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TESTING ADAPTIVE RADIATION AND KEY INNOVATION HYPOTHESES IN SPIDERS

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Abstract.—We combine statistical and phylogenetic approaches to test the hypothesis that adaptive radiation and key innovation have contributed to the diversity of the order Araneae. The number of unbalanced araneid clades (those whose species numbers differ by 90% or more) exceeds the number predicted by a null Markovian model. The current phylogeny of spider families contains 74 bifurcating nodes, of which 31 are unbalanced. As this is significantly more than the 14.8 expected unbalanced nodes, some of the diversity within the Araneae can be attributed to some deterministic cause (e.g., adaptive radiation). One of the more highly unbalanced (97%) bifurcations divides the orb-weaving spiders into the Deinopoidea and the larger Araneoidea. A simple statistical model shows that the inequality in diversity between the Deinopoidea and the Araneoidea is significant, and that it is associated with the replacement of primitive cribellar capture thread by viscous adhesive thread and a change from a horizontal to a vertical orb-web orientation. These changes improve an orb-web's ability to intercept and retain prey and expand the adaptive zone that orb-weaving spiders can occupy and are, therefore, considered to be "key innovations."

Key words.—Adaptive radiation, Araneae, key innovation, null Markovian model, orb web evolution.

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Adaptive radiation, "diversification into different ecological niches by species derived from a common ancestor" (Futuyma 1986, p. 32), is commonly invoked to explain disparate diversity patterns, or clade imbalance, among major animal lineages. The success of a large clade is often attributed to one or more key innovations unique to that lineage (e.g., birds: Mayr 1963; plethodontids: Larson et al. 1981; cichlid fishes: Liem 1973; flowering plants: Sanderson and Donoghue 1994). Key innovations are thought to be "critical new adaptations" (Futuyma 1986, p. 356) that allow a lineage to enter a new "adaptive zone" (sensu Simpson 1944; i.e., the environment is composed of a finite and more or less clearly delimited set of zones or areas often occupied by a group of closely related species) and thereby utilize resources that were previously unavailable (Futuyma 1986). Adaptive radiation potentially follows a shift in adaptive zone as a lineage proliferates into the newly available habitat (Guyer and Slowinski 1993). Although paradigms regarding these macroevolutionary phenomena may seem intuitive and appear to be a recurring theme in nature, tests of these hypotheses within a scientific framework are difficult.

This study addresses the issues of adaptive radiation and key innovation within the arachnid order Araneae, the clade to which all spiders belong. This order is ideal for such an investigation: it is diverse (> 34,000 species distributed among 105 families); a family-level phylogeny has been hypothesized (summarized by Coddington and Levi 1991); and its members occupy a wide range of habitats and vary considerably in morphology, behavior, and physiology. One group that has attracted considerable attention are the orb-weaving spiders that compose the Orbicularia clade. This large clade can be divided into the Deinopoidea that comprises the primitive orb-weavers and the Araneoidea that includes the "modern" orb-weavers. The divergence of these clades occurred during the early Cretaceous and was marked by a change in the type of capture thread found in orb-webs (Coddington 1986c, 1990b; Selden 1989; Coddington and Levi 1991; Opell 1997a,b, in press). Deinopoids produced

dry cribellar capture threads like those found in the less highly organized webs of their ancestors (Fig. 1a), whereas araneoids replaced these with viscous adhesive capture threads (Fig. 1b).

Cribellar threads derive their stickiness from thousands of fine, looped fibrils that are produced by the spigots of a cribellum spinning plate located at the posterior of the spider's abdomen. These fibrils form the outer surface of a spider's composite cribellar capture threads and are supported internally by a pair of larger axial fibers produced by flagelliform glands and spun from spigots on the posterior spinnerets (Peters 1983, 1984, 1986, 1992; Eberhard 1988; Eberhard and Pereira 1993; Opell 1990, 1993, 1994a–d, 1995, 1996). In contrast, the axial fibers of adhesive capture threads (Fig. 1b) are surrounded by a complex chemical solution that is produced by aggregate glands whose spigots open near those of the flagelliform glands (Vollrath et al. 1990; Townley et al. 1991; Vollrath and Tillinghast 1991; Vollrath 1992; Tillinghast et al. 1993; Foelix 1996). This solution quickly coalesces into a series of regularly spaced droplets that owe their stickiness to internal glycoprotein nodules (Vollrath et al. 1990; Vollrath and Tillinghast 1991; Tillinghast et al. 1993; Peters 1995). A number of authors (e.g., Craig et al. 1994; Opell 1997b) consider this shift in the type of capture thread to be one of the causal factors associated with a major increase in spider species and suggest that it should be regarded as a key innovation. But does the large number of araneoid species represent an adaptive radiation? If so, can it be objectively ascribed to this putative key innovation?

Possible Key Innovations

Several features that distinguish deinopoid and araneoid orb-webs may have contributed to the greater diversity of the latter clade. Compared to cribellar threads produced by spiders of similar size, the adhesive capture threads of araneoids: (1) reflect less ultraviolet light and are, therefore, less visible to insects (Craig et al. 1994); (2) achieve their stickiness at a greater material economy and allow araneoid orb-webs to

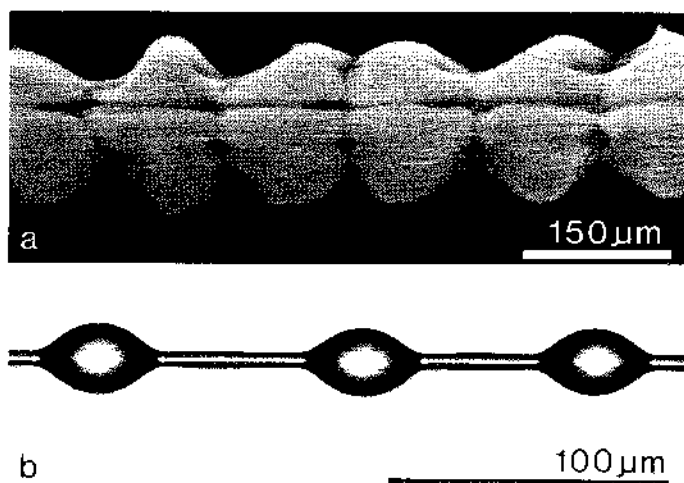


FIG. 1. Capture threads of orb-weaving spiders. (a) Cribellar thread of *Hyptiotes cavatus* (scanning electron micrograph); (b) adhesive thread of *Argiope trifasciata* (light micrograph).

achieve a greater total stickiness that enhances prey capture (Chacón and Eberhard 1980; Eberhard 1989; Opell 1997b, in press); (3) have axial fibers and are larger and, therefore, probably stronger than those of cribellar threads (Opell 1997a); and (4) have a unique self-tensing mechanism that resides in each droplet and helps maintain capture thread tension under windy conditions and may also contribute to overall web extensibility and, therefore, better equip the web to absorb the force of insects strikes through aerodynamic dampening (Vollrath and Edmonds 1989; Köhler and Vollrath 1995; Lin et al. 1995).

Web orientation may be another feature that distinguish the Deinopoidea and Araneoidea. It has long been recognized that most deinopoid orb-webs are oriented horizontally and most araneoid orb-webs are oriented vertically (e.g., Emerton 1902, p. 216; Comstock 1940, p. 262; Gertsch 1949, p. 150). However, there are exceptions to this generalization and web orientation has never been critically evaluated in a phylogenetic context. Vertical artificial orb-webs capture more insects and retain them for longer periods of time than do horizontal orb-webs having the same capture thread stickiness (Chacón and Eberhard 1980). When the orientation of araneoid orb-webs was changed, vertically oriented webs retained prey longer than did horizontally oriented webs (Eberhard 1989). Additionally, insects that struggled free of vertical orb-webs were more often recaptured by the web's other threads than those that struggled free of horizontal orb-webs (Eberhard 1989). Thus, if the transition from horizontal to vertical orb-web orientation distinguishes the Araneoidea, this feature may also be a key innovation that favored the success of this clade.

To demonstrate that adhesive thread is a key innovation that facilitated an adaptive radiation in the Araneoidea, we address three basic questions. First, are clades significantly imbalanced in the order Araneae? Second, is the diversity in the Araneoidea significantly greater than that of the Deinopoidea? Third, if so, can this imbalance in diversity be attributed to key innovations associated with changes in thread features? To qualify as a key innovation, our analysis requires

that a feature: (1) be a synapomorphy; (2) be functionally advantageous; and (3) be capable of facilitating a change or an expansion of adaptive zone.

The Approach

We use a multistep approach to evaluate adaptive radiation and key innovation in the Araneae clade. Our approach is unique in that it combines statistical approaches to analyzing clade diversity (e.g., Guyer and Slowinski 1993; Sanderson and Donoghue 1994) with character optimization techniques for evaluating adaptation (e.g., Coddington 1988, 1990a). We first test the diversity of the order Araneae for departure from the null Markovian model by evaluating each of the internal bifurcating nodes of its family-level phylogeny as either balanced or unbalanced. This test uses the null Markovian model developed by Slowinski and Guyer (1989), Slowinski (1990), and Guyer and Slowinski (1991, 1993) and addresses only a global departure in the Araneae from the null model (i.e., it does not identify which unbalanced clades are due to chance alone). To determine if differences in species numbers between the Deinopoidea and Araneoidea are significant, we use Slowinski and Guyer's (1989) model to make this single sister group comparison, as suggested by Nee and Harvey (1994) and Nee et al. (1996) as a simple alternative to Sanderson and Donoghue's (1994) maximum likelihood approach. After demonstrating that this pattern of diversity differs from that predicted by the implementation of both null models, we use character optimization techniques to identify synapomorphies of the large araneoid orb-weaving spider clade that may be key innovations.

The optimization aspect of this study combines newly analyzed data on orb-web orientation with data obtained from the literature to address the functional advantage of modern, adhesive orb-webs over primitive, cribellate orb-webs. However, attempting to associate the origin of adhesive thread with an increase in clade diversity poses an interesting set of problems. Because this is a unique historical event (Coddington and Levi 1991), a multiple test similar to that implemented by Mitter et al. (1988) is not possible. Undeniably, features that have evolved only once in the history of life (phenotypes that are uniquely derived and thus are apomorphic) present some of the most intriguing and thought provoking paradigms in evolutionary biology. Consequently, a large body of literature has developed on the study of unique adaptational events (e.g., Coddington 1988, 1990a, 1994; Carpenter 1989, 1991; Donoghue 1989; Wannatorp et al. 1990; Baum and Larson 1991). However, the study of unique historical events, termed the "homology approach" by Coddington (1994), has been largely criticized by proponents of the multiple test approach. They argue that parallel or convergent evolution provides a more statistically robust method for investigating adaptation and key innovation (Coddington 1994) and that adaptational or key innovation hypotheses about unique events are no more than "plausible suggestion" (e.g., Rohde 1996), as they lack statistical rigor. These opposing views emphasize that the issue of homology versus convergence in adaptational studies is still controversial and is at present unresolved in the formal literature. However, we agree with Coddington (1994) that "the study of historical

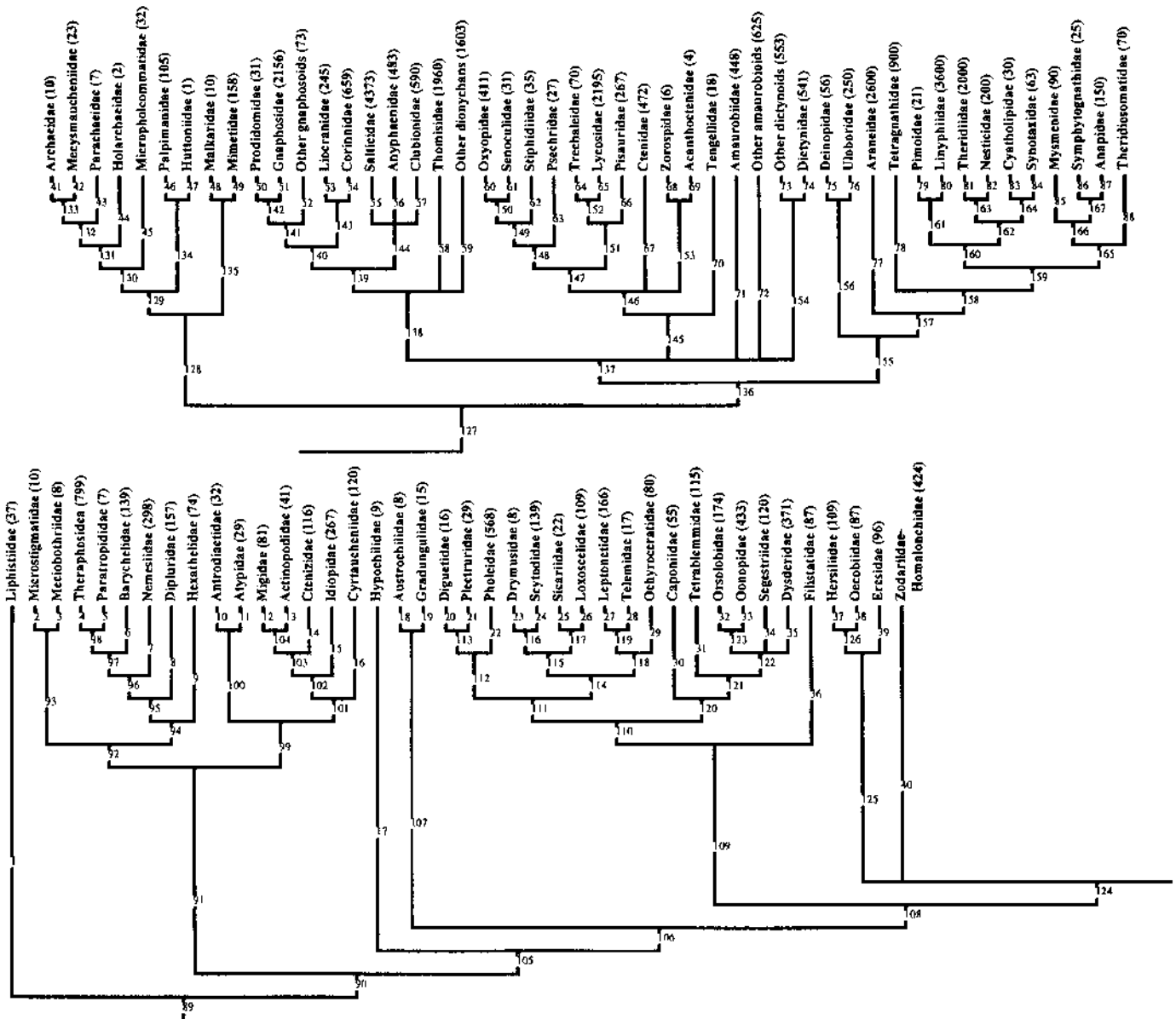


FIG. 2. Composite phylogeny of the spider families from Coddigton and Levi (1991). Numbers along branches correspond to the clade numbers listed in Table 1, numbers following family names indicate the number of species in each family.

uniques addresses the important and interesting questions of evolutionary innovation, and whether or how innovations have shaped evolutionary history."

METHODS

Application of the Null Markovian Model

The phylogeny used in this investigation (Fig. 2) is the composite phylogeny of spider families summarized by Coddigton and Levi (1991), with the Araneoid phylogeny (node 155) modified to reflect the studies of Griswold et al. (1997). We assume that this phylogeny is sound and do not attempt to evaluate it in this study. We can reject ($\chi^2 = 97.01$; $P < 0.001$) Guyer and Slowinski's (1991, 1993, 1995) proportional-to-distinguishable-arrangements (PDA) null model,

which they claim tests whether a phylogeny can be distinguished from the pool of random trees. However, we agree with Cunningham (1995) that the PDA model is too restrictive and is a superficial means by which to test the robustness of a phylogenetic hypothesis. The number of species for each of the terminal branches (families) were obtained from Platnick (1989, and unpubl. species list). It is important to note that we are assuming that the number of taxa considered in this analysis is complete and acknowledge that incomplete sampling could affect the outcome of this study (Sillen-Tullberg 1993). However, with only a few exceptions, the diversity in most spider families has been thoroughly documented. Therefore, it is unlikely that the results reported in this study have been compromised by sampling bias. At each dichotomous node (the six polytomies in the cladogram were

TABLE I. Comparison of sister clades in Araneae. *R* = number of species in smaller clade, *S* = number of species in larger clade, *P* = proportion of taxa contained in larger clade, + indicates that node is unbalanced ($P > 0.90$), and - indicates that node is balanced. For unnamed clades, clade is designated by taxon with greatest number of species, given in parentheses. Clades in bold type indicate family level dichotomies.

Clade #	Taxon	<i>R</i>	<i>S</i>	<i>P</i>	+/-
89	Mesothelae/Opisthothelae	37	33,714	0.99	+
90	Mygalomorphae/Araneomorphae	2178	31,536	0.94	+
105	Paleocribellatae/Neocribellatae	9	31,527	0.99	+
106	Austrochiloidea/Araneoclada	23	31,504	0.99	+
108	Haplogynae/Entelegynae	2509	29,018	0.92	+
127	Palpimanoidea/RTA-Oribiculariae	348	27,931	0.99	+
136	Oribiculariae/RTA	10055	17,876	0.64	-
155	Deinopoidea/Araneoidea	306	9749	0.97	+
157	Araneidae/Higher Araneoids	2600	7149	0.73	-
158	Tetragnathidae/"Linyphiidae"	900	6249	0.87	~
159	"Anapidae"/"Linyphiidae"	335	5914	0.95	+
165	Theridiosomatidae/"Anapidae"	70	265	0.79	-
166	Mysmenidae/"Anapidae"	90	175	0.66	-
167	Symphytognathidae/Anapidae	25	150	0.86	-
160	"Theridiidae"/"Linyphiidae"	2293	3621	0.61	~
161	Pimoidae/Linyphiidae	21	3600	0.99	+
162	"Synotaxidae"/"Theridiidae"	93	2200	0.96	+
163	Nesticidae/Theridiidae	200	2000	0.91	+
164	Cyatholipidae/Synotaxidae	30	63	0.68	-
156	Deinopidae/Uloboridae	56	250	0.82	-
145	Tengellidae/Lycosoidea	18	3518	0.99	+
154	"Dictynoids"/Dictynidae	541	553	0.51	-
153	Acanthoctenidae/Zorospidae	4	6	0.60	-
147	"Oxyopidae"/"Lycosidae"	504	2532	0.84	-
151	Pisauridae/"Lycosidae"	267	2265	0.89	-
152	Trechaleidae/Lycosidae	70	2195	0.97	+
148	Psechridae/"Oxyopidae"	27	477	0.95	+
149	Stiphidiidae/"Oxyopidae"	35	442	0.93	+
150	Senoculidae/Oxyopidae	31	411	0.93	+
139	"Gnaphosidae"/"Salticidae"	3164	5446	0.63	-
140	"Corinnidae"/Gnaphosoidea	904	2260	0.71	-
142	Other Gnaphosids/"Gnaphosidae"	73	2187	0.97	+
142	Prodidomidae/Gnaphosidae	31	2156	0.99	+
143	Liocranidae/Corinnidae	245	659	0.73	-
128	"Mimetidae"/"Palpimanidae"	168	180	0.52	-
135	Malkaridae/Mimetidae	10	158	0.94	+
129	"Micropholcommatidae"/"Palpmanidae"	74	106	0.59	-
130	Micropholcommatidae/"Mecysmaucheniidae"	32	42	0.57	-
131	Holarchoaeidae/"Mecysmaucheniidae"	2	40	0.95	+
132	Parachaeidae/"Mecysmaucheniidae"	7	33	0.83	-
133	Arachaeidae/Mecysmaucheniidae	10	23	0.70	-
134	Huttonidae/Palpimanidae	1	105	0.99	+
125	Erisidae/"Hersiliidae"	96	196	0.67	-
126	Oecobiidae/Hersiliidae	87	109	0.56	-
109	Filistatidae/"Higher Haplogynes"	87	2422	0.97	+
110	Scytodoids/"Oonopidae"	1154	1268	0.52	-
120	Caponidae/"Oonopidae"	55	1213	0.96	+
121	Tetrablemmidae/"Oonopidae"	115	1098	0.91	+
123	Orsolobidae/Oonopidae	174	433	0.71	-
111	"Leptonetidae"/"Pholcidae"	613	655	0.52	-
114	"Scytodidae"/"Leptonetidae"	263	278	0.51	-
118	Ochyroceratidae/"Leptonetidae"	80	183	0.70	-
119	Telemidae/Leptonetidae	17	166	0.91	+
115	"Loxoscelidae"/"Scytodidae"	131	147	0.53	-
116	Drymusidae/Scytodidae	8	139	0.95	+
117	Sicariidae/Loxoscelidae	22	109	0.83	-
112	"Plectruridae"/Pholcidae	45	568	0.93	+
113	Diguetidae/Plectruridae	16	29	0.64	-
107	Austrochilidae/Gradungulidae	8	15	0.65	-
91	Fornicephalae/Tuberculotae	686	1492	0.69	-

TABLE 1. Continued.

Clade #	Taxon	R	S	P	+/-
99	Atypoidina/Rastelloidina	61	625	0.91	+
101	Cyrtachenidae/"Idiopidae"	120	505	0.81	-
102	"Ctenizidae"/Idiopidae	238	267	0.53	-
103	Ctenizidae/"Migidae"	116	122	0.51	-
104	Actinopodidae/Migidae	41	81	0.66	-
100	Atypidae/Antrodiaetidae	29	32	0.52	-
92	"Microstigmatidae"/"Theraphosidae"	18	1474	0.99	+
94	Hexathelidae/"Theraphosidae"	74	1400	0.95	+
95	Dipluridae/Crassitarsae	157	1243	0.89	-
96	Nemesiidae/Theraphosoidina	298	945	0.76	-
97	Barychelidae/"Theraphosidae"	139	806	0.85	-
98	Paratropidae/Theraphosidae	7	799	0.99	+
93	Meciobothriidae/Microstigmatidae	8	10	0.56	-

ignored) the number of taxa in each branch was compared (Table 1). The topology (Q) arising from each node in the cladogram has a Markovian probability, P_m , and is determined by the recursive formula: $P_m(Q) = 2(n - 1)^{-1}P_m(R)P_m(S)$, given n terminal taxa with subclades R and S (Slowinski 1990). Additionally, the cumulative probability, P_c , of the tree being partitioned into subclades r and s can be computed by using the following formula: $P_c(r, s) = 2r(n - 1)^{-1}$ for $r < s$ (Slowinski and Guyer 1989). We follow Guyer and Slowinski's (1993) conservative approach by considering a dichotomous node to be unbalanced only if the more diverse clade contains at least 90% of the total number of species in the two sister groups.

*Permutations of the Null Markovian Model:
Addressing the Issue of Independence*

The null Markovian model of investigating clade diversity patterns has only been applied by Guyer and Slowinski (1991, 1993) in a theoretical sense to unrelated groups (e.g., angiosperms, insects, and tetrapods) to address large scale trends in diversity. The application of the model has been limited to this scale to ensure the statistical independence of the nodes being used in the analysis. Such an application of the model, however, limits its utility in addressing the allocation of diversity within any single large clade. Our application of the null Markovian model requires us to address the issue of independence because the diversity at the tips of our cladogram contributes in a successive fashion to that of the nodes

below. For example, the family Salticidae (node 55, Fig. 2), which contains 4373 species, contributes to the diversity at the 12 nodes below it.

We address the issue of independence in two ways. First, we repeat the Markovian analysis for only the terminal, family-level dichotomies. The nodes used in this restricted analysis are indicated in bold in Table 1. As in the global analysis, we considered nodes to be unbalanced if the more diverse clade contains at least 90% of the total number of species. Second, in an attempt to evaluate the influence of speciose terminal taxa, the cladogram (Fig. 2) was randomly rerooted 10 times using a random number generator and the global Markovian analysis was repeated for each tree produced (Table 2).

Araneoidea/Deinopoidea Diversity Comparison

To compare the diversity of the Araneoidea and Deinopoidea (Fig. 2, node 155), we used the single sister group comparison of Guyer and Slowinski (1993) in which the probability of an inequality in clade size as large or larger than that observed is described by the formula: $P = 2(n - r)/(n - 1)$ (Nee and Harvey 1994; Nee et al. 1996), where n is equal to the total number of taxa and r the number of taxa in the larger clade. This analysis was conducted once with the Deinopoidea as the sister group to all the araneoid families (Fig. 3a) and a second time with the Deinopoidea plus Araneidae as a sister group to the remaining araneoid taxa (Fig. 3b).

Character Optimization

The phylogeny used in this aspect of the study is that of Coddington and Levi (1991), modified to include the more detailed studies of Araneoidea (Griswold et al. 1997), Araneidae (Scharff and Coddington 1997), and Theridiosomatidae (Coddington 1986b, 1990b) phylogeny. In the analysis of orb-web orientation the Pimoidea-Synotaxidae clade, which is sister to the Mysmenidae-Theridiosomatidae clade, was excluded since its members do not construct orb-webs. Genera whose web forms or orientations are unknown were excluded from the analysis, as were those with highly modified webs, such as the uloborid genera *Hyptiotes* and *Miagrammopes* and the araneid genera *Cyrtophora* and *Mecynogea* (Levi 1980; Opell 1982, 1990; Lubin 1986). The in-

TABLE 2. Summary of Markovian model results from random rooting of Araneae phylogeny. Note that "Node" indicates nodes at which reroot occurred in phylogeny illustrated in Figure 1. All χ^2 values were significant ($P < 0.001$).

Node	Unbalanced	Balanced	χ^2
6	31	42	35.6
9	33	40	29.0
22	33	40	29.0
32	33	49	29.0
50	31	42	23.0
61	31	42	23.0
84	32	41	25.9
100	32	41	25.9
132	32	41	25.9
156	29	44	17.8

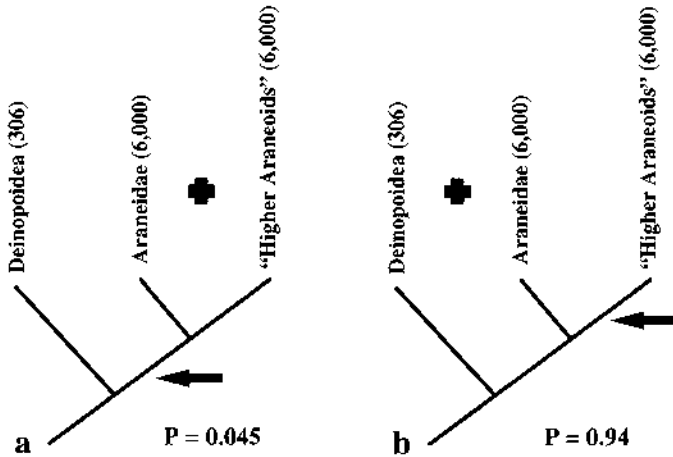


FIG. 3. Sister-group analyses of Orbicularian diversity. (a) Deinopoidea:(Araneidae + higher Araneoids) has greater diversity than the Deinopoidea; (b) the "higher Araneoids" do not have greater diversity than the Deinopoidea + Araneidae. Therefore, features promoting araneoid diversification were acquired at the basal node of the Araneoidae.

clusion of the genera that construct highly modified web forms does not, however, affect the final outcome of the analysis.

The computer program MacClade (vers. 3.02, Maddison and Maddison 1992) was used to phylogenetically optimize four characters on the cladogram using the "show all most parsimonious states at each node" character tracing option (Figs. 4, 5): (1) the spectral properties of spider silks; (2) the light environments in which spiders forage; (3) thread type; and (4) orb-web orientation. All multistate characters were treated as unordered in each analysis. The spectral properties of spider silks and light environment character states were

obtained from Craig et al. (1994) and thread type was scored from the review of Coddington and Levi (1991). The reanalysis of data from Craig et al. (1994) was performed on those spider families included in their analysis. To establish the araneoid ancestral character state for web orientation we scored this character for as many araneoid and deinopoid genera as possible. Character states were determined from natural history observations included in various monographs and other publications (listed at the tips of the cladogram in Fig. 5). Web orientation was defined as horizontal, vertical, or variable. Variable includes those webs that are constructed in both horizontal and vertical planes or at variable angles.

As the specific outgroup of the Orbiculariae has not been determined, it was also necessary to evaluate and score web orientation for members of its sister group, the RTA clade, to establish the polarity of web orientation at the basal node of the orbicularian clade. The RTA clade is a large lineage that includes 34 families (Coddington and Levi 1991). Of these, we included in the analysis only cribellate families because the basal group of the Orbiculariae, the Deinopoidea, produce cribellar thread. We further restricted the analysis to those genera whose members constructed planar, cribellate, sheet webs whose orientation could be evaluated as horizontal, vertical, or variable. This excluded three-dimensional, space-filling webs and webs whose capture lines radiated from a retreat and formed a sheet only when the contour of the adjacent substrate so dictated.

Testing Adaptive Radiation and Key Innovation Hypotheses: Three Criteria

For change in capture thread composition and web features to qualify as key innovations, we propose that three criteria must be met: (1) they must be synapomorphic for araneoids; (2) these features must confer a functional advantage over

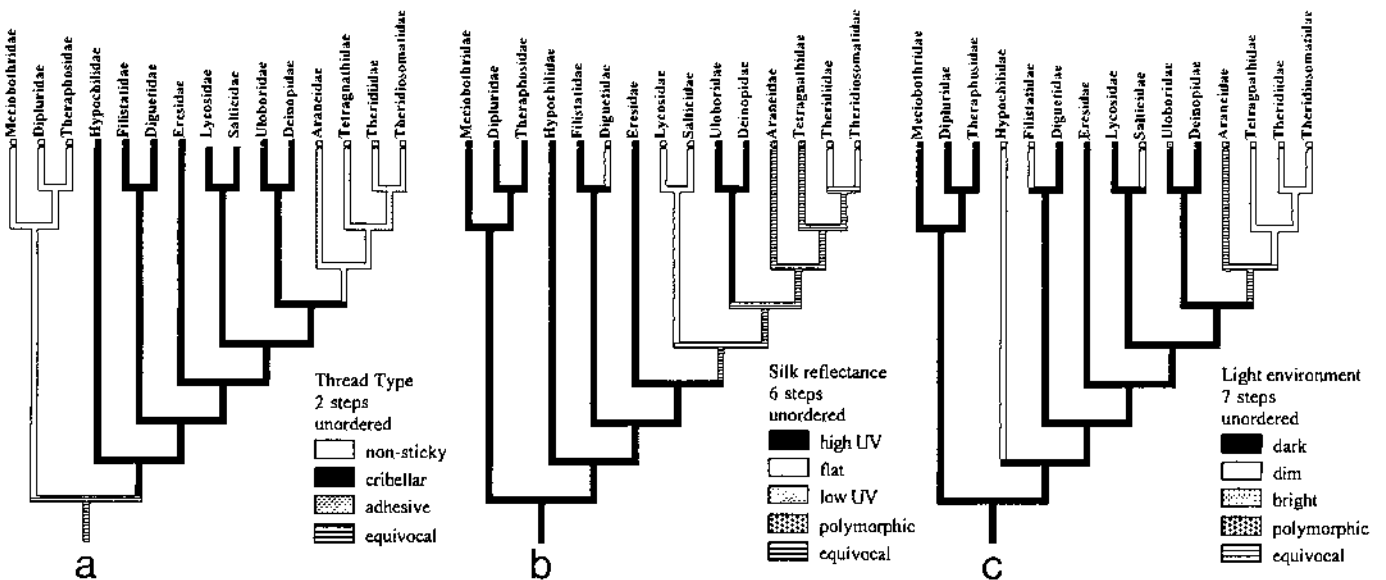


FIG. 4. Character optimizations of silk features and foraging environment. (a) Thread type, showing that the origin of cribellar thread was associated with the Hypochilidae and adhesive thread with the appearance of the araneoid orb-weavers (Araneidae - Theridiosomatidae); (b) silk reflectance, showing that high UV reflectance is characteristic of the Deinopoidea (Deinopidae + Uloboridae) and low or flat UV reflectance is equivocally characteristic of the Araneoidae; (c) light environment, showing that the Deinopoidea are associated with dark environments and that the Araneoidae tend to be associated with dim-light environments.

overestimates the number of unbalanced clades expected by chance alone. Based on the simulation studies of Losos and Adler (1995) and our combination of analyses, we have demonstrated that the relative diversity of clades within the Araneae is different than that expected by chance and that some deterministic mechanism (Guyer and Slowinski 1993) has resulted in the disparate allocation of diversity within the Araneae clade.

Is the Diversity of the Araneoidea Greater than That of the Deinopoidea?

The simple sister group comparison (Slowinski and Guyer 1989; Nee et al. 1996) was used to determine if the Araneoidea is significantly more diverse than the Deinopoidea (Fig. 3a), and indicates that the greater diversity of the Araneoidea is only marginally significant ($P = 0.061$). However, Scharff and Coddington (1997) and Coddington and Levi (1991) note that recent revisions of neotropical araneids show that their diversity is much greater than currently recognized, and estimate that 6000–7000 species exist. Using the lower estimate, we find the inequality in deinopoid and araneoid diversity to be unequivocal ($P = 0.045$; Fig. 3a). Consequently, it is not surprising that when the diversity of the Araneidae plus Deinopoidea is compared to that of the remaining araneoid diversity (Fig. 3b) there is no longer an inequality ($P = 0.937$ for the higher-diversity estimate; $P = 0.578$ for the lower-diversity estimate). These data show that the Araneoidea are more diverse than the Deinopoidea and that the features promoting diversification were acquired at the base of the araneoid lineage (Nee et al. 1996).

Character Optimization

Figures 4a–c and Figure 5 summarize the optimizations of thread type (Fig. 4a), silk reflectance (Fig. 4b), light environment (Fig. 4c), and web orientation (Fig. 5). We found adhesive threads, dim/dark (unequivocally dim using ACCT-RAN optimization) light environment, and vertical web orientation all to be synapomorphic for the Araneoidea (i.e., these changes occur at the araneoid ancestral node). In their analysis, Craig et al. (1994) found flat UV reflectance to be synapomorphic for the Orbiculariae clade with a reversal to high UV reflectance in the Deinopoidea. In contrast, we found high UV reflectance to be plesiomorphic for the Orbiculariae and flat and low UV reflectance to occur equivocally at the base of the Araneoidea (Fig. 4b). The differences between the two optimizations is most likely due to the use of an updated phylogeny. In summary, Figures 4a, 4b, and 5 show thread type and spectral properties as well as web orientation change at the base of the araneoid lineage respectively. It is important to note that in this study we have addressed only synapomorphies that are directly related to prey capture. Therefore, we do not consider some of the 12 synapomorphies of the Araneoidea (Griswold et al. 1997). We do not argue that these omitted characters have not contributed to the observed clade imbalance. However, comparative functional studies of all of these characters are beyond the scope of this paper, and we address only the functionality of thread and web features, as this is a testable hypothesis in its own right.

DISCUSSION

The implementation of the Markovian model, globally and in the single sister group comparison of deinopids and araneoids, demonstrates that adaptive radiation has occurred in spiders and the major increase in araneoid diversity noted by Craig et al. (1994) is statistically significant. Additionally, we conclude that this increase in diversity is located at the basal node of the Araneoidea and is associated with changes in web orientation and capture thread composition that alter orb-web cost, stickiness, strength, extensibility, and UV reflectance, thereby fulfilling the synapomorphy component of our key innovation hypothesis (criterion 1). Furthermore, we will demonstrate below that these changes confer complementary functional advantages to the araneoid orb-weavers (criterion 2) and are capable of facilitating an expansion of the adaptive zones they can occupy (criterion 3).

Criterion 2: Functional Advantage.—The prey capture success of orb-webs depends on the availability of insects and the web's ability to intercept them, to absorb the force generated when insects strike the web, and to retain insects long enough for a spider to subdue them (Chacón and Eberhard 1980; Craig 1987b). Insect availability is determined by the habitat in which a web is placed (Reichert and Cady 1983; Wise and Barata 1983; Craig 1988, 1990). The web's ability to intercept these insects is influenced by its area (Eberhard 1986), its orientation (Eberhard 1989), its invisibility or attractiveness to insects (Craig 1988, 1990; Craig and Bernard 1990; Craig et al. 1994), and by the visibility of a spider positioned at the web's hub (Craig and Freeman 1991; Craig and Ebert 1994). A web's architecture, strength, and extensibility equip it to absorb and dissipate the force of a prey strike (Denny 1976; Eberhard 1986a, 1989; Craig 1987a,b; Lin et al. 1995) and its sticky, spirally arrayed capture thread equip it to retain prey (Chacón and Eberhard 1980; Eberhard 1989; Opell 1990, 1994a, 1996).

As documented in this paper's introduction, vertically oriented, adhesive orb-webs possess complementary functional properties that confer advantages over horizontally oriented, cribellate orb-webs at every phase of prey capture. The lower UV reflectance of many of these webs makes them less visible to insects and allows them to be placed in more brightly lighted habitats where insect abundance may be greater. Vertically oriented orb-webs intercept more prey than do horizontally oriented webs and, for a given stickiness, retain prey longer. The axial fibers of adhesive threads are larger and, therefore, probably stronger than those of cribellar threads. The self-tensing mechanism of adhesive capture threads increases their extensibility and may contribute to the web's overall extensibility and its ability to employ aerodynamic dampening as a mechanism of dissipating the force of insect strikes. Adhesive capture thread achieves its stickiness at a greater material economy than cribellar threads and, consequently, adhesive orb-webs have a greater total stickiness that equips them to both retain prey longer and retain larger prey than cribellate orb-webs can.

In this context, it is important to note that Coddington (1988) defines an adaptation as an apomorphy arising through natural selection that appears to have some advantageous selective value when compared to the plesiomorphic condi-

tion. We have implemented Coddington's homology approach to our treatment of unique thread features in the Araneoidea. However, like the adaptational definition of Baum and Larson (1991), this definition assumes that a feature's historical and current functional roles and selective regimes are similar. Both assumptions are untestable when considering the derivation of complex changes in silk features, spinning apparatus, and web-building behavior. Therefore, we consider our test of functionality limited to the current biological role of the character in question, as it is likely that only some of the components, or the complex once derived in its entirety, have an adaptational origin.

Criterion 3: Adaptive Zone.—Explanations of key innovations typically invoke shifts in adaptive zone (e.g., Simpson 1944; Futuyma 1986). However, like Liem's (1973) study of morphological innovation in cichlids, we suggest that the changes in orbicularian capture thread features lead to an expansion of, rather than a shift, in the orbicularian "adaptive zone." Our reanalysis of data presented by Craig et al. (1994) indicate that the Orbiculariae originally foraged in a dark environment, whereas the Araneoidea now also forage in dim and bright-light environments. Associated with this change in environment are changes in the spectral properties of the capture threads and the orientation of the orb-web. The cribellar capture threads of deinopoid orb-webs reflect a great deal of UV light, whereas the adhesive capture threads of most araneoid orb-webs reflect very little (Craig and Bernard 1990). Craig et al. (1994) suggest that this change in thread spectral properties permitted araneoids to use orb-webs in more brightly lighted habitats where the greater UV reflectance of deinopoid orb-webs would make them more visible to insects and, therefore, less effective in intercepting prey (Craig 1988). However, the production of capture threads that reflect little UV light does not prevent araneoids from accruing the benefits of UV reflective silks. By adding other types of UV reflective threads to their webs, araneoids can attract certain types of insects to the web (Craig and Bernard 1990), create a visual screen to protect against predators (Cushing and Opell 1990; Craig and Freeman 1991; Schoener 1992), or advertise the web's presence to birds and thereby prevent its destruction (Eisner and Nowicki 1983).

The lower UV reflectance of adhesive capture threads complements the vertical orientation of araneoid orb-webs. Horizontal deinopoid webs probably capture more erratically flying insects, insects that fall from the forest canopy, and insects that fly upward from low vegetation. Only in the latter case is the orb-web's visibility likely to be a major factor in prey interception. However, if there is sufficient light to make a horizontal araneoid orb-web visible, an insect that is flying upward will either see the webs against the sky, in which case the web will be camouflaged by its UV reflection, or the insect will be attracted to the web because of its high UV reflectance (Craig 1988, 1990). In contrast, vertically oriented orb-webs are more conspicuous to insects, as many of the objects in their background do not reflect UV light. Thus, vertical orb-web orientation favors lowered UV reflectance.

Key Innovation

Our analysis demonstrates that adaptive radiation has occurred in orbicularian clade and that this diversification was

associated with changes in capture thread and web features. We conclude that these changes conferred complementary functional advantages that allowed araneoid orb-weavers to occupy a greater number of adaptive zones. Additionally, we hypothesize that these changes in web orientation and capture thread composition were rapid. This is supported by the complementary nature of these changes and the likelihood that any one change would be of limited benefit by itself. Larson et al. (1981) propose a similar explanation for the diversity of the plethodontid salamander genus *Aneides*, in which the complimentary rearrangement of carpals and tarsals better adapt species for climbing. This may explain why no species show intermediate or partial combinations of features.

The changes in orb-web design and function that marked the origin of the Araneoidea also reduce the amount of niche overlap between deinopoid and araneoid orb-weavers. Thus, the lower number of deinopoid orb-weaving species cannot be ascribed principally to competitive exclusion by the Araneoidea. Given the wide geographic distribution of the Deinopoidea (Opell 1979), the size of this clade may reflect lower rates of speciation than found in the Araneoidea rather than higher rates of extinction.

Our conclusions raise two critical questions about the study of key innovation: (1) Can complex multicharacter traits be regarded as key innovations? (2) Can the functional-homology approach be used to determine if unique events are responsible for an adaptive radiation? Since spiders that produce adhesive capture threads use different combinations of spinning spigots, silk glands, and behaviors than spiders that produce cribellar threads (Foelix 1996), these key innovations are actually a suite of complementary characters. One potential criticism of the concept of key innovation is that there is seldom a single feature that can be designated as the evolutionary novelty responsible for clade diversification. Instead, the more diverse clade is often distinguished by a suite of adaptive features (Lauder and Liem 1989; Cracraft 1990). We agree with this assessment, but we do not believe that it refutes the validity of key innovations.

If a key innovation is defined as the appearance of a new capability that facilitates the proliferation of the lineage that possesses it, then one or more characters may contribute to the key innovation. In the case of character complexes, a key innovation is not functional and therefore not present until all of its components are present. Thus, the key innovation appears at the point in a group's phylogeny where the last of the functionally linked suite of characters appears. Because a phylogeny depicts cladogenesis and not fine-grain evolution (i.e., phyletic evolution), it is not surprising that several components of the key innovation appear at the same node. The character, or characters, that complete the suite may, therefore, be thought of as "key characters" as they are, in retrospect, the limiting factor of the key innovation. Orb-web architecture appeared when the Orbiculariae diverged from the RTA clade, but it was not until adhesive capture thread replaced cribellar thread and orb-webs became vertically oriented that clade diversity increased. Thus, these latter two features can be considered the key characters that facilitated the adaptive radiation of modern orb-weaving spiders.

A second question raised by this study is whether the func-

tional-homology approach can be used to determine if unique events are causal mechanisms of adaptive radiation. Cracraft (1990) argues that differences in speciation and extinction rates are attributable to factors at the population level. However, we maintain that the presence of a key feature, derived once in the history of a lineage and maintained throughout, can demonstrably confer a functional advantage upon the clade in question (i.e., to the individuals in that clade). As suggested by Maddison (1996) "clades with diversity-favoring traits will be more successful over the long term than others, and this will be reflected in the shape of the phylogenetic tree, with these clades being larger than their sisters." If the comparative approach is used to assess the functionality of one particular organismal feature (e.g., adhesive threads vs. cribellar threads) relative to another, a testable functional advantage can be associated with unbalanced clade diversity. This approach deals with key innovations as testable hypotheses. That is, there is not a functional advantage associated with a character versus there is a functional advantage for a particular character state, and if adaptive, the feature in question at some point was favored by selection and resulted in a shift in or expansion of adaptive zone. Our approach is similar to that of Lauder and Liem (1989), as it focuses on homologous characters and their states. Additionally, our approach permits the investigation of putative key innovations that have evolved only once and does not establish a priori, arbitrary, limitation on evolutionary processes.

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