

CLADISTIC ANALYSIS OF THE *ATYPOIDES* PLUS *ANTRODIAETUS* LINEAGE OF MYGALOMORPH SPIDERS (ARANEAE, ANTRODIAETIDAE)

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ABSTRACT. Cladistic analyses of the antrodiaetid spider genera *Atypoides* O.P.-Cambridge 1883 and *Antrodiaetus* Ausserer 1871 yield a much more completely resolved phylogeny than that proposed by Coyle in 1971. Twenty-nine potentially informative characters were used in the analyses, which were performed using PAUP's *a posteriori* weighting options. Three independent analyses were performed, each with a different outgroup. These outgroups were 1) the antrodiaetid genus *Aliatypus* Smith 1908, the putative sister group of *Atypoides* plus *Antrodiaetus*, 2) *Aliatypus gulosus* Coyle 1974, the most primitive *Aliatypus* species, and 3) a hypothetical ancestral taxon based on character states found in *Aliatypus* and the Atypidae, the latter being the putative sister group of the antrodiaetids. These three analyses produced a total of eight most parsimonious trees which support the following principal conclusions: 1) *Atypoides*, as defined by Coyle, is paraphyletic (*Atypoides riversi* O. P.-Cambridge 1883 plus *At. gertschi* Coyle 1968 share with *Antrodiaetus* a common ancestor not shared with *At. hadros* Coyle 1968). 2) *Antrodiaetus roretzi* (L. Koch 1878) is a relict species which shares a unique common ancestor with all other *Antrodiaetus* species. 3) Coyle's *unicolor* group of nine *Antrodiaetus* species is paraphyletic; six of these form a recently-derived clade, (*Antrodiaetus occultus* Coyle 1971 (*An. yesoensis* [Uyemura 1942], *An. cerberus* Coyle 1971, (*An. montanus* [Chamberlin & Ivie 1933], (*An. pugnax* [Chamberlin 1917], *An. hageni* [Chamberlin 1917])), and the other three species, *An. pacificus* (Simon 1884), *An. robustus* (Simon 1890), and *An. unicolor* (Hentz 1841), are derived from more ancestral stock. 4) Coyle's *lincolnianus* group of three *Antrodiaetus* species, *An. lincolnianus* (Worley 1928), *An. stygius* Coyle 1971, and *An. apachecus* Coyle 1971, represents a valid clade. Our phylogeny suggests that two separate vicariance events led to the evolution of the two east Asian members of this otherwise North American assemblage. Vicariance events that are indicated by geological evidence and consistent with our phylogeny are postulated to account for the present distribution of North American species. New putative synapomorphies of *Antrodiaetus*, and of *Antrodiaetus* plus *Atypoides*, are proposed.

The monophyly of the Antrodiaetidae (defined to include *Aliatypus*, *Antrodiaetus* and *Atypoides*) has survived the collapse of the Atypoidea brought about by the recent cladistic revolution in arachnology (Platnick & Gertsch 1976; Platnick 1977). Although all phylogenies of the Mygalomorphae published within the last decade postulate that these three genera form a monophyletic Antrodiaetidae (Raven 1985; Eskov & Zonshteyn 1990; Coddington & Levi 1991; Goloboff 1993), Coyle (1994) has drawn attention to the tenuousness of this hypothesis, arguing that many of the proposed syn-

apomorphies may be either plesiomorphies or homoplasies.

The three species of *Atypoides* and 13 species of *Antrodiaetus* were hypothesized by Coyle (1968, 1971) to form a monophyletic group. This relationship has been supported by the following putative synapomorphies: 1) a strongly developed inner conductor sclerite (ICS) that surrounds the embolus and has a tip which is clearly separate from the outer conductor sclerite (OCS) (Raven 1985; Coyle 1994); 2) reduction of the anterior lateral spinnerets (ALS) (Coyle 1971; Raven 1985); 3) the presence of a cheliceral apophysis (or its vestige) in mature males (Coyle 1971; Raven 1985); 4) a longitudinal thoracic fovea (Coyle 1971, 1994). Coyle (1994) has discussed the problematic nature of synapomorphy 2, ex-

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Table 1.—Quantitative character values for *Atypoides* and *Antrodiaetus* species. Range, mean, and standard deviation (if $n > 4$) are given for all ratio characters; range and mean only for meristic characters. PTT/PTL and ITL/IML are male characters; all others are female characters. See Methods section for character definitions.

	<i>n</i> females	<i>n</i> males	CMT	IMS	IVCTR
<i>At. hadros</i>	6	15	2–5 2.9	8–10 8.7	3–4 3.5
<i>At. riversi</i>	86	25	6–33 18.3	17–32 23.0	6–11 7.3
<i>At. gertschi</i>	57	20	9–26 17.7	18–35 23.6	4–10 7.2
<i>An. roretzi</i>	2	2	6	15	4
<i>An. pacificus</i>	56	105	9–24 16.8	9–15 12.3	1–6 4.0
<i>An. robustus</i>	13	11	11–18 13.9	9–14 10.6	2–5 3.6
<i>An. unicolor</i>	225	104	6–23 12.0	9–15 11.6	1–6 3.5
<i>An. occultus</i>	0	21			
<i>An. yesoensis</i>	1	2	7	10	4
<i>An. cerberus</i>	4	4	12–19 15.7	11–13 11.7	4–5 4.5
<i>An. montanus</i>	12	23	16–29 21.9	12–16 12.9	3–5 3.9
<i>An. hageni</i>	7	8	13–18 15.1	13–15 13.7	2–5 4.0
<i>An. pugnax</i>	24	24	8–17 12.1	9–13 11.1	4–6 4.2
<i>An. lincolnianus</i>	2	6	23–27	13	0–1 0.5
<i>An. stygius</i>	3	8	14–19 17.0	11–13 12.0	0–2 1.3
<i>An. apachecus</i>	3	8	10–16 13.0	11–12 11.3	0–2 1.0

plaining that the ALS of *Atypoides* may be at least as well developed as those of the atypids, but the other three synapomorphies appear to be valid. We have identified a new putative synapomorphy of *Atypoides* plus *Antrodiaetus*: these taxa share a spermathecal bowl—apparently either the result of the sclerotization of the proximal portion of the spermathecal bulb itself or of the expansion of the distal end of the sclerotized spermathecal stalk (Coyle 1968, figs. 80–94; 1971, figs. 270–311)—which is not found in *Aliatypus* or the

Atypidae, and may be unique among the Mygalomorphae.

Coyle (1971) constructed a working hypothesis of the phylogeny of the *Atypoides* plus *Antrodiaetus* lineage using a protocladistic approach. However, much of that tree was unresolved. Eight of the ten characters used to construct that phylogeny have been used in our current study, although some of these have been redefined, quantified, or split into several discrete characters. By modifying these characters, utilizing 14 ad-

Table 1.—Extended.

IML/CL	ITL/IML	PTT/PTL	IVML/CL
0.36–0.38	0.81–0.86	0.42–0.47	0.50–0.53
0.38 ± 0.01	0.84 ± 0.01	0.45 ± 0.01	0.52 ± 0.01
0.51–0.65	0.66–0.77	0.32–0.50	0.55–0.70
0.56 ± 0.03	0.71 ± 0.03	0.46 ± 0.03	0.63 ± 0.03
0.50–0.59	0.71–0.80	0.30–0.33	0.70–0.86
0.55 ± 0.02	0.75 ± 0.02	0.32 ± 0.01	0.77 ± 0.04
0.45–0.46	0.75–0.76	2.78	0.57–0.58
0.42–0.51	0.65–0.81	0.33–0.48	0.51–0.65
0.47 ± 0.02	0.72 ± 0.04	0.40 ± 0.03	0.58 ± 0.03
0.38–0.42	0.77–0.83	0.40–0.47	0.52–0.57
0.40 ± 0.01	0.80 ± 0.02	0.43 ± 0.02	0.55 ± 0.02
0.35–0.48	0.74–0.85	0.38–0.54	0.49–0.68
0.44 ± 0.02	0.81 ± 0.03	0.45 ± 0.04	0.60 ± 0.04
	0.81–0.90	0.45–0.49	
	0.85 ± 0.02	0.47 ± 0.02	
0.41	0.95–0.99	0.45–0.47	0.56
0.43–0.46	0.92–0.93	0.39–0.41	0.62–0.67
0.44	0.93	0.40	0.65
0.44–0.52	0.83–0.91	0.35–0.40	0.60–0.65
0.48 ± 0.02	0.88 ± 0.02	0.38 ± 0.01	0.64 ± 0.02
0.43–0.48	0.88–0.90	0.37–0.41	0.61–0.65
0.46 ± 0.02	0.90 ± 0.01	0.39	0.64 ± 0.02
0.39–0.48	0.82–0.91	0.37–0.44	0.56–0.65
0.43 ± 0.02	0.88 ± 0.03	0.42 ± 0.01	0.60 ± 0.03
0.41–0.42	1.00–1.04	0.23–0.24	0.56
	1.02 ± 0.02	0.24 ± 0.0	
0.35–0.38	0.87–0.94	0.31–0.34	0.48–0.53
0.37	0.90 ± 0.02	0.32 ± 0.01	0.51
0.40–0.44	0.89–0.99	0.29–0.34	0.50–0.54
0.42	0.94 ± 0.04	0.33 ± 0.02	0.52

ditional characters, and employing modern cladistic methods, we hope to generate a phylogeny which more closely approaches real history.

METHODS

Following the methods of Coyle (1994), we searched for phylogenetically informative characters by carefully screening the descriptions, illustrations and quantitative character tables in Coyle (1968, 1971) for character states which distinguish two or more species

from the rest. A total of 29 potentially informative characters were selected by this process and eventually used in the analyses. Nineteen of these characters were adopted from species descriptions and illustrations, three from a table of male leg I macrosetation, and seven (three meristic characters and four ratios of measurements used to represent proportions and shapes) from quantitative character tables. The data set contains ten genitalic characters (six male and four female) and 19 characters of somatic morphology. All eight

triple-state characters were treated as ordered because all appear to have discrete intermediate character states. The range, mean and standard deviation for each of the ratio and meristic characters are given in Table 1. These characters were selected from the much larger set of quantitative characters surveyed in this study because they distinguish clusters of species with nonoverlapping values or with mean values significantly different ($P < 0.05$) from other such clusters (see, for example, Figs. 1, 2). Thiele (1993) has argued convincingly and demonstrated with botanical data sets that quantitative (morphometric) characters are useful in cladistic analyses, and the second author has found this to be true in his cladistic analyses of other mygalomorph spider genera (Coyle 1994, 1995).

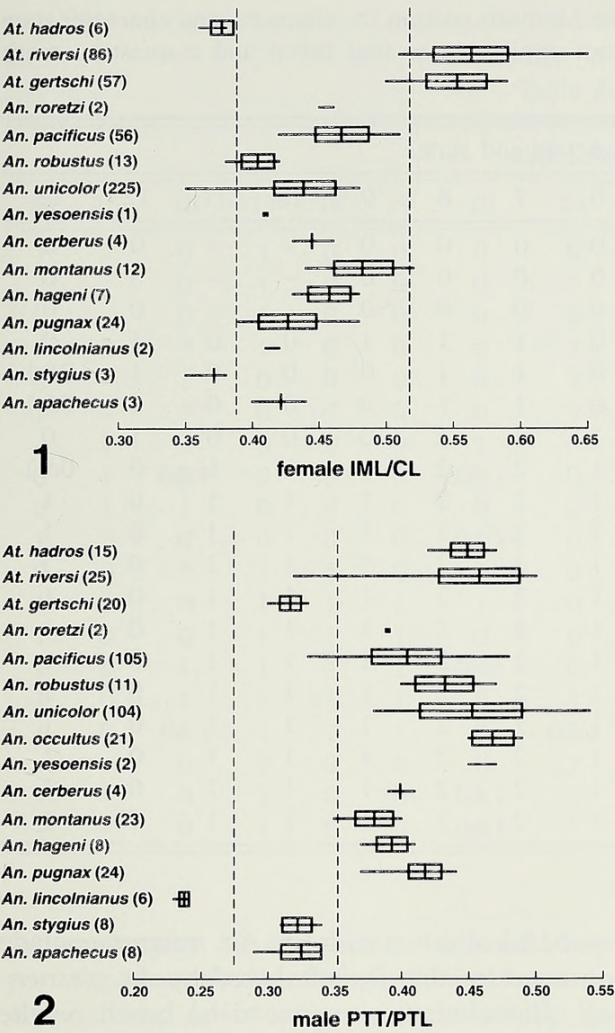
Three outgroup taxa were used to polarize character evolution: the genus *Aliatypus*, *Aliatypus gulosus*, and a hypothetical ancestral taxon. Despite problems with the putative synapomorphies that unite *Aliatypus* with the other antrodiaetids, current consensus places *Aliatypus* as the sister genus of the *Atypoides* plus *Antrodiaetus* lineage (Raven 1985; Goloboff 1993; Coyle 1994). *Aliatypus gulosus* is the most primitive *Aliatypus* species and shares with *Antrodiaetus* plus *Atypoides* certain apparently plesiomorphic traits of the male and female genitalia that have probably been modified in all other *Aliatypus* species (Coyle 1974, 1994). For both of these outgroups, character states were determined from data in Coyle (1974). The hypothetical ancestral taxon was based on the most probable primitive character states exhibited by species of *Aliatypus* and the family Atypidae, which is considered to be the sister group of the Antrodiaetidae (Raven 1985; Coddington & Levi 1991; Goloboff 1993) or, along with the mecicobothriids, part of the sister group of the antrodiaetids (Eskov & Zonshtein 1990). We determined these putative ancestral states by examining hypotheses and data on *Aliatypus* (Coyle 1974, 1994), *Sphodros* (Gertsch & Platnick 1980), and *Atypus* (Schwendinger 1989, 1990), and by studying specimens of *Sphodros rufipes* (Latrielle) and *Sphodros abboti* Walckenaer. The use of a hypothetical outgroup taxon was deemed desirable because *Aliatypus* appears to be a highly derived assemblage of species in which many ancestral conditions seem to have been modified, in

part, at least, during an adaptive shift into a xerophyllic/trapdoor adaptive zone (Coyle & Icenogle 1994).

Independent cladistic analyses were performed using each of the three outgroup taxa. Each data matrix was analyzed using the branch and bound tree searching algorithm of PAUP version 3.1 for the Apple Macintosh (Swofford 1993). Successive *a posteriori* character weighting of the resulting trees was performed using each of the three options available in PAUP: the consistency index (CI), the retention index (RI), and the rescaled consistency index (RC). Further analysis was conducted using MacClade version 3.0 (Maddison & Maddison 1992).

Character states.—The character state data used in the analysis are presented in Table 2 and Fig. 3. Abbreviations and definitions for measurements, meristic characters and structures are given in Coyle (1968, 1971). In brief, they are: ALS, anterior lateral spinnerets; CL, carapace length; CMT, number of microteeth on each chelicera; ICS, inner conductor sclerite of the male palpus; IML, length of metatarsus I; IMS, number of ensiform macrosetae (spines) on female metatarsus I; ITL, length of tibia I; IVCTR, number of teeth on retrolateral claw of left tarsus IV; IVML, length of metatarsus IV; OCS, outer conductor sclerite of the male palpus; PTL, length of palpal tibia; PTT, maximum diameter of palpal tibia, in lateral view. An expanded treatment of each character used in the analysis follows. Characters 6, 10, 11, and 12 describe conditions that are visible when the prolateral surface of the left male palp is viewed with the conductor tips pointing upwards (as in Coyle 1971, figs. 188, 190, etc.).

1. Number of microteeth on female chelicera: 0 = large (mean CMT > 11); 1 = small (mean CMT < 8). 2. Number of ensiform macrosetae on female metatarsus I: 0 = small (mean IMS = 8–15); 1 = large (mean IMS = 22–25). 3. Number of teeth on retrolateral claw of female left tarsus IV: 0 = small (mean IVCTR < 2); 1 = moderate (mean IVCTR = 3–4); 2 = large (mean IVCTR > 6). 4. Female metatarsus I: 0 = relatively short (mean IML/CL = 0.37–0.38); 1 = of moderate length (mean IML/CL = 0.40–0.48); 2 = relatively long (mean IML/CL = 0.55–0.56). 5. Male tibia I prolateral mating setae: 0 = absent; 1 = present. 6. Left arm of ICS base: 0



Figures 1, 2.—Diagrams comparing quantitative character values of *Atypoides* and *Antrodiaetus* species to demonstrate method used for coding quantitative characters. Horizontal bar represents the range, vertical bar the mean, and box the standard deviation (when $n > 4$). Sample size is given next to species name. Vertical dashed lines separate clusters of species with mean values significantly different ($P < 0.05$) from other such clusters; these are the character state boundaries. 1, Female IML/CL; 2, Male PTT/PTL.

= weak; 1 = strong and heavily sclerotized. 7. Cheliceral apophysis: 0 = absent; 1 = well developed; 2 = vestigial. All *Antrodiaetus* males have an anterior-dorsal cheliceral prominence which, because of its position, is very probably a homologue of the cheliceral apophysis of *Atypoides* (Coyle 1971). We agree with Coyle (1971) that the high intra- and interspecific variability in the size and form of this prominence, and its small size in all species, support the hypothesis that it is a nonfunctional vestige of the cheliceral apoph-

ysis. Our coding represents this hypothesis. Coding the prominence as rudimentary (as state 1, intermediate between the well developed apophysis of *Atypoides* and the outgroup condition in which no sign of this structure is evident), does not alter the topology of the shortest trees, but it lengthens and increases the homoplasy of these shortest trees. 8. ALS with: 0 = two articles; 1 = one article; 2 = absent. 9. Spermathecal stalks: 0 = long; 1 = short. 10. Dorsal profile of ICS tip (the left side of the terminal part of the ICS): 0 = concave; 1 = convex. 11. Apex of OCS: 0 = on left side of ICS tip; 1 = on right side of ICS tip. 12. OCS: 0 = narrow distally; 1 = broad distally. 13. Anterior margin of bursa copulatrix: 0 = bilobed; 1 = not bilobed. 14. Percent of male tibia I ventral retrolateral macrosetae which are ensiform: 0 = rarely $> 30\%$; 1 = rarely $< 40\%$. 15. Percent of male tibia I prolateral macrosetae which are ensiform: 0 $> 30\%$; 1 $< 30\%$. 16. Floor of bursa copulatrix: 0 = weakly sclerotized; 1 = with areas of moderate to heavy sclerotization. 17. Male tibia I: 0 = considerably shorter than metatarsus I (mean $ITL/IML = 0.71-0.81$); 1 = slightly shorter than metatarsus I (mean $ITL/IML = 0.85-0.99$); 2 = slightly longer than metatarsus I (mean $ITL/IML > 1.0$). 18. Male tibia I prolateral profile: 0 = more or less straight; 1 = strongly convex. 19. Male tibia I ventral retrolateral macrosetae: 0 = scattered; 1 = clustered. 20. Male metatarsus I distal macroseta: 0 = present; 1 = absent. 21. Seta-less area on upper ectal surface of chelicera: 0 = present; 1 = absent. 22. Male metatarsus I ventral retrolateral protuberance: 0 = absent; 1 = present. 23. Spermathecal bowl: 0 = large and heavily sclerotized; 1 = small and weakly sclerotized. 24. OCS surface sculpture: 0 = strongly file-like to serrate; 1 = smooth or weakly file-like. 25. Male tibia I prolateral mating setae: 0 = large (macrosetae); 1 = small (bristles). 26. Male palpal tibia in lateral view: 0 = thickest proximally; 1 = cylindrical; 2 = thickest distally. 27. Male palpal tibia: 0 = relatively short and thick (mean $PTT/PTL = 0.37-0.47$); 1 = of moderate length and thickness (mean $PTT/PTL = 0.31-0.33$); 2 = relatively long and thin (mean $PTT/PTL < 0.24$). 28. Sclerotization of OCS: 0 = weak to moderate; 1 = strong. 29. Female metatarsus IV: 0 = relatively short (mean $IVML/CL < 0.53$); 1 = of moderate length

Table 2.—Data matrix used for cladistic analyses. See Methods section for character and character state descriptions. A hyphen indicates that a character is not applicable to that taxon and a question mark indicates that the character state is unknown.

Taxa	Characters and states												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Aliatypus</i>	0&1	0&1	0	0	0	0	0	0	0	-	-	0	0
<i>Al. gulosus</i>	0	0	?	0	0	0	0	0	0	-	-	0	0
hypoth. ances.	0	0	1	0	0	0	0	0	0	-	-	0	0
<i>At. hadros</i>	1	0	1	0	1	0	1	1	1	0	0	1	0
<i>At. riversi</i>	0	1	2	2	0	0	1	1	0	0	0	1	0&1
<i>At. gertschi</i>	0	1	2	2	0	0	1	1	0	0	0	1	0&1
<i>An. roretzi</i>	1	0	1	1	1	1	2	2	0	0	0	1	0
<i>An. pacificus</i>	0	0	1	1	1	1	2	2	1	1	1	0	0&1
<i>An. robustus</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. unicolor</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. occultus</i>	?	?	?	?	1	1	2	2	?	1	1	0	?
<i>An. yesoensis</i>	1	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. cerberus</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. montanus</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. hageni</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. pugnax</i>	0	0	1	1	1	1	2	2	1	1	1	0	1
<i>An. lincolnianus</i>	0	0	0	1	1	1	2	2	1	1	1	0	1
<i>An. stygius</i>	0	0	0	0	1	1	2	2	1	1	1	0	1
<i>An. apachecus</i>	0	0	0	1	1	1	2	2	1	1	1	0	1

(mean IVML/CL = 0.55–0.65); 2 = relatively long (mean IVML/CL > 0.67).

RESULTS AND DISCUSSION

Regardless of which outgroup was used, a branch and bound tree search followed by *a posteriori* weighting (using either the RI or RC) generated the same set of four shortest trees (Figs. 3, 4). These four trees differed only in the relationships among *An. pacificus*, *An. robustus*, and *An. unicolor*. All four trees contained a trichotomy involving *An. yesoensis*, *An. cerberus* and the *An. montanus* clade (clade 9 in Fig. 3). Re-weighting using the CI generated these same four trees plus four additional equally short trees identical in topology to the other four except that this trichotomy was resolved. All eight trees were shortest (length (TL) = 68, CI = 0.71, RI = 0.76, RC = 0.53) when using the hypothetical ancestral outgroup, longer (TL = 71, CI = 0.68, RI = 0.73, RC = 0.50) when *Aliatypus gulosus* was the outgroup, and even longer (TL = 77, CI = 0.71, RI = 0.74, RC = 0.53) when the genus *Aliatypus* was the outgroup.

The resolution of clade 9 generated by *a posteriori* weighting using the CI shows *An.*

cerberus sharing with the *An. montanus* clade an ancestor that is not shared by *An. yesoensis*. However, this seems to be based on the weighting of the highly homoplastic character 20. Because of the high degree of polymorphism exhibited by this character, particularly in species with large sample sizes, and because *An. cerberus* and *An. yesoensis* are represented by small sample sizes, we consider this resolution to be dubious. The reduction of the seta-less area of the chelicera in some females of *An. cerberus* (Coyle 1971) may provide additional evidence that it and the *An. montanus* clade (which is united, in part, by the synapomorphic loss of the seta-less area in both sexes, character 21) share a recent common ancestor. However, we prefer to consider these relationships unresolved until more convincing evidence can be found to support a solution to the trichotomy.

The monophyly of the *An. lincolnianus* clade (clade 10) is strongly supported by characters 3 and 23–28 (Fig. 3). A sister species relationship between *An. stygius* and *An. apachecus* is supported by character 29. Monophyly of the *An. occultus* clade (clade 7) is supported by character 18. Clade 8 is supported by

Table 2.—Extended.

Characters and States															
14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
?	-	0	1	0	0	0	0	0	-	0&1	-	1&2	0&2	0	0&1
?	-	0	1	0	0	0	?	0	-	0	-	1	2	0	0
?	-	0	1	0	0	0	0	0	-	0	-	0	0	0	1
0	0	?	1	0	0	0	?	0	0	0	0	0	0	1	0
0	-	1	0	0	0	0	?	0	0	0	-	0	0	1	1
1	-	?	0	0	0	0	?	0	1	0	-	1	1	1	2
-	1	?	0	0	0	1	0	0	1	0	0	0	0	1	1
0	1	0&1	0	0	0	0&1	0	0	0	0	0	0	0	1	1
0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
1	0	0	0	0	0	0&1	0	0	0	0	0	0	0	1	1
0	0	?	1	1	0	1	0	0	?	0	0	0	0	1	?
1	0	0	1	1	1	1	0	0	?	0	0	0	0	1	1
1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1
1	0	1	1	1	1	0&1	1	0	0	0	0	0	0	1	1
1	0	1	1	1	1	0	1	1	0	0	0	0	0	1	1
1	0	0&1	1	1	1	0	0&1	1	0	0	0	0	0	1	1
-	-	0	2	0	0	0	?	0	1	1	1	2	2	0	1
-	-	0	1	0	0	0&1	?	0	1	1	1	2	1	0	0
-	-	0	1	0	0	0&1	?	0	1	1	1	2	1	0	0

synapomorphy 19. Characters 16 and 21 support the monophyly of clade 9, the *An. montanus* clade. A sister species relationship between *An. hageni* and *An. pugnax* is supported by synapomorphy 22. The monophyly of clade 6 is weakly supported by character 17, which appears to have undergone a reversal in the progenitor of this clade. Clade 5 is weakly supported by characters 14–16. Character 14 could be interpreted as a synapomorphy of clade 8 with a parallelism in *An. unicolor* or as a synapomorphy of clade 5 with a reversal in *An. occultus*; both scenarios are equally parsimonious. Characters 15 and 16 both appear to be reversals to the outgroup condition. *Antrodiaetus roretzi* is clearly the most plesiomorphic species in the genus, with all other *Antrodiaetus* species forming a clade (clade 3) defined by characters 9–12, the last of which appears to involve a reversal. The monophyly of *Antrodiaetus* (clade 2) is strongly supported by synapomorphies 5–8. Coyle (1971) incorporated two of these synapomorphies (7, 8) in his phylogeny; we are proposing the other two (5, 6) for the first time. A sister species relationship between *At. riversi* and *At. gertschi* is well supported by characters 2–4. While characters 4 and 17

support the monophyly of clade 1, it should be noted that character 5 seems to contradict this resolution, supporting a sister relationship between *At. hadros* and *Antrodiaetus* to the exclusion of *At. riversi* plus *At. gertschi*. Although relationships among *An. pacificus*, *An. robustus*, and clade 5 are ambiguous and cannot be resolved by this data matrix, there is evidence (albeit weak) to support our preferred phylogeny (Fig. 3). The vestigial male cheliceral apophysis is usually more prominent in *An. pacificus* than in other *Antrodiaetus* species (Coyle 1971), suggesting that this apophysis may have undergone further degeneration in the ancestor of all other North American *Antrodiaetus* species (clade 4). Also, the population of *An. pacificus* in eastern Washington, eastern Oregon and Idaho has a bilobed bursa copulatrix (character 13); this presumably ancestral condition is distinct from the unlobed condition of clade 4. We should also point out, however, that *An. robustus*, alone among the *Antrodiaetus* species, retains minute ALS vestiges (Coyle 1971), suggesting that loss of these spinnerets was not yet complete when this species diverged, and therefore that the lineage leading to this species may have originated earlier than *An.*

pacificus. Our preferred phylogeny (Fig. 3) requires a less complex biogeographic history that can be more easily correlated with known events than is the case for the other equally short trees (see below).

Our cladistic analyses have produced a phylogeny that is not only better resolved than Coyle's (1971, fig. 69) phylogeny, but significantly different in other ways. We have concluded that the three species of *Atypoides* (*sensu* Coyle 1968, 1971) probably comprise a paraphyletic group and that Coyle's *An. unicolor* species group (which included all *Antrodiaetus* species but *An. roretzi* and the three *An. lincolnianus* group species) is likewise paraphyletic. Our analyses support Coyle's hypotheses that *Antrodiaetus* is monophyletic, the *An. lincolnianus* group is monophyletic, and *An. stygius* and *An. apachecus* are sister species. They likewise support his contention that *An. roretzi* is a relict of a branch attached near the base of the *Atypoides* plus *Antrodiaetus* tree. We do not feel any urgency to formalize our hypothesis that *Atypoides* is paraphyletic. If further studies corroborate our findings, then *Atypoides* should be designated a junior synonym of *Antrodiaetus*.

BIOGEOGRAPHY

Mygalomorph spiders have been featured prominently among the few papers that have dealt with the historical biogeography of spiders (Pocock 1903; Raven 1980; Platnick 1981; Griswold 1991). Although early work on spider biogeography assumed that continents were stable and areas of high diversity were centers of origin (Pocock 1903), plate tectonics and cladistics have caused a drastic paradigm shift. Armed with an improved phylogeny, and knowledge and methodologies unavailable to Coyle in 1971, we should be able to improve upon his hypotheses about the biogeographic history of *Atypoides* and *Antrodiaetus*. Our biogeographic analysis proceeds from the model of vicariance biogeography as described by Croizat et al. (1974) and first applied to spiders by Platnick (1976). Briefly stated, we will presume that sister clades diverged from a common ancestor in response to a physical or ecological barrier which divided its range to prevent gene flow between the incipient sister taxa. We will also assume that clades evolved more or less in place.

All three species of *Atypoides* and 11 of the

13 *Antrodiaetus* species are endemic to North America (Coyle 1971). The North American species occupy three isolated provinces of endemism (Fig. 5): a western province containing *At. riversi*, *At. gertschi*, *An. pacificus*, *An. occultus*, *An. cerberus*, *An. montanus*, *An. pugnax* and *An. hageni*; an eastern province including *At. hadros*, *An. robustus*, *An. unicolor*, *An. lincolnianus* and *An. stygius*; and a southwestern province occupied solely by *An. apachecus*. The remaining two species, *An. roretzi* and *An. yesoensis*, are known only from the Japanese islands of Honshu and Hokkaido, respectively.

The *An. occultus* clade (Clade 7), with the exception of the Japanese species *An. yesoensis*, occurs only in the western province, and the *An. lincolnianus* clade (clade 10) is rooted in the eastern province. Thus, for all four candidate phylogenies (Figs. 3, 4), we can imagine the common ancestor of these two clades (the progenitor of clade 6) being split by a barrier into an eastern (*An. lincolnianus*) and a western (*An. occultus*) lineage. Later range expansions and vicariance events are required to explain the existence of *An. yesoensis* on Hokkaido and *An. apachecus* in Arizona and New Mexico. The other species in these two clades can be thought of as having differentiated as the result of more localized isolation.

In an attempt to resolve the ambiguous relationships among *An. pacificus*, *An. robustus*, and *An. unicolor*, we can evaluate the merits of our four competing phylogenies (Figs. 3, 4) by considering the biogeographic consequences of each. The trichotomy in Fig. 4a makes this cladogram uninformative regarding the biogeographic history of *An. pacificus*, *An. robustus*, and *An. unicolor*. The tree in Fig. 4b requires that an ancestral population would have to be divided into eastern and western taxa and then the western lineage would have to expand its range to the east and be divided again. All this would have to predate the origin of the *An. occultus* plus *An. lincolnianus* clade. The cladogram in Fig. 4c requires the same number of interprovincial range expansions and vicariance events, but the event that led to the divergence of *An. pacificus* and *An. robustus* need not have occurred before the rise of the *An. occultus* plus *An. lincolnianus* clade. Our preferred cladogram (Fig. 3) is biogeographically more par-

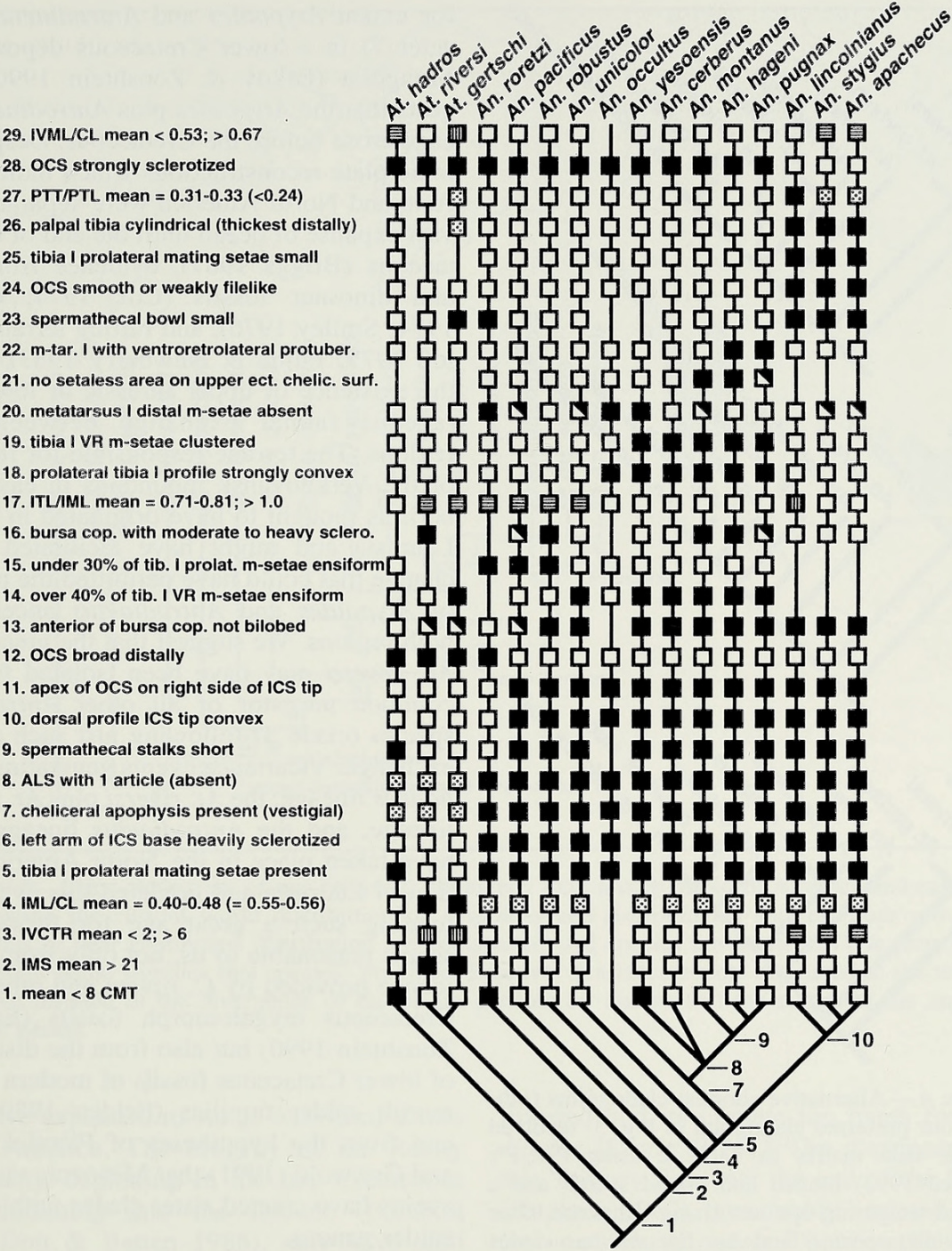


Figure 3.—Preferred cladogram of *Atypoides* and *Antrodiaetus* species. Numbers at nodes are used to identify clades discussed in the text. The plesiomorphic character state (i.e., the state of the hypothetical ancestral taxon) is denoted by a white box. For those characters (10, 11, 15, 23, and 25) where the outgroup state is unknown or not applicable, the state exhibited by *A. hadros* is denoted by a white box. Apomorphic states are described to the left of the cladogram and designated by patterned boxes. For binary characters, the apomorphic state is denoted by a black box. For triple-state characters where the two derived states are closer to each other than one of them is to the ancestral state, the intermediate state is described first and denoted by grey (stipples) and the extreme apomorphic state is described in parentheses and denoted by black. For triple-state characters where each derived state is closer to the ancestral state than to the other derived state, the first described state is designated by horizontal lines and the state following a semicolon is designated by vertical lines. Polymorphic taxa (exhibiting two or more states) are denoted by half white, half black boxes.

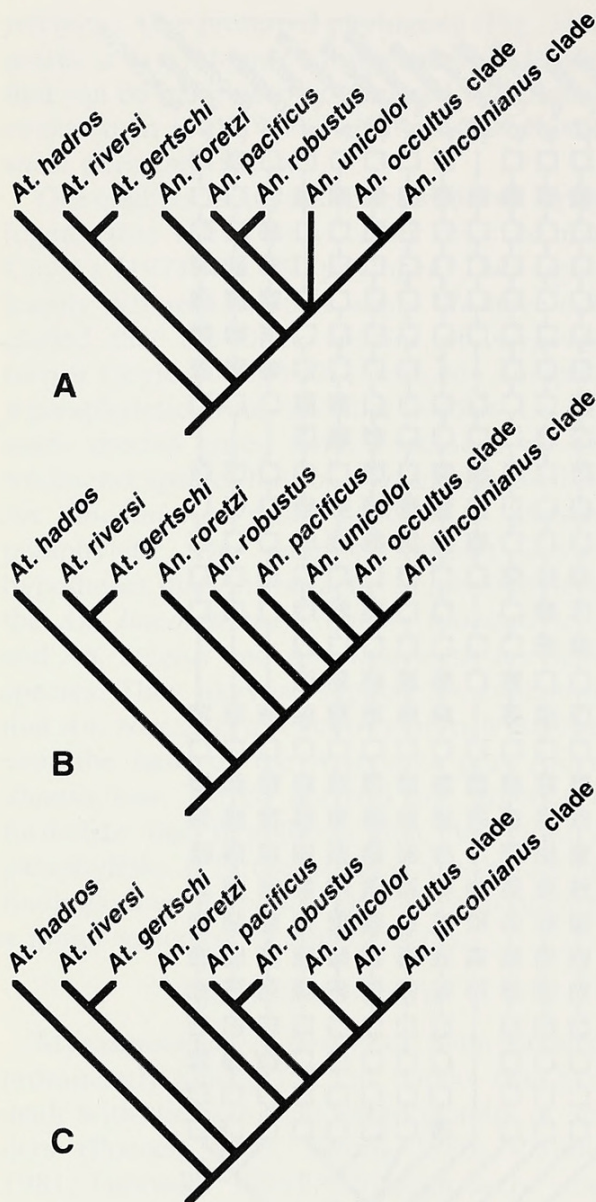


Figure 4.—Alternative shortest cladograms (other than our preferred cladogram in Fig. 3) resolved from the data matrix in Table 2 using PAUP's (Swofford 1993) branch and bound search and a posteriori weighting options. Using either the RI or RC, the *An. occultus* and *An. lincolnianus* clades are identical to clades 7 and 10, respectively, in the Fig. 3 cladogram.

simonious because it requires the fewest interprovincial range expansion events.

Proceeding from this preferred phylogeny, we will propose a scenario using known or suspected geological and ecological events which could have produced the observed distribution of *Antrodiaetus* species. The discovery of a fossil mygalomorph spider, *Cretacatyma raveni* Eskov & Zonshtein 1990, with a cheliceral apophysis (a unique synapomorphy

for extant *Atypoides* and *Antrodiaetus*, character 7) in a lower Cretaceous deposit from Mongolia (Eskov & Zonshtein 1990), suggests that the *Atypoides* plus *Antrodiaetus* lineage arose before the Cretaceous. Despite tectonic plate reconstructions which indicate that Asia and North America were separated by a vast expanse of ocean until the end of the Cretaceous (Briggs 1987), evidence from plant and dinosaur fossils (Cox 1974; Cracraft 1974; Smiley 1976), and rafting terranes (Pie-lou 1979; Fujita & Newberry 1983) suggest the existence of upper Jurassic or lower Cretaceous faunal exchange between these regions. The terrane responsible for the uplift of the Verkhoyansk mountains in eastern Siberia is thought to have originated in western Laurasia and might have facilitated an exchange that could have permitted the presence of *Atypoides* and *Antrodiaetus* ancestors in both regions. We suggest that the precursor of *An. roretzi* may have been isolated from the common ancestor of all other *Antrodiaetus* species (clade 3) following just such a faunal exchange. Vicariance events generating the *At. hadros* lineage, the *At. riversi* plus *At. gertschi* lineage, and the *Antrodiaetus* lineage would have taken place in the North American portion of Laurasia and predated this event. Postulating such a great age for these events seems reasonable to us, not only from the evidence provided by *C. raveni* and other lower Cretaceous mygalomorph fossils (Eskov & Zonshtein 1990) but also from the discoveries of lower Cretaceous fossils of modern araneomorph spider families (Selden 1989, 1990) and from the hypotheses of Platnick (1976) and Griswold (1991) that Mesozoic vicariance events have created sister clades within extant spider genera.

The next important vicariance event in the history of the lineage, the isolation of the progenitor of *An. pacificus* from that of all other *Antrodiaetus* species (clade 4), may have been caused by the formation of the Mid-Continental Seaway separating eastern and western North America in the mid-Cretaceous (Cox 1974; Hallam 1979; Briggs 1987). By the beginning of the Tertiary, the Mid-Continental Seaway had receded (Cox 1974; Cracraft 1974), and during the early Tertiary, much of North America was covered by tropical to warm-temperate forests (Cracraft 1974). Under these conditions, the ancestor of clade 6

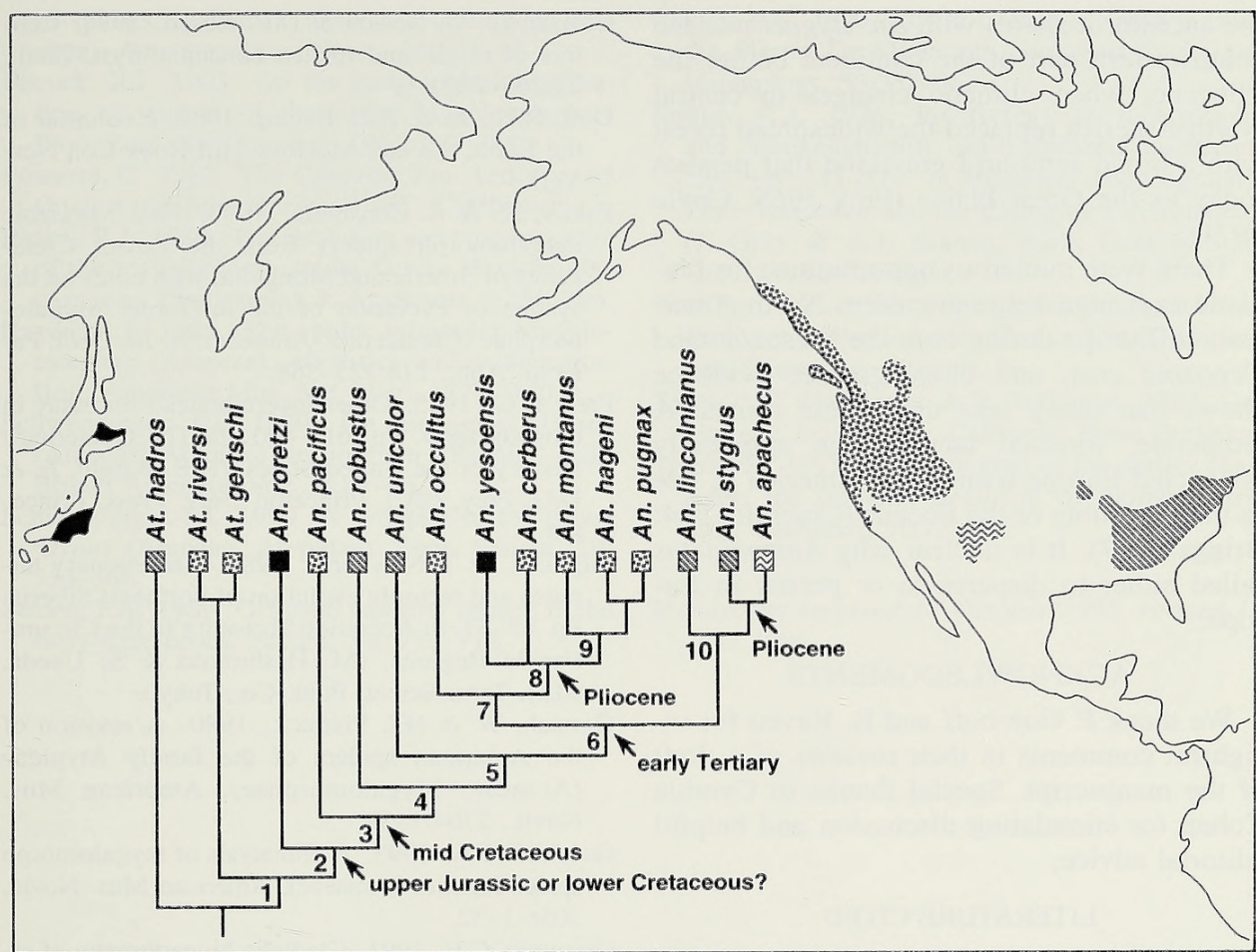


Figure 5.—Area cladogram of our preferred phylogeny with a map of North America and eastern Asia and showing the current world distribution of *Atypoides* and *Antrodiaetus* species. Four provinces of continuous or near continuous distribution are demarcated. All species are limited to one province. Box near species name signifies that species' province. Putative vicariance events discussed in the text which may have resulted in the divergence of clades are denoted by arrows and the names of the appropriate geologic period.

may have expanded its range westward across North America. The orogeny of the Rocky Mountains, beginning in the late Cretaceous and continuing into the Eocene (Pomeroy 1982; Dott & Batten 1988), may have split this clade into western (clade 7) and eastern (clade 10) clades. The importance of the uplift of these mountains is supported by the current absence of antrodiaetid spiders from all but the southern-most outliers of the Rocky Mountains.

During the late Oligocene and mid-Miocene, a region of mixed mesophytic forest which connected the North Pacific from Oregon to Japan via a Bering land connection (Hopkins 1967) offered the last ecologically favorable opportunity for the expansion of *Antrodiaetus* into east Asia (Coyle 1971). (The more recent Pleistocene connection was un-

forested and its climate too harsh for *Antrodiaetus* [Coyle 1971].) The disappearance of this Tertiary link near the end of the Pliocene (Hopkins 1967) presumably isolated the ancestor of *An. yesoensis*. The remarkable physiographic and climatic fluctuations in the Pacific Northwest during the Pliocene and Pleistocene may have fostered the divergence of *An. montanus*, *An. pugnax*, *An. hageni* and *An. cerberus* (see Coyle 1971, p. 399). Land connections between Japan and the Asian mainland are believed to have developed periodically beginning in Mesozoic times and occurred as recently as the Pleistocene (Takai et al. 1963) and must be responsible for the existence of both *An. roretzi* and *An. yesoensis* on Japanese islands.

The western distribution of *An. apachecus* is probably the result of a range expansion by

the ancestor it shares with *An. stygius* into the southwestern part of the continent before the Pliocene, when climatic changes in central North America replaced the widespread forest with a broad semi-arid grassland that persists today as the Great Plains (Frey 1965; Coyle 1971).

There were numerous opportunities for faunistic exchange between eastern North America and Europe during both the Mesozoic and Cenozoic eras, and biogeographic evidence shows that many taxa used these routes. A temperate, forested land bridge apparently connected Europe with North America as late as the beginning of the Eocene (Cracraft 1974; Briggs 1987). It is unclear why *Antrodiaetus* failed either to disperse to or persist in Europe.

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