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PHYLOGENETIC REVIEW OF THE GENUS *MIAGRAMMOPES (SENSU LATO)* (ARANEAE, ULOBORIDAE)

Brent D. Opell

Department of Biology
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

ABSTRACT

The genera *Miagrammopes (sensu stricto), Ranguma, Huanacauria, Mumaia,* and *Miagrammopsidis* are synonymized to reform the traditional genus *Miagrammopes.* This genus is a sister group of *Hyptiotes* and is characterized by construction of a single-line web, loss of the anterior eyes, a carapace with lateral apodemes and flexible anterior margins, a divided sternum, and a male palpus with a radix that has taken over the conductor's function. Cladistic analysis divides *Miagrammopes* into eight species groups that do not correspond to previous genera. Major patterns of diversity result from differences in eye and lateral apodeme position, thoracic region and abdominal lengths, and sternum width.

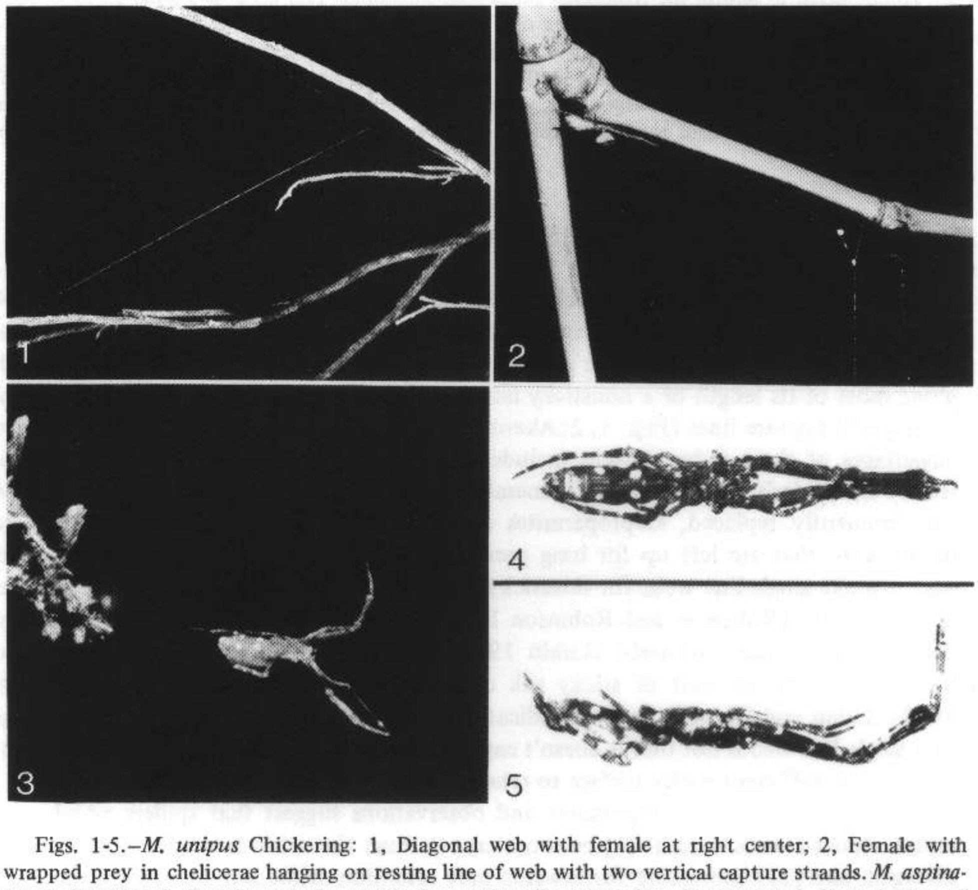
INTRODUCTION

The genus *Miagrammopes (sensu lato)* contains approximately 20 Neotropical, 14 Australian, 4 Ethiopian, and 10 Oriental species. All species that have been observed spin reduced webs consisting of either a single, usually horizontal, strand with cribellar silk along most of its length or a nonsticky horizontal resting line with one or several vertical or diagonal capture lines (Figs. 1, 2; Akerman 1932, Lubin *et al.* 1978). Possible selective advantages of these reduced webs include: (1) they are less easily seen and, therefore, reduce the spider's visibility and its vulnerability to predation; (2) because they are simple and frequently replaced, kleptoparasites do not accumulate in these webs as they do in orb-webs that are left up for long periods (Vollrath 1976); (3) nematoceran insects may mistake single-line webs for nonsticky framework or drag lines and choose them as "resting" sites (Robinson and Robinson 1976); (4) insects may have more difficulty in detecting them than orb-webs (Lubin 1974, Turnbull 1960); and (5) the number of insects captured per unit of sticky silk decreases with silk length (Lubin and Dorugl 1982). Lubin and Dorugl's findings indicate that in the tropics the primary disadvantage of a single-line web is not that it doesn't capture sufficient insects to support a spider, but that it lacks sufficient sticky surface to retain struggling insects.

Taken together, these hypotheses and observations suggest that spiders which construct reduced webs would: (1) be more cryptic than the orb-weavers from which they diverged, and (2) compensate for lowered prey retention of the web by actively monitoring or manipulating it during prey capture. Both predictions appear borne out in *Miagrammopes* and its araneid analogues, the bolas spiders (Eberhard 1980, Gertsch 1955).

In each, the spider's shape and posture contribute to its crypsis. Slender, brown or green *Miagrammopes* rest with their legs extended (Figs. 1,2), making them either eucryptic or affording protective resemblance to twigs or moss (Robinson 1969); whereas globose, light bolas spiders rest with their legs drawn in, making them eucryptic or resemble bird droppings. Despite these convergent features, the form and use of the reduced web and the spider's associated anatomical modifications differ radically in the two families. Bolas spiders swing a short silk strand with a terminal adhesive mass to catch male moths attracted by an allomone that mimics the sex attractant of female moths (Eberhard 1977); whereas *Miagrammopes* monitor and actively jerk longer, attached cribellar capture lines to reduce the likelihood of prey escaping (Lubin *et al.* 1978). *Miagrammopes* shows no evidence of pheromone production (Lubin *et al.* 1978), instead, the genus is characterized by extreme carapace modifications that appear to facilitate this active web use (Opell 1984).

It was the most striking of these carapace modifications, loss of the anterior eye row (Figs. 11-13), that led O. Pickard-Cambridge (1869) to first describe the genus *Miagrammopes* and shortly thereafter (1870) to erect the family Miagrammopidae for it. However, it was not until 1932 that Akerman first characterized the web of this genus. Thorell (1873) placed the genus in the Uloboridae, subfamily Miagrammopinae, which was later divided by Lehtinen (1967) into the genera *Miagrammopes (sensu stricto), Ranguma,*

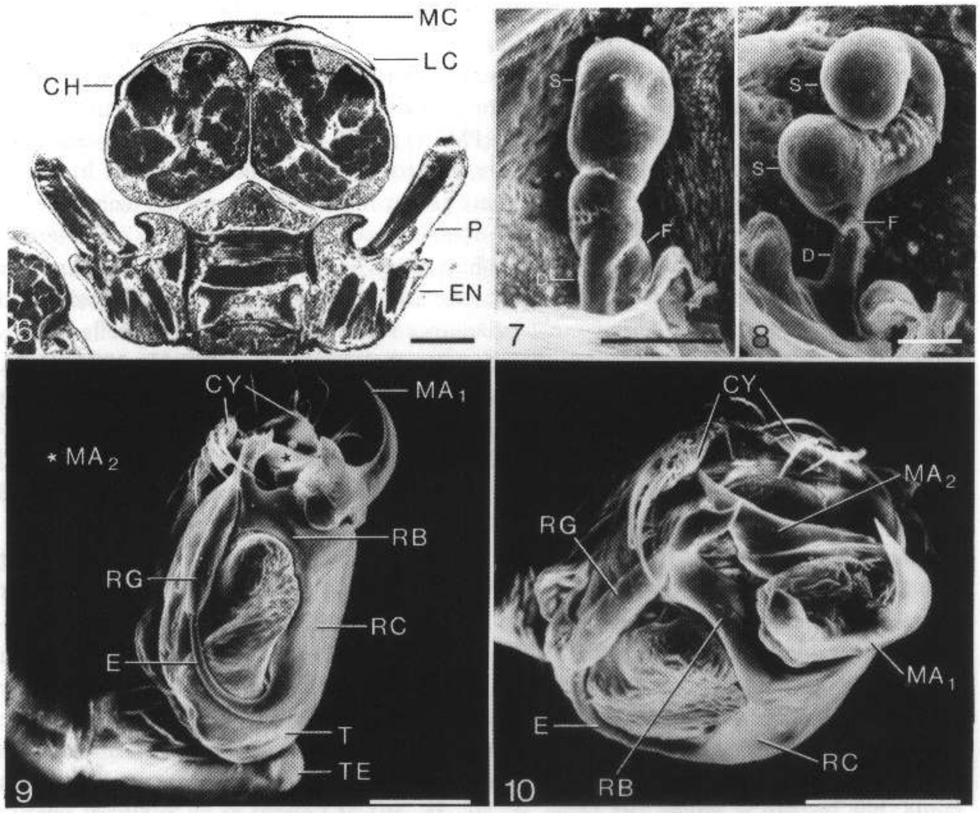


Figs. 1-5.–*M. unipus* Chickering: 1, Diagonal web with female at right center; 2, Female with wrapped prey in chelicerae hanging on resting line of web with two vertical capture strands. *M. aspinatus* Chickering: 3, Female actively monitoring capture line extending from moss; 4, Ventral view of female; 5, Lateral view of female. Cephalothorax-abdomen lengths of all specimens about 9 mm.

Huanacauria, and *Mumaia*. To this Wunderlich (1976) added *Miagrammopsidis*. In 1979 I treated the genus in its traditional, pre-1967 sense, concluding only that it was a monophyletic sister group of the Chilean genus *Sybota*, whose web was, at that time, unknown. The purpose of this paper is to reevaluate the phylogenetic placement of *Miagrammopes*, further characterize it, cladistically analyze its diversity, and give a key to its species groups. This will provide an overview of the group and its characters and establish the framework for future species and species group revisions.

GENERIC POSITION

My previous conclusion that *Miagrammopes* is a sister group of *Sybota* (Opell 1979) is incorrect. It resulted from an incomplete understanding of diversity within *Miagrammopes*, an oversight of several important characters, and unresolved details of the *Miagrammopes* male palpus. The close relationship of *Miagrammopes* and *Sybota* and of



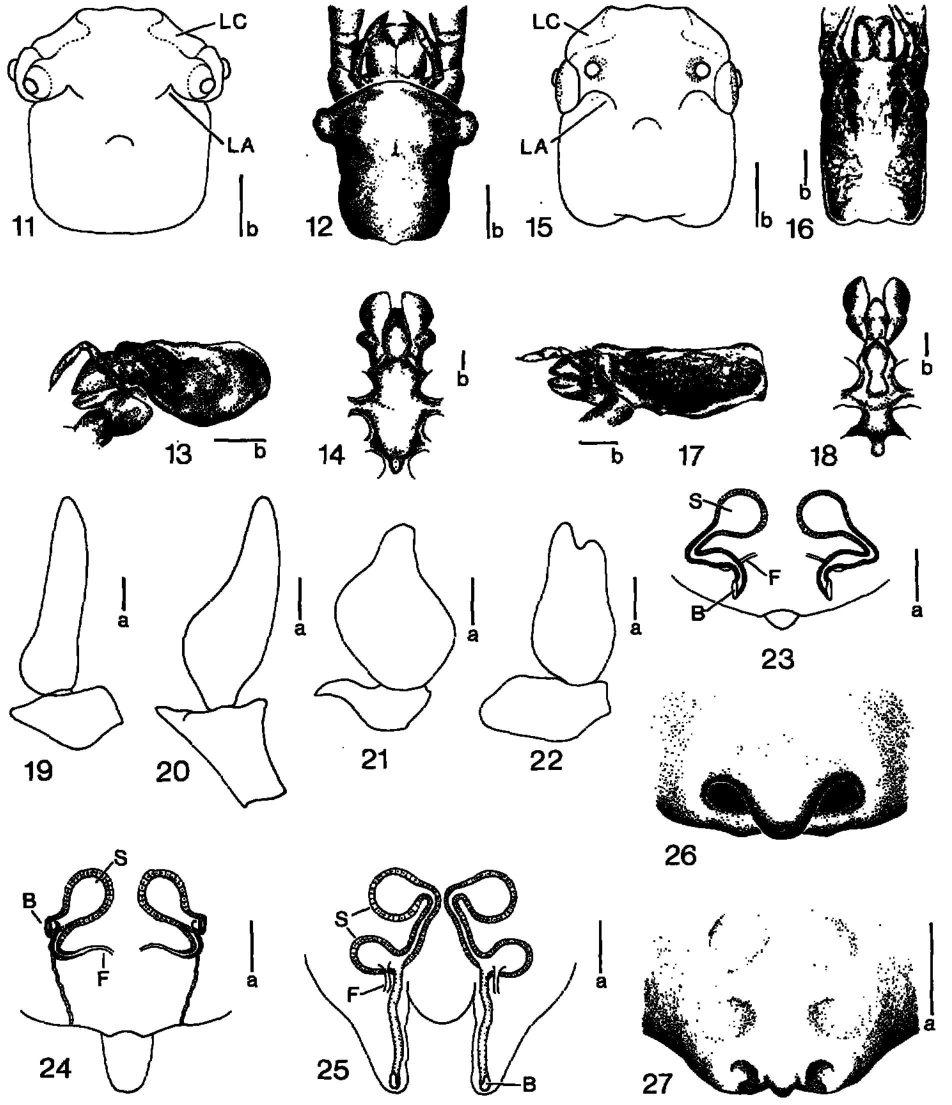
Figs. 6-10.–6, Cross section through anterior carapace region of *M. aspinatus* Chickering, showing the endites (EN), palpal bases (P), anteriorly-directed chelicerae (CH), thicker median carapace region (MC), and thin, flexible anterior lateral carapace margin (LC); 7-8, Left half of female internal genitalia of *M. simus* Chamberlin and Ivie (7) and *M. orientalis* Bösenberg and Strand (8) showing sperm ducts (D), spermathecae (S), and fertilization ducts (F); 9-10, Retrolateral (9) and apical (10) views of *M. longicaudatus* O. P.-Cambridge male left palpus showing tarsal extension (TE), tegulum (T), cymbium (CY), embolus (E), radix bridge (RB), radix corpus (RC), radix guide (RG), conductor (C), primary median apophysis (MA1), and secondary median apophysis (MA2). Scale bar in Fig. 8 represents 50 μm, all others 100 μm.

Hyptiotes and *Siratoba* has been shown to be problematic by observations of N. I. Platnick and V. D Roth, respectively (personal communications). The webs of both *Sybota* and *Siratoba* are now known to be horizontal orbs, making each a less likely sister group of a genus characterized by a reduced, vertical web. It now seems clear that *Miagrammopes* and *Hyptiotes* are sister groups, united by the following seven synapomorphies: (1) reduced web monitored and operated by a single line, (2) narrow anterior cephalic region, (3) reduced or absent anterior eyes, (4) calamistrum about three-fourths rather than half as long as metatarsus IV, (5) tarsus IV about one-third rather than half as long as metatarsus IV, (6) ventral comb macrosetae extending two-thirds rather than one-third the length of metatarsus IV (Opell 1982 a), and (7) male palpus with a broad radix lobe that has a looped reservoir at its base (Fig. 35; Opell 1979, fig. 64, Wiehle 1953, fig. 256).

Three synapomorphies unite *Miagrammopes* and *Hyptiotes* with *Polenecia:* (1) the presence of a median apophysis extension, (2) the production of a reduced, vertical web, and (3) the absence of a second instar or adult male sheet or "baby" type capture web (Lubin *et al.* 1978, Opell 1982 b, H. M. Peters, personal communication), reported for orb-weaving uloborids (Eberhard 1976, Opell 1979, Szlep 1961). Reevaluation of the palpal sclerites of other uloborids, such as *Ariston* and *Siratoba* may show the median apophysis extension to unit additional genera. A feature that is presently known only in *Hyptiotes* and *Miagrammopes* is the anterior lateral extension of the endosternite so that its arms lie near the posterior median eyes (PME's) (Opell 1984). However, this character has not been assessed in *Orinomana, Sybota, Ariston, Siratoba, Polenecia,* and *Waitkera,* because there are few representatives of these genera in collections and the technique for studying the endosternite destroys a specimen's cephalothorax. As this endosternite modification is associated with a reduced web, it may also be found in *Polenecia.* Another possible synapomorphy of *Polenecia, Hyptiotes,* and *Miagrammopes* is the deposition of cribellar silk along radii. This is most pronounced in *Polenecia* where cribellar silk is added to radii and some framework threads after their production (Wiehle 1931, H. M. Peters, personal communication). If the capture lines of *Miagrammopes* are homologues of radii, the feature is also present in this genus. The cribellar silk of *Hyptiotes* is deposited across radii, but is attached to each radius for a distance of several millimeters (Opell 1982 b, fig. 1) rather than at a single point as is typical of orb-weaving uloborids (Opell 1979, plate 1-f, g).

Miagrammopes has seven autapomorphic characters: (1) its capture web lacks radiating elements, (2) its anterior eyes have been lost, (3) weakly sclerotized, flexible, anterior lateral carapace margins are present (Fig. 3), (4) the carapace has a pair of lateral apodemes posterior or median to PME's (Figs. 11, 15), (5) the sternum is divided between the second and third, and the third and fourth coxae by narrow, transverse, weakly sclerotized, flexible regions (Figs. 14, 18), (6) a broad radix bridges over the bases of the two median apophyses to give rise to a grooved, distal extension that acts as an embolus guide (Figs. 9, 10, 33-41), and (7) the true conductor no longer functions as an embolus guide, but instead is either lost (Figs. 9, 10, 35, 36) or present as an auxiliary sclerite adjacent to the radix guide (Figs. 37, 39). Although all species studied spin reduced webs, Lubin *et al.* (1978) describe a nocturnal eggsac web of one species that contained both rudimentary nonsticky radial and cribellar spiral elements. Likewise, evidence of anterior median eyes is seen in small, dark pigment spots of some specimens. However, no cornea is present and cross sections fail to show any characteristic internal eye anatomy. Because these spots can be detected only in lightly colored specimens, they are of little use in assessing phylogeny.

Many of the autapomorphies cited above appear to facilitate use of the reduced *Miagrammopes* web. The flexible anterior lateral carapace regions and the divided sternum permit the legs to extend directly anteriorly and posteriorly. Eye tubercles and lateral carapace apodemes reflect reorganization of leg muscles to permit the first legs to extend directly forward and exert force more nearly parallel to the midsaggital body plane (Opell 1984). This latter study, and unpublished observations of Y. D. Lubin,



Figs. 11-27.–Female cephalothorax of : 11, *M. alboguttatus* F. P.-Cambridge, dorsal view; 12-13, *M. aspinatus* Chickering, dorsal (12) and lateral (13); 14, *M. bambusicola* Simon, dorsal view; 15-16, *M. auriventer* Schenkel, dorsal (15) and lateral (16) view. Female sternum of: 17, *M. aspinatus* Chickering; 18, *M. auriventer* Schenkel. Male cymbium and tibia of: 19, *M. aspinatus* Chickering; 20, *M. rubipes* Mello-Leitão; 21, *M. pinopus* Chickering; 22, *M. sexpunctatus* Simon. Internal female genitalia of: 23, *M. aspinatus* Chickering; 24, *M. simus* Chamberlin and Ivie; 25, *M. pinopus* Chickering. Epigynae of: 26, *M. aspinatus* Chickering; 27, *M. rubipes* Mello-Leitão. Scale bar "a" represents 100 μm, scale bar "b" 400 μm.

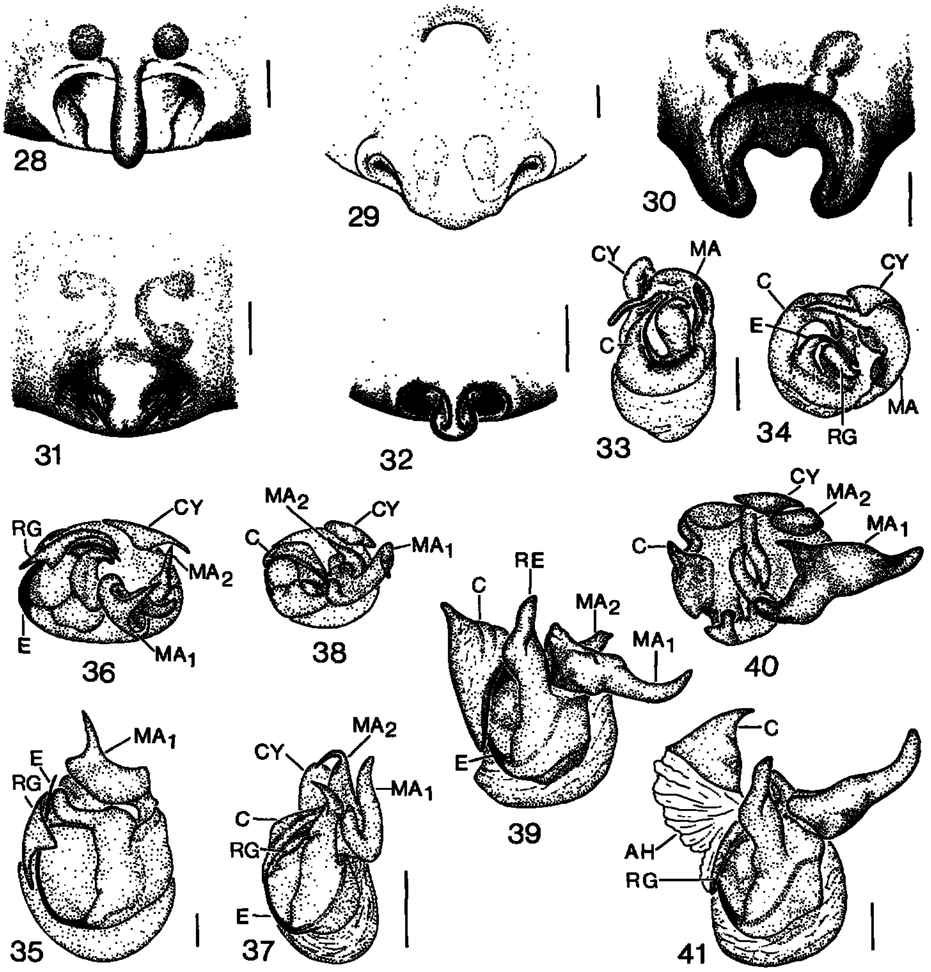
suggest that PLE tubercles also extend ventrally a spider's vision to enhance detection of approaching predators.

Details of the *Miagrammopes* male palpus are more similar to those of *Hyptiotes* and *Polenecia* than to those of *Sybota.* The palpus of each contains an embolus that arises from a broad, free, heavily sclerotized tegular extension that, in retrolateral view, extends in a clockwise direction (Figs. 9, 10). In *Sybota* a branched median apophysis and a grooved conductor arise near the base of the tegular extension (Opell 1979, plate 6-a, b). In this genus the median apophysis is surrounded by the embolus and the conductor enfolds the embolus tip. In *Hyptiotes* (Opell 1979, plate 4) and *Miagrammopes* (Figs. 9, 10, 35, 36) a broad radix extends from the inner surface of the tegular extension at the point where it narrows abruptly to form the embolus. A narrower radix is found in many other uloborids (Opell 1979), but, unlike those of *Hyptiotes* and *Miagrammopes,* these do not have a reservoir loop at their bases. In *Miagrammopes* the radix tip forms a proximally-directed distal extension that serves to guide the embolus. In most species this enfolds at least half of the embolus' length (Fig. 10), although in *M. flavus* (Fig. 33, 34), the groove is restricted to the radix tip. The radix guide has taken over the true conductor's function, allowing the latter sclerite to assume a new function or to be lost. In members of the *aspinatus, rubipes, simus* (in part), and *brevior* species groups the conductor is present as an apparently vestigial, soft sclerite appressed either to the conductor or to the palp's posterior surface (Figs. 37, 38). In *M. bambusicola* and some members of the *simus* species group, the more heavily sclerotized conductor is borne on an apical hematodocha which, when artificially (osmotically) expanded, moves the sclerite apically and anteriorly (Figs. 39-41). In these species, the conductor probably inserts under a narrow epigynal rim (Fig. 29) and, in this way, may aid in coupling or alignment of the male palpus. Although other *Miagrammopes* species have epigynal rims (Fig. 30), only species with an expandible conductor have the rim situated so far anteriorly. In members of the *animotus, biroi,* and *orientalis* species groups the conductor appears to have been lost (Figs. 9, 10, 35, 36). The radix guide often has a pointed, grooved apical extension (Figs. 9, 10) and in some species the radix bridge region bears a pointed or cupped distal extension (Figs. 37, 39; Opell 1979, plate 5 b-d). At the apex of the palpus are two sclerites, a more retrolateral one previously termed median apophysis 1, and a more prolateral one termed median apophysis 2 (Opell 1979). These are homologous with the median apophysis extension and median apophysis (median apophysis spur), respectively, of *Hyptiotes* (Opell 1979, plate 4). Because the shapes and apparent specific functions of these sclerites differ between the two genera as well as within *Miagrammopes,* they will be referred to only as primary and secondary median apophyses. Contrary to my previous conclusions (Opell 1979), *Hyptiotes* and *Miagrammopes* both have a middle haematodocha, it just isn't very large or expandible in many members of these genera.

The entelegyne female genitalia of *Miagrammopes* are simple, both externally and internally. Like *Ariston, Polenecia, Siratoba,* and *Hyptiotes* many have a short, posteriorly-directed median scape with a concave dorsal surface. In some this forms a rim which may either be free (Fig. 26) or fused with lateral lobes to set off a deep posterior, median groove in whose lateral recesses bursal openings are found (Fig. 30). In other species this rim bears a prominent scape that extends over more anteriorly situated bursae (Fig. 28). Several Oriental and Australian species lack an obvious scape and the bursae are found either at the posterior of the epigynum in a configuration similar to that shown in Fig. 29, but without an anterior rim or within paired crypts that have migrated anteriorly, forming a median partition between the bursae (Figs. 31, 32). The internal genitalia of many species contain two pairs of spermathecae with sperm ducts connected at the narrow region separating them and fertilization ducts issuing from the median surface of the posterior pair (Figs. 8, 25). I examined trypsin-cleaned genitalia of three species under the scanning electron microscope. Large surface pits that apparently denote the insertion of secretory cells (Opell 1983) were present only in the region of sperm duct attachment and not on the spermathecae themselves. In species with only a single pair of spermathecae (Figs. 7, 24) or with one large and one small pair (Fig. 23), these pits are situated near the origin of the fertilization duct. In the *brevior* species group, sperm ducts are long and convoluted, in all other species they are short and curved (Figs. 24, 25).

GENERIC DIVERSITY AND CONCLUSIONS

The cladogram presented in Fig. 42 includes the characters whose states can be distinguished and whose polarity can be established by outgroup comparison with *Hyptiotes*.



Figs. 28-41.—Epigynae of: 28, *M. simus* Chamberlin and Ivie; 29, *M. zenzesi* Mello-Leitão; 30, *M. cubanus* Banks; 31, *M. sexpunctatus* Simon; 32, *M. biroi* Kulczynski. Male palpi of: 33-34, *M. flavus* Wunderlich, retrolateral (33) and apical (34) views; 35-36, *M. biroi* Kulczynski, retrolateral (35) and apical (36) views; 37-38, *M. aspinatus* Chickering, retrolateral (37) and apical (38) views; 39-41, *M. zenzesi* Mello-Leitão, retrolateral (39), apical (40), and retrolateral expanded (41) views. All scale bars represent 100 μm.

Table 1.—Characters used in the cladistic analysis of *Miagrammopes*. l = length, w = width, s = separation; CR = cribellum, EF = epigastric furrow, PCW = posterior carapace width, PLE = posterior lateral eyes, PME = posterior median eyes.

CHARACTER	PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Female Sternum I (l/w)	Wide (≤ 1.60)	Narrow (2.30-3.09)
2. Female Abdomen (EF-CR/PCW)	Short (1.40-1.80)	Long (2.14-3.90)
3. Eye Curvature	Recurved	a. Straight b. Procurved
4. Cymbium Length (l/w)	Long (1.80-3.00)	Short (≤ 1.60)
5. Thoracic Region (l/PCW)	Short (♂ 0.71) (♀ 0.80)	Long (♂ 0.85-1.00) (♀ 0.90-1.22)
6. Conductor	Present	Absent
7. PME Separation (PME s/PCW)	Small (♂ ≤ 0.53) (♀ ≤ 0.64)	Great (♂ 0.67-0.92) (♀ 0.76-0.98)
8. Lateral Apodeme	Behind PME's	Between PME's
9. Median Epigynal Projection	Present	Absent
10. Cymbial Tip	Narrow, Pointed	Broad, Bifurcate
11. PLE Tubercles (PLE s/PCW)	Low (1.03-1.13)	High (1.20-1.24)
12. Epigynal Ducts	Simple	Coiled
13. Lateral Epigynal Lobes	Absent	Present
14. Female Bursae	Small or Posterior	Deeply Indented to Form a Median Ridge

Species groups take their names from common or typical species and in this paper are not treated as formalized taxa. The analysis is based on 13 double- and one triple-state characters that together require a minimum of 15 evolutionary steps. The cladogram requires 19 steps, with one extra step required to explain the apomorphic state of character 2 in some species of the *simus* group, two required to explain apomorphic states of character 4 in the *bambusicola* and some species of the *simus* group, and one required to explain the apomorphic state of character 11 in the *rubipes* group.

Although some characters used in the cladistic analysis are specified by ratios, most can be assessed without taking measurements. For example, the tubercles of widely spaced PME's (character 7) are confluent with posterior lateral eye (PLE) tubercles, and a long thoracic region (character 5) has a length about two rather than one times that of the cephalic region. In establishing ratios to more precisely describe character states, some commonly used reference measurements proved unsatisfactory. Carapace length and maximum width could not be used because length of the post-thoracic-groove carapace region and prominence of PLE tubercles were themselves characters used in the analysis. Instead, I used carapace width taken just posterior to the PLE tubercles as a standard by which to divide most distance measurements to produce ratios presented in Table 1. An eye row was considered procurved if a line across the PME's anterior margins passed through the center or posterior half of the PLE's and recurved if a line across the PME's posterior margins passed through the center or anterior half of the PLE's.

More characters support the separation and subsequent division of the *brevior-orientalis* branch than the *bambusicola-simus* branch (Fig. 42). No synapomorphy unites the *bambusicola* group with the *aspinatus-simus* branch and the *aspinatus* group is united to the *rubipes-simus* branch only by a change in eye row curvature. Because a straight eye row is intermediate between recurved and procurved eye rows, I consider the straight eye row of the *aspinatus* group as a feature uniting it with the *rubipes-simus* branch. However, if procurved and straight eye rows are considered only alternate apomorphic states, *aspinatus* also lacks a synapomorphy that would unite it with the *rubipes-simus* branch. The clearest synapomorphies in the *bambusicola-simus* branch are changes in PME and apodeme position (characters 3, 7, 8). Because these characters appear to be associated with reorganization of cephalothoracic musculature (Opell 1984), changes in their states may be associated and the possibility of their convergence may therefore be greater than at first seems likely.

Most of the species groups defined by the cladistic analysis comply with the common usage of a species group to contain spider species with similar genitalic patterns. The only exception is the *simus* group. Here the female genitalia may have either a median rim (Fig. 29) or a rim with a central scape of varying lengths (Fig. 28). When a scape is present the bursae are situated anteriorly in a broad, common depression (Fig. 28). When only a rim is present the bursae are situated posterior laterally (Fig. 29).

Cephalothoracic features are important both in characterizing the genus *Miagrammopes* and in helping to depict its diversity. Almost as many cephalothoracic features are used in the cladogram as male and female genitalic characters combined, and a disproportionate number of the former delineate more inclusive splits. The most strikingly different kinds of *Miagrammopes* are those of the *rubipes* and *simus* groups which have undergone major ocular and apodeme changes, and those of the *animotus*, *biroi*, and *orientalis* groups which have narrow sternae and elongate carapaces and abdomens. This suggests that changes in the first two species groups may be largely functional, whereas changes in the latter may serve primarily to enhance crypsis. Unfortunately, the only species whose behavior has been studied in detail (Lubin *et al.* 1978) belong to the *aspinatus*, *rubipes*, and *simus* groups.

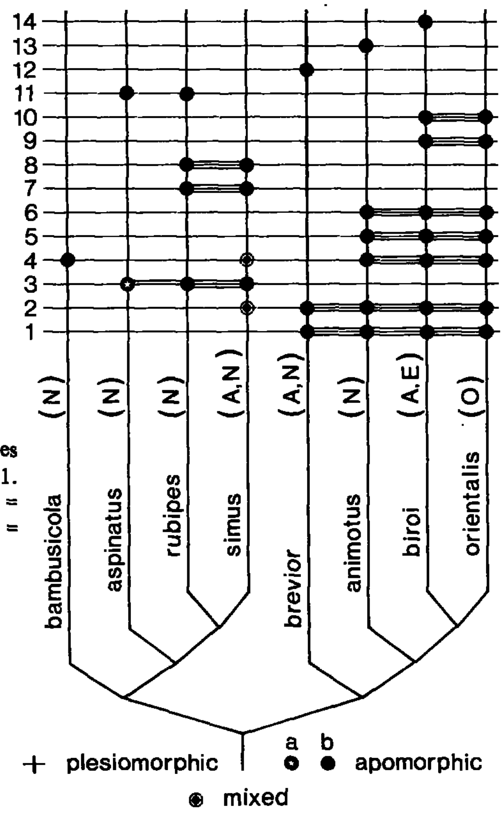


Fig. 42.–Cladogram of *Miagrammopes* species groups using characters presented in Table 1. Known distributions are given in parentheses. A = Australian, E = Ethiopian, N = Neotropical, O = Oriental.

CONCLUSIONS AND CLASSIFICATION

Although *Miagrammopes* is a most diverse genus, this study shows it to be a monophyletic sister group of *Hyptiotes*, and therefore, properly considered one rather than five genera. For this reason, I synonymize below the five genera into which *Miagrammopes* was formerly divided and comment briefly on correspondence between these and the species groups separated by the cladogram. This is followed by a key to the species groups that will serve as a transition between this study and subsequent revisionary work on *Miagrammopes* species.

Miagrammopes O. Pickard-Cambridge

Miagrammopes O. Pickard-Cambridge 1869:400. Type species by virtue of first listing in publication: *M. thwaitesi* O. Pickard-Cambridge, 1869. The type species of this genus belongs to the *biroi* group.

Ranguma Lehtinen 1967:262, 395. Type species by original designation, *Miagrammopes similis* Kulczynski 1908. NEW SYNONYMY. The type species of this genus belong to the *biroi* group.

Huanacauria Lehtinen 1967:239, 395. Type species by original designation *Miagrammopes bambusicola* Simon 1892. NEW SYNONYMY. This genus contains the *bambusicola* group and two other species whose types are either lost or immature.

Mumaia Lehtinen 1967:250, 395. Type species by original designation, *Miagrammopes corticeus* Simon 1892. NEW SYNONYMY. The type species of this genus belongs to the *animotus* group; Lehtinen also assigned to this genus some species of the *simus* group.

Miagrammopsidis Wunderlich 1976:116. Type species by original designation and monotypy *Miagrammopsidis flavus* Wunderlich 1976. NEW SYNONYMY. The type species of this genus belongs to the *simus* group.

KEY TO SPECIES GROUPS

1. Eye row procurved, PME's widely separated, their tubercles confluent with those of PLE's (Fig. 11), lateral apodemes between PME's 2
   Eye row straight (Fig. 12) or recurved (Figs. 15, 16), PME and PLE tubercles not confluent, lateral apodemes posterior to PME's 3
2. Prominent PLE tubercles present (Fig. 12), epigynum with a shallow median depression (Fig. 27), but without a rim or scape; palp with a radix guide that encloses about four-fifths of embolus, but lacks a conspicuous conductor. . . . .*rubipes*
   Low PLE tubercles (Fig. 11), epigynum with either a median rim or scape (Figs. 28, 29); radix guide encloses only about half of embolus (Fig. 37) or, if more, a large conductor is present (Figs. 39,41). . . . .*simus*
3. Eye row straight, PLE tubercles well-developed (Fig. 12), epigynum with a median scape (Fig. 26), male palpus with slender cymbium (Figs. 19, 20). . . . . *aspinatus*
   Eye row recurved, PLE tubercles small (Figs. 15, 16), epigynum with a central rim (Fig. 30) or ridge (Figs. 31, 32) or lacking a central projection, cymbium about half as wide as long (Figs. 21, 22). 4
4. Length of first division of female sternum about one-third width (Fig. 14), male palpus without tibial extension . . . . *bambusicola*
   Length of first division of female sternum no more than one-quarter width (Fig. 18), male palpus with long tibial extension (Figs. 21, 22) or if tibial extension absent, thorax at least 0.85 posterior carapace width (Fig. 16) .5

5. Thoracic region short (Fig. 15). . . . . *brevior*
   Thoracic region long (Fig. 16) 6
6. Epigynum with median rim or a very narrow flange and lateral lobes (Fig. 30), cymbium of male palp pointed (Fig. 21) . . . . *animotus*
   Epigynum with central mound or deep lateral bursae (Figs. 31, 32), but no median rim or lateral lobes; cymbium tip bifurcate (Fig. 22) 7
7. Epigynum with deeply recessed bursae that often set off a median ridge (Figs. 31-32), male palpus with a broad primary median apophysis that bears a central spike, tip of radix guide usually lacks a long, pointed tip (Figs. 35, 36). . . . . *biroi*
   Epigynum with a central mound and narrow, broadly separated, diagonal bursae similar to Fig. 29, but without anterior median rim; male palpus with a long, anteriorly directed, sickle shaped primary median apophysis, radix guide usually with a long, pointed tip (Figs. 9, 10) . . . . *orientalis*

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LITERATURE CITED

Akerman, C. 1932. On the spider *Miagrammopes* sp. which constructs a single-line snare. Ann. Natal Mus., 7:137-43.

Eberhard, W. G. 1976. The webs of newly emerged *Uloborus diversus* and of a male *Uloborus* sp. (Araneae, Uloboridae). J. Arachnol., 4:210-16.

Eberhard, W. G. 1977. Aggressive chemical mimicry by a bolas spider. Science, 198:1173-75.

Eberhard, W. G. 1980. The natural history and behavior of the bolas spider, *Mastophora dizzydeani* sp. n. (Araneae). Psyche, 87:143-69.

Gertsch, W. J. 1955. The North American bolas spiders of the genera *Mastophora* and *Agathostichus*. Bull. Mus. Nat. Hist., 106:221-54.

Lehtinen, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool., Fennici, 4:199-468.

Lubin, Y. D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zool. J. Linn. Soc. London, 54:321-39.

Lubin, Y. D., W. G. Eberhard, and G. G. Montgomery. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche, 85:1-23.

Lubin, Y. D. and S. Dorugl. 1982. Effectiveness of single-thread webs as insect traps: sticky trap models. Bull. British Arachnol. Soc., 5:399-407.

Opell, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. Comp. Zool., 148:443-549.

Opell, B. D. 1982a. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). Bull. British Arachnol. Soc., 5:338-43.

Opell, B. D. 1982b. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). J. Arachnol., 10:185-91.

Opell, B. D. 1983. The female genitalia of *Hyptiotes cavatus* (Araneae: Uloboridae). Trans. Am. Micros. Soc., 102:97-104.

Opell, B. D. 1984. Comparison of carapace features in the family Uloboridae (Araneae). J. Arachnol., 12:105-113.

Pickard-Cambridge, O. 1869. Descriptions and sketches of two new species of Araneida, with characters of a New Genus. J. Linn. Soc. London, 10:398-405.

Pickard-Cambridge, O. 1870. [1871]. Arachnida. Zool. Rec., 7:207-24.

Robinson, M. H. 1969. Defense against visually hunting predators. Evol. Biol., 3:225-59.

Robinson, M. H. and B. Robinson. 1976. A tipulid associated with spider webs in Papua New Guinea. Entomol. Mon. Mag., 112:1-3.

Szlep, R. 1961. Developmental changes in web-spinning instinct of Uloboridae: construction of the primary-type web. Behaviour, 27:60-70.

Thorell, T. 1873. Remarks on synonyms of European spiders, 4. Upsala [Uppsalla], pp. 375-645.

Turnbull, A. L. 1960. The prey of the spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). Canadian J. Zool., 38:859-73.

Vollrath, F. 1976. Konkurrenzvermeidung bei tropischen kleptoparasitischen Haubennetzspinnen der Gattung *Argyrodes* (Arachnida: Araneae: Theridiidae). Entomol. Germanica, 3: 104-08.

Wiehle, H. 1931. Neue Beiträge zur Kenntnis des Fanggeweben der Spinnen aus den Familien Argiopidae, Uloboridae, und Theridiidae. Zeits. Morph. Ökol. Tiere, 22:349-400.

Wiehle, H. 1953. Spinnentiere oder Arachnoidea (Araneae). IX: Orthognatha – Cribellatae – Haplogynae, Entelegynae. *In* Dahl, F., ed., Die Tierewelt Deutschlands, Pt. 42, Gustav Fischer, Jena, pp. 1-150.

Wunderlich, J. 1976. Spinnen aus Australien. I. Uloboridae, Theridiosomatidae und Symphytognathidae (Arachnida, Araneida). Senckenbergiana Biol., 57:113-24.

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