been collected at 1,000 meters above sea level (Sherriffs, 1919), this species is often associated with aquatic environments, living for instance near reservoirs or beaches. In mangroves, it lives among the vegetation near the high water mark. The web of mature females measures 4.5 - 6.0 cm in diameter. Egg sacs, white in colour, are placed, in a single row like a string of beads, along a radial line which passes through a free sector at the upper part of the web. As many as 7 egg sacs may be found in one string. The spider sits at the centre of the web with legs retracted, thus achieving the effect of simulating the last bead in the chain. Webs without egg sacs do not have a free sector. In this case, the spider places pellets of debris along a vertical line above and below the hub on which it sits, thereby presenting itself as another pellet in the same chain.

**Distribution.** - A widespread species ranging from Africa to Japan and Papua New Guinea.

### ***Cyrtophora* Simon, 1864**

*Cyrtophora* species build a highly modified orb web in the form of a finely-meshed, non-adhesive dome. The dome is suspended in a barrier web in the form of a three-dimensional tangle. Unlike most araneids, they do not remake their web everyday. Their webs are durable structures that may last several weeks. The abdomen of *Cyrtophora* tends to be high with the anterior end overhanging the cephalothorax. The embolus of the male palp is enclosed in the conductor. The eight species found in Singapore can be separated into three groups as follows:

- a. Species without any abdominal humps or tubercles : *C. beccarii* (Thorell), *C. exanthematica* (Doleschall), *C. eczematica* (Thorell);
- b. Species with two abdominal tubercles : *C. moluccensis* (Doleschall), *C. unicolor* (Doleschall), *C. cylindroides* (Walckenaer);
- c. Species with four abdominal tubercles : *C. cicatrosa* (Stoliczka), *C. citricola* (Forskal).

The presence of *C. eczematica* and *C. citricola* in Singapore was recorded by Workman (1896), but there have been no recent records.

### ***Cyrtophora beccarii* (Thorell, 1878)**

(Figs. 13-14)

**Materials examined.** - Singapore - 2 females, rubber estate along Lorong Kerepek, off Mandai Road, (15.ii.1976); 1 female, same locality, (16.iv.1976); 2 females, garden at Tanjong Irau near Sungei Seletar (20.ii.1985); 1 female, among mangrove vegetation, Sungei Seletar (17.iii.1985); 1 female, wasteland fringing mangrove, northern end of Lim Chu Kang Road (25.iii.1989).

**Diagnosis.** - The abdomen is white and hairy unlike *C. exanthematica*, the posterior tip of the abdomen is smoothly rounded and not bifid. An illustrated description of the spider is given by Chrysanthus (1960: 25, fig. 9-13, male, female).

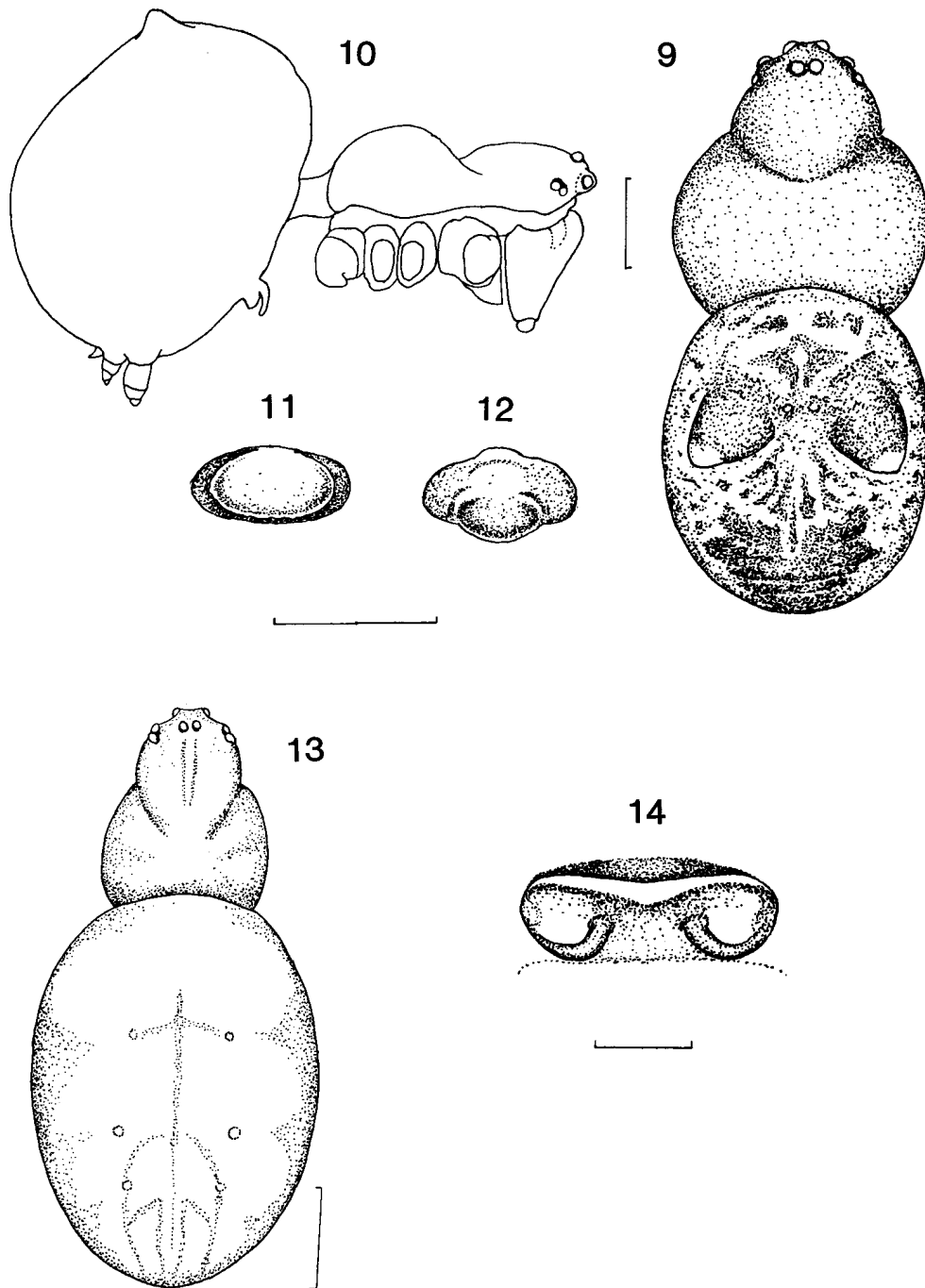


Fig. 9-12. *Cyclosa mulmeinensis* (Thorell) female : 9. Dorsal view. 10. Lateral view. 11. Epigyne with scape intact. 12. Epigyne with scape removed. Scale line : 0.5 mm. Fig. 13-14. *Cyrtophora beccarii* (Thorell) female : 13. Dorsal View. 14. Epigyne. Scale line : 1.0 mm (Fig. 13), 0.25 mm (Fig. 14).

**Natural History.** - The spider lives well into the seaward edge of the mangrove forest, but can also be found inland, e.g., among bushes along rural paths. The web has been described by Workman (1896) and photographed by Koh (1989). The spider is nocturnal and hides in the silken tube within the web during the day. It often drops out of the tube whenever it is disturbed and "plays dead" by retracting all legs close to the body and remaining immobile.

**Distribution.** - From Malaysia to Papua New Guinea and Polynesia.

***Cyrtophora moluccensis* (Doleschall, 1857)**

(Figs. 15-17)

**Materials examined.** - Singapore - 1 female, edge of secondary forest, Buona Vista Road, (20.ii.1983); 1 female, wasteland fringing mangrove, Lim Chu Kang Road, (25.iii.1989); 1 female, same locality, (28.i.1991).

**Diagnosis.** - *C. moluccensis* differs from other Southeast Asian *Cyrtophora* species with a pair of abdominal tubercles by its elaborate pattern and the characteristic shape of the median septum of its epigyne (Fig. 17). Colour illustrations of the spider are given by Clyne (1969: 135, fig. 164-165, male, female), Yaginuma (1986: 117, pl. 81, fig. 62.1, male, female) and Chikuni (1989: 214, pl. 81, fig. 53, male, female). Description and drawings are also provided by Chrysanthus (1959: 199, fig. 1, 9, 30, female), Tikader (1982: 172, fig. 326-330, female) and Davies (1988: 320, pl. 42, male, female).

**Natural History.** - *C. moluccensis* is often associated with open, disturbed habitat from coastal areas (Marples, 1955) to the mountainous interior (Lubin, 1980). In Singapore, it can be found at the edges of secondary forests and landward fringes of mangroves. This species has a tendency to congregate, and a single "communal web" can cover an area of 15 m<sup>2</sup> and accommodate more than 400 individuals, with close to 50 adults (Berry, 1987). However, those in Singapore mangroves build only solitary webs, each measuring up to 150 cm in height, with a dome 60 cm across in diameter. Four to five adults may live within 1-3 meters from one another, but they have not been seen forming colonies with shared structural threads in Singapore. However, spiderlings of *C. moluccensis* do make their little tents within the barrier web of the presumed mother. Some *C. moluccensis* webs may also host *Argyrodes miniaceus* and spiderlings of two other species of unidentified araneids which make orb webs within the upper tangle. Other aspects of *C. moluccensis* biology have been studied in detail by Lubin (1974, 1980) and Berry (1987).

**Distribution.** - This is a widespread species which ranges from India to Japan and Australia.

***Cyrtophora cicatrosa* (Stoliczka, 1869)**

(Figs. 18-19)

**Materials examined.** - Singapore - 1 female, wasteland fringing mangrove, Sungei Seletar, (20.ii.1985); 1 female, among mangrove foliage, Sungei Seletar, (7.vii.1985).

**Diagnosis.** - *C. cicatrosa* has four abdominal tubercles but can be separated from *C. citricola* (Forsk.) by the absence of a bifid caudal hump. Diagnostic drawings of the species are given

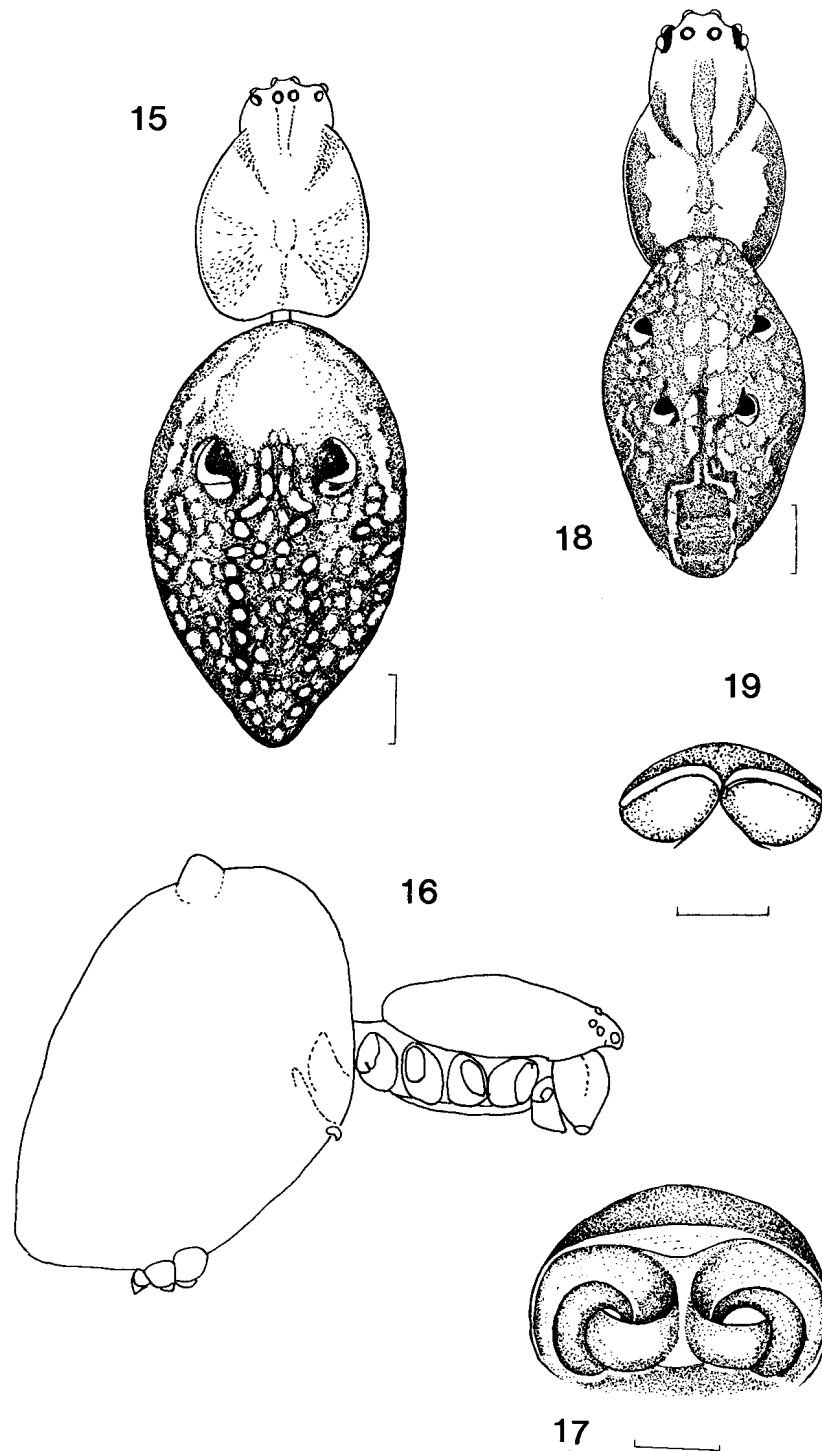


Fig. 15-17. *Cyrtophora moluccensis* (Doleschall) female : 15. Dorsal view. 16. Lateral view. 17. Epigyne. Scale line : 2.0 mm (Fig. 15-16), 0.5 mm (Fig. 17). Fig. 18-19. *Cyrtophora cicatrosa* (Stoliczka) female : 18. Dorsal view. 19. Epigyne. Scale line : 0.5 mm (Fig. 18), 0.25 mm (Fig. 19).

in *Chrysanthus* (1960: 28, fig. 19-23, male, female) and *Tikader* (1982: 179, fig. 341-345, female).

**Natural History.** - This is another common and widespread *Cyrtophora* which makes occasional appearances at mangrove fringes. The egg sacs, numbering from 3 to as many as 12, are arranged in a string and are suspended vertically over the dome-shaped web. When alarmed, the spider drops readily from its web and darkens its colour to blend with the ground. Gravely (1921) has reported that the webs of *C. cicatrosa* in India are invaded by reduviid bugs of the genus *Eugubinus* which consume the eggs of the spiders.

**Distribution.** - From India and Burma to Papua New Guinea and Polynesia.

**Acknowledgements.** - I wish to thank Dr. H. Levi for confirming that *Argiope mangal* is new to science and for encouraging me to describe it. I am also grateful to Mr. David Court and Dr. Peter K. L. Ng for their advice. Associate Professor D.H. Murphy, a great teacher with a special talent for infusing his students with his wide-ranging interests (including mangrove ecology) and inspiring them to take a closer look of the world around them, gave many valuable suggestions and provided the final push to get this paper published. I therefore take great pleasure in dedicating this paper to him on the occasion of his 60th birthday.

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