COMPARISON OF CARAPACE FEATURES
IN THE FAMILY ULOBORIDAE (ARANEAE)

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ABSTRACT

Cluster analyses of 51 quantified carapace features from each of 34 species representing all known uloborid genera fail to produce a consistent pattern of overall similarity. However, a minimum spanning tree and a principal axis analysis of these features shows that formation of PLE tubercles and other anterior lateral carapace changes are most responsible for explaining carapace diversity within the Uloboridae. Many of these same features are shown by discriminant analysis to be most highly correlated with web type, indicating that they are functionally linked to changes in web monitoring and use. A survey of the endosternites of *Hyptiotes*, *Miagrammopes*, and *Philoponella*, and carapace musculature of the latter two genera shows many changes in carapace form to be associated with muscle reorientation that facilitates use of a reduced orb-web. The presence of eye tubercles associated with the most extremely modified carapaces also appears to ventrally extend the spider's vision.

INTRODUCTION

Carapace modification was strongly reflected in early classifications of the family Uloboridae (O. Pickard-Cambridge 1869, Simon 1874, 1892, Dahl 1904). The subfamily Uloborinae traditionally contained orb-weavers with a generalized, pear-shaped carapace (Fig. 4); Hyptiotinae, triangle-web weavers with a broad, anteriorly narrowed carapace (Fig. 6); and Miagrammopinae, members with a rectangular carapace that bore only the four posterior eyes (Fig. 8) and were later found to construct reduced webs of only one or a few lines (Akerman 1932, Lubin et al. 1978). The number of uloborid genera has increased from an initial one per subfamily to 22 (Lehtinen 1967, Lubin et al. 1982, Opell 1979, in press a), 14 of which would fall within the traditional bounds of the Uloborinae. However, shifting emphasis from carapace form and eye arrangement to other characters such as details of male and female genitalia caused Lehtinen (1967) to establish the subfamily Tangaroinae, and me (Opell 1979) to conclude that uloborids with a generalized carapace are not monophyletic.

The purpose of this study is to quantify and compare carapace features of representatives of all known uloborid genera in order to assess the significance of carapace shape within the family. Carapace form may mirror the family's phylogeny or it may more closely reflect muscle reorientation or other functional changes associated with orb-web modification. These hypotheses do not entirely exclude one another, as the use of reduced, vertical webs is characteristic of the related genera *Polenecia*, *Hyptiotes*, and *Miagrammopes* (Opell 1979, in press b). However, modified orb-webs are constructed

by other genera (Table 1), making it possible to assess the significance of carapace shape in three ways. First, if carapace shape reflects phylogeny, then a phenogram based on overall carapace similarity should more closely resemble the family's phylogeny than a breakdown of its web types. Second, if carapace form is closely related to web type, then features most responsible for explaining carapace differences should correspond to those showing the greatest correlation with web type. Finally, a correct understanding of carapace features should permit a logical interpretation of internal cephalothoracic differences.

METHODS AND MATERIALS

Measurements were made from drawings or enlarged photographs of uloborid carapaces placed on a clear plastic sheet beneath which a large protractor was mounted. These illustrations were positioned so that a needle extending from the protractor's center passed through the intersection of the carapace's midsagittal plane and thoracic groove and so that the midsagittal plane passed through the protractor's 0- and 180-degree points. A transparent scale was placed over the illustration with its zero point inserted through the exposed needle and its distal end extending over the protractor scale. By rotating this scale the angle and distance from the thoracic groove of the carapace margin, eyes, and eye tubercles could be measured. Figure 1 presents the 51 features which were measured for each species and Table 1 the 34 species which were studied. If a feature was not present its coordinates were recorded as zeros. Distance measurements were divided by carapace length. Because males do not construct capture webs and are not known for several genera, analysis was performed only on females.

Webs reported in Table 1 were classified as orb-web (0), orb-plus-cone-webs (OC), orb-webs with a vacant sector through which a signal line passes (OS), spiralless-orb-webs with cribellar silk deposited on radii and framework threads (SO), triangle-webs (T), or single-line-webs with only one or a few capture lines (S). This was established by personal observations, by personal communications with W. G. Eberhard, R. R. Forster, Y.D. Lubin, H. M. Peters, N. I. Platnick, and V. D. Roth; and from the work of Comstock (1913), Eberhard (1969), Forster (1967), Kaston (1948), Lubin (in press), Lubin et al. (1978, 1982), Muma and Gertsch (1964), Opell (1979, 1982, 1983, in press a), Trail (1982), and Wiehle (1927, 1931).

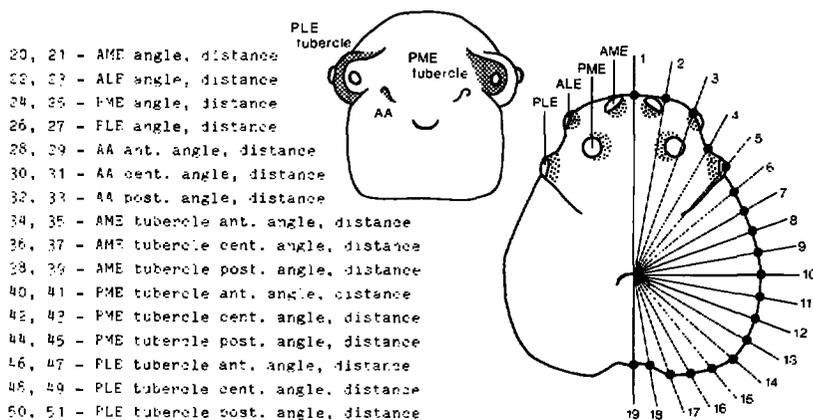|	
20, 21	— AME angle, distance
22, 23	— ALE angle, distance
24, 25	— PME angle, distance
26, 27	— PLE angle, distance
28, 29	— AA ant. angle, distance
30, 31	— AA cent. angle, distance
32, 33	— AA post. angle, distance
34, 35	— AME tubercle ant. angle, distance
36, 37	— AME tubercle cent. angle, distance
38, 39	— AME tubercle post. angle, distance
40, 41	— PME tubercle ant. angle, distance
42, 43	— PME tubercle cent. angle, distance
44, 45	— PME tubercle post. angle, distance
46, 47	— PLE tubercle ant. angle, distance
48, 49	— PLE tubercle cent. angle, distance
50, 51	— PLE tubercle post. angle, distance

Fig. 1.—Carapace features used in the cluster analysis. Features 1-19, carapace contour; 20-27, eye position; 28-33, anterior apodeme (unique to *Miagrammopes*) position; 34-51, eye tubercle positions.

Table 1.—Species included in the analysis of carapace features. O = orb-web, OC = orb-plus-cone-web, OS = orb-web with vacant sector, SO = spiralless orb-web, T = triangle-web, S = single-line-web, - = web unknown.

SPECIES	WEB TYPE	PLE ANGLE	PLE DISTANCE	PLE ANGLE X DISTANCE	PLE TUBERCLE
Waitkera waitkerensis (Chamb.)	O	29	0.55	16.0	+
Tangaroa beattyi Opell	O	27	0.46	12.4	-
Siratoba referena (M. & G.)	O	36	0.41	14.8	-
Sybota abdominalis (Nicolet)	O	41	0.48	19.7	+
Uloborus campestratus Simon	O	30	0.46	13.8	-
Uloborus glomosus (Walckenaer)	O	28	0.49	13.4	-
Octonoba octonaria (Muma)	O	30	0.48	14.4	-
Zosis geniculatus (Olivier)	O	24	0.47	11.3	-
Philoponella divisa Opell	O	18	0.54	9.7	-
Philoponella fasciata (M-L.)	O	22	0.55	12.1	-
Philoponella oweni (Chamberlin)	O	21	0.48	10.1	-
Philoponella republicana (Simon)	O	21	0.51	10.7	-
Philoponella tingena (Ch. & Iv.)	O	22	0.51	11.2	-
Uloborus albolineatus Opell	OC	30	0.38	11.4	-
Uloborus bispiralis Opell	OC	23	0.45	10.4	-
Uloborus conus Opell	OC	21	0.47	10.0	-
Conifaber parvus Opell	OC	53	0.26	13.8	-
Lubinella morobensis Opell	OS	35	0.48	16.8	+
Polenecia producta (Simon)	SO	28	0.46	12.9	-
Hyptiotes cavatus (Hentz)	T	67	0.55	36.9	+
Miagrammopes intempus (Chick)	S	69	0.55	38.0	+
Miagrammopes simus (Ch. & Iv.)	S	54	0.60	32.4	+
Miagrammopes sp.	S	45	0.48	21.6	+
Miagrammopes sp.	S	53	0.39	20.7	+
Tangaroa tahitiensis (Berland)	-	29	0.49	14.2	-
Ariston aristus Opell	-	27	0.50	13.5	-
Sybota mendozae Opell	-	32	0.49	15.7	+
Orinomana bituberculata (Keys.)	-	42	0.48	20.2	+
Uloborus metae Opell	-	27	0.41	11.1	-
Octonoba sp.	-	31	0.47	14.6	-
Zosis peruvianus (Keyserling)	-	24	0.40	9.6	-
Purumitra grammica (Simon)	-	31	0.47	14.6	-
Ponella lactescens (Mello-L.)	-	27	0.54	14.6	-
Daramuliana gibbosa (L. Koch)	-	39	0.38	14.8	-

Overall similarity of carapace features was evaluated with seven cluster analysis programs included in Rohlf et al. (1979): unweighted pair-group method using arithmetic averages, weighted pair-group method using arithmetic averages, complete linkage cluster analysis, single linkage cluster analysis, weighted pair-group method using Spearman's sums of variables, unweighted pair-group method using centroid averaging, and unweighted pair-group method using centroid averaging. This statistical series was also used to compute the minimum spanning tree of carapace features used to identify those features most important in explaining carapace differences. A principal axis analysis (verimax preliminary rotation and oblique analytical rotation) from the SAS Institute Inc. (P. O. Box 10066, Raleigh, N. C. 27605) was also used to study the relationship of carapace features. The latter statistical package also provided the stepwise discriminant analysis (generalized squared distance based on a pooled covariance matrix, prior probabilities

proportional to sample size, $p < 0.05$) used to determine the eight carapace features most highly correlated with web type. These features were then checked with an unweighted discriminant model that predicted web types of species included in the study.

Specimens used for histological study were relaxed with carbon dioxide, fixed at 20-26°C for 12-18 hours in 3% formaldehyde/3% glutaraldehyde buffered in 0.1 M sodium cacodylate buffer (pH 7.3), rinsed and stored in 0.1 M sodium carodylate buffer, dehydrated through a graded series of acetone, and embedded in Spurr's epoxy resin. Prior to examination, 1 μm thick sections made with a Sorvall JB-4 microtome were stained with 1% toluidine blue in 1% borate buffer.

Endosternites from alcohol preserved specimens were cleaned of muscle tissue with trypsin. Prior to scanning electron microscope study they were dehydrated in alcohol, critical-point-dried, and sputter-coated with gold.

RESULTS

Cluster analyses of carapace similarity produced phenograms that differed greatly both in the taxa they most closely united and in the levels at which clusters were fused. Attempts to manipulate taxa and characters failed to clarify appreciably such patterns. This lack of congruity precluded arbitrary use of one phenogram for assessing patterns of overall carapace similarity and shifted emphasis to a comparison of those character sets most important in explaining carapace shape and most highly correlated with web type.
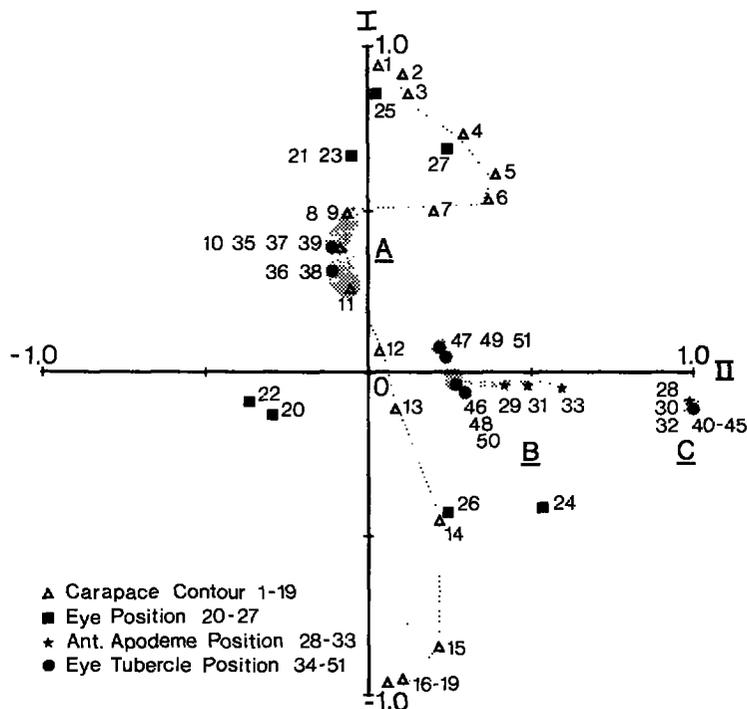

Fig. 2.—Factor analysis of carapace features. Together factors I and II explain 34% of the eigenvalues of carapace features.

Factor analysis (Fig. 2) shows three closely associated sets of nine carapace features each (shaded areas A-C). Cluster A is comprised of carapace contour points in the 70-100 degree sector and angle and distance measurements of the anterior eye tubercle. Cluster B contains distance points of the anterior apodeme and angle and distance measurements of the posterior lateral eye tubercle. Cluster C contains angle and distance measurements of the posterior median eye tubercle and angle measurements of the anterior apodeme. Clusters B and C correspond closely to the carapace features shown by a minimum spanning tree to be least correlated with other carapace features and, therefore, most important in explaining differences in carapace shape (Fig. 3). They also correspond to many of the carapace features shown by discriminant analysis to be highly correlated with web form. Arranged form greatest to least importance, these features are numbers 23, 50, 48, 22, 46, 44, 21, 37. A PLE tubercles appear only in species for which the product of PLE angle and relative distance from the thoracic groove exceeds 15.6 (Table
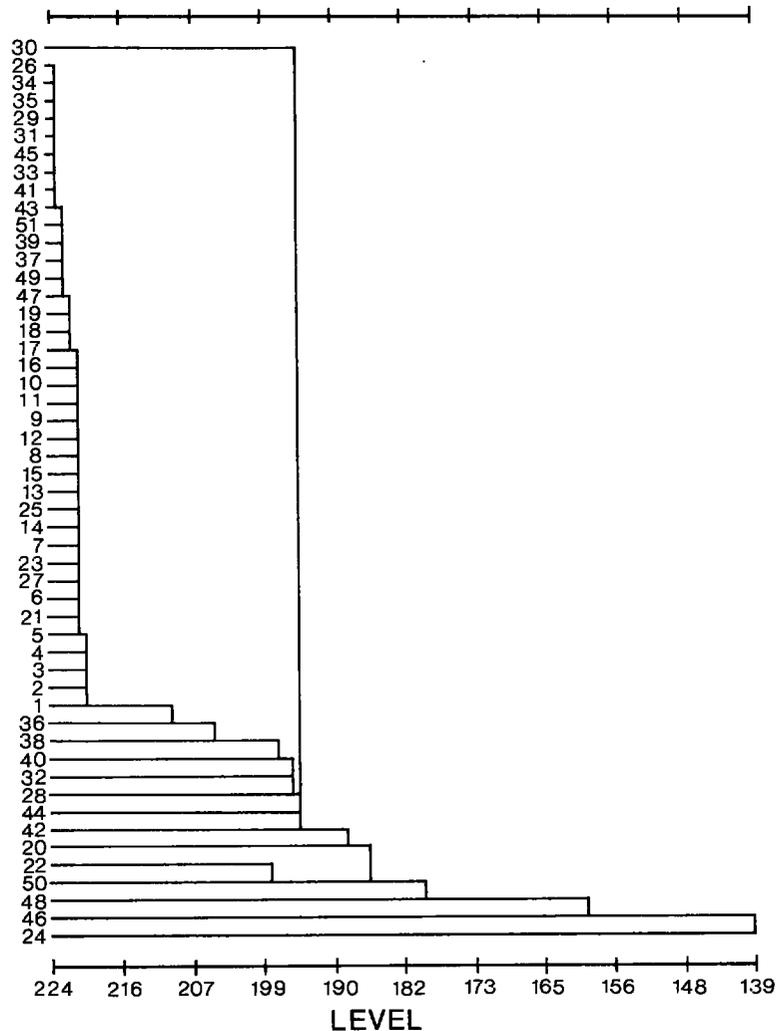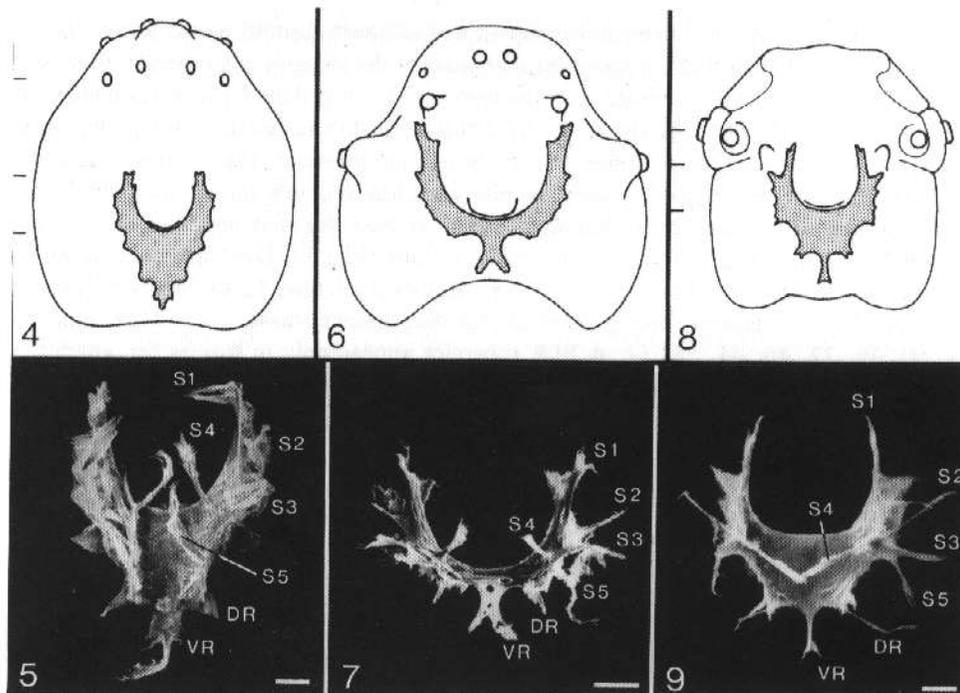

Fig. 3.—Minimum spanning tree of carapace features. Features united at higher levels are more closely correlated.

Figs. 4-9.—Dorsal views of endosternites of *Philoponella republicana* (4, 5), *Hyptiotes cavatus* (6, 7), and *Miagrammopes simus* (8, 9). S1-S5 = endosternite dorsal rays for insertions of suspensor muscles 1-5, respectively; DR = dorsal retractor muscle insertion; VR = ventral retractor muscle insertion (terminology after Whitehead and Rempel 1959). Scale lines represent 100 μm.

1). Perhaps a point is reached beyond which shape change and muscle reorganization cannot occur without the added space or strength afforded by eye tubercles.

When the eight features associated with web form are used to group species by web type, they correctly classified web form (posterior probability > 0.95) of the 22 species whose webs were known. However, the web of a subadult *Sybota* (probably *abdominalis*) photographed by N. I. Platnick after this analysis was completed produced what is probably a horizontal orb-web rather than the single-line-web predicted for it.

The conclusion that major carapace differences are strongly influenced by web type is also supported by a preliminary survey of differences in internal cephalothorax anatomy. The endosternites of *Hyptiotes cavatus* and *Miagrammopes simus*, members of genera characterized by prominent PLE tubercles, are proportionally larger and extend further forward than that of *Philoponella republicana* which lacks eye tubercles (Figs. 4-9). As the endosterno-coxalis muscles of legs I and II originate at the ventral surface of the endosternite's anterior processes (Fig. 10; Whitehead and Rempel 1959, Palmgren 1981; terminology after latter author), they too are more laterally displaced in the former two genera (Figs. 6-9) and, consequently, extend forward more nearly parallel to the midsagittal body plane than in *Philoponella* (Figs. 4-5). In the more dorsally-ventrally compressed carapace of *Miagrammopes* these muscles are situated medially to the PLE and tergo-coxalis medius and profundus muscles originate between the PME and PLE (Figs. 10, 14-16). The more posteriorly situated endosternite and more convex carapace of *Philoponella* result in the endosterno-coxalis muscles extending more obliquely anteriorly and ventrally and not passing through the ocular region (Figs. 10, 11-13). Cephalothoracic
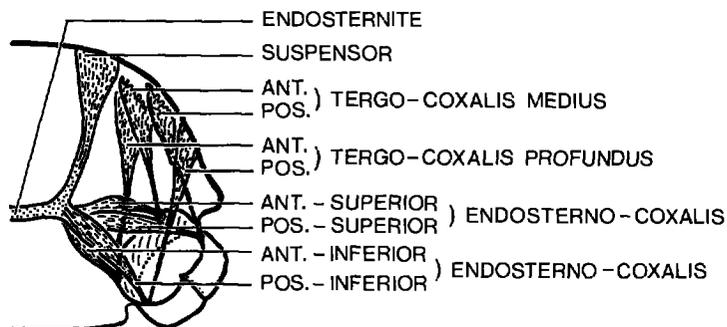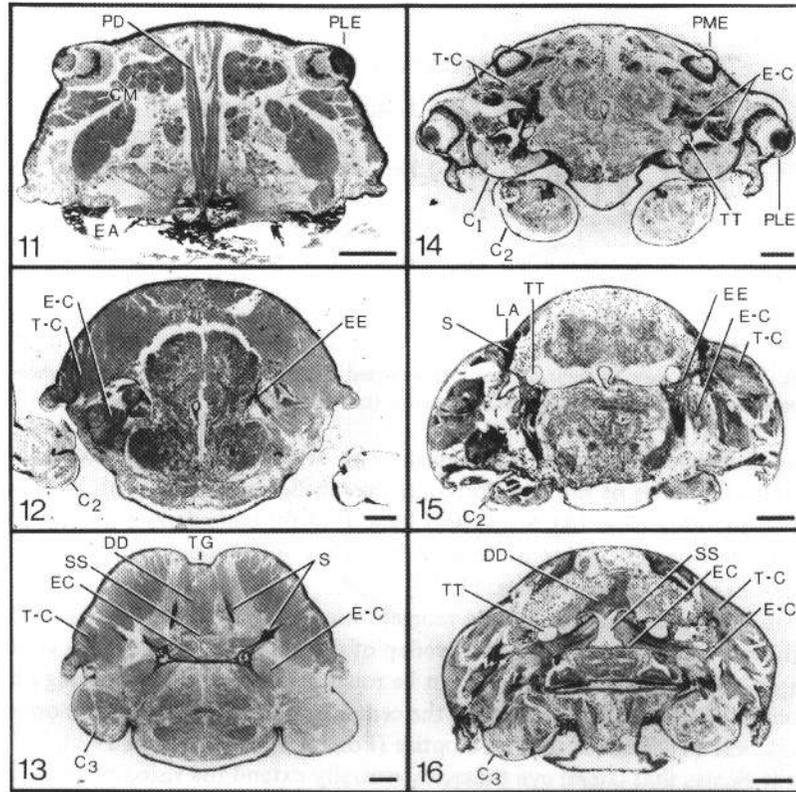
ENDOSTERNITE
SUSPENSOR
ANT.
POS.) TERGO–COXALIS MEDIUS
ANT.
POS.) TERGO–COXALIS PROFUNDUS
ANT. – SUPERIOR
POS. – SUPERIOR) ENDOSTERNO – COXALIS
ANT. – INFERIOR
POS. – INFERIOR) ENDOSTERNO – COXALIS

Fig. 10.–Posterior view of right half of a generalized spider carapace cross section showing endosternite suspensor muscle and extrinsic coxal muscles (terminology after Palmgren 1981).

shortening in *Miagrammopes* sp. may explain why origins of the tergo-coxalis muscles of leg I as well as muscles of the anteriorly-directed chelicerae are concentrated lateral and posterior to the PME (Fig. 14). Suspensors I and II of the endosternite also originate here (Fig. 9). In *P. tingena* origins of these muscles are more evenly distributed over the anterior region of the carapace (Figs. 11, 12).

In addition to providing for muscle reorganization, eye tubercles may alter the visual field of the eyes they bear or the visual overlap of these and other eyes. On a cross section photograph, the visual field of an eye can be roughly estimated by extending a line from the periphery of its retinal cells through the center of its lens. Although this only approximates a detailed analysis of the eye's optics (Forster 1982, Homann 1928, 1971, Land 1969), it indicates that lateral eye tubercles ventrally extend the vision of those uloborids in which they appear (Figs. 10, 13). The approximately 80° visual field of a *P. tingena* PLE extends ventrally to within about 61° of a sagittal plane passing through this eye, whereas the 90° visual field of a *Miagrammopes* sp. PLE extends ventrally to within about 10° of such a sagittal plane. In the latter case, this excludes from vision only the area immediately ventral to the spider.

DISCUSSION

The intermittent tugging behavior characteristic of all uloborids as they hang from a single line or monitor their webs (Eberhard 1969, Lubin in press, Lubin et al. 1978, 1982 Marples 1962, Marples and Marples 1937, Opell 1979, 1982) a) may have predisposed the group to many of the web and carapace changes described above. The fact that the first and, to a lesser extent, second legs, are responsible for this tugging may explain why most changes occur in the anterior lateral carapace region. It is in this region that muscles and endosternite suspensors associated with movement of the first two pairs of legs attach. Although web modification seems to play a major role in shaping the carapace, several other factors may also be involved. Differences in the resting postures of some genera (Opell and Eberhard, in press) may be reflected in carapace shape, since, like web monitoring, these postures involve differences in leg placement. The apparent ventral shift of the PLE's vision associated with development of an eye tubercle may also be a contributing factor. Both *Hyptiotes* and *Miagrammopes* monitor the attachment line of their reduced, vertical webs while resting on or near a twig. Here, the spider may be more vulnerable to predation, both because of its proximity to the twig and because it no

Figs. 11-13.—*Philoponella tingena:* 11, carapace cross section through PLE; 12, anterior endosternite extension; 13, anterior endosternite corpus; see lines in Fig. 4 for approximate positions.

Figs. 14-16.—*Miagrammopes* sp.: 14, carapace cross sections through PME and PLE; 15, anterior endosternite extension; 16, anterior endosternite corpus; see lines in Fig. 8 for approximate positions. C = coxae, CM = cheliceral muscles, DD = dorsal dilator of sucking stomach, E = endosternite corpus, EA = endite articulation, E-C = endosterno-coxalis muscles, EE = endosternite extension, LA = lateral apodeme, PD = posterior dilator of pharnyx, PLE = posterior lateral eye, PME = posterior median eye, S = suspensor muscle, SS = sucking stomach, T-C = tergo-coxalis muscles, TG = thoracic groove, TT = trachael trunk. Scale lines represent 100 μm.

longer hangs beneath an orb-web that can provide both protection and warning. In such a situation, more ventrally extended vision should be an advantage in predator detection.

Changes in the carapace of *Miagrammopes* exemplify extreme modifications associated with use of a modified orb-web. Here, morphological changes appear to facilitate the monitoring and jerking of one or a few lines, a behavior requiring the spider to exert force parallel to the sagittal plane. The direct anterior extension of legs I and II that makes these movements possible is accompanied by a number of cephalothoracic changes: 1. The chelicerae extend anteriorly rather than ventrally in a manner that does not interfere with first leg movement. 2. The anterior eye row has been lost, perhaps to accommodate cheliceral bases and allow for reorientation of their musculature. 3. The endosternite is expanded anteriorly and laterally (Figs. 8, 9) so that muscles inserting on coxae I and II run less obliquely to the sagittal plane and, consequently, to the direction of force. 4. To accommodate this lateral muscle displacement and perhaps also to ventrally extend vision, PLE tubercles form. 5. Smaller PME tubercles may also allow greater muscle bulk and, along with their perimetric apodemes, may strengthen the area of concentrated

muscle origins in the anterior lateral carapace. 6. The lateral muscle apodeme just posterior to the PLE tubercle and the more medial anterior apodeme also serve as attachment and strengthening devices for muscles that operate the chelicerae and legs I and for the endosternite's anterior suspensors (Fig. 9) that transfer force from endosterno-coxalis muscles of the first coxae (Fig. 10).

Because of their extremism, the adaptive significance of carapace changes is more apparent in *Miagrammopes* than in most uloborid genera. Nevertheless, similar changes have occurred in other genera. The PLE tubercles of the New Guinea genus *Lubinella* are clearly convergent with those of *Hyptiotes* and *Miagrammopes* (Opell, in press a, b). Members of this genus construct an oval orb-web with its hub and empty sector nearer to a retreat than to the opposite side of the web (Lubin, in press). Extending through the vacant sector is a signal line used by the spider to monitor the web from its retreat. Although this is a different kind of web modification than that found in *Miagrammopes* and *Hyptiotes*, its use also requires the spider to hang from and monitor a single line until a prey is detected and the spider runs to the hub to locate and wrap it. In this case the visual corollary of eye tubercle significance is less plausable because the spider monitors its web from a retreat. Since *Miagrammopes* is no longer considered most closely related to *Sybota* and *Orinomana* (Opell, in press b), the PLE tubercles of these latter two genera may be a third case of their convergent appearance within the family. Unfortunately, the latter's web is unknown and details of the former's web are sketchy, so the manner in which they monitor their webs is unclear.

Like *Miagrammopes*, *Hyptiotes* is characterized by a short carapace with a reduced anterior region and PLE tubercles (Figs. 6, 7), but *Polenecia*. the sister group of these two, exhibits none of these features. This lack of modification is at first surprising in view of the latter's vertical, spiralless web (Wiehle 1931). However, the web's hub on which the spider rests is attached to a twig (H. M. Peters, personal communication), permitting the spider to simultaneously monitor the many cribellar-silk-covered radii without actively keeping a thread under tension. By contrast, the triangle-web of *Hyptiotes* with its single attachment line requires such continual monitoring and active use during prey capture (Marples and Marples 1937, Opell 1982, Peters 1938, Wiehle 1927) as might be enhanced by those carapace modifications cited for *Miagrammopes*.

These methods for quantifying and analyzing carapace features may prove useful in other spider taxa which exhibit diverse eye and carapace features. Although the endosternite has been used in insect systematics (e.g., Crowson 1938, 1955), it has received little comparative study in spiders. This structure provides clues to muscle reorganization which can subsequently be studied histologically to provide a more complete picture of changes in a group's functional morphology.

ACKNOWLEDGMENTS

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