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Original article

Geographic variation in *Varroa jacobsoni* (Acari, Varroidae) : application of multivariate morphometric techniques

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Summary — *Varroa jacobsoni* is an ectoparasitic mite which attacks the honey bees *Apis mellifera* and *Apis cerana*. A morphological and taxonomic study was conducted using 462 female mites collected from *A. mellifera* and *A. cerana* from 17 countries (including two recent introduction sites in the United States). Thirteen morphological characteristics were measured.

While univariate analyses indicated a statistically significant difference in mean body length of *V. jacobsoni* collected from *A. mellifera* and *A. cerana*, the distributions overlapped broadly with a weak bimodality (by host). There was a weak correlation, on average, between the size of *V. jacobsoni* and the size of the host. However, there was sufficient size variance and plasticity that shifts in mite body size could accommodate interspecific host shifts.

Principal component analysis, discriminant function analysis and clustering (UPGMA) of Mahalanobis distances were used to determine phenetic similarity among populations. Results indicated that populations of *V. jacobsoni* show remarkable stability in character variance across their geographic range. There is no reason to suspect the occurrence of more than one cosmopolitan species. Since the US samples were more similar to *V. jacobsoni* collected from Brazil, than to European or Asian populations, it was concluded that the origin of the introduction into the United States was South America. The origin of the US introduction is discussed in terms of evolutionary implications and potential virulence of biotypes.

***Varroa jacobsoni* — morphometrics — geographic variation — multivariate analysis**

Introduction

The Asian honey bee mite, *Varroa jacobsoni* Oud. (Acari : Varroidae), is an obligate ectoparasite which attacks the honey bees *Apis cerana* Fabr. (Asian or Indian honey bee) and *Apis mellifera* L.

(European honey bee) (Eickwort, 1988). *Apis cerana* is the smaller of the two bee species, and is the original host of *V. jacobsoni* (Oudemans, 1904; Delfinado-Baker, 1988). The two hosts, *A. cerana* and *A. mellifera*, represent genetically isolated gene pools which are allopatric and do not naturally coexist over the

extent of their ranges (Ruttner and Maul, 1983). *Apis mellifera* however, has been successfully introduced into many regions, including Southeast Asia (with the exception of Sri Lanka, Nepal, and probably Sumatra), imposing an artificial sympatry on both bee and mite distributions. Because of man's intervention and apicultural practices, *V. jacobsoni* is now almost cosmopolitan in distribution, occurring in all temperate and tropical regions of the world except Central and South Africa, Australia and New Zealand (Griffiths and Bowman, 1981). Until recently, *V. jacobsoni* had not been present in Central or North America. In September 1987, however, mites were found in the state of Wisconsin. By May, 1988, *V. jacobsoni* has been reported in fourteen states: Florida, Illinois, Indiana, Maine, Michigan, Mississippi, Nebraska, New York, Ohio, Pennsylvania, South Carolina, South Dakota, Washington and Wisconsin. The origin of the United States introduction is unknown, but the most likely possibilities are that the mites arrived on bees entering from South America or on bees attending unspecified queens shipped illegally from Europe or Asia.

Varroa jacobsoni has secondarily become a successful parasite of *A. mellifera* where the two bee species experience geographic proximity. The coevolutionary association of *V. jacobsoni* and *A. cerana* has resulted in host-parasite accommodation and reduce mortality to *A. cerana* colonies (Peng and Fang, 1988). In contrast *A. mellifera*, without benefit of a long historical association, experiences hive mortality as a common outcome of infestation. This difference in mortality results, in part, from the fact that *V. jacobsoni* usually confines its feeding to drone brood of *A. cerana*, but attacks both drone and worker brood of *A. mellifera* (Koeniger *et al.*, 1981; De

Jong, 1988). Reduced infestation on *A. cerana* is also due to worker recognition of *Varroa* and the removing of mites from their bodies (Peng *et al.*, 1987; Peng and Fang, 1988), to juvenile hormone titers in *A. cerana* females which are insufficient to stimulate ovulation in the mite (Hänel, 1983), and perhaps to a shorter post-capping developmental period (Schousboe, 1986). Loss of potential workers in domestic *A. mellifera* hives threatens all functions of the hive, and has become a serious threat to commercial beekeeping and pollination biology.

Morphological studies of *V. jacobsoni* have been pursued to better understand the biology, systematics and geographic variation of this mite (Delfinado and Baker, 1974; Delfinado-Baker, 1984; Grobov *et al.*, 1980; Akimov and Yastrebtsov, 1985; Akimov *et al.*, 1988). *Varroa jacobsoni* was found to be morphologically conservative, and best diagnosed on the basis of female characters. In general, mites from the smaller bee species, *A. cerana*, appear to be smaller than those from *A. mellifera* (Delfinado-Baker, 1988). While geographic variability in body size, shape, and chaetotaxy exists among females of *V. jacobsoni*, conventional approaches have yielded no features useful for taxonomic identification and discrimination of mites collected from *A. mellifera* and *A. cerana*. Because mite behavior and infestation-impact differ in *V. jacobsoni* associated with *A. mellifera* and *A. cerana*, it has been suggested that *V. jacobsoni* may represent a species complex, as has been shown in other acarines (Griffiths *et al.*, 1983).

This study is an extension of previous morphological work on *V. jacobsoni* and addresses three issues:

— whether multivariate morphological procedures are useful in interpreting

patterns of character variation and covariation in mites associated with *A. mellifera* and *A. cerana*;

— whether multivariate patterns of morphological variation in *V. jacobsoni* can be differentiated by country or region of collection; and

— whether the origin of the populations introduced into the United States can be clarified with any degree of certainty on grounds of morphological similarity.

Materials and Methods

Samples and characters

462 females of *Varroa jacobsoni* were collected from *Apis cerana* ($N=92$) and *Apis mellifera* ($N=370$) from 17 countries representing 5 geographic regions (Table I). Among these, two recent introduction-sites in the United States (Wisconsin and Florida) were sampled.

Mites were processed in 5% KOH and mounted in Hoyer's medium. Characters were measured using a phase contrast microscope

Table I. Geographic regions, countries, and species of *Apis* from which *Varroa jacobsoni* were collected.

Geographic region	Country	N	Species of <i>Apis</i>
Old world :			
Europe	Germany (1977)	28	<i>Apis mellifera</i>
	Poland (1980)	25	<i>Apis mellifera</i>
	USSR (1964)	28	<i>Apis mellifera</i>
	Netherlands (1983)	27	<i>Apis mellifera</i>
Mediterranean	Tunisia (1975)	31	<i>Apis mellifera</i>
	Iran (1978)	31	<i>Apis mellifera</i>
	Israel (1984)	26	<i>Apis mellifera</i>
Asia	Nepal	17	<i>Apis cerana</i>
	Sri Lanka (1983)	36	<i>Apis cerana</i>
	Malaysia (1963)	14	<i>Apis cerana</i>
	Thailand (1968)	25	<i>Apis cerana</i>
	China (1958)	23	<i>Apis mellifera</i>
	Korea (1960)	28	<i>Apis mellifera</i>
	P. New Guinea (1986)	24	<i>Apis mellifera</i>
	Philippines (1960)	24	<i>Apis mellifera</i>
New World :			
North America	USA : Wisconsin (1987)	23	<i>Apis mellifera</i>
	USA : Florida (1987)	28	<i>Apis mellifera</i>
South America	Brazil (1978)	24	<i>Apis mellifera</i>
	Total	462	

Groupings by region are consistent with Figures 4, 6B and 7B. Dates following country designations are dates of detection of *V. jacobsoni*.

equipped with ocular micrometer. Bilateral measurements were averaged for each specimen.

Morphological characters (Fig. 1) measured included: maximum body length, maximum body width, the distance between the first pair of sternal setae (ST1), the distance between the second pair of sternal setae (ST2), the width of the genital shield, the width of the anal shield, the distance between the first and second pairs of sternal setae, the width of the metapodal shield, the length of the metapodal shield, the length of the tarsus of leg I, the number of sternal setae, the number of dorsal shield marginal setae, and the number of metapodal marginal setae. All distances are in micrometers.

Statistical procedures

Body size was examined as a univariate character (body length) and as a latent variable (general size) contributing to character variance. A Manova procedure using the General Linear Model was used to estimate the influence of geographic region and *Apis* host-species on morphological characters. The Tukey studentized range test on all main-effect means determined statistical differences among groups ($\alpha = 0.05$).

Principal components analysis (PCA), based on the covariance matrix of log-

transformed data, was performed and multivariate allometric coefficients calculated. Character lengths were first converted to natural logarithms to equalize variances, preserve (linearize) allometric relationships among characters, and produce a scale-invariant covariance matrix. Because we wished to examine patterns of variation independent of differences in body size, size was partitioned from the data set on a character-by-character basis in the following manner. The first eigenvector of the PCA represents a general-size factor, derived from the within-group variance-covariance matrix. Each log-transformed character was independently regressed on this size factor (PC1). The size-free residuals were calculated and a discriminant function analysis (DFA) was subsequently performed, by group, on these residuals. The scores were then plotted as scattergrams. This provided interpretation of morphological patterns in form as size-free contrasts, independent of the allometric consequences of size change.

Centroids (± 1 SD) of the scores of individuals on DF1 and DF2 were calculated by country and by extended geographic region (i.e. Europe, Mediterranean, Asia, North and South America). Centroid analysis characterizes the "average" individual variance on DF1 and DF2 for the size-corrected data. This point, and one standard deviation about this point, represents the focus about which individuals vary in multivariate space.

Mahalanobis distances (D^2) were calculated among groups on the primary discriminant axes (DF1 and DF2) and a clustering algorithm (UPGMA) was used to determine phenetic similarities, by country and region. Resulting dendrograms are not interpretable as statements of phylogenetic relationships because they do not distinguish primitive from derived similarity.

A 3-D contour plot of the centroids of DF1-DF3 (± 1 SD) was constructed to visually show the continuity in morphology across the geographic range of *V. jacobsoni*. The first three components were used because the variance structure reflected in DF4, and beyond, was minimal and reflected non-biological (measurement) variance.

The SAS-PC statistical package was used on an IBM PC/AT microcomputer for calculation of univariate means, the Manova and the PCA. The DFA procedures were run on mainframe SAS using a VAX system.

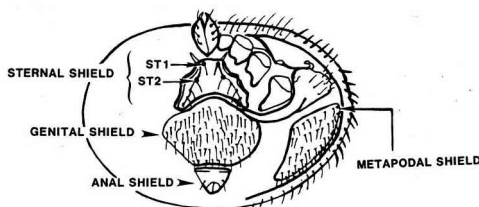


Fig. 1. Distance measured across the form of *Varroa jacobsoni* females. For taxonomic details see Delfinado and Baker (1974).

RESULTS

The difference in mean body length of *Varroa jacobsoni* collected from *Apis cerana* (mean = $1\,037.52\ \mu\text{m} \pm 49.38$) and from *Apis mellifera* (mean = $1\,106.31\ \mu\text{m} \pm 33.19$) is statistically significant ($F_{12,440} = 8.91$; $P \geq F = 0.000\ 1$), while the distributions of body length overlap broadly with a weak bimodality by host (Fig. 2A). The frequency distribution of general-size (scores of PC1) parallels that of body length for *V. jacobsoni* collected from *A. mellifera* and *A. cerana* (Fig. 2B)

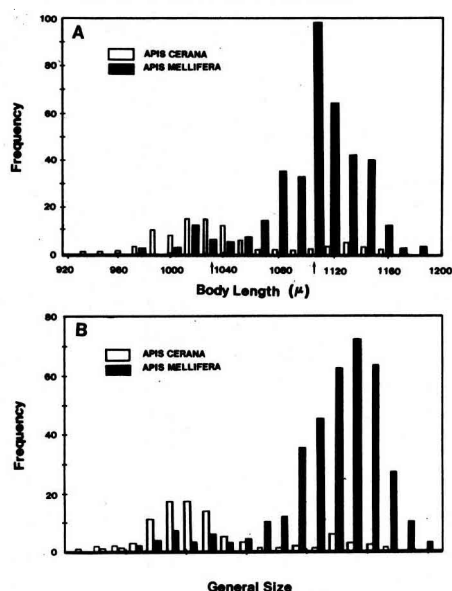


Fig. 2 A. Frequency distribution of body length (μm) of *Varroa jacobsoni* collected from *Apis cerana* and *Apis mellifera*. Means are indicated by arrows along the abscissa. Although the mean body length for mites on *A. cerana* (mean = $1\,037.52\ \mu\text{m} \pm 49.38$) is statistically less than that on *A. mellifera* (mean = $1\,106.31\ \mu\text{m} \pm 33.19$), the distributions overlap with a weak bimodality by host.

B. Frequency distribution of general size (PC1) of *V. jacobsoni* collected from *A. cerana* and *A. mellifera*. The PCA was based on the covariance matrix of log-transformed data.

indicating that size is the first component in PCA.

The PCA offered no separation or resolution of groups. The first eigenvector accounted for 38% of the total variance, while the second accounted for 28%. All allometric coefficients reflected positive allometry of characters except for the distance between the first pair of sternal setae and the number of metapodal marginal setae. These two characters exhibited a decrease in magnitude with an increase in general size.

When weighted by country, the primary size-free discriminant axis (DF1) accounted for 36% of the variance structure, while DF2 accounted for 21%. The remainder of the variance was relatively equally partitioned among the remaining functions. Significant character coefficients (expressed as correlations of characters with discriminant functions) demonstrate that the length of the metapodal shield (0.57), the length of tarsus I (-0.67), and the number of metapodal setae (0.45) contribute most to the size-free discrimination.

Discriminant function analysis, by country (Fig. 3), resulted in discrimination among only nine of the 153 pair-wise comparisons (5.9%) (Table II). This level of discrimination is not dissimilar to that expected due to sampling error alone (where $\alpha = 0.05$).

When examined by region (Fig. 4), DF1 accounted for 75% of the variance in the data set and DF2 accounted for 19%, with regions not discriminated on any axis. Character variance overlapped on DF1 and DF2 with no indication of discriminatory pattern. In addition, no discrimination could be assigned to host (Fig. 5). The primary axes of DFA by host-species accounted for 100% variance (as is always the case for a two-group comparison).

Table II. Mahalanobis distances are given the lower left diagonal of the matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Brazil	1	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sri Lanka	2	4.0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
China	3	5.7	0.4	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Florida, USA	4	0.8	3.6	5.6	0	+	+	+	+	+	+	+	+	+	+	+	+	+
Germany	5	5.0	0.7	0.2	6.0	0	+	+	+	+	+	+	+	+	+	+	+	+
Iran	6	4.3	0.3	0.1	4.8	0.1	0	+	+	+	+	+	+	+	+	+	+	+
Israel	7	4.4	4.2	3.3	7.7	2.0	2.5	0	+	+	+	+	+	+	+	+	+	+
Korea	8	5.4	0.6	0.0	6.1	0.0	0.1	2.6	0	+	+	+	+	+	+	+	+	+
Malaysia	9	0.7	1.4	2.9	0.6	2.7	2.0	4.2	2.8	0	+	+	+	+	+	+	+	+
Nepal	10	11.4	5.3	7.8	6.9	9.7	8.1	18.7	8.8	7.0	0	+	+	+	+	+	+	+
Netherlands	11	1.9	0.6	1.0	2.6	0.8	0.5	2.1	0.9	0.7	8.4	0	+	+	+	+	+	+
New Guinea	12	4.9	2.6	1.6	7.4	0.8	1.2	0.4	1.1	3.8	15.4	1.4	0	+	+	+	+	+
Philippines	13	4.7	0.5	0.1	5.5	0.1	0.0	2.3	0.0	2.4	8.9	0.6	1.0	0	+	+	+	+
Poland	14	4.4	0.9	0.4	5.7	0.1	0.2	1.4	0.2	2.5	10.7	0.6	0.5	0.1	0	+	+	+
Thailand	15	0.2	2.6	4.4	0.3	4.1	3.3	4.9	4.3	0.2	8.4	1.3	4.8	3.8	3.7	0	+	+
Tunisia	16	2.0	1.5	1.5	3.5	0.9	0.8	1.0	1.2	1.2	11.5	0.2	0.7	0.9	0.6	1.8	0	+
USSR	17	3.5	1.1	0.7	5.0	0.3	0.3	1.0	0.5	2.1	11.2	0.4	0.3	0.3	0.1	3.0	0.2	0
Wisconsin, USA	18	0.4	4.0	6.3	0.1	6.1	5.0	6.9	6.3	0.7	8.6	2.6	7.0	5.6	5.7	0.2	3.2	4.8

A plus (+) in the upper right diagonal of the matrix indicates that, in the DFA, the two countries overlapped in variance distribution. A minus (-) indicates that the plot of DF1 vs. DF2 resulted in no overlap of variance patterns. An asterisk (*) signifies that the centroids on DF1 and DF2 are statistically different at $\alpha = 0.05$.

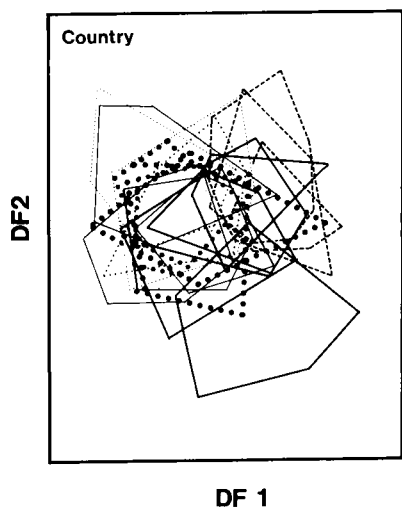


Fig. 3. Primary and secondary DFA scores, plotted by country of origin, for *Varroa jacobsoni*. Data are pooled across host-species. Populations which have non-overlapping distributions are indicated in Table II.

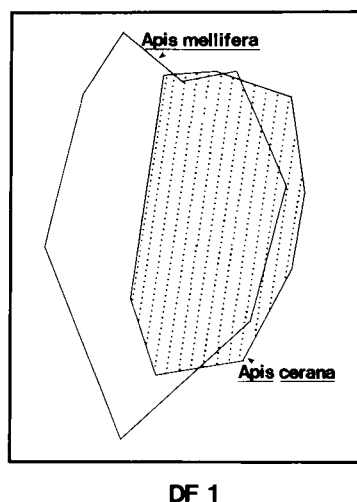


Fig. 5. Primary and secondary DFA scores, plotted by host-species, for *Varroa jacobsoni*. Data are pooled across countries of collection.

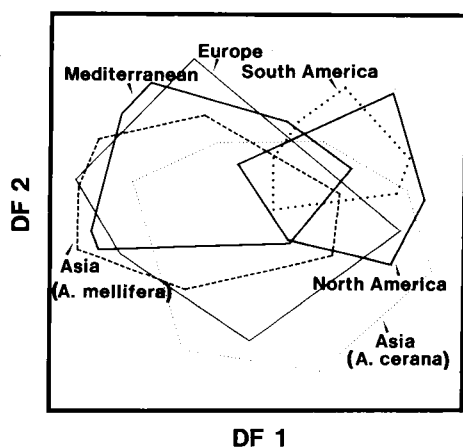


Fig. 4. Primary and secondary discriminant function scores, plotted by region, for *Varroa jacobsoni*. Data are pooled across host-species.

Further structure in the data was resolved by centroid analysis. Centroids (± 1 SD) of the character-distributions on DF1 and DF2 were plotted by country and by region (Fig. 6A,B). Significant differences among centroids occurred in 49.7% of the comparisons (Table II) and reflected character shifts, among populations, following mite establishment.

Mites from Nepal (Fig. 6A) are distinctly different from all others. *Varroa jacobsoni* from Brazil, Wisconsin, and Florida form a cluster and are more similar to one another than each is to any other population. The Mediterranean and European localities (Fig. 6B) provide only slight character contrast when compared with other groups. Phenetic cluster analysis among regions (Table III, Fig. 7 A, B) indicates that mites from North America (Wisconsin and Florida) are most similar in morphology to those of South America ($D^2 = 1.16$).

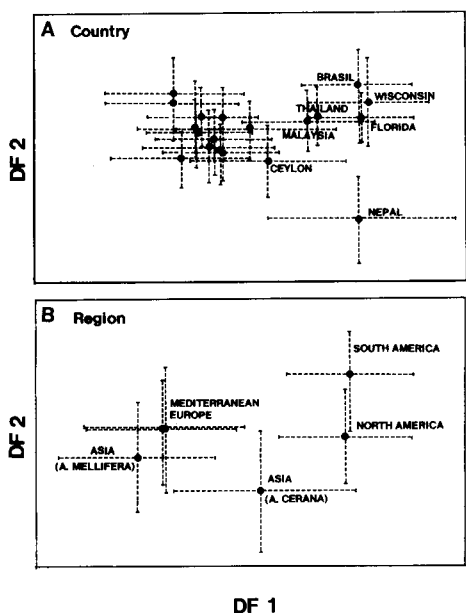


Fig. 6A. Centroids (± 1 SD) of the primary and secondary discriminant functions, calculated by country, for *Varroa jacobsoni*. **6B.** Centroids (± 1 SD) of the primary and secondary discriminant functions, calculated by region, for *Varroa jacobsoni*. Centroid analysis positions the "average" individual variance on DF1 and DF2 for the size-corrected data. This point, and one standard deviation about this point, represent the focus about which variation rotates in multivariate space.

Discussion

The difference in mean body length of *Varroa jacobsoni* collected from *Apis cerana* and *Apis mellifera* is statistically significant, while the distributions of body length overlap broadly. The smallest mites from *A. mellifera* overlap the central tendency of those from *A. cerana* and *vice versa*. This indicates that there is a weak correlation, on average, between the size of *V. jacobsoni* and the size of the host. However, there is sufficient size variance and plasticity that shifts in mite body size could accommodate interspecific host shifts.

The smallest mites occurred on *A. cerana* from Sri Lanka. It is interesting that the largest specimens of *V. jacobsoni* were those from Nepal (mean = $1\,125.58\ \mu\text{m} \pm 20.66$). These mites were removed from the same bees from which the type-specimens of *Varroa underwoodi* were obtained (Delfinado-Baker and Aggarwal, 1987). *Apis cerana* is the natural host for both *V. jacobsoni* and *V. underwoodi*. Sympatry of the mite species may have resulted in character displacement for body size, since *V. underwoodi* is about 20% smaller on

Table III. Mahalanobis distances among regions from which *Varroa jacobsoni* were collected.

		1	2	3	4	5	6
Asia (<i>Apis mellifera</i>)	1	0					
Europe	2	2.5	0				
Mediterranean	3	2.6	0.0	0			
North America	4	1.9	4.9	5.1	0		
Asia (<i>Apis cerana</i>)	5	2.6	0.3	0.3	6.6	0	
South America	6	5.2	6.0	6.2	1.2	8.8	0

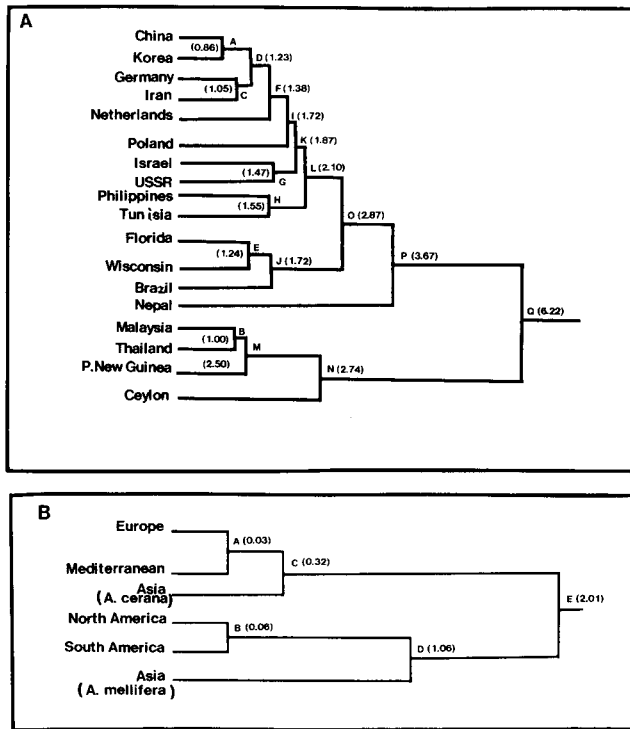


Fig. 7A. Cluster diagram of Mahalanobis distances, by country, for *Varroa jacobsoni*. Values in parentheses are the Mahalanobis distances. Branch lengths are proportional to these distances. **7B.** Cluster diagram of Mahalanobis distances, by region, for *Varroa jacobsoni*. Values in parentheses are the Mahalanobis distances. Branch lengths are proportional to these distances.

average (mean = 758 μm) than the smallest *V. jacobsoni* (mean = 934 μm) collected from any locality in this study, and *V. jacobsoni* is most divergent in size in sympatry. This is a hypothesis which could be tested if additional mites in sympatry are compared with mites in allopatry.

These results, taken in concert and in context, indicate that populations of *V. jacobsoni* show remarkable stability in character variance across their geographic range with transitions in variation from continent to continent (Fig. 8). The observed morphological consistence may

reflect a relatively short period of geographic isolation and/or diffuse and recurrent redistribution of domesticated *A. mellifera*. There is no reason to suspect the occurrence of more than one cosmopolitan species.

Because character deviation has presumably been weak since the radiation of *V. jacobsoni* from its area of origin, an examination of mean differences in multivariate character space was appropriate. Centroid analysis, Mahalanobis distances, and clustering methods indicate that the Wisconsin and Florida samples are more similar to *V. jacobsoni*

VARROA:DF1-DF3 BY COUNTRY

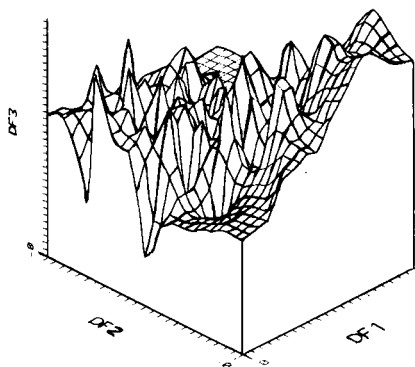


Fig. 8. Three-dimensional plot of centroids of scores (± 1 SD) on DF1-DF3 for all characters. Each peak represents an individual country from which *Varroa jacobsoni* was collected. The transitions and nature of the variance structure represent non-discrete groupings.

collected from Brazil than they are to the European or Asian populations. The most parsimonious conclusion would be that the origin of the introduction into the United States was South America, and that the introduction was recent. The fact that character variation occurs among Brazilian and US mites indicates that either :

- the temporal separation of the Brazilian and US gene pools has provided sufficient time for real morphological divergence to occur, or
- that the observed variance reflects the sampling of hives in Brazil which are different from Brazilian hives contributing to the US introduction.

An auxiliary finding in this study is that the Mahalanobis distances portray the mites from Brazil as similar to the Asian lineage, and most likely not of European origin (Fig. 7A,B). This conclusion

concerning transport route is quite realistic since samples of *V. jacobsoni* were known to have been carried to Paraguay in 1971 on queens and comb imported from Japan. Mites were subsequently introduced from apiaries in Paraguay to Brazil in 1972 (De Jong and Goncalves, 1981), producing the phenetic similarity of the Asian and South American mites.

This character analysis has offered several conclusions concerning *V. jacobsoni* that could not have been obtained by conventional methods. Through a multivariate approach we have determined the extent of morphological plasticity in *V. jacobsoni*, the phenetic relationships among sampled populations, and the probable origin of the introduction into North America. This study also establishes a data base for further evolutionary studies on the range-extension and adaptation of a host-parasite association, and may contribute to the predictive power concerning the potential virulence of infestation in the United States.

Delfinado-Baker (1988) has identified three mite biotypes :

- Biotype A infests *A. mellifera* of European origin and parasitizes both drone and worker broods causing heavy losses in all European races of bees;
- Biotype B infests *A. cerana* drone brood only and results in minimal colony damage; and
- Biotype C infests both drone and worker brood of Africanized bees causing brood damage but usually not colony mortality, partly because of the shorter postcapping period (9.6—11 days), and hence shorter pupation period of the bees, and resulting restricted mite reproduction under these conditions (Camazine, 1986; Moritz and Hänel, 1984; Shousboe, 1986). Since the origin

of infestation in North America is most likely Africanized Brazilian bees, these mites may be of less virulence than had they been derived from European parentage, if virulence is a reflection of mite biology. However, it is equally likely that biotypes reflect the host biology or some covariance parameters of host and parasite.

However encouraging this lesser evil may seem, the prospects for losses of bees, honey and migratory pollination services will continue to be high. Contributing to the overall problem is the paucity of available information concerning this mite's biology in the United States. Previous generalities developed under European and Asian climatic regimes, management practices, and breeding programs may not extrapolate to United States situations.

The European Economic Community (EEC) is the leader in *Varroa* research and development in both the basic and applied sciences (Bruce and Chiesa, 1988). Concentrated support for *Varroa* biology is needed in the United States, as well as workers willing to contribute their talents to a crisis likely to be a far more serious threat to apiculture and agriculture than any experienced so far in modern history.

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Résumé — Variation géographique de *Varroa jacobsoni* (Acari, Varroidae) : application des techniques morphométriques multivariées. *Varroa jacobsoni* est un acarien ectoparasite qui attaque les abeilles *Apis mellifica* et *Apis cerana*. Les acariens sont une sérieuse menace pour la vigueur et la survie des colonies qu'ils infestent. En raison de l'infestation et du comportement de l'acarien différents selon l'hôte, on a pensé qu'il pouvait s'agir d'un complexe d'espèces avec une spécificité stricte de l'hôte. On a réalisé une étude morphologique et taxonomique des femelles adultes de *V. jacobsoni* provenant de divers hôtes récoltés dans diverses parties du monde. On décrit dans cet article la variabilité morphologique que présente *V. jacobsoni* sur les deux espèces d'abeilles. Avec les techniques morphométriques multivariées, on a examiné et mesuré 13 caractères morphologiques, chez les acariens femelles adultes, prélevés dans 17 localités à travers le monde, y compris deux endroits aux Etats-Unis. L'analyse en composantes principales, l'analyse de la fonction discriminante et la classification phénétique des distances de Mahalanobis ont été utilisées pour

déterminer la ressemblance entre les échantillons. Les caractères étudiés sont les suivants : longueur du corps, largeur du corps, distance entre les setae sternaux de la 1^{re} paire, distance entre les setae sternaux de la 2^e paire, distance entre la 1^{re} et la 2^e paire de setae sternaux, largeur du sclérite épigynial, largeur du sclérite anal, largeur du sclérite métapodal, longueur du sclérite métapodal, longueur du tarse de la patte I, nombre de setae sternaux, nombre de setae dorsaux marginaux et nombre de setae métapodaux marginaux.

L'analyse des caractères a fourni plusieurs conclusions concernant la taxonomie de *Varroa*, impossibles à obtenir par les méthodes taxonomiques traditionnelles. Les techniques morphologiques multivariées ont permis de déterminer le degré de plasticité de *V. jacobsoni* et l'origine géographique de la souche introduite aux Etats-Unis. La différence dans la longueur moyenne du corps de *V. jacobsoni* sur *Apis mellifica* et *Apis cerana* est statistiquement significative, alors que les distributions de la longueur du corps des deux parasites se recouvrent largement. Les acariens les plus petits venant d'*Apis mellifica* recouvrent la tendance centrale de ceux qui viennent d'*Apis cerana* et vice versa. Les plus gros spécimens de *V. jacobsoni* sont ceux du Népal sur *Apis cerana*; les plus petits viennent de Ceylan, sur *Apis cerana* aussi. L'ensemble des résultats indique que les populations de *V. jacobsoni* présentent une remarquable stabilité dans la variance des caractères sur toute leur aire de répartition géographique avec des transitions continues douces dans les variations d'un continent à un autre. Il n'y a aucune raison pour suspecter l'existence de plus d'une espèce cosmopolite infestant *Apis cerana* et *Apis mellifica*. La méthode du centroïde, les distances de Mahalanobis

et les méthodes de classification par agrégation montrent que les échantillons du Wisconsin et de Floride sont bien plus proches des *V. jacobsoni* prélevés au Brésil que de ceux des populations européennes ou asiatiques. On conclut que l'introduction aux Etats-Unis s'est faite à partir de l'Amérique du Sud. On discute l'origine de l'introduction en termes d'implications pour l'évolution et de virulence des biotypes.

***Varroa jacobsoni* — morphométrie — variation géographique — analyse multivariable**

Zusammenfassung — Geographische Variabilität von *Varroa jacobsoni* (Acari, Varroidae) : Analyse unter Verwendung multivariater morphometrischer Methoden. *Varroa jacobsoni* ist eine ektoparasitische Milbe, welche die Honigbienen *Apis mellifera* und *Apis cerana* anfällt. Die Milbe bedroht ernstlich Lebenskraft und Überlebensfähigkeit der Bienenvölker, die sie befällt. Da sowohl Befall wie Verhalten der Milbe auf beiden Bienenarten verschieden ist, wurde vermutet, *V. jacobsoni* könnte einen Artenkomplex mit enger Wirtsspezifität bilden. Deshalb wurde eine morphologische und taxonomische Untersuchung von weiblichen erwachsenen Milben aus verschiedenen Wirtsvölkern und aus verschiedenen Teilen der Erde vorgenommen.

In dieser Arbeit wird die morphologische Variabilität von *V. jacobsoni* auf den beiden Bienenarten beschrieben. Unter Einführung von multivariaten morphologischen Techniken in die *Varroa*-Taxonomie wurden 13 morphologische Merkmale von erwachsenen weiblichen Tieren aus 17 Ländern untersucht und

gemessen, einschließlich zweier Orte in den Vereinigten Staaten. Zur Feststellung von Ähnlichkeiten zwischen den Proben wurden die statistischen Verfahren der Hauptkomponentenanalyse (PCA), Diskriminanzanalyse und der phänetischen Clusteranalyse (UPGMA) von Mahalanobis-Distanzen benutzt. Es wurden folgende Merkmale untersucht: Körperlänge, Körperbreite, Abstand zwischen dem ersten Paar sternaler Borsten, Abstand zwischen dem zweiten Paar sternaler Borsten, Abstand zwischen den ersten und den zweiten Paaren sternaler Borsten, Breite von Genital- und von Analfeld, Breite von metapodalem Feld, Tarsuslänge von Bein I, Anzahl der Sternalborsten, Anzahl der dorsalen Randborsten und Anzahl der metapodalen Randborsten (Fig. 1).

Diese Merkmalsanalyse hat einige Schlußfolgerungen zur Taxonomie von *Varroa* ermöglicht, die mit den konventionellen taxonomischen Methoden nicht zu erzielen sind. Die multivariaten morphologischen Techniken haben Angaben über die Variationsbreite und über ihren wahrscheinlichen Einwanderungsweg in die Vereinigten Staaten erbracht.

Der Unterschied in der mittleren Körperlänge von *V. jacobsoni* parasitierend auf *Apis cerana* und auf *Apis mellifera* ist statistisch signifikant, aber die Einzelwerte für die Körperlänge überlappen sich stark. Die kleinsten Milben auf *Apis mellifera* überlappen die mittleren Größen der Milben auf *Apis cerana*, und umgekehrt. Die größten Exemplare von *V. jacobsoni* wurden in Völkern von *Apis cerana* in Nepal gefunden; die kleinsten Milben kamen ebenfalls auf *Apis cerana* vor, und zwar auf Ceylon (Sri Lanka). Das Gesamtergebnis zeigt eine bemerkenswerte Stabilität der Merkmalsvarianz der Populationen von *V. jacobsoni* über ihr geographisches Verbreitungsgebiet mit

kontinuierlichen allmählichen Übergängen in der Variabilität von Kontinent zu Kontinent.

Es gibt keinen Grund für den Verdacht, daß mehr als eine einzige kosmopolitische Art existiert, die sowohl auf *Apis cerana* wie auf *Apis mellifera* parasitiert. Die Analyse der Zentroide, der Mahalanobis-Distanzen und der Resultate der Cluster-Analysen haben ergeben, daß die Proben aus Wisconsin und aus Florida der *V. jacobsoni* aus Brasilien ähnlicher waren als die Proben aus Europa und aus Asien. Es wird daraus der Schluß gezogen, daß die in die Vereinigten Staaten eingeschleppten Milben aus Südamerika stammen. Die Herkunft der Einschleppung wird unter dem Aspekt der evolutionären Bedeutung und der Virulenz der Milbenstämme diskutiert.

***Varroa jacobsoni* — Morphometrie — geographische Variabilität — multivariate Analyse**

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