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David L. Stern

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PHYLOGENY OF THE TRIBE CERATAPHIDINI (HOMOPTERA) AND THE EVOLUTION OF THE HORNED SOLDIER APHIDS

DAVID L. STERN¹

Wellcome/CRC Institute and Department of Genetics, University of Cambridge, Tennis Court Road, Cambridge CB2 1QR, UK

Abstract.—The horned soldier aphids of the Cerataphidini, unlike most social insects that reside in nests, live on the open surface of plants. The lack of a nest and other obvious ecological correlates makes it unclear why secondary-host soldiers might have evolved. Here I present a molecular phylogenetic analysis of 32 species of the Cerataphidini, including 10 species from the genera *Ceratovacuna* and *Pseudoregma* that produce horned soldiers. The phylogeny suggests that horned soldiers evolved once and were lost once or twice. Most horned soldiers are a morphologically specialized caste and two species that have unspecialized soldiers are independently derived from species with specialized castes. The genus *Ceratovacuna* appears to have undergone a relatively rapid radiation. Mapping secondary-host plants and geographic ranges onto the phylogeny suggests that bamboos were the ancestral secondary-host plants and that the Asian tropics and subtropics were the ancestral geographic regions for the genera *Astegopteryx*, *Ceratoglyphina*, *Ceratovacuna*, *Chaitoregma*, and *Pseudoregma* and possibly for the entire tribe. There is evidence for vicariant events that separate the tropical and subtropical lineages in all of the major lineages of the tribe and for dispersal of some lineages. Based on these results, I present hypotheses for the causes and consequences of horned-soldier evolution.

Key words.—Biogeography, Cerataphidini, eusociality, mitochondrial DNA, molecular phylogenetics, social behavior, soldier aphids.

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The social insects have intrigued biologists since before Darwin and have been the touchstone ever since for theory explaining the existence of social and altruistic behavior (e.g., Haldane 1923; Fisher 1930; Hamilton 1964; Maynard Smith 1964; Wilson 1971, 1975). Despite extensive study of the social insects, there is a paucity of evidence relevant to the origins of sociality. This may be because the best studied social insects (social bees, wasps, ants, and termites) live in colonies with complex social systems that are not representative of the initial conditions of social evolution. Relevant data must come from species that display primitive forms of sociality and preferably from taxa that display variation in the presence and extent of sociality (Choe and Crespi 1997).

The recently discovered soldier-producing aphids (Aoki 1977) provide a novel and rich source for studies of the early stages of insect sociality (Stern and Foster 1996, 1997). Soldiers have evolved many times in the two sister families Hormaphididae and Pemphigidae (Aoki and Miyazaki 1985; Aoki 1987; Aoki and Kurosu 1989a; Stern 1994; Stern and Foster 1996). Since aphids do not forage—each individual derives all its nutrition by plugging into plant vascular tissue—the primary social activity is defense, although some species have also evolved the altruistic behavior of cleaning their residence (Kurosu and Aoki 1991; Benton and Foster 1992; reviewed in Stern and Foster 1996). Aphids are also unusual among the social insects in that they reproduce parthenogenetically. There should be no genetic conflict of interest within a colony derived from a single foundress. This focuses the study of social evolution in aphids on two issues: the extent of clonal mixing within colonies and the ecological conditions favoring soldier production (Stern and Foster 1996). These studies should be set in a historical framework

to allow robust comparative analysis (Harvey and Pagel 1991). Although there is little genetic data as yet (Fukatsu and Ishikawa 1994), the expected lack of genetic conflict within colonies suggests that soldiers should evolve easily (Krebs and Davies 1993). Soldiers are expected to evolve when benefits to the clone (rather than the individual) outweigh costs to the clone (Stern and Foster 1996). However, only 1% of aphids produce soldiers, which suggests that clonality is not sufficient to promote sociality.

The horned-soldier aphids of the Cerataphidini and several species of *Colophina* in the family Pemphigidae are unique among the social insects because they do not live in anything remotely resembling a nest. The horned-soldier aphids live in colonies on the surface of plant stems or leaves. All other soldier-producing aphids live in plant galls, and galls have apparently favored the evolution of soldiers (Foster and Northcott 1994; Stern and Foster 1996, 1997) as nests have promoted the evolution of sociality in other groups (Abe 1991; Alexander et al. 1991; Crespi 1994). No other social arthropod is known to live in such an exposed manner (cf. social mites in webs [Saito 1986], ants, bees, wasps, and termites in various nests [Wilson 1971], and social shrimp in sponges [Duffy 1996]) and the highly social vertebrates, such as the naked mole rats, also live within well-protected nests (Sherman et al. 1991).

Horned soldiers are limited to two closely related (Stern 1994) genera, *Ceratovacuna* and *Pseudoregma*. In most of these species, first-instar larvae are dimorphic and soldiers are the larger morph (Fig. 1; Aoki and Miyazaki 1978; Aoki et al. 1981; Stern et al. 1996). In two species, *C. lanigera* and *P. near-bambucicola* (Stern et al. 1997b), larvae are monomorphic, but at least some of the first-instar larvae attack predators with a behavior similar to the other horned soldiers, piercing predators with their enlarged cephalic horns (Aoki and Kurosu 1987).

Most cerataphidine aphids alternate between two host

¹ Present address: Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; E-mail: ds205@cus.cam.ac.uk.

plants, the primary host, where they produce a gall, and the secondary host (see Stern et al. 1997a). The horned soldiers occur on the secondary host. In galls on the primary host, all cerataphidines produce soldiers. Behavioral, morphological, and phylogenetic evidence suggest that primary- and secondary-host soldiers are not homologous and that horned soldiers evolved after the primary-host soldiers (Aoki 1987; Aoki and Kurosu 1989a; Fukatsu et al. 1994; Stern 1994).

The unusual biology of the horned soldiers suggests that they may have evolved sociality for novel reasons. Because there are no clear correlates of sociality in these species, it is important to clarify the history of this group, including the number and pattern of origins and losses of soldiers and the evolution of possible correlates of soldiers. Here I present a molecular phylogenetic analysis of 32 species of the Cerataphidini. I use the phylogeny to examine the patterns of horned-soldier evolution, the evolution of secondary-host plant use, and historical geographic distributions. Based on these observations, I generate hypotheses for the causes of the evolution of horned soldiers and for their current geographic distribution.

MATERIALS AND METHODS

Insect Samples, DNA Extraction, PCR Amplification, and DNA Sequencing

Aphids were collected and DNA sequenced as previously described (Stern 1994; Stern et al. 1997a). Regions of the mitochondrial Cytochrome Oxidase I and II gene were sequenced (see Stern et al. 1997a). Table 1 shows the samples used in this study, together with lifecycle and soldier information, collection data, the amount of sequence data collected, and the Genbank accession numbers. Specimens of all samples were deposited in the Natural History Museum, London.

Phylogenetic Analysis

I utilized three methods of phylogeny estimation: neighbor joining, maximum parsimony, and maximum likelihood. The neighbor-joining (NJ) algorithm (Saitou and Nei 1987) was implemented with the computer program NEIGHBOR of PHYLIP vers. 3.53c (Felsenstein 1993). Distance matrices were estimated with the maximum-likelihood (ML) method of DNADIST (PHYLIP) with a transition/transversion ratio of 1.45. A second distance matrix was calculated assuming four different rates of evolution at the three codon positions and the tRNA positions, respectively. The number of changes at each kind of site was estimated with the "Character Steps/etc." option of MacClade calculated over the original NJ tree. The relative probability of change was calculated as the number of steps at each kind of site divided by the total number of steps (codon position 1 = 1.19; position 2 = 0.52; position 3 = 3.36; tRNA = 0.77). One-hundred bootstrap replicates were performed assuming equal rates of evolution at all sites. PHYLIP does not allow for bootstrapping with variable rates among sites.

I implemented maximum-parsimony (MP) analysis (for reviews see Felsenstein 1983; Swofford and Olsen 1990) with the Heuristic algorithm of the computer program PAUP vers.

3.1.1 with 10 random addition sequences and TBR branch swapping (Swofford 1993). I ran 100 bootstrap replicates using the heuristic search algorithm. Two analyses were run, one with all sites weighted equally and one with sites weighted relative to their probability of change as described above.

ML estimation of the phylogeny was performed with the computer program fastDNAML (Felsenstein 1981; Olsen et al. 1994). Since extensive searching of trees was prohibitively time consuming with the ML method, I performed global branch-swapping starting with the MP tree. For the ML search, I used the same transition/transversion ratio and four categories of substitution as above.

To compare the results from the different methods, I generated the strict consensus tree of all three methods, since regions of agreement between methods are likely to represent well supported groups (Kim 1993). For all subsequent analyses I used each tree and also the strict consensus tree separately and compared the results.

Testing Alternative Hypotheses of Horned-Soldier Evolution

I tested whether qualitatively different hypotheses of horned-soldier evolution were plausible by comparing the highest-likelihood phylogenies that supported alternative hypotheses using the paired-sites test (Kishino and Hasegawa 1989) as implemented in fastDNAML. Three hypotheses were tested: (1) the horned soldier-producing aphids are monophyletic; (2) the horned soldier-producing aphids with dimorphic larvae are monophyletic; (3) the genus *Ceratovacuna* is monophyletic (Fig. 4).

Mapping Traits

I mapped three traits onto the trees using the computer program MacClade (Maddison and Maddison 1992) under both ACCTRAN and DELTRAN assumptions: (1) presence or absence of horned soldiers (Table 1); (2) secondary-host plant, primarily at the family level; and (3) the geographic region where the species is found. In addition, I used dispersal-vicariance analysis (Ronquist 1997) to further explore the historical biogeography of the tribe.

Secondary-host plant data were compiled from my collection data, a survey of all cerataphidine samples in the Natural History Museum, London, and from Noordam (1991) and Blackman and Eastop (1994). For the Gramineae, host plants were divided into bamboos or broad-leaved grasses, such as *Oplismenus* and *Microstegium*.

All cerataphidine aphids are found within Southeast Asia, and several species have spread pantropically (for example *Pseudoregma panicola* [Aoki 1982], *Cerataphis brasiliensis*, *C. lataniae*, and *C. orchidearum* [Stern et al. 1995; Russell 1996]). The complete geographic distributions for most of the species studied here are unknown, primarily due to the poor sampling of mainland China. Cerataphidine aphids have been relatively well sampled from Japan (Takahashi 1958; S. Aoki and U. Kurosu, pers. comm.), Taiwan (Takahashi 1921, 1931, 1936; S. Aoki and U. Kurosu, pers. comm.), Peninsular Malaysia (Takahashi 1950; this study), Java (Noordam 1991), Sumatra (Takahashi 1936; U. Kurosu and S. Aoki, pers. comm.), and India (Ghosh et al. 1974). Cerataphidines are

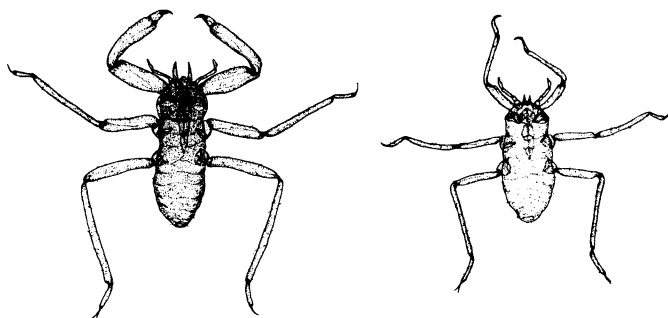


FIG. 1. Secondary-host first-instar larvae of *Pseudoregma bambucicola*. Larvae are dimorphic with soldier larvae (left) attacking predators with their enlarged forelegs and pointed cephalic horns.

rare in the Philippines (Calilung 1967) and Sulawesi (unpubl. obs.).

I defined three geographic regions to examine the historical distribution of lineages: region A includes Peninsular Malaysia, Sumatra, and Java; region B is Taiwan; and region C is Japan. These areas exclude large regions where cerataphidine aphids exist and some of the species in this study spread beyond the sampled regions. This study includes limited sampling of region A, but complete sampling of cerataphidines from Japan (region C) and nearly complete sampling from Taiwan (region B).

RESULTS

The Data

For most species, approximately 800 bp were sequenced (Table 1); 20 bp of uninterpretable length variation, positions 214–229 and 245–248, were excluded from the analyses. The sequences were submitted to Genbank (Table 1) and the aligned dataset is available from <http://www.chu.cam.ac.uk/aphids/home.html>.

Phylogenetic Analysis

The three methods (NJ, MP, and ML) produced trees with a similar basic structure. The tree from the ML analysis is shown in Figure 2 with the bootstrap values from the MP and NJ analysis. Dissimilarities between the trees arose at nodes that had low bootstrap support for both MP and NJ and relatively short branches. In particular, MP placed *Glyphinaphis bambusae* within the genus *Cerataphis*, whereas NJ and ML placed this species basal to the entire clade. The relative positions of all other genera were similar in the different trees. The strict consensus of all three trees is shown in Figure 3.

The paraphyly of *Ceratovacuna* is supported by all of the methods. There is low MP and NJ bootstrap support for most groupings within *Ceratovacuna* (Fig. 2). In addition, the different methods produced different branching orders for these species (Fig. 3). Finally, the internal branch lengths for *Ceratovacuna* are relatively short (Fig. 2, Table 2), suggesting a possible rapid radiation of these species. The terminal branches of *Ceratovacuna* were not significantly longer than the terminal branches of the other genera combined (Mann-Whitney $U = 66$, $P = 0.48$), but the internal branches were ap-

proximately five times shorter than the internal branches of *Cerataphis*, *Ceratoglyphina*, and *Tuberaphis*, and significantly shorter than all other internal branches combined (Mann-Whitney $U = 15$, $P < 0.05$). The ratio of the terminal to internal branches was two to five times larger for *Ceratovacuna* than for any other genus (Table 2). Considerably more data will be required to resolve the phylogeny of this genus.

All of the trees give the same support for the general conclusions that are drawn below with respect to soldier and host plant evolution and biogeography. The different topologies either rearrange parts of the tree that are irrelevant to horned-soldier evolution or rearrange the genus *Ceratovacuna* such that the same general conclusions are drawn. This is illustrated further by the tests of alternative hypotheses of horned-soldier evolution. For illustrative purposes, the character mappings are shown only on the ML tree.

Testing Alternative Hypotheses of Horned-Soldier Evolution

The highest-likelihood phylogeny supporting the monophyly of horned soldiers (Fig. 4A) had a significantly lower likelihood than the ML tree (Table 3). Therefore, the horned soldiers evolved once, and subsequently some species probably lost soldiers.

The highest-likelihood phylogeny supporting the monophyly of soldier-producing species with dimorphic larvae (Fig. 4B) was not significantly less likely than the ML phylogeny (Table 3). However, this alternative would require either the independent acquisition of monomorphic horned soldiers in *Ceratovacuna lanigera* or the loss of soldier behavior in the common ancestor of *C. nekoashi* and *C. sp. B*. There is some evidence to suggest that the latter scenario is correct. The soldier behavior of *C. lanigera* is similar to the behavior of dimorphic soldiers; all use their forelegs and horns for attack (Aoki 1987; Aoki and Kurosu 1989a; Stern and Foster 1996). In contrast, on the secondary-host, first-instar larvae of the horned aphid *Astegopteryx bambucifoliae* use their stylets for attack (Aoki and Kurosu 1989b), as do the larvae of *Tuberaphis takenouchii* (Kurosu et al. 1994), and both represent independent acquisitions of soldier behavior (Stern 1994; Stern and Foster 1996). In addition, a species of *Pseudoregma* that produces monomorphic first-instar larvae that attack with their horns has recently been discovered (Stern et al., 1997b), further indicating that morphological dimorphism can be lost while soldier behavior is retained.

The highest-likelihood phylogeny supporting the monophyly of *Ceratovacuna* (Fig. 4C) was not significantly less likely than the ML phylogeny (Table 2). However, if *Ceratovacuna* is monophyletic, at least one loss of horned soldiers is still required.

Mapping Traits onto the Phylogeny

Horned Soldiers

Horned soldiers are reconstructed as evolving once in the common ancestor of *Ceratovacuna* (Fig. 5). They were then either lost and then regained in *C. lanigera* or they were lost twice, once in *C. nekoashi* and once in *C. sp. B*. The MP and

TABLE 1. Samples used in this study with host affiliations, collection data, presence or absence of soldiers data collected, and Genbank accession numbers.

Genus ³	Species ⁴	Num-ber of spe-cies ⁵	Host ¹		Secondary ⁷	Number ⁸	Collection		Soldiers ²		bp data	Genbank accession no. ⁹	
			Primary ⁶	Secondary ⁷			Locality	Locality	1° host	2° host			
<i>Astegopteryx</i>	<i>bambucifoliae</i>	25	<i>suberifolia</i>	Gramineae	90-10	Puli, Taiwan	Di	Mono	784	L27324			
	<i>basalis</i>		<i>benzoin</i>	Gramineae		92-369E	Gombak, Malaysia	Di	No	460	U58037, L38296		
	<i>formosana</i>		?	Gramineae		90-15	Sun Moon Lake, Taiwan	?	No	804	L27326		
	<i>malaccensis</i>		<i>benzoin</i>	Gramineae		93-54A	Gombak, Malaysia	Di	No	428	L38295		
	<i>mui</i>		?	Zingiberaceae		92-97	Gombak, Malaysia	?	No	809	U58038		
<i>Cerataphis</i>	<i>bambusifoliae</i>	7	?	Gramineae	90-44A	Kuangyinshan, Taiwan	?	No	834	L27327			
	<i>brasiliensis</i> ¹⁰		<i>benzoin</i>	Palmae	92-407	Gombak, Malaysia	Di	No	834	L38298			
	<i>freycinetae</i>		?	Pandanaceae	93-17	FRIM, Gombak, Malaysia	?	No	820	U58041			
	<i>lataniae</i>		?	Palmae	93-21	Univ. Malaysia, KL, Malaysia	?	No	849	U58042			
	<i>pothophila</i>		?	Araceae	93-136	Bogor Bot. Garden, Java	?	No	700	U58043			
	<i>vandermeermohri</i>		<i>serrulata</i>	?	?	Araceae	93-155	Urung Tama, Sumatra	Di	?	818	L38299	
<i>Ceratoglyphina</i>	<i>bambusae</i>	5	<i>benzoin</i>	Gramineae	92-72	Gombak, Malaysia	Di	No	838	U58040, U58044			
	<i>styracicola</i>		<i>suberifolia</i>	Gramineae	91-46	Gombak, Malaysia	Di	No	851	L27330			
	<i>roepkei</i>		<i>parallelo-neura</i>	Monoecious	90-34A	Sun Moon Lake, Taiwan	Di	No	779	L38297			
<i>Ceratovacuna</i>	<i>japonica</i>	18†	<i>japonica</i>	Gramineae	90-5C	Kumagaya, Japan	Di	Di	838	L27328			
	<i>lanigera</i>		?	Gramineae	90-86	Kumagaya, Japan	?	Mono	840	L39995			
	<i>longifila</i>		?	Gramineae	90-32B	Sun Moon Lake, Taiwan	?	Di	829	L40002, L40003, L39996, L40004, L40005			
	<i>nekoashi</i>		<i>japonica</i>	Gramineae	90-1A	Kuangyinshan, Taiwan	Di	No	843	L27329			
	sp. "B" ¹¹		?	Gramineae	90-83	Saitama, Japan	?	No	827	L39997			
<i>Chaitoregma</i>	sp. "C"	2†	?	Gramineae	91-13A	Tokyo, Japan	?	Di	831	L39998			
	sp.		?	Gramineae	93-75	Shomaru Pass, Japan	?	Di	815	L39993			
	<i>tattakana</i>		?	Gramineae	94-14B	Cameron Highlands, Malaysia	?	No	825	L39994			
	<i>bambusae-1</i>		?	Gramineae	92-119	Puli, Taiwan	?	No	825	L27331			
	<i>bambusae-2</i>		?	Gramineae	90-14	Sun Moon Lake, Taiwan	?	No	632	L40001			
<i>Neothoracaphis</i>	<i>yanonis</i>	11	<i>Disyllum</i> ¹²	Fagaceae	91-10	Tokyo, Japan	No	No	850	L27334			
	<i>alexanderi</i>		?	Gramineae	90-89A	Sun Moon Lake, Taiwan	?	Di	827	L27335			
<i>Pseudoregma</i>	<i>bambucicola</i>	15	<i>suberifolia</i>	Gramineae	90-25	Sun Moon Lake, Taiwan	Di	Di	818	L38300			
	<i>koshunensis</i>		<i>suberifolia</i>	Gramineae	90-26	Sun Moon Lake, Taiwan	Di	Di	838	L27336			
	<i>nicolai</i>		<i>parallelo-neura</i>	Gramineae	92-165	Cameron Highlands, Malaysia	?	Di	820	L38301			
	<i>panicola</i>		?	Gramineae	90-46	Kuangyinshan, Taiwan	?	Di	802	L39999			
	<i>coreana</i>		<i>formosana</i>	Loranthaceae	92-47	Kanagawa, Japan	?	No	829	L40000			
<i>Tuberaphis</i>	<i>leuveni</i>	15	<i>serrulata</i>	Monoecious	93-149	Mt. Sibayak, Sumatra	Di	NA	724	L40008			
	<i>styraci</i>		<i>obassia</i>	Monoecious	91-17B	Shomaru Pass, Japan	Di	NA	834	L38307			
	<i>takenouchii</i>		<i>japonica</i>	Loranthaceae	93-146	Sun Moon Lake, Taiwan	Di	Mono	795	L27338			
					93-154	Urung Tama, Sumatra					L40022		

TABLE 1. Continued.

1 Host information is provided only for the first sample of each species.
 2 Presence of soldiers on the primary or secondary host. Mono = monomorphic larvae that attack predators, Di = dimorphic larvae with a specialized soldier caste, No = soldiers not yet found, NA = species does not occur on this host. Soldier information is provided only for the first sample of each species. See Stern and Foster (1996) for further discussion of soldier types.
 3 This list includes all known genera of the Cerataphidini (Neothoracapsis is a member of the Nipponaphidini). Blackman and Eastop (1994) have placed four other genera within the Cerataphidini, but their position there is dubious. *Doraphis populi* feeds on *Populus* and is possibly more closely related to the Pemphigidae. *Hoplothoracaphis manipurensis* resembles *Parathoracaphis* from the Nipponaphidini (Aoki, pers. comm.). *Indoregma bambusae* is possibly synonymous with *Ceratovacuna indica* (Aoki, pers. comm.). Finally, the position of *Neothoracaphis* is unknown. I did not obtain samples of any of these genera for study.
 4 Replicates of the same species are indicated with a dash and replicate number immediately following the species name.
 5 The approximate number of species from each genus, as estimated by Blackman and Eastop (1994), except values marked with †, which were estimated by Eastop and Hille Ris Lambers (1976).
 6 Species of *Syrax*. Question mark indicates the primary host is unknown.
 7 Family of secondary host. Question mark indicates the secondary host is unknown. Monoecious indicates that the species does not migrate to the secondary host.
 8 Collection number of DLS.
 9 Many of these sequences were first published in Stern (1994, 1995) and Stern et al. (1997a).
 10 Russell (1996) synonymized *C. palmae*, *variabilis*, and *fransseni* with *brasiliensis*. This sample is referred to as *C. fransseni* in Stern (1995).
 11 *Ceratovacuna* sp. "B" and sp. "C" are described in Takahashi (1958).
 12 Species of the Nipponaphidini feed on species of the genus *Distylium* as the primary host. *N. yanonis* feeds on *D. racemosum*.

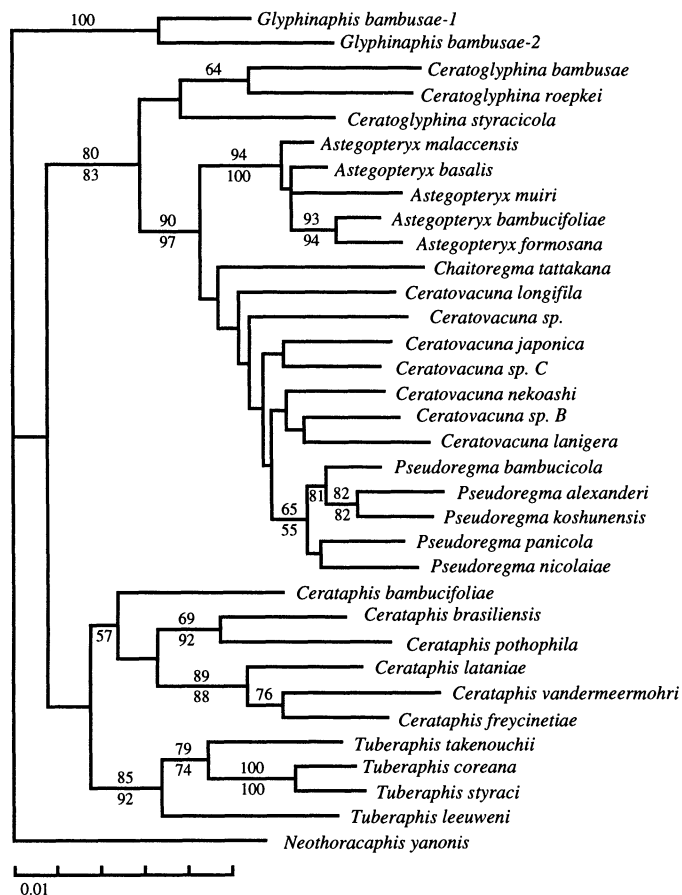


FIG. 2. The maximum-likelihood tree. The maximum-parsimony and neighbor-joining bootstrap values greater than 50% are shown above and below branches, respectively. The scale bar is marked in units of 0.01 expected substitutions per nucleotide position.

NJ trees support independent losses of soldiers in *C. nekoashi* and *C. sp. B* (not shown).

Secondary-Host Plants

The common ancestor of *Ceratoglyphina*, *Astegopteryx*, *Chaitoregma*, *Ceratovacuna*, and *Pseudoregma* is reconstructed as feeding on bamboos as a secondary host (Fig. 6). The secondary-host plant of the common ancestor of all cerataphidines is equivocal but may have been bamboos. The common ancestor of *Tuberaphis* fed on Loranthaceae, but the secondary host of the ancestor of *Cerataphis* is unclear, although it was probably a monocot. Feeding on gingers has evolved at least twice independently, once in *Astegopteryx* and once in *Pseudoregma*. The use of broad-leaved grasses is a recent innovation in *Ceratovacuna* and *P. panicola*.

Biogeography

The geographic distributions of cerataphidine aphids sampled for this study are shown in Figure 7. Parsimony mapping of areas and dispersal-vicariance analysis (Ronquist 1997) suggests four conclusions. First, the ancestral geographic regions for the common ancestor of *Astegopteryx*, *Ceratoglyphina*, *Ceratovacuna*, *Chaitoregma*, and *Pseudoregma* ap-

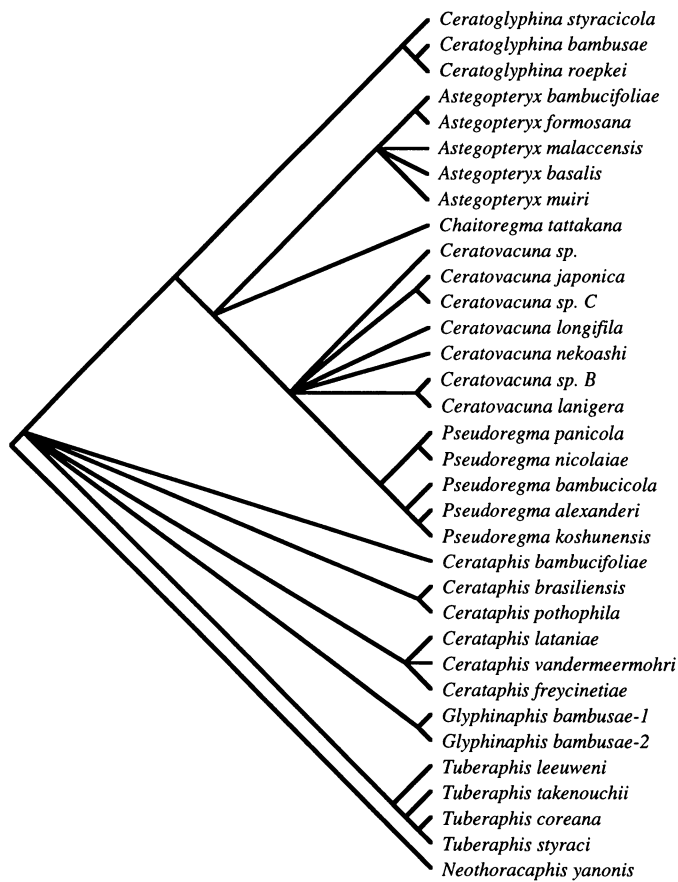


FIG. 3. Strict consensus tree of MP, NJ, and ML trees. This tree shows only the groupings that are found by all of the methods.

pears to be tropical and subtropical Asia, regions A and B. There is weaker evidence that this is the ancestral geographic region for the entire tribe. Populations of *Glyphinaphis bambusae* are also found in region A, although these populations were not included in the analysis, and their inclusion would favor an ancestral geographic region for the tribe that includes all three areas, A, B, and C. Second, there appear to be six vicariance events separating lineages between regions A and B. Most of these vicariance events appear at a similar depth along the ML phylogeny (Fig. 7) suggesting that there may be a general explanation for this pattern. Third, the presence of species in region C (Japan) appears to represent dispersal events from regions A and B. Region C was the most completely sampled region (i.e., species from this region are overrepresented in the phylogeny) so their reconstruction as recent dispersers is unlikely to represent underrepresentation due to sampling bias. Fourth, the *Ceratovacuna* and *Pseudoregma* species in region C are derived from lineages that produced horned soldiers. That is, these species dispersed to region C shortly after the origin of horned soldiers in regions A and B.

DISCUSSION

The goal of this study was to explore the history of the Certaphidini and particularly the two aphid genera producing

TABLE 2. Comparison of the average terminal and internal branch lengths for each genus from the maximum-likelihood phylogeny.

Genus	Mean branch lengths		Terminal/ Internal
	Terminal branches (N)	Internal branches (N)	
<i>Astegopteryx</i>	0.01423 (5)	0.00455 (3)	3.13
<i>Cerataphis</i>	0.03503 (6)	0.01420 (4)	2.47
<i>Ceratoglyphina</i>	0.04084 (3)	0.01696 (1)	2.41
<i>Ceratovacuna</i>	0.02992 (7)	0.00360 (6)	8.31
<i>Pseudoregma</i>	0.01980 (5)	0.00542 (3)	3.65
<i>Tuberaphis</i>	0.02735 (4)	0.01673 (2)	1.63

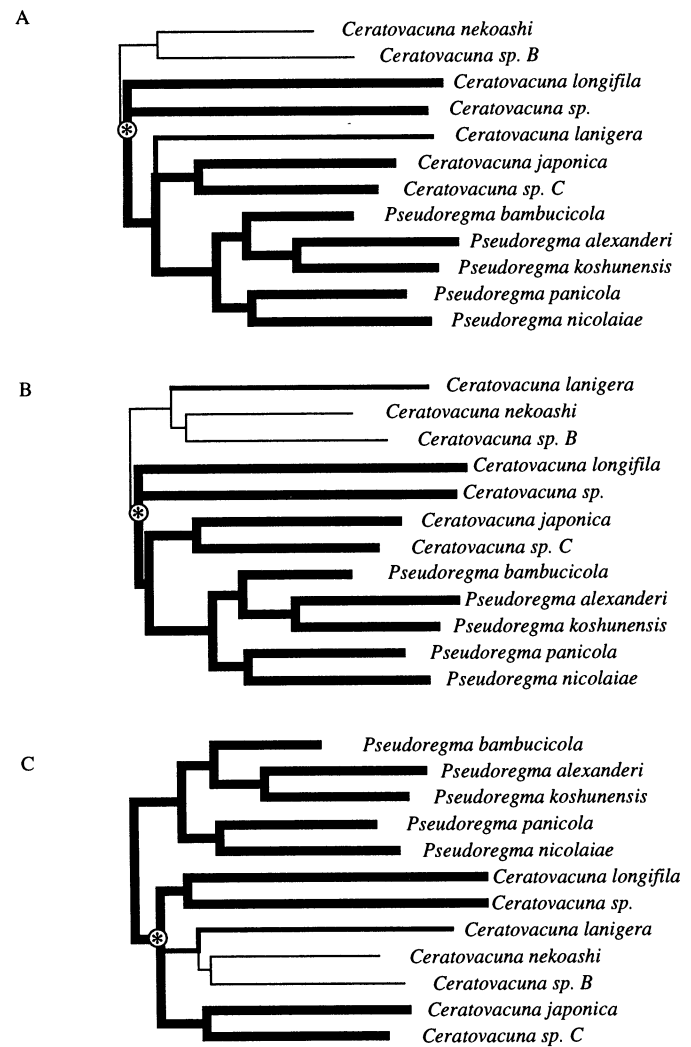


FIG. 4. The variable parts of the highest-likelihood constraint trees used to test alternative hypotheses of soldier evolution (see text and Table 2). Species producing horned soldiers are indicated by lineages with thickened lines. The thickest lines indicate species producing dimorphic larvae and the medium thickness lines indicate species producing monomorphic larvae. The relevant monophyletic group is indicated with an asterisk. (A) Horned soldiers, including species with monomorphic larvae, form a monophyletic group. (B) Species with dimorphic larvae and horned soldiers form a monophyletic group. (C) The genus *Ceratovacuna* is monophyletic.

TABLE 3. Paired-sites tests (Kishino and Hasegawa 1989) of alternative phylogenies against the maximum-likelihood phylogeny.

Alternative phylogenetic hypothesis ¹	LL ²	ΔLL ³	SD ⁴	Z-score
Maximum-likelihood tree	-7525.88972			
Secondary-host soldiers are monophyletic	-7550.69949	-24.80976	11.9264	2.08*
Secondary-host dimorphic soldiers are monophyletic	-7543.18137	-17.29164	9.4803	1.82
<i>Ceratovacuna</i> is monophyletic	-7538.12354	-12.23382	9.5931	1.28

* $P < 0.05$.

¹ Alternative hypotheses are the highest-likelihood phylogenies that satisfy this constraint. The relevant section of each alternative phylogeny is shown in Figure 4.

² Log likelihood of the tree.

³ Difference in the log likelihoods between the ML tree and the focal tree.

⁴ Standard deviation of the difference in site-by-site log likelihoods between the ML tree and the focal tree.

horned soldiers, *Ceratovacuna* and *Pseudoregma*. Species of these genera possess a novel form of sociality, the horned soldiers, and the historical analysis was designed to explore the possible causes and consequences of horned-soldier evolution. Below, I first discuss the reconstruction of horned-soldier evolution. Second, I discuss a hypothesis of the causes for the origin of the horned soldiers. In the third section, I discuss the biogeographic findings, and in the final section, I discuss the possible consequences of horned-soldier evolution and present a hypothesis for the historical ecology and biogeography of horned-soldier aphids.

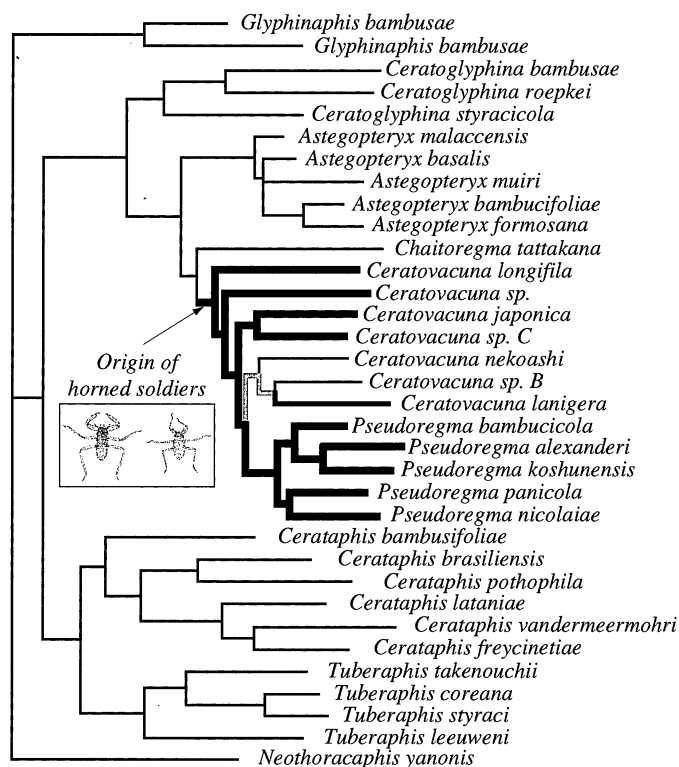


FIG. 5. The distribution of horned soldiers mapped onto the ML phylogeny. Lineages producing soldiers and dimorphic larvae are indicated by the boldest lines, the lineage producing soldiers and monomorphic larvae (*C. lanigera*) is indicated with a medium-thickness line, and equivocal ancestral lineages are mapped with a medium-thickness gray line. The origin of the horned soldiers is indicated.

A Single Origin of the Horned Soldiers

Previous phylogenetic analysis with two species from each genus, *Ceratovacuna* and *Pseudoregma*, suggested that the horned soldiers evolved once and were lost once (Stern 1994). This analysis, with seven species of *Ceratovacuna* and six species of *Pseudoregma*, supports these observations; horned soldiers appear to have evolved once and been lost once or twice (Fig. 5).

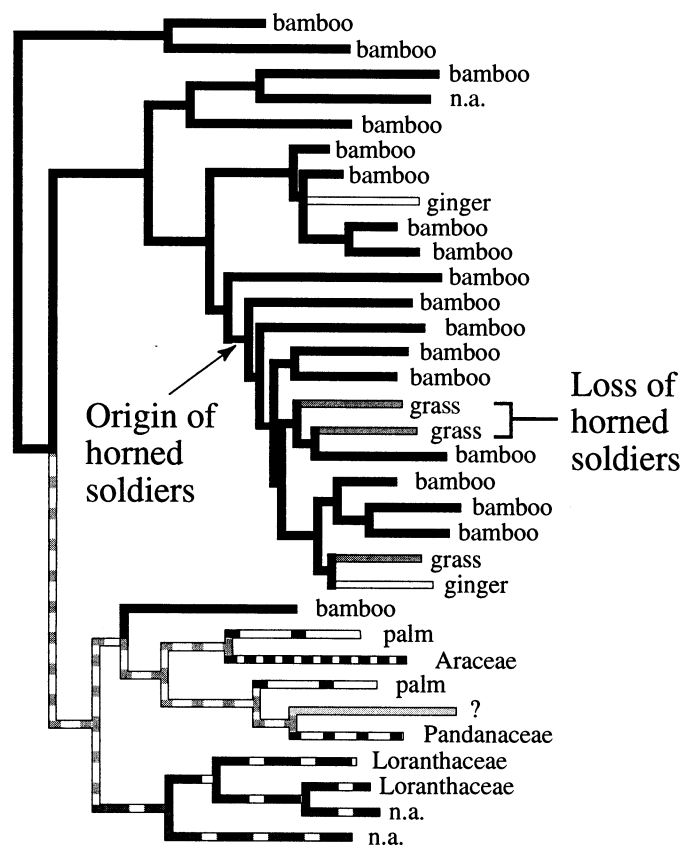


FIG. 6. Secondary-host plants mapped onto the ML phylogeny. Ancestral states are indicated with patterned branches that match the patterns in terminal branches. For example, bamboos are indicated with solid black branches and the common ancestor of the tribe is reconstructed as feeding on bamboos. Equivocal branches have a broken light gray pattern. The branches leading to the out-group, *Neothoracaphis yanonis*, are deleted from this and subsequent figures.

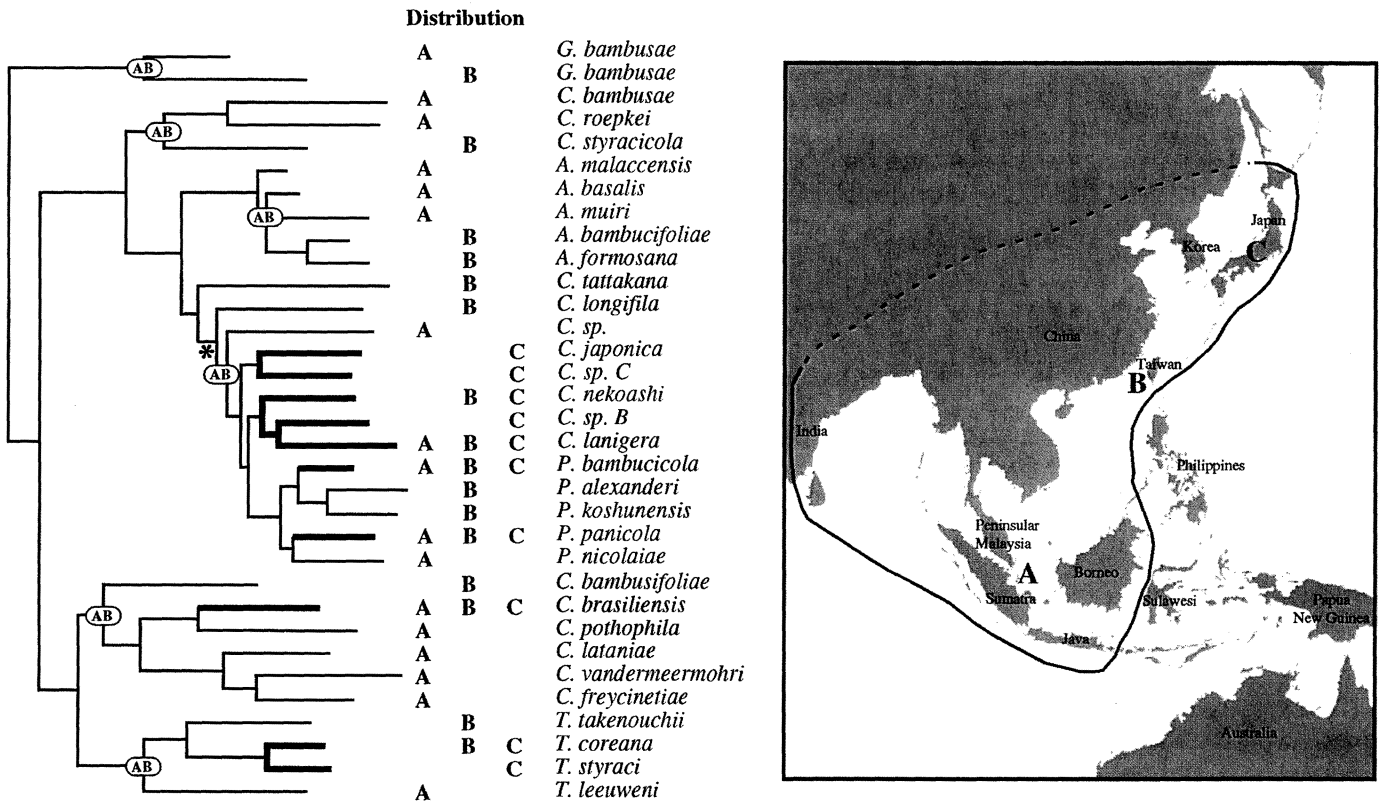


FIG. 7. The biogeography of the Cerataphidini. The ML phylogeny is shown on the left. A map of Asia is shown on the right with the primary geographic range of cerataphidine aphids circled. The broken line indicates that there is considerable uncertainty about the range of cerataphidines in this region. Some cerataphidine aphids are found outside of this area, but they tend to be species with widespread geographic distributions, including regions outside of Asia. The three general regions used in the biogeographic reconstructions are indicated: Region A includes Peninsular Malaysia, Sumatra, and Java; region B is Taiwan, and region C is Japan. For each of the species, except *Glyptinaphis bambusae*, the distribution columns indicate whether the species is found in regions A, B, or C. For *G. bambusae* the samples from regions A and B showed highly divergent DNA sequences and they were treated as distinct populations. Populations of *G. bambusae* are also found in region C. Six nodes on the phylogeny are labeled with an oval containing "AB" to indicate that the ancestral population was likely to occupy both regions A and B. The origin of horned soldiers is indicated with a star. Lineages that were confidently resolved as present in region C are shown as bold lines.

The phylogeny of species of the genus *Pseudoregma* is relatively well resolved and this genus appears to be monophyletic (Figs. 2, 3). In contrast, the phylogeny of species of the genus *Ceratovacuna* is unresolved. Most of the analyses support the hypothesis that *Ceratovacuna* is paraphyletic with respect to *Pseudoregma* (Figs. 2, 3), but this hypothesis was not statistically significantly supported (Table 3). The genus *Ceratovacuna* may have undergone a relatively rapid burst of speciation events soon after its origin. Although the branching order remains obscure, the rapid series of divergent events is well supported.

The Causes for the Evolution of the Horned Soldiers

The horned soldiers possess few of the ecological traits that are thought to favor the evolution of sociality. They do not live in a nest and there is apparently nothing preventing mixing of clones. Nonetheless, horned soldiers display the ultimate in reproductive altruism, they are reproductively sterile. There must be an advantage to producing soldiers that derives from the specific ecology of these species.

Analytical (Stern and Foster 1996) and simulation (Aki-moto 1996) models both predict that soldiers are selectively

advantageous when the intrinsic growth rate of a colony is depressed. This prediction is analogous to the predictions of ecological constraints models for the evolution of helping behavior (Emlen 1982). Altruistic behavior is advantageous when ecological conditions are unfavorable: in birds, when nesting sites are limited; in aphids, when the colony's growth rate is depressed by factors other than predation. The ultimate benefit of soldiers is to reduce predation on the colony. But this strategy of fighting against predators is only advantageous when the colony is unable to adopt the more typical aphid strategy of developing as quickly as possible and running or flying away to colonize a new, predator-free host plant. Since aphids are dependent on their host plant for nutrition, they may get stuck, both ecologically and evolutionarily, on host plants that do not allow rapid aphid reproduction and development. In such cases, a colony that does not defend itself may be at a disadvantage.

One ecological hypothesis is that the secondary-host plants provide relatively poor nutrition that does not allow rapid growth of colonies, thus selecting for soldiers. However, the fact that horned soldiers have evolved only once suggests that the origin of this trait may not be as malleable by eco-

logical conditions as required for a robust comparative test. In fact, mapping secondary-host plant use onto the phylogeny (Fig. 7) suggests that there has not been a dramatic switch of host plants near the origin of the horned soldiers that might have selected for soldiers.

It is possible that bamboos, which are the ancestral secondary-host plant for the clade containing the horned soldiers, are a relatively poor host and that horned soldiers have provided one means of counteracting slow growth on these plants. This hypothesis has the disadvantage that many species of cerataphidine aphids without soldiers live on bamboos. It is possible that these other aphids pursue alternative defensive strategies, such as recruiting ant protection. However, there is no clear correlation between soldier production and ant attendance (Stern and Foster 1996), although this relationship may entail more subtle costs and benefits than have been measured.

This problem will only be solved with more ecological data on the growth rates and general performance of species on different host plants and the nature of interactions with ants and predators. This is not a trivial undertaking. A more immediately fruitful avenue for testing the importance of ecological parameters may be to study the species that have lost horned soldiers, *Ceratovacuna nekoashi* and *C. sp. B*, in comparison with the other species of *Ceratovacuna* that have soldiers. One striking pattern of host-plant evolution is that the two species that lost soldiers feed on broad-leaved grasses, whereas all the soldier-producing species feed on bamboos (Fig. 6). The evolutionary loss of soldiers may provide the clues to their origin.

Biogeography of the Cerataphidini

The modern distribution of related species may be due to both vicariance and dispersal events. There is evidence for both in the tribe Cerataphidini (Fig. 7). The ancestral geographic distribution for much of the tribe appears to be regions A and B, the Southeast Asian tropics and subtropics. Each of the major lineages gives evidence for a variance event that splits the lineage between regions A and B. The species *G. bambusae* provides the best, and most surprising, evidence for this event. This species has a wide geographic distribution and the sexual generation has only been reported from temperate areas (Buchner 1965, p. 329). The phylogenetic data suggest that in tropical areas this species may represent an ancient asexual lineage (the mtDNA sequences from the samples from Taiwan and Malaysia differ by 6.7%).

The best evidence for dispersal is the presence of cerataphidine species in Japan, region C. All of the trees and reconstruction methods suggest that the contemporary presence of cerataphidine aphids in Japan represents dispersal from regions A and B. The species of *Ceratovacuna* and *Pseudoregma* in Japan is apparently due to dispersal soon after the origin of horned soldiers.

The biogeographic analysis yielded several unexpected results, but they should be taken with two caveats, and therefore treated as hypotheses requiring further study. First, the phylogeny used is an incomplete and biased sample of the tribe. Species were sampled primarily to study horned-soldier evolution. Second, the complete geographic distributions of all

of these species are unknown and it is unclear how this uncertainty influences the conclusions.

The Consequences of Horned-Soldier Evolution

Horned soldiers represent a novel life-history strategy for aphids living on a secondary host. I have discussed the possible causes for the origins of defensive behavior on the secondary host, but there were also likely to be ecological consequences of soldier evolution. Soldiers defend the aphid colony against predators and the generalist predators that attack aphids on the secondary host were the most likely to suffer. Some specialist predators have evolved that attack soldier-producing aphids (reviewed in Stern and Foster 1996). In addition, numerous predator species have probably evolved novel behavior patterns for dealing with soldiers, including "hit-and-run" tactics that are not necessary for soldierless aphid colonies. Have these life-history and ecological changes had any evolutionary consequences, in turn, for the aphids? Two pieces of evidence suggest that the origin of horned soldiers may have influenced the evolution of the aphids.

There is evidence that the genus *Ceratovacuna* underwent a relatively rapid diversification after the origin of horned soldiers. This burst of diversification coincided with or slightly preceded the move of some species into the temperate zone of Asia (Fig. 7). These three events, the origin of horned soldiers, the increased speciation rate, and the biogeographic shift, may be related. To understand why, two aspects of aphid biology are important.

First, most aphids are found in the northern temperate regions and relatively few are found in the tropics. Both ecological (Dixon et al. 1987) and historical (Heie 1994) hypotheses have been forwarded to explain this unusual geographic distribution. For most of aphid evolution, most aphids have lived in the temperate regions and so accordingly have most of their specialist predators. In addition, the primary life-history strategy of most temperate aphids is to reproduce quickly and escape predators by dispersal (Dixon 1985).

The second pertinent fact is that, although hormaphidid aphids only reproduce sexually on the primary host, the abundance, geographic distribution, and phenology of their secondary host is probably crucial to determining reproductive isolation. The presence or absence of a secondary host can determine the presence or absence of species in an area. Equally important, different secondary-host plant phenologies could temporally shift the development of colonies of the same population, leading to eventual reproductive isolation (Smith 1988; Butlin 1990; Guldemond and Dixon 1994; Guldemond and MacKenzie 1994; MacKenzie and Guldemond 1994).

Synthesizing these observations, the evolution of horned soldiers might have both increased the speciation rate of the genus *Ceratovacuna* and increased their geographic distribution, particularly into the temperate regions. Secondary-host soldiers would have allowed colonies to deal more effectively with predators in the tropics, leading to increased population sizes and chances for dispersal, increased geographic ranges, and eventual isolation by distance. More importantly, horned soldiers may have allowed these aphids to

invade the temperate regions, where non-soldier-producing species had already attracted a large spectrum of aphid-specialist predators. The temperate regions, with their hordes of aphid predators, do not present an environment conducive to slow-growing aphids. Horned soldiers may have provided an alternative life-history tactic to the typical aphid strategy, thereby promoting ecological and geographic expansion in concert with an enhanced speciation rate.

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Corresponding Editor: R. DeSalle