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~~Bi~~ogeography and Taxonomy of *Mononychellus* species associated with *Manihot esculenta* Crantz in the Americas

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Biogeography and Taxonomy of *Mononychellus* species associated with *Manihot esculenta* Crantz in the Americas

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RUNNING HEAD Biogeography and Taxonomy of *Mononychellus* Spp

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ABSTRACT

We mapped the distribution of *Mononychellus* spp. associated with cassava based on survey of 1264 fields in thirteen Central and South American countries. We collected *M tanajoa* (Bondar) in Panama, Colombia, Venezuela, Guyana, Trinidad & Tobago, Brazil and Paraguay, but not north of Panama, nor south of Colombia in the Andean region. *M. tanajoa* was primarily associated with humid to seasonally dry lowlands except in northeast Brazil, where the ecological range extends to semiarid lowland areas *M caribbeanae* (McGregor) was the most geographically widespread species, and was the predominant species of *Mononychellus* on cassava in semiarid lowland areas, except in northeast Brazil, Peru or Paraguay where it does not occur. We found *M* *mcgregori* Flechtmann & Baker in humid highlands (interandean valleys) of Colombia, Ecuador and Peru, in subtropical southern Brazil, and in the Colombian region of the Amazon Basin (humid lowlands). *M* *planki* (McGregor) was collected from one field in northeast Brazil and from five fields in Colombia. *Mononychellus* *tanajoa* (Bondar) is a polymorphic species with considerable variability in the length of the dorsocentral setae D1, D2 and D3 We found polymorphic populations of *M* *tanajoa* in throughout its known range in the Americas, except in northeast Brazil where setal morphology is skewed towards the short extreme of the phenotypic range The largest number of *Mononychellus* species on cassava and a high degree of setal polymorphism in *M* *tanajoa* ocurred in Colombia. Several implications for biological control of *M* *tanajoa* follow from the existence of a geographical subpopulation distinct from other populations in the American of African range of this species.

KEYWORDS. *Mononychellus* *tanajoa*, *Mononychellus* *caribbeanae*, *Manihot* *esculenta*, Cassava Green Mite, biological control, electrophoresis, taxonomy, biogeography

INTRODUCTION

Taxonomy of CGM

The taxonomic controversy surrounding the so-called cassava green mite (CGM) complex led to uncertainty about the number of species of *Mononychellus* introduced to Africa, and has been reviewed Yaninek and Herren (1988). Analyses of African specimens by Gutierrez (1987) based on the form of the aedeagus, by Rogo *et al*. (1988) based on 22 morphological characters in addition to the aedeagus, and by Murega (1989) based on hybridizations between individuals from different geographical populations, concurred that only one species was introduced Gutierrez (1987) reported that differences between and within populations were common with respect to the lengths of the dorsal setae of the genus *Mononychellus*. This type of variation had been previously reported for other tetranychid genera such as *Eutetranychus* (Gutierrez 1985) Rogo, Gutierrez and Murega did not agree, however, on whether CGM in Africa should be called *M tanajoa* or *M*. *progresivus* Doreste (1981). *M*. *tanajoa* was the name given in the original description of the species (Bondar 1938), however type specimens collected from cassava in northeast Brazil can not be located (Gutierrez 1987).

M. *progresivus* is a species described from cassava in Venezuela. This name entered the literature when variation in the lengths of the dorsocentral setae of green mites collected from cassava in the Americas led Doreste (1981) to describe two new species, *M*. *progresivus*, and *M manihoti*, supposed sibling species of *M tanajoa* Rogo *et al* (1987) studied the lengths of the dorsocentral setae D1, D2, and D3, of specimens from Venezuela, representing the topotype of *M. progresivus*, from Brazil, representing the topotype for *M. tanajoa*, and from several African countries, concluding that these characters alone could not be used to distinguish between the two species since their lengths varied in a continuous gradient from the shorter *tanajoa* to the longer *progresivus* type. Subsequently, Rogo *et al.* (1988) found a relationship between the lengths of the dorsocentral setae and the geographical origin of African specimens of *M. tanajoa*, and concluded that populations could be classified into short, intermediate and long setal forms.

The Origin of the Cassava Green Mite

Classical biological control programs generally begin by exploring for natural enemies in the likely areas of origin of the pest (Waage 1990) *M tanajoa* was accidentally introduced to Africa in the 1970s (Yaninek & Herren 1988) from the Neotropics (Nyiira 1972, unpublished; Lyon 1974). Areas of the Neotropics which are ecologically similar to CGM-affected areas of the African cassava-growing belt are priority areas for exploration for natural enemies of CGM for introduction to Africa (Yaninek & Bellotti 1987, Bellotti *et al.* 1987) A second strategy, compatible with the agroecological homologue approach, is suggested by the trophic relationship between CGM and cassava CGM feeds almost exclusively on *Manihot*, the cassava genus, in the Neotropics (Byrne 1980, Moraes & Flechtmann 1981, Moraes *et al* submitted), and has maintained this trophic habit under African conditions (Yaninek & Herren 1988) The oligophagous relationship between CGM and Manihot in the Neotropoics suggests a close coevolutionary relationship between Manihot and CGM (Yaninek & Bellotti 1987) More specific knowledge of the origin of CGM within the Neotropics would contribute selection of areas for natural enemy exploration.

We measured dorsocentral setal lengths and evaluated other taxonomic characters for a large sample of *M. tanajoa* specimens from the Americas to determine the degree of variability of these characters, and to test Rogo's hypothesis of geographic variation in morphology Based on these taxonomic analyses and other supporting data, we present a hypothesis for the area of origin of the trophic relationship between *Mononychellus* species and cassava, and discuss implications for biological control of *M tanajoa*.

METHODS AND MATERIALS

Specimen Collection

Specimens were obtained during exploration trips made for collection and characterization of CGM natural enemies. The countries visited and the areas searched within countries were selected according to a system of priority based on agroecological homology between the Americas and CGM-affected areas of Africa (Yaninek & Bellotti 1987, Bellotti *et al* 1987) Homology maps were prepared based on Carter`s (1986) cassava microregion classification for S. America, and highest priority was given to tropical, seasonally dry (4-6 months/year with < 60 mm precipitation), isothermic lowlands Lowland, tropical, semiarid (7-9 dry months/year) isothermic areas, and seasonally dry or semiarid isothermic highlands were given second and third priority respectively The most geographically extensive cassava-growing ecosystem in the Americas is the wet (0-3 dry months/year), lowland, tropical zone This ecosystem also received coverage in the exploration campaign, as did subtropical southern Brazil and Paraguay.

With the exception of Bolivia, explorations were conducted in all countries containing priority areas. In the Caribbean and Central America, abrupt changes in terrain occur over short distances, precluding the generation of reliable homologue maps (P. Jones pers. com), therefore, areas visited were chosen based on primary sources of climate and crop distribution information from available weather data, atlases and national agricultural institutions. CGM were found in 673 of the 1264 cassava fields surveyed in 13 countries The CGM specimens included in our analyses were from the 266 of these 673 fields which yielded specimens with measurable dorsocentral setae plus an additional 259 Brazilian specimens from 49 fields not included in the survey The latter specimens were obtained by J. G. de Moraes

Specimen Preparation

CGM were collected, cleared in lactophenol and mounted in Hoyer's medium as described in Flechtmann (1982) Slides were dried for 3-4 days at 40°C before examination under a phase contrast microscope (400 X). The dorsocentral setae D1, D2 and D3 of female specimens were measured The right and left dorsocentral setae were found to be of unequal length in some specimens These were excluded from the analyses. One to 45 mites per site were measured for a total of 1862 specimens The form of the aedeagus was evaluated for male specimens prepared according to McGregor (1950). From 120 male specimens, we obtained 50 high quality slides

Statistical Analyses

We performed cluster analysis on the means of the lengths of the dorsocentral setae of CGM specimens obtained from each sampling site, using Ward's method (SAS Institute 1989) to minimize the variance within clusters. We based our decision on the number of clusters to accept on cophenetic correlation (Sneath and Sokal 1973) Subsequently, we performed a discriminant analysis (SAS Institute 1989) to find a mathematical function for more objective and rigorous classification of setal lengths into groups We assumed the frequency distribution of cluster membership was proportional rather than equiprobable, reflecting our empirical observation that some clusters are more frequently represented in nature than others. A pooled covariance matrix could not be specified, therefore, we used a quadratic discriminant function based on the estimated miminum total probability of misclassification for normal populations as given in Johnson and Wichern (1982).

We based the initial cluster analysis on the mean length of the dorsocentral setae of 1-45 specimens per site from 266 sampling locations in order to be able to map the distribution pattern. However, this approach obscures variability in setal length within clusters across sites In order to determine how well the relative frequency of cluster types based on analysis of individual specimens was represented by the mapping approach, we assigned each specimen to a cluster based on the discriminant function generated from the original data, and calculated the frequency of cluster membership within countries, regions and within clusters across sites.

Follow-up Studies

After completing the cluster and discriminant analyses, we made several additional studies to investigate phenomena observed during the evaluation of the specimens, or suggested by the data We analyzed anomalies in the number of tactile and sensory setae, and applied several electrophoretic techniques to determine whether mites with different setal lengths or from different geographical areas could be distinguished electrophoretically.

Electrophoresis

After failing to obtain bands on gels stained for glutamic oxalacetic transaminase we tested malate dehydrogenase but did find not polymorphism. We report results of electrophoreses performed on specimens of CGM from several sites in Colombia (Malagana [n=30] and Arjona [n=30], Bolivar; Luruaco [n=30], Atlantico; and Palmira, Valle [n =48]) and Brazil (Cruz das Almas, Bahia [n=59]) to determine

1) whether geographical races could be distinguished and

2) whether race and setal length are related

We used vertical polyacrylamide slab gradient and discontinuous gels (MiniBioRad) prepared according to methods modified from Hussain et al. (1988) and Poehling & Neuhoff (1980), with one mite per sample and staining for α- and ß-esterases.

Anomalies in the number of tactile and sensory setae in CGM

The number of tactile and sensory setae on tarsus I and tibia I were recorded for a subsample of 20-29 randomly selected female specimens from each cluster. The frequency of occurrence of anomalies in the number of tactile and sensory setae was classified according to cluster membership. The anomalies were:

1) presence of more than one sensory seta on either tarsus I or tibia I ("masculinization", according to Guttierez 1987);
2) differences between the left and right tarsus I and/or tibia I in the number of tactile or sensory setae;
3) more or less than five tactile setae on tarsus I;
4) more or less than nine tactile setae on tibia I

X^2 goodness-of-fit tests were applied to the data.

RESULTS

Distribution of Mononychellus Species in the Neotropics

One thousand two hundred sixty four cassava fields were surveyed in 13 countries (Colombia, Venezuela, Trinidad and Tobago, Brazil, Cuba, Mexico, Nicaragua, Honduras, Panama, Peru, Paraguay, Guyana, and Ecuador; see Table 1)) Forty five and 47%

respectively of cassava fields where *M tanajoa* was detected were in humid lowland or seasonally dry lowland zones The remaining 8% were distributed between semiarid lowlands, and humid, seasonally dry and semiarid highland ecosystems. Forty-two and 49% respectively of the cassava fields samples in humid (n=544) and seasonally dry lowlands (n=488) were infested with CGM Only 18% of 112 fields surveyed in semiarid lowlands were infested and 12 of these 20 fields were in northeast Brazil Outside Brazil, *M. caribbeanae* was present in 64% of the semiarid fields surveyed This species was not found in Brazil

M tanajoa was present in 56% of 52 fields in our survey of northeast Brazil, and in 89% of 427 additional fields sampled by Moraes (unpublished data) for an overall frequency of 85%. In Colombia and Venezuela, *M tanajoa* was identified in 48 and 85% respectively of fields visited None were collected from 132 Ecuadorian sites or from 92 sites visited in Mexico, Peru, Nicaragua, Honduras, and Cuba The most frequently encountered species of *Mononychellus* in Ecuador, Mexico, Nicaragua and Cuba was *M caribbeanae* (McGregor) (Table 1) The only regions where *M caribbeanae* was not detected were in Brazil, Peru and Paraguay (Fig 1). Records of *M caribbeanae* in Brazil have appeared in several unpublished reports (Yaseen 1977, 1978, Yaseen and Bennett 1978), however, these do not mention how the specimens were identified, nor were specimens available for examination (P Baker, Director, CAB International, Trinidad and Tobago Station, pers com.) Apart from this discrepancy, good agreement was found between the results of our survey and published reports on the distribution of Mononychellus species in the Neotropics (Table 2) M. caribbeanae was not identified in Moraes' (unpublished) survey of 427 cassava fields in northeast Brazil.

We found M. mcgregori in the humid highlands (interandean valleys) of Colombia, Ecuador and Peru, in the Colombian region of the Amazon Basin and in the state of Santa Catarina in southern Brazil (Table 1, Fig. 1). We could not confirm unpublished reports (Yaseen & Bennett 1978) of this species in Trinidad.

Dorsocentral Setal Lengths of CGM

Measurements of the dorsal setae of CGM collected in the Americas indicate the presence of short setal forms fitting the description of M. tanajoa, and long setal forms fitting Doreste's (1981) original description of M. progresivus. Intermediate types between the two extremes also occur in a continuous gradient (Fig. 2). M tanajoa populations were divided into five clusters based on the mean lengths of the setae D1, D2, and D3 (Table 3), resulting in a multivariate r^2 of 0.87 The decision to accept five clusters was based on cophenetic correlation, arbitrarily high values of r^2 could be attained by further increasing the number of clusters, however, the increase resulting from adding an new cluster was small when the number of clusters exceeded five The division into five clusters provides an heuristic nomenclature for referring to setal length. Clusters can conveniently be called very short, short, intermediate, long and very long (Table 3, Fig. 3) and will henceforth be referred to as morphotypes

The multivariate distances between morphotypes were statistically significant (Wilk's Lambda: F = 100.06, df = 12, P = 0.0001) Morphotype membership was assigned differently by discriminant analysis for 1.9% of the 266 samples. This low apparent error rate suggests that accepting five morphotypes is statistically robust The discriminant function is given in the appendix.

All morphotypes were found in in Colombia, Brazil and Venezuela where sample sizes were large (Table 4). Eighty-two % of sites (Table 5) and 85% of specimens (Table 4) from Brazil were classified as having either the very short or short morphotypes In Colombia 20% of sites (Table 5) and 18% of specimens were of the short morphotypes In Venezuela 97% of sites (Table 5) and 93% of specimens (Table 4) were of the short, intermediate or long morphs

Fewer than 15 sites were sampled in each of the other countries where *M. tanajoa* was collected. In Paraguay, both extremes of variability were found (Table 5) and analysis of individual specimens revealed mites of all but the intermediate morphotype in a sample of 11 females In Trinidad, 100% of the eight sites had the long morphotype (Table 5), and individual specimens (n=64) of all morphs except the very short were found (Table 4) In Panama 80% of sites (Table 5) and 94% of individual specimens (Table 4) were of the short morph The long morphotype occurred in the remaining 20% of sites (Table 5)

In general, where sample size was adequate, good agreement was obtained between analyses based on mean setal lengths from each collection site and from individual specimens When the individual specimens from all sites classified to a given morphotype were classified by the discriminant function, the existence of polymorphism within morphotypes across sites emerged (Table 6) We found less polymorphism at the short extreme of the phenotypic range than at the long extreme. Sites classified as having the intermediate morphotype are highly polymorphic (Table 6)

Geographical analysis of the unusual distribution of setal length in Brazil revealed that the skewness towards the short morphs was due to the high frequency of short morphotypes in the northeast region (Fig. 4). Fifty-three of the 54 populations from northeast Brazil had short or very short mean setal lengths (Table 7). The other 1.8% of sites and 6 1% of specimens were of the intermediate morph (Table 8). Northeast Brazil was the only large contiguous region sampled where mites with long setae were not found (Fig 4, Table 8)

Of the 266 sites analyzed, only fourteen were in highland areas. One hundred six sites were in humid lowlands, 123 were in seasonally dry lowlands and 22 were in semiarid lowlands. All setal morphs occurred in humid lowlands and in seasonally dry lowlands (Fig 5) The short morph had a higher frequency than expected in semiarid lowland areas ($X^2 = 36.78$, 4 d f $P \leq$ 0 001)

The Aedeagus

Variation in the form of the aedeagus of male specimens from different sites was negligible (Fig. 6). The shape of the aedeagus was similar to a drawing made by Tuttle *et al* (1977) for *M tanajoa*. The aedeagi examined did not resemble the drawings made by Flechtmann (1982) or Gutierrez (1987), however, it is not clear whether the latter drawing was based on conventional preparations or on males prepared according to the mounting technique described in Gutierrez (1985)

Sensory and Tactile Setae

Doreste (1981) reported 4 tactile and 1 sensory setae for *M. tanajoa* and 4 tactile and no sensory setae on tarsus I for *M progresivus* when he proposed the existence of three different species in the group then called *M. tanajoa* We examined 20-29 specimens chosen randomly from each morphotype. All had sensory setae on tarsus I. In general, five tactile setae were present on tarsus I, and nine were present on tibia I, as described by Flechtmann & Baker (1970) and Nokoe & Rogo (1988) for *M. tanajoa*. However, several types of anomalies were observed 32% of specimens had fewer or more than five tactile setae on tarsus I; 0 8% had fewer or more than nine tactile setae on tibia I, 0 8% of specimens were masculinized, with more than one sensory seta on tarsus I and/or tibia I (see Gutierrez 1987), 29 and 11 % of specimens had diferences between the number of right and left tactile and sensory setae on tarsus I and tibia I, respectively The probability of possessing normal morphology was equal for all morphotypes (Table 9, X^2 goodness-of-fit test, NS) With respect to specific types of anomalies, the probability of possessing

1) unequal number of right and left sensory and tactile setae or
2) more or less than 5 tactile setae on tarsus I

was equal for all morphotypes (Table 9, X^2 goodness-of-fit test; NS)

Electrophoresis

Polymorphism was not found for malate dehydrogenase or glutamic oxalacetic transaminase. The banding patterns for α- and β-esterases from *M. tanajoa* collected from the Caribbean coast (Malagana and Arjona, Bolivar, Colombia; Luruaco, Atlantico, Colombia), an interandean valley (Palmira, Valle, Colombia) and northeast Brazil (Cruz das Almas, Bahia) were identical (Figs 7,8), however, greater esterase activity, expressed as darker bands, was consistently found in specimens with short setae (Fig. 8)

DISCUSSION

Morphological Variability

Our data corroborate Rogo's *et al* (1988) conclusion that *M progresivus* and *M. tanajoa* comprise a single polymorphic species, and that morphotype may be associated with the geographical origin of specimens

Rogo *et al* (1987) report a range in variation in setal lengths for CGM collected in Africa similar to that reported here for northwest S America, Central and Southern Brazil and Paraguay Assuming that setal length is genetically determined, if the introduction of CGM to Africa was from a site with a highly polymorphic population, a single introduction of CGM to Africa could account for the polymorphism in Africa. It is unlikely that the origin of CGM in Africa was from northeast Brazil, where variability in setal length is limited.

A similar degree of variability in length is present in the lateral hysterosomal setae of _M_. _caribbeanae_ (Guerrero unpub. data) The short setal forms fit the the description of _M_ _caribbeanae_ (McGregor 1950) and the long setal forms fit the description of _M_ _erythrinae_ (Tuttle _et al_ 1976), a species described from Mexico on _Erythrina_ sp A continuous gradient of intermediate forms occurs between these extremes (Guerrero unpub data).

Distribution and Ecological Adaptation of Mononychellus spp.

Comparison of our collection records of _Mononychellus_ species on cassava in the Neotropics with reports in the literature indicates that _M_. _tanajoa_ is present in Colombia, Venezuela, Brazil, Guyana and Paraguay (See Table 2) In Central America CGM has been reported in Panama and Costa Rica, and in the Caribbean, in Trinidad and Tobago and Haiti. _M_. _bondari_ Paschoal, which we consider to be a junior synonym of _M_ _tanajoa_, which has been reported once from cassava in Brazil, and once from Colombia (see Table 2) was not detected in our survey We found _M_. _mcgregori_ in interandean valleys of Colombia, Ecuador, and Peru (Fig 1) and in subtropical southern Brazil, corroborating the reports of Samways & Ciociola (1980), but were unable to confirm unpublished reports (Yaseen 1978; Yaseen & Bennett 1978) of this species in northeast Brazil or Trinidad and Tobago. *M caribbeanae* occurs from southern Florida (Peña & Wadill 1982, Peña *et al* 1984), throughout the Caribbean basin (see Table 2) and in Ecuador, however we could not corroborate unpublished reports of this species in northeast Brazil (Yaseen 1977, 1978, Yaseen & Bennett 1978). Other Neotropical species of *Mononychellus* (see Table 2) have been reported primarily from Mexico on species other than *Manihot*. Northeast Brazil and Paraguay are unique in that neither *M*. *caribbeanae* nor *M*. *mcgregori* were detected in our survey.

M caribbeanae was collected in zones with 0 to 9 dry months/yr, and with mean annual precipitation between 401 to 3023 mm/yr The mean number of dry months/yr for these sites was 5 6 compared to 3 1 for *M tanajoa*, indicating that *M caribbeanae* distribution is skewed towards subhumid areas, whereas CGM distribution is skewed towards more humid zones. The absence of *M caribbeanae* in northeast Brazil is particularly noteworthy given the sizeable seasonally dry to semiarid cassava-growing area where *M*. *caribbeanae* would presumably be well adapted. The absence of *M*. *mcgregori* in northeast Brazil, on the other hand, is not as surprising, since 80% of cassava fields where this species has been detected in our survey were in humid interandean valleys

Origin of the Trophic Relationship between Mononychellus and cassava

The largest number of species of Mononychellus on cassava occurs in Colombia, with the number dropping off with distance both towards Central America and the Caribbean, and to the south, suggesting a center of genetic diversity for the genus. The antiquity of cassava cultivation in northwest S. America is well documented (Shultes 1987), and this region is an area of primary genetic diversity of cassava (Gulick *et al* 1983) and may be a one of several possible areas of domestication (Sauer 1969, Lathrap 1973; Spath 1973, Renvoise 1973). Colombia also has the greatest diversity of phytoseiid predators of tetranychid mites reported on cassava (CIAT 1991, Botelho *et al*. submitted). Together these patterns point to a possible area of origin of the trophic association between Mononychellus and cassava in northwest S America

Hypotheses about Mononychellus tanajoa in Northeast Brazil

The absence in northeast Brazil of the setal polymorphism associated with *M. tanajoa* throughout the rest of its range is unique. CGM with short dorsocentral setae can be distinguished electrophoretically from specimens with long setae by their enhanced esterase activity, suggesting some physiological differentiation and the possible existence of a geographical subpopulation in northeast Brazil It is striking that in Moraes' survey of 427 cassava fields in northeast Brazil (CIAT 1990, 1991) and in cassava germplasm screening sites (CIAT 1992), heavy infestations of CGM were found in semiarid areas, a pattern not seen elsewhere in tropical America or in Africa, where CGM does not appear to have colonized semiarid areas of Nigeria (M Porto pers. com) or Benin (Yaninek & Onzo 1988, unpublished)

A hypothesis which accounts both for the absence of other *Mononychellus* species and the limited setal polymorphism skewed toward the short extreme of polymorphic variability in *M tanajoa* in northeast Brazil is that CGM was introduced inadvertently to the area. The absence of the long morphs over such an extensive area could have come about if the founder population had short setae, and a high degree of genetic isolation was maintained. Alternatively, after introduction of a polymorphic founder population, selection may have favored the short morphotypes leading to elimination of the others. The absence of competition from other *Mononychellus* species, particularly *M. caribbeanae* may have contributed to the success of the short morphotypes of *M tanajoa* in northeast Brazil and to its unique adaptation to semiarid environments Molecular techniques have recently been applied in acarological phylogenetic research (Kaliszewski *et al* 1992, Navajas *et al*. 1992) The application of these techniques in studies of phylogenetic relationships of *Mononychellus* spp may provide a conclusive means to assess whether a distinct CGM biotype occurs northeast Brazil.

The variability in setal length, the relatively high frequency of anomalies in the numbers of tactile and sensory setae found in *M. tanajoa*, and the high frequency of similar phenomena in *M. caribbeanae* suggests that rapid evolutionary change is occurring in these species in the Americas, perhaps in response to the great range of edaphic and climatic factors under which cassava is grown We collected *M* *tanajoa* over a range of altitudes (2-1820 m), and precipitation zones (425-4468 mm/yr) with widely varying rainfall patterns (1-9 dry months/yr). The diversity of ecological conditions under which cassava has been cultivated in the Andean zone and the patchiness of cassava distribution there (Carter 1986) are both related to the mountainous topography of the region. Less agroecological and topographical variability occurs in northeast Brazil, where we collected *M*. *tanajoa* from 30-900 m above sea level in rainfall zones from 425-2083 mm/yr Agroecological diversity and patchy distribution may have been incisive in the speciation of *Mononychellus* associated with *Manihot* and in the appearance of setal polymorphism in CGM and *M*. *caribbeanae*

Implications for Biological Control

CGM is considered an important pest of cassava in northeast Brazil, particularly in seasonally dry and semiarid areas (Veiga, 1985) Alternatives for control of CGM in northeast Brazil have focused on host plant resistance, and improving the level of resistance to CGM is a high priority for cassava breeders working in the states of Ceara, Paraiba, Pernambuco, Alagoas and Bahia (C Iglesias pers. com.). To date no effort has been made to improve levels of biological control, even though the phytoseiid fauna in cassava all agroecological zones of northeast Brazil is less diverse than that in homologous zones in northwest S

America (CIAT 1991, Moraes et al submitted) Introduction of exotic species or strains may provide an ecologically sound pest management option in northeast Brazil if species or strains which are well adapted to semiarid conditions can be found The largest diversity of phytoseiid species in a semiarid area occurs in coastal Ecuador (Braun 1993). Introduction of exotic natural enemies for control of CGM in Brazil should be implemented in conjunction with other plant protection measures such as augmentation and conservation of natural enemies, habitat manipulation and the deployment of host plant resistance

The possibility that the trophic relationship between *Mononychellus* and *Manihot* evolved in northwest S. America suggests that this area should receive high priority as a source of phytoseiid predators and fungal pathogens (*Neozygites* spp.) of natural enemies of CGM for introduction to Africa and Brazil.

A high degree of host specificity of *Neozygites* spp. can be deduced from the difficulty of culturing this fungus on artificial media (Alvarez 1990, Evans 1991). Since our data point to differences in morphotype composition and ecological adaptation between CGM from northeast Brazil and Africa, we recommend broadening the effort to introduce fungal pathogens from northeast Brazil to include *Neozygites* species/strains obtained elsewhere in the Americas

The use of ecological homologue mapping for prioritizing the search for natural enemies and deciding which natural enemies to introduce to particular regions of the African cassava belt has been proposed by Yaninek & Bellotti (1987), and is compatible with a strategy based on searching in the area of origin of the trophic relationship between CGM and cassava.

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Table 1 Inventory of *Mononychellus* species on cassava in the Americas.

Country	No fields sampled	Species Reported	No fields present
Brazil	52	*M. tanajoa*	29
		M planki	1
		M mcgregori	1
Cuba	43	*M caribbeanae*	23
Ecuador	132	*M caribbeanae*	65
		M. mcgregori	13
Colombia	869	*M. tanajoa*	420
		M. caribbeanae	71
		M. mcgregori	59
		M. planki	5
Mexico	27	*M caribbeanae*	16
Nicaragua	2	*M caribbeanae*	1
Honduras	3	*M caribbeanae*	3
Panama	17	*M caribbeanae*	13
		M tanajoa	3
Venezuela	84	*M tanajoa*	76
		M. caribbeanae	36
Peru	14	*M mcgregori*	5
Paraguay	7	*M. tanajoa*	5
Trinidad & Tobago	12	*M caribbeanae*	11
		M tanajoa	8
Guyana	2	*M. caribbeanae*	1
		M. tanajoa	1

Table 2 *Mononychellus* species reported in the Neotropics

Species	Country	Reference
M *hispidosetus*[1]	Mexico[a]	Beer & Lang 1958, Tuttle *et al* 1976
M *hyptis*[2]	Mexico[a]	Tuttle *et al* 1974, 1976
M *estradai*[3]	Mexico[a]	Tuttle *et al* 1976
	Nicaragua[a]	Baker & Pritchard 1962
M *erythrinae*[2]	Mexico[a]	Tuttle *et al* 1976
M *flabellosetus*[1]	Mexico[a]	Beer & Lang 1958 Tuttle *et al* 1976
M *chapalensis*[2]	Mexico[a]	Tuttle *et al* 1976
M *willardiae*[2]	Mexico[a]	Tuttle *et al* 1976
M *wainsteini*[2]	Mexico[a]	Tuttle *et al* 1976, 1977
M *eysenhardtiae*[2]	Mexico[a]	Tuttle *et al* 1976
M *tephrosiae*[2]	Mexico[a]	Tuttle *et al* 1974 1976
M *psidium*[4]	Mexico[a]	Estebanes & Baker 1968, Tuttle *et al* 1976
M *vilaricensis*	Brazil[a]	Paschoal 1971c
M *bondari*[5]	Brazil	Paschoal 1970a, Flechtmann & Baker 1970, Yaseen & Bennett 1978[b]
	Colombia	Urueta 1975
M *mcgregori*[6]	Brazil	Yaseen 1978[b], Samways & Ciociola 1980,
	Colombia	Urueta 1975 Yaseen & Bennett 1977[b], 1978[b] Guerrero & Bellotti 1980, CIAT[c]
	Trinidad	Yasseen & Bennett 1978[b]
	Argentina[a]	Pritchard & Baker 1955
	Panama	CIAT[c]
	Peru	CIAT[c]

(continued)

Table 2 (cont) *Mononychellus* species reported in the Neotropics

Species	Country	Reference
M manihoti[8d]	Venezuela	Doreste 1980, 1981
	Trinidad	CIBC 1982[b]
M progresivus[8d]	Bolivia, Colombia	Yaseen 1978[b]
	Venezuela	Yaseen 1978[b]
	Paraguay,	Yaseen 1988
	Trinidad	Yaseen 1978[b]
M tanajoa[9]	Brazil	Bondar 1938, Paschoal 1971a, Flechtmann & Abreu 1973, Flechtmann & Bastos 1972, Costa 1975, Tuttle *et al* 1977, Yaseen & Bennett 1977[b], 1978[b], Flechtmann 1987, Yaseen 1978[b], Farias *et al* 1978, 1979, 1981, Samways & Ciociola 1980, CIAT[c]
	Paraguay	Aranda & Flechtmann 1971, CIAT[c], Yaseen & Bennett 1977[b]
	Costa Rica	Salas 1978
	Colombia	Urueta 1970, 1975, Yaseen & Bennett 1977[b], 1978, Guerrero & Bellotti 1980, CIAT[c]
	Venezuela	Quiroz 1977, Yaseen & Bennett 1978[b], Doreste 1981, CIAT[c]
	Haiti	Lenoir *et al* 1981
	Guyana, Trinidad	Yaseen & Bennett 1977[b], 1978[b], CIAT[c]
	Bahamas, Surinam	Yaseen 1977[b], Yaseen & Bennett 1978[b]
	French Guyana	Yaseen 1978[b]
	Panama	CIAT[c]

[a] Reports on host plants other than *Manihot* spp

[b] Unpublished

[c] Specimens deposited in a reference collection at Centro Internacional de Agricultura Tropical (CIAT)

(Continued)

Table 3 Mean dorsocentral setal lengths of female *Mononychellus tanajoa* from 266 sites in the Americas

Cluster	Morphotype	n	Seta	Mean length (μm)	Range (μm)
1	Very short	29	DC1	20.37	17.85-22.24
			DC2	21.45	17.85-25.50
			DC3	24.87	20.40-28.22
2	Short	73	DC1	24.05	20.40-26.78
			DC2	25.32	22.95-28.90
			DC3	30.68	26.07-37.05
3	Intermediate	32	DC1	25.64	22.10-28.05
			DC2	28.26	25.50-30.60
			DC3	38.83	33.15-45.05
4	Long	94	DC1	28.85	23.80-34.00
			DC2	34.99	28.90-45.90
			DC3	46.35	35.21-61.20
5	Very long	38	DC1	36.17	30.60-54.40
			DC2	44.82	34.00-56.10
			DC3	54.19	44.20-64.60

Table 4 Distribution of dorsocentral setal length morphotypes in *Mononychellus tanajoa* specimens from the Americas.

Country	No specimens measured	% specimens/morphotype[1] 1	2	3	4	5
Brazil	611	28.6	55.8	12.1	1.0	2.5
Colombia	716	2.9	15.5	24.3	16.8	40.5
Venezuela	440	1.6	25.9	48.9	18.6	5.0
Trinidad	64	0.0	7.8	84.4	6.25	1.6
Panama	18	0.0	94.4	5.6	0.0	0.0
Paraguay	11	36.4	9.1	0.0	45.5	9.1
Guyana	2	0.0	0.0	0.0	100.0	0.0

[1] 1=very short, 2=short; 3=intermediate; 4=long; 5=very long.

Table 5 Geographic distribution of *Mononychellus tanajoa* dorsocentral setal length morphotypes in Brazil.

Region[2]	No sites sampled	% sites/morphotype[1]				
		1	2	3	4	5
North	5	100.0	0.0	0.0	0.0	0.0
Northeast	54	27.8	70.4	1.8	0.0	0.0
Central West	16	12.5	12.5	18.8	31.3	25.0
Southeast	8	12.5	62.5	12.5	12.5	0.0
South	1	100.0	0.0	0.0	0.0	0.0

[1] 1=very short, 2=short; 3=intermediate, 4=long, 5=very long

[2] States sampled in regions are North-Amazonas, Northeast-Ceara, Piaui, Bahia, Alagoas, Sergipe, Paraiba, Pernambuco, Maranhao, Central West-Matto Grosso do Sul, Brasilia D F , Southeast-Sao Paulo, South-Santa Catarina.

Table 6. Variability within dorsocentral setal morphotypes of *Mononychellus tanajoa* from the Americas.

			% specimens/morphotype[1]			
Morphotype	No females measured	VS	S	I	L	VL
VS	208	60.4	39.6	0.0	0.0	0.0
S	589	5.5	88.6	5.9	0.0	0.0
I	518	0.4	42.0	29.0	27.8	0.8
L	218	0.0	10.3	12.1	63.5	14.2
VL	329	0.0	1.4	2.1	26.0	70.6

[1] VS=very short, S=short, I=intermediate, L=long, VL=very long.

Table 7. Geographic distribution of *Mononychellus tanajoa* dorsocentral setal length morphotypes in Brazil

		% sites/morphotype[1]				
Region[2]	No. sites sampled	VS	S	I	L	VL
North	5	100.0	0.0	0.0	0.0	0.0
Northeast	54	27.8	70.4	1.8	0.0	0.0
Central West	16	12.5	12.5	18.8	31.3	25.0
Southeast	8	12.5	62.5	12.5	12.5	0.0
South	1	100.0	0.0	0.0	0.0	0.0

[1] VS=very short, S=short, I=intermediate; L=long, VL=very long

[2] States sampled in regions are. North-Amazonas, Northeast-Ceara, Piaui, Bahia, Alagoas, Sergipe, Paraiba, Pernambuco, Maranhao; Central West-Matto Grosso do Sul, Brasilia D F , Southeast-Sao Paulo, South-Santa Catarina

Table 8. Distribution of *Mononychellus tanajoa* dorsocentral setal length morphotypes in Brazil.

		% specimens/morphotype[1]				
Region[2]	No specimens measured	VS	S	I	L	VL
North	15	100.0	0.0	0.0	0.0	0.0
Northeast	459	29.4	64.5	6.1	0.0	0.0
Central West	73	16.4	17.8	38.4	6.8	20.5
Southeast	58	13.8	55.2	31.0	0.0	0.0
South	6	100.0	0.0	0.0	0.0	0.0

[1] VS=very short, S=short, I=intermediate; L=long; VL=very long.

[2] States sampled in regions are. North-Amazonas; Northeast-Ceara, Piaui, Bahia, Alagoas, Sergipe, Paraiba, Pernambuco, Maranhao; Central West-Matto Grosso do Sul, Brasilia D.F.; Southeast-Sao Paulo; South-Santa Catarina.

Table 9 Comparative frequencies of anomalies in the sensory and tactile setae of *Mononychellus tanajoa* morphotypes

		Anomaly type[1]				
Morphotype[2]	n	1	2	3[3]	4[4]	5
very short	23	14	1	6	7	0
short	20	10	0	9	10	0
intermediate	25	14	0	6	10	0
long	29	20	0	7	9	0
very long	25	21	0	3	3	1

[1] 1 = normal; 2 = masculinized; 3 = unequal number of right and left sensory or tactile setae; 4 = more or less than 5 tactile setae on tarsus I; 5 = more or less than 9 tactile setal on tibia I. The probability of possessing normal morphology is equal for all morphotypes (X^2 = 5 95, df = 4, P = 0 20, NS).

[2] Morphotype was determined by cluster analysis of lengths of dorsocentral setae D1, D2 and D2.

[3] The probability of possessing an unequal number of right and left sensory and tactile setae is equal for all morphotypes (X^2 = 4 96, df = 4, P = 0.29, NS).

[4] The probability of possessing more or less than 5 tactile setae on tarsus I is equal for all morphotypes (X^2 = 5 73, df = 4, P = 0.22, NS).

Figure Legends

Fig 1 The geographical distribution of *M. tanajoa*, *M caribbeanae*, *M planki* and *M. mcgregori* in the Americas

Fig 2 Variation in the length of the dorsocentral setae D1, D2, and D3 of *M tanajoa* (Morphotypes: A = very short; B = short, C = intermediate; D = long).

Fig. 3 Continuous gradient in variability in the mean length of the dorsocentral setae D1, D2, and D3 of *M. tanajoa* from 266 sites in the Americas and their distribution in morphotypes.

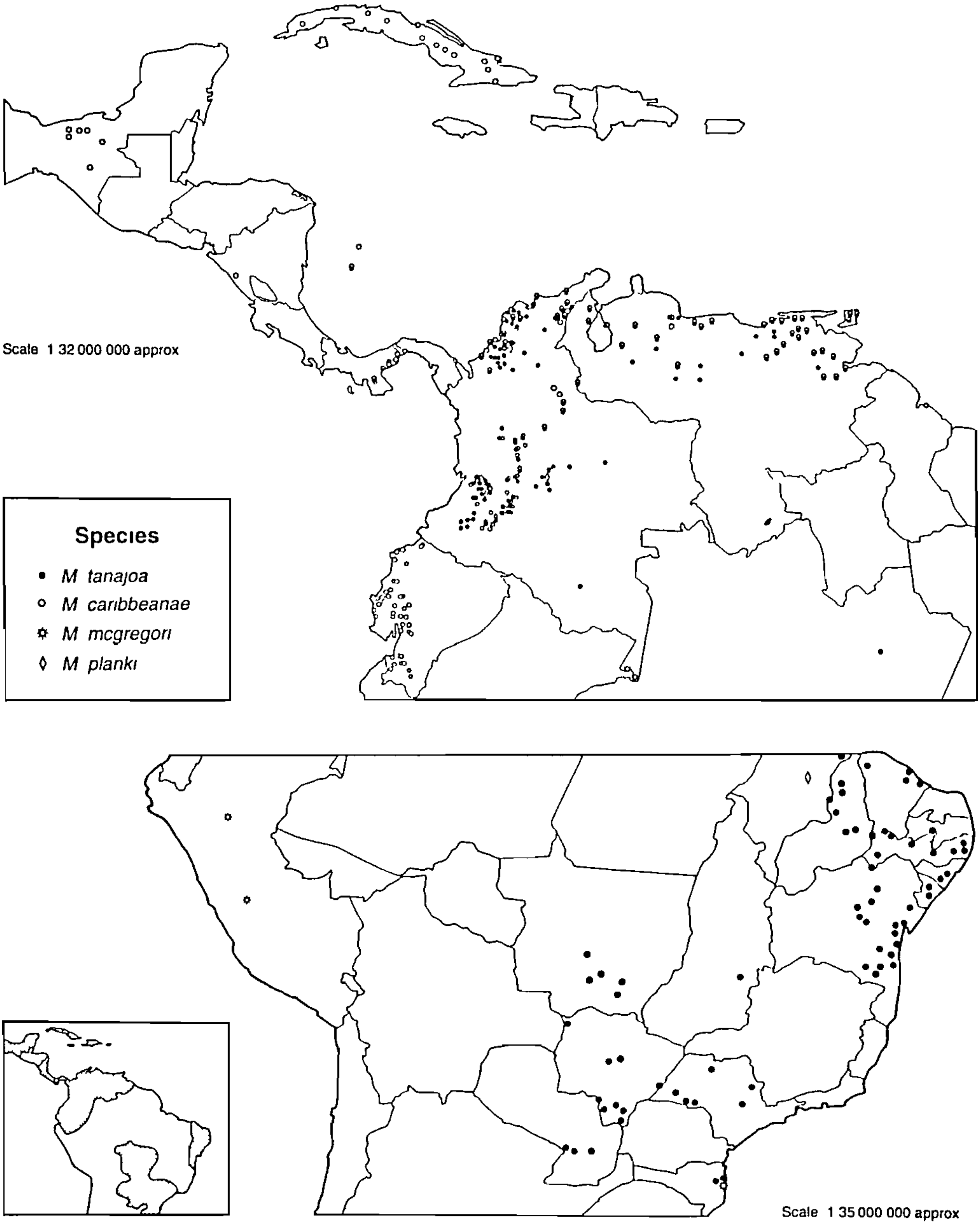
Fig 4 Geographical distribution of *M. tanajoa* morphotypes in the Americas.

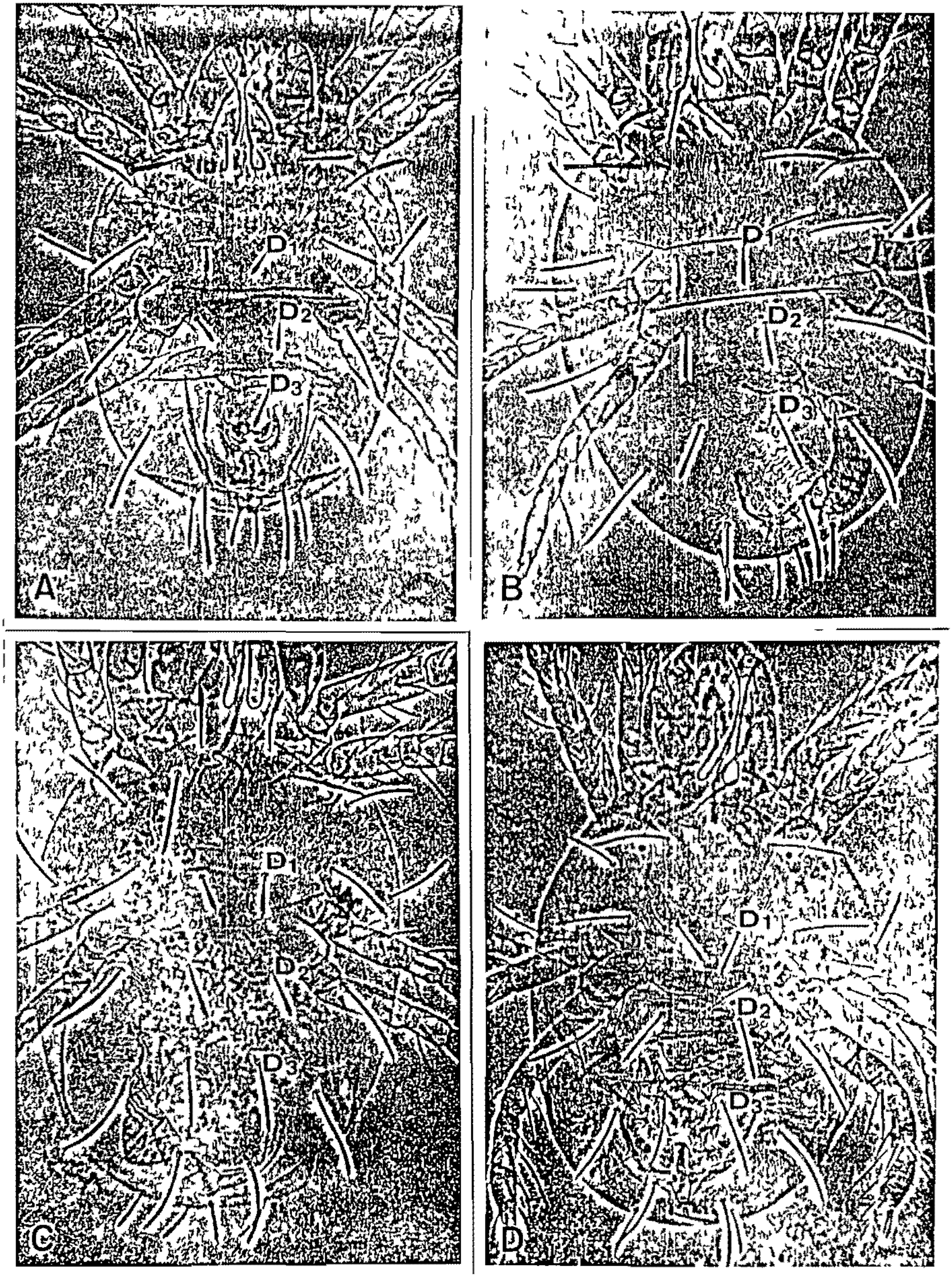
Fig. 5 Frequency of *M. tanajoa* morphotypes in humid (HL), seasonally dry (SDL), and semiarid (SAL) lowlands of the Americas (Morphotypes: VS = very short, S = short, I = intermediate, L = long, VL = very long).

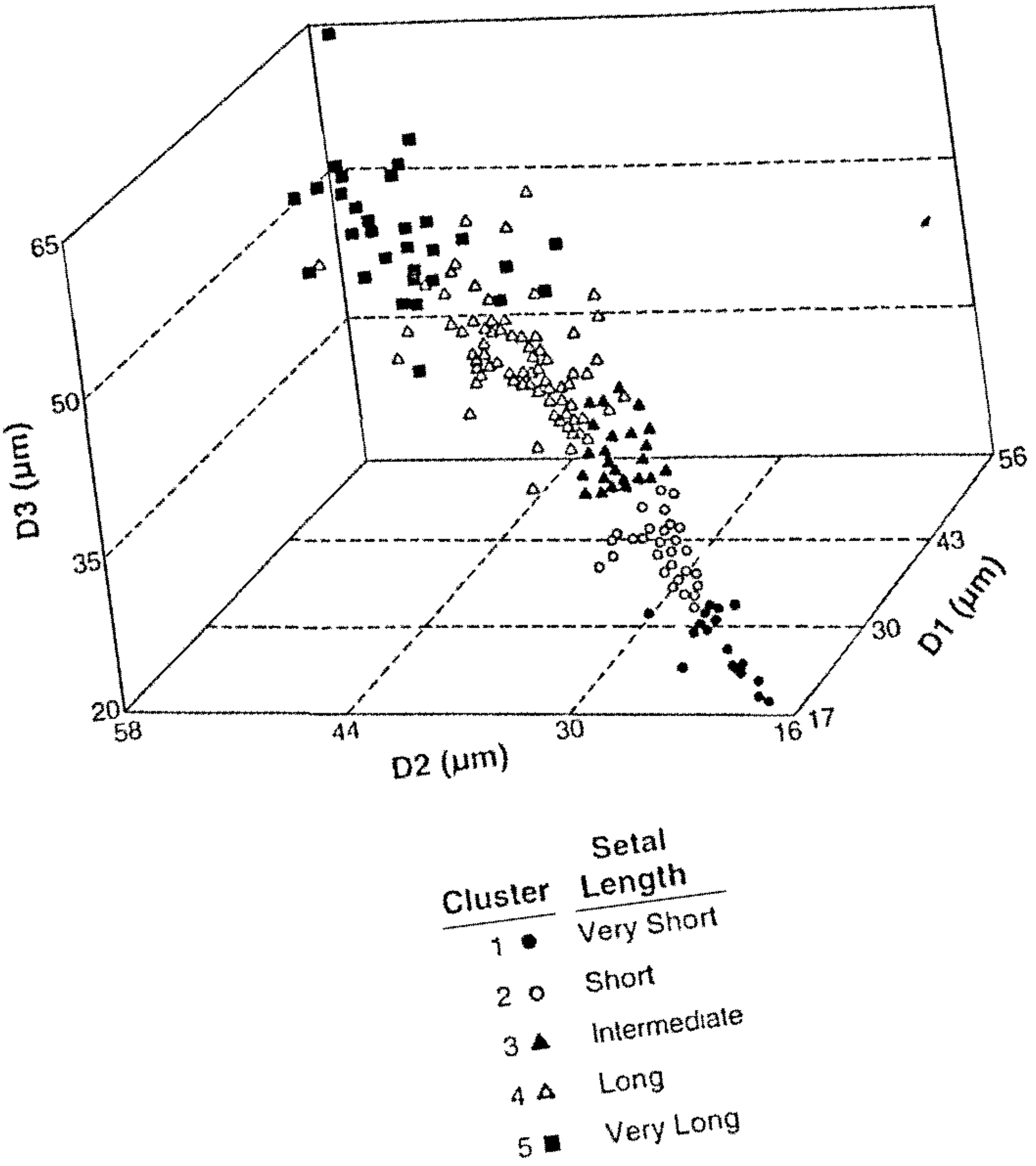
Fig 6 Aedeagi of male *M tanajoa* from Colombia (A), Venezuela (B) and Brazil (C)

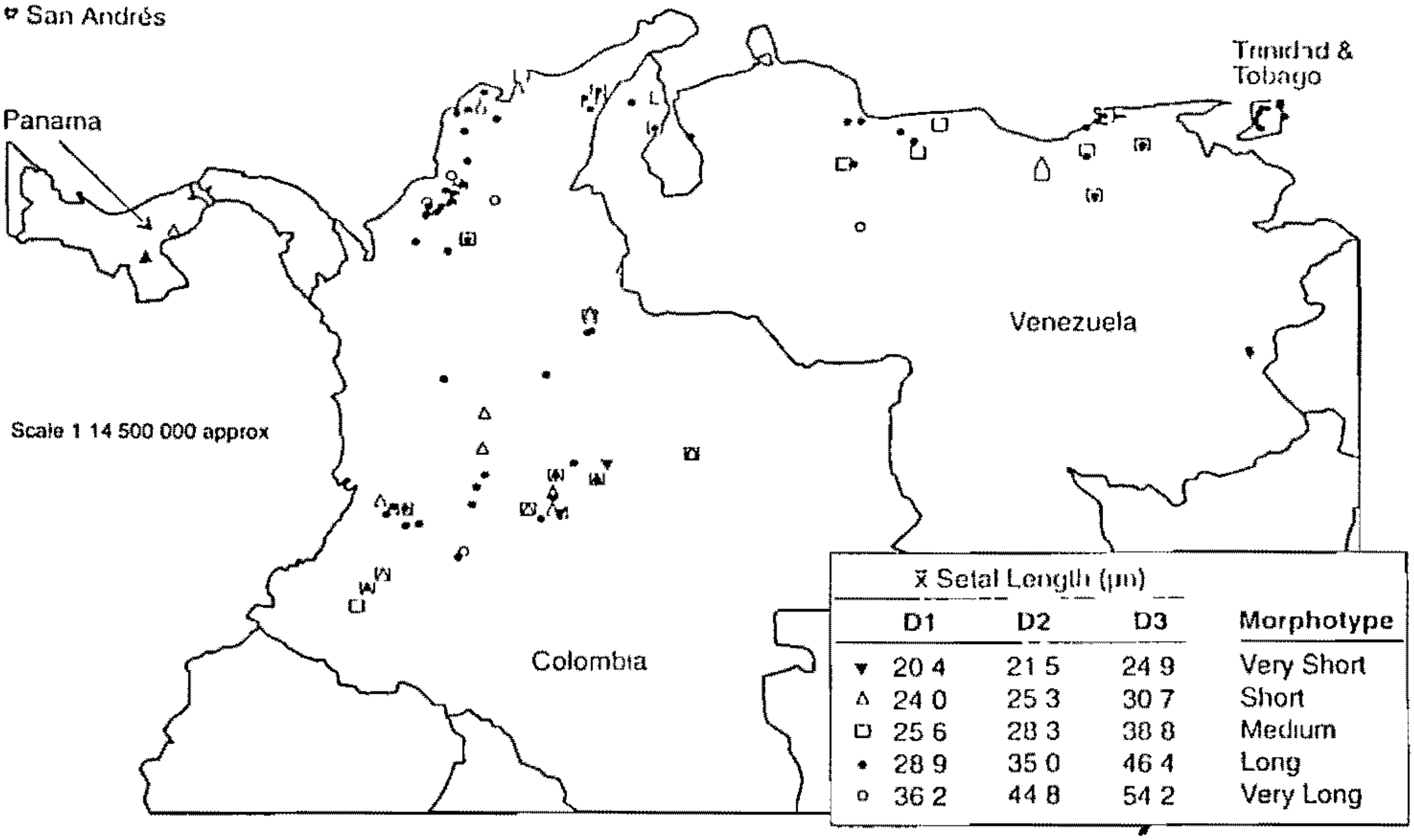
Fig 7 Banding patterns for α- and β-esterases from *M. tanajoa* from the Caribbean coast (Malagana [lanes 1-3] and Arjona [lanes 4-6], Bolivar, Colombia, Luruaco [lanes 7-9], Atlantico, Colombia)

Fig 8 Banding patterns for α- and β-esterases from *M tanajoa* with short dorsocentral setae from an interandean valley (Palmira, Colombia; lanes 1-3) and Northeast Brazil (Cruz das Almas, lane 8), and with long setae from an interandean valley (Palmira, Colombia; lane 4-7).

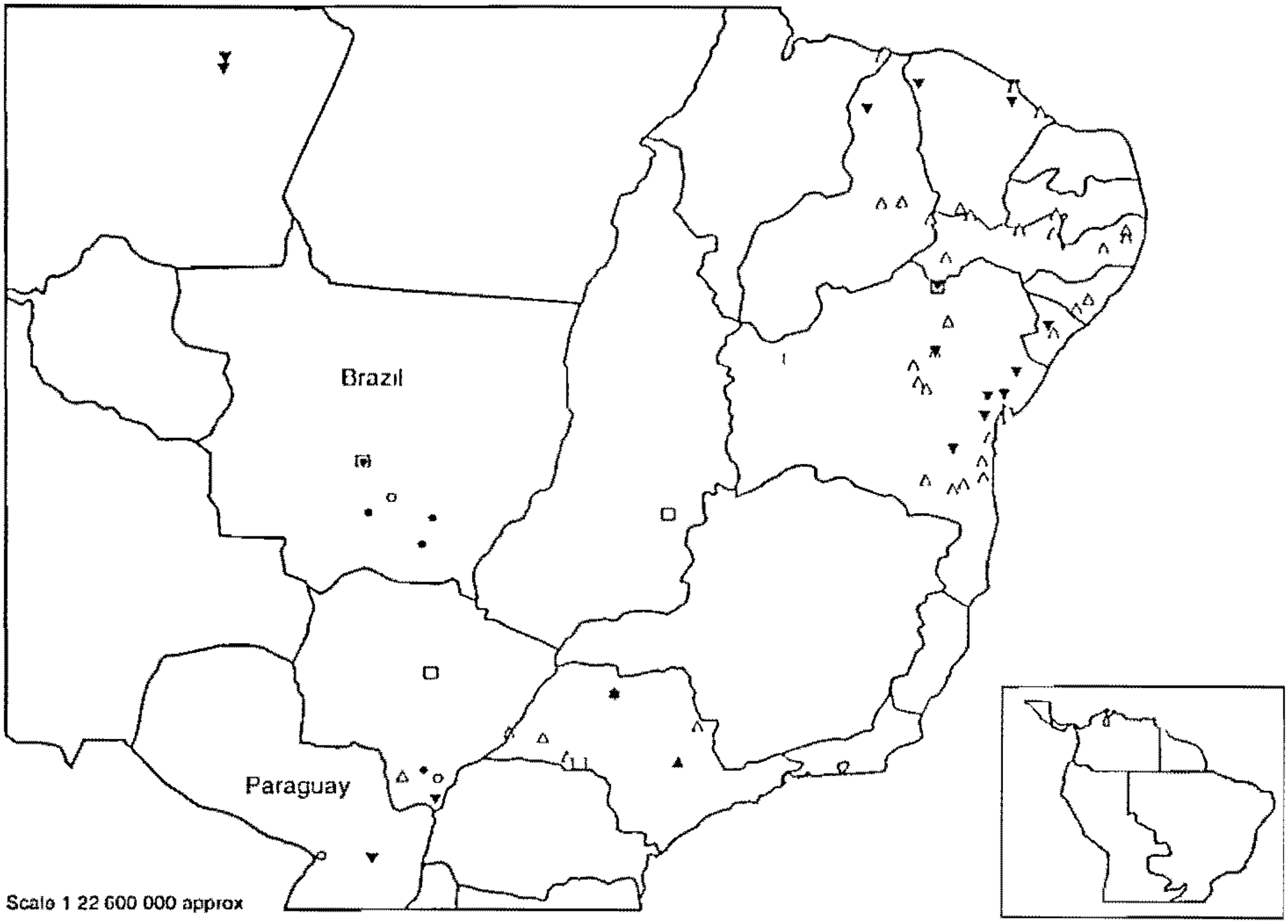

Scale 1 32 000 000 approx
Species
● M tanajoa
○ M caribbeanae
✡ M mcgregori
◊ M planki
Scale 1 35 000 000 approx

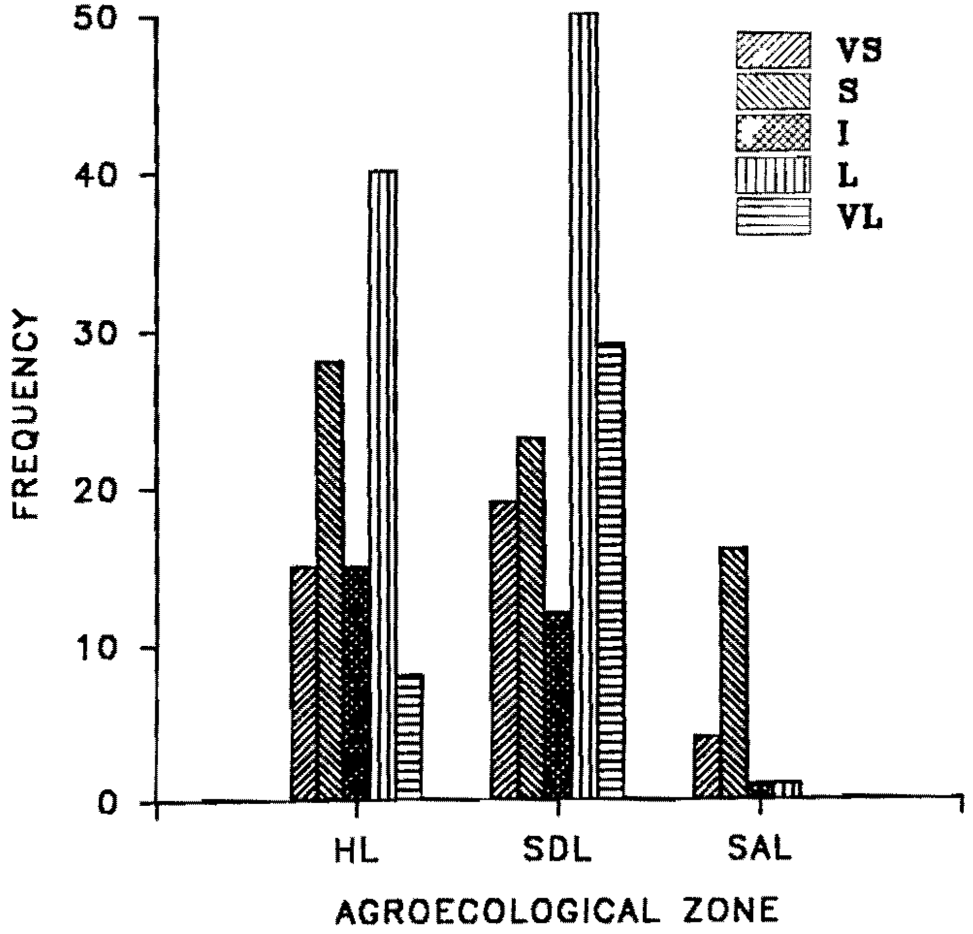

A
D_1
D_2
D_3
B
D_1
D_2
D_3
C
D_1
D_2
D_3
D
D_1
D_2
D_3


D3 (μm)
65
50
35
20
D2 (μm)
58
44
30
16
D1 (μm)
17
30
43
56
Cluster
Setal Length
1 ● Very Short
2 ○ Short
3 ▲ Intermediate
4 △ Long
5 ■ Very Long

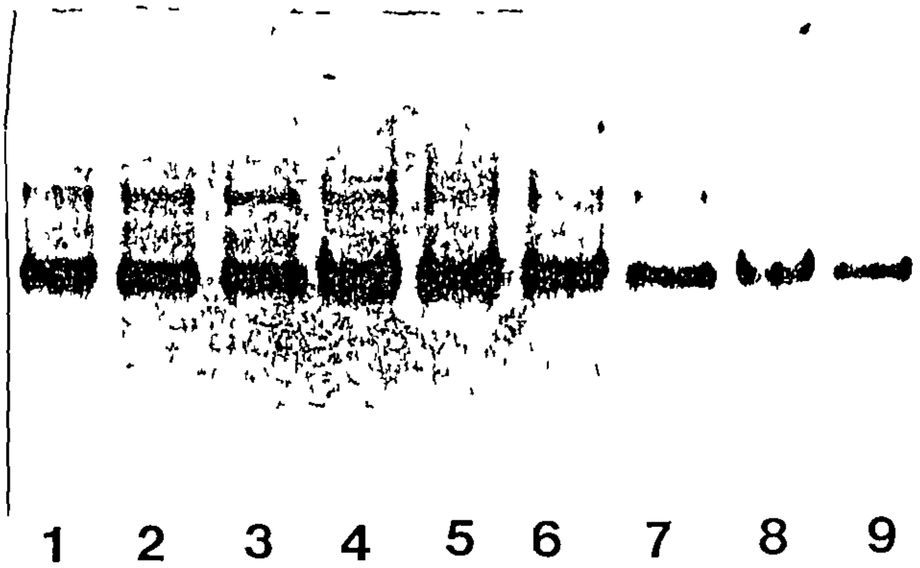


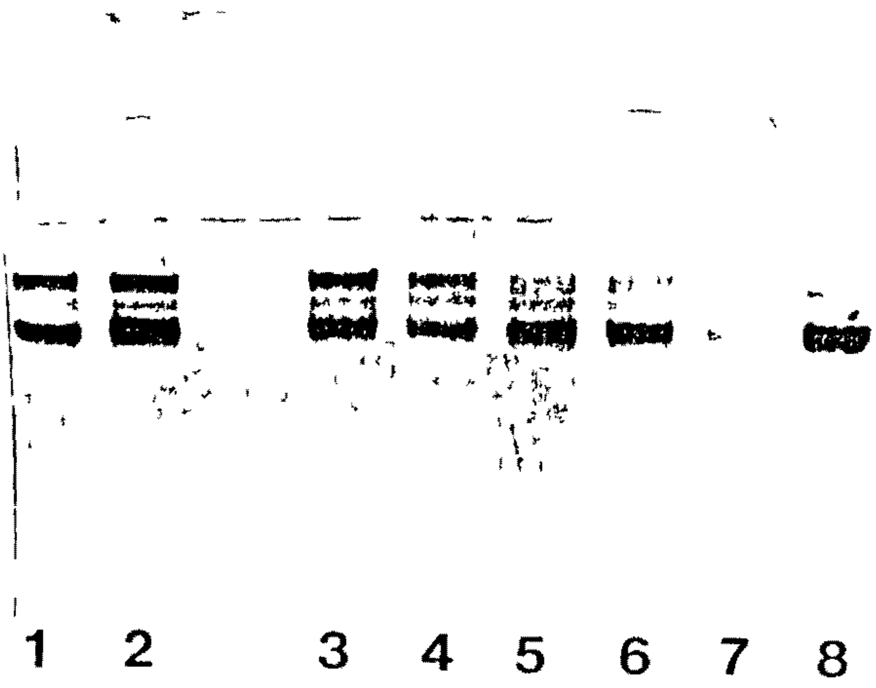
x̄ Setal Length (µm) D1	D2	D3	Morphotype
▼ 20 4	21 5	24 9	Very Short
△ 24 0	25 3	30 7	Short
□ 25 6	28 3	38 8	Medium
• 28 9	35 0	46 4	Long
○ 36 2	44 8	54 2	Very Long




50
40
30
20
10
0
FREQUENCY
VS
S
I
L
VL
HL
SDL
SAL
AGROECOLOGICAL ZONE


A
B
C


1
2
3
4
5
6
7
8
9


1
2
3
4
5
6
7
8

Appendix

The estimate of the quadratic discrimination score is

$$\hat{d}_i^{Q}(X) = \ln\left|S_i\right| + (X - \bar{X}_i)' S_i^{-1}(X - \bar{X}_i) - 2\ln(P_i)$$

X = vector of values, D1, D2, D3, to be assigned to a morphotype

S_i = sample covariance matrix in morphotype i.

$\bar{X}_i$ = sample mean vector of morphotype i.

P_i = prior probability of membership in morphotype i.

Allocate X to morphotype Π_k if the quadratic discrimination score $\hat{d}_k^{Q}(X)$ is the largest of the $\hat{d}_i^{Q}$, $i = 1,2,\ldots,g$. The S_i are as follows:

$$S_1 = \begin{pmatrix} 2.394 & 2.176 & 2.373 \\ 2.176 & 3.900 & 2.926 \\ 2.373 & 2.926 & 4.620 \end{pmatrix}$$

$$S_2 = \begin{pmatrix} 1.969 & 0.146 & -0.704 \\ 0.146 & 1.321 & 1.097 \\ -0.704 & 1.097 & 7.080 \end{pmatrix}$$

$$S_3 = \begin{pmatrix} 2.018 & 0.544 & -0.837 \\ 0.544 & 1.972 & -0.026 \\ -0.837 & -0.026 & 9.352 \end{pmatrix}$$

$$S_4 = \begin{pmatrix} 5.761 & 2.420 & 1.435 \\ 2.420 & 12.181 & 8.730 \\ 1.435 & 8.730 & 25.062 \end{pmatrix}$$

$$S_5 = \begin{pmatrix} 17.182 & 11.539 & 7.887 \\ 11.539 & 23.528 & 9.180 \\ 7.887 & 9.180 & 20.101 \end{pmatrix}$$

The $\overline{X}_i$ are as follows.

$$\overline{X}_1 = \begin{pmatrix} 20\ 371 \\ 21\ 454 \\ 24\ 868 \end{pmatrix}$$

$$\overline{X}_2 = \begin{pmatrix} 24\ 047 \\ 25\ 319 \\ 30\ 681 \end{pmatrix}$$

$$\overline{X}_3 = \begin{pmatrix} 25\ 640 \\ 28\ 261 \\ 38\ 833 \end{pmatrix}$$

$$\overline{X}_4 = \begin{pmatrix} 28\ 852 \\ 34.989 \\ 46\ 355 \end{pmatrix}$$

$$\overline{X}_5 = \begin{pmatrix} 36.168 \\ 44\ 817 \\ 54\ 187 \end{pmatrix}$$