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South American species of the subgenus *Anisotarsus* Chaudoir (genus *Notiobia* Perty: Carabidae:Coleoptera). Part II: Evolution and Biogeography

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South American species of the subgenus *Anisotarsus* Chaudoir (genus *Notiobia* Perty: Carabidae:Coleoptera).
Part II: Evolution and Biogeography

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Abstract: In this paper I postulate the following origin and evolution of the species. Phylogenetic relationships of extant forms are as in Figure 1. *Anisotarsus* arose in Tertiary times in southern South America, were restricted there until the climate cooled in Miocene, and with climatic cooling enlarged their range northward. During Miocene to Pliocene times the ancestral stock diverged into the *tucumana* and *cupripennis* branches. The latter then diverged into the *cupripennis* and *mexicana* stocks. Vicariance among descendants of the *cupripennis* stock led to speciation. Pliocene uplift of the Andes isolated populations in western South America, giving rise to *N. aguilarorum.* Pleistocene interglacial sea level rise may have isolated populations in present day Uruguay, giving rise to *N. latiuscula.* Pleistocene glaciation isolated populations in the Andes, giving rise to *N. schnusei.* The balance of the gene pool of the common ancestor of these latter two species evolved into *N. cupripennis.* The three species of the *peruviana* branch arose as a result of events accompanying Andean uplift. There were two dispersals of *Anisotarsus* into Central and North America: the *tucumana* branch during Miocene to Pliocene times when northern South America was more arid than now; and the *mexicana* stock during Miocene to Pliocene times or less likely during Pleistocene arid periods. *Anisotarsus* have undergone a series of taxon pulses (sensu Erwin, 1979) starting with generalists in temperate lowland grasslands and savannas, continuing with generalists in mid elevation Andean grasslands, and ending with high Andean specialists such as *N. moffetti.* I use Popper's criteria to test the above hypotheses and conclude they are valid.

The bulk of the paper analyizes geographical differentiation in presumed Pleistocene and post Pleistocene core areas or refugia in the Andes of Ecuador and Peru and the lomas of the coastal desert of Peru.

The method of analysis is from Vanzolini and Williams (1970). Areas of character state uniformity for many characters are assumed to each have a well integrated genome due to geographical differentiation during past isolation of populations there. The primary test organism for elucidation of refugia is *Notiobia (Anisotarsus) peruviana* Dejean, a widespread species ideally suited to such analysis.

Detailed examination of 13,989 specimens of *N. peruviana* from 95 sites suggests the following hypothesis. A series of drier-warmer and wetter-cooler climatic periods altered the potency of barriers within the Andes of Ecuador and Peru and the lomas of the Peruvian coastal desert. During drier-warmer periods populations contracted into refugia or core areas and differentiated there. With development of wetter-cooler climates, populations expanded, came into secondary contact, and introgression occurred. The cycles of such contractions and expansions resulted in the production and dispersal of new forms and produced the present pattern of geographical differentiation. The six refugia or core areas recognized are: I, the Andes of Ecuador and extreme northern Peru; II, the southern end of the Río Santa Valley, Peru; III, the Junin Plateau area, Peru; IV, the coastal lomas of Peru; V, the Central Valley extending through the Andes of central and southern Peru; and VI, the Andean highlands around Cuzco, Peru. During drier-warmer periods barriers operated as follows: the Huancabamba Depression or "northern Peru low" served as barrier between core area I and the others; highland to the east, west, and south and lowlands to the north of the Río Santa Valley isolated populations in core area II; populations retreated to the higher parts of core area III; the Río Apurimac and its tributaries became an even more potent barrier between core areas V and VI. The coastal lomas expanded or contracted according to the amount of coastal fog during different climatic periods.

Popper's four criteria for scientific hypotheses serve as a partial test of the hypothesis. The hypothesis explains (criteria one) the present patterns of geographical differentiation and (two) is internally consistent. Criteria three and four are partially tested by six potentially falsifiable predictions: (1) geological data as they become available will support concept of past climatic cycles (already shown); (2) study of core areas will show their boundaries correspond at least partially to potential barriers (such correspondence established by examination of geography, topography, and climate of core areas); (3) hypothesis will agree with taxon pulse postulated for all *Anisotarsus* (it does); (4) available data on other terrestrial Andean grassland organisms (plants, vertebrates, and invertebrates) will show that at least some have been affected by same barriers as *N. peruviana* (so shown, but detailed studies needed of other groups); (5) alternative hypothesis for local selection as cause of geographical differentiation will not adequately explain such variation (it doesn't); and (6) data from studies of non morphological characters will support the hypothesis (such studies still to be done).

Key index words: Biogeography; Carabidae, Evolution; Geographical Differentiation; *Notiobia peruviana* Dejean; Pleistocene; post Pleistocene; Refugia; Vicariance.

Resumen

En esta parte propongo la hipótesis siguiente sobre el origen y la evolución de las especies. Las afinidades filogenéticas de las formas que todavía existen se muestran en el esquema número uno. *Anisotarsus* aparecieron durante el Terciario en el sur de Sudamérica, se limitaron a esta región hasta que el clima se enfrió en el Mioceno, y conel enfriamiento climático su distribución geográfica se extendió hacia el norte. Durante el Mioceno hasta el Plioceno el linaje ancestral se divide en las ramas *tucumana y cupripennis.* Luego ésta se dividió en los linajes *cupripennis* y *mexicana.* El vicarismo entre los descendientes del linaje *cupripennis* dio lugar a la evolución de las especies. El levantamiento plioceno de los Andes aisló las populaciones en el oeste de Sudamérica, lo cual dio origen a *N. aguilarorum.* La crecida del nivel del mar durante el Pleistoceno interglacial puede haber aislado populaciones en lo que actualmente es hoy Uruguay para dar origen a *N. latiuscula.* La glaciación pleistocena aisló populaciones en los Andes para dar origen a *N. schnusei.* El resto del conjunto genético del ancestro común de éstas dos últimas especies evolucionó a *N. cupripennis.* Las tres especies de la rama *peruviana* aparecieron como resultado de los acaecimientos que acompañaron el levantamiento de los Andes. Hubieron dos dispersiones de *Anisotarsus* a Centroamérica y a Norteamérica: la rama *tucumana* durante el Mioceno hasta el Plioceno cuando el norte de Sudamérica estaba más árido que lo que actualmente es; y el linaje *mexicana* durante el Mioceno hasta el Plioceno o, con menos probabilidad, durante los periodos áridos del Pleistoceno. Los *Anisotarsus* han experimentado una serie de "taxon pulses" (sensu Erwin, 1979): primero las especies que son "generalistas" en los llanos y las sabanas de las tierras bajas, luego con las especies que se adaptan a varios medios dentro de las sabanas andinas a media altura, y finalmente con las especies que son "especialistas" de las tierras altas de los Andes como *N. moffetti.* Para evaluar las hipótesis aquí mencionadas uso los criterios de Popper y concluyo que las hipótesis son válidas.

La mayor parte de esta monografía es un análisis de la evolución de formas geográficamente distintas en las supuestas "core areas" o la "refugia" durante el Pleistoceno y el post-Pleistoceno en los Andes ecuatorianos y peruanos y en las "lomas" del desierto de la costa del Perú. El método de análysis es de Vanzolini y Williams (1970). Las áreas geográficas donde los valores de muchas características son uniformes, se suponen que comprenden un conjunto genético bien integrado a causa de la diferenciación geográfica durante el aislamiento en las populaciones pasadas. El organismo más apto para la elucidación de "refugia" es *Notiobia (Anisotarsus)* peruviana Dejean, una especie que se encuentra en muchas áreas y que está bien adecuada para esta clase de análisis.

Un examen detallado de 13,989 especimenes de *N. peruviana* de 95 sitios sugiere la hipótesis siguiente. Una serie de períodos climáticos más secos y calientes, más lluviosos y fríos alteró la fuerza de los límites en los Andes de Ecuador y del Perú y de las "lomas" del desierto de la costa peruviana. Durante los periodos más secos y calientes las populaciones se reducieron a la "refugia" o a las "core areas" y allá evolucionaron. Con el desarrollo de climas más lluviosos y fríos, las populaciones se extendieron, se pusieron en contacto de nuevo y hubo un intercambio de genes. Los ciclos de contracciones y expansiones de esta manera dio como resultado la producción y dispersión de nuevas formas y produjo la diferenciación geográfica actual. Las seis "refugia" o "core areas" que se reconocen son: I, los Andes de Ecuador y del extremo norte del Perú; II, la parte sur del valle del Río Santa, Perú; III, el área del altaplanicie Junin, Perú; IV, las "lomas" costeras del Perú; V, el "Valle Central" que se extiende por lo largo de los Andes del centro y del sur del Perú; y VI, las tierras altas andinas alrededor de Cuzco, Perú. Durante los períodos más secos y calientes los límites fueron estos: La Depresión Huancabamba o "northern Peru low" sirvió de barrera entre la "core area" I y las otras; las tierras altas al este, al oeste y al sur y las tierras bajas al norte del valle Río Santa aislaron las populaciones en la "core area" II; las populaciones se refugiaron en los lugares más altos de la "core area" III; el Río Apurimac y sus afluentes llegó a ser una barrera aún más completa entre las "core areas" V y VI. Las "lomas" costeras se extendieron o se reducieron según la cantidad de neblina costera durante los diferentes períodos climáticos.

Los cuatro criterios de Popper para poner a prueba las hipótesis científicas sirven para verificar parcialmente la hipótesis. La hipótesis (criterio número uno) explica las distribuciones actuales de diferenciación geográfica y (criterio número dos) afirma la consistencia interna. Seis predicciones que pueden ser falsificadas ponen a prueba parcialmente los criterios tres y cuatro: (1) los datos geológicos, en cuanto estén disponibles, darán razón al concepto de ciclos climáticos en el pasado (que ya se ha demostrado); (2) un estudio de las "core areas" demostrará que sus límites corresponden por lo menos en parte a las barreras potenciales (tal correspondencia se establece al analizar la geografía, la topografía y el clima de las "core areas"); (3) las hipótesis estarán de acuerdo con el "taxon pulse" postulado para todos los *Anisotarsus* (y así pasa); (4) los datos disponibles sobre otros organismos terrestres de las sabanas andinas (plantas, vertebrados, invertebrados) mostrarán que por lo menos algunos han sido afectados por las mismas barreras que las de *N. peruviana* (ya demostrado pero se necesitan estudios detallados de otros grupos); (5) una hipótesis alternativa para la selección local como causa de la diferenciación geográfica no explicaría de una forma adecuada tal variación (no lo hace); (6) los datos de los estudios de características no morfológicas servirán de apoyo a la hipótesis (estos estudios quedan por llevarse a cabo).

Palabras importantes para el índice —
Biogeografía, Carabidae, Evolución, Diferenciación geográfica; *Notiobia peruviana* Dejean; Pleistoceno; post-Pleistoceno; "Refugia"; Vicarismo.

Introduction

This is the second paper in a two-part treatment of South American species of the subgenus *Anisotarsus* Chaudoir (genus *Notiobia* Perty). The first part (Noonan, Milwaukee Public Museum, Contributions in Biology and Geology Number 44) treats the systematics and natural history of the ten known species. Part II discusses evolutionary history and biogeographic topics such as present and past refugia and centers of differentiation in the Andes of Ecuador and Peru and coastal desert of Peru.

Evolutionary History of the South American Species of *Anisotarsus*

Introduction. The aim of this section is to propose a recontructed phylogeny of the extant species and discuss the evolution and historical zoogeography of *Anisotarsus*. Methods are as in Noonan (1973, 1979).

Classification as plesiotypic or apotypic of the character states used to reconstruct the phylogeny.

Character 1. Length of the apex of the median lobe. Two states: plesiotypic, moderately long (Figs. 17-25, 28, Part I); apotypic, short (Figs. 77, 79 in Noonan, 1973). Many specimens of *N. peruviana* and all specimens of the other South American species have moderately long apices. Short apices are regarded as a state that evolved in some populations of *N. peruviana,* in the ancestor of the two North American members of the *mexicana* stock, and in various North American *Anisotarsus* of the *tucumana* branch.

Character 2. Large proximal spine on internal sac of median lobe. Two states: plesiotypic, present (Fig. 38, Part I); apotypic, absent (Figs. 29-37, Part I). This classification is based on presence of the spine in *N. tucumana,* 11 North American species of the *tucumana* branch, and many or most species of Australian *Anisotarsus* and of subgenera *Notiobia* and *Diatypus.*

Character 3. Apex of ligula. Two states: plesiotypic, narrow (Fig. 15, Part I); apotypic, markedly expanded laterally (Fig. 16, Part I). The ligula apex is narrow in all *Anisotarsus* but *N. tucumana* and narrow in most or all species of subgenera *Notiobia* and *Diatypus.*

Character 4. Mental tooth. Three states: plesiotypic, present and moderate sized in all specimens of species or group; intermediate apotypic, varied from present and moderate sized to vestigial or absent in some specimens of species or group; apotypic, absent in all specimens. This classification is based on most species of *Anisotarsus* having all adults with a moderate mental tooth.

Character 5. Lateral beads of pronotum. Two states: plesiotypic, thin and not prominent (Figs. 5-14, Part I); apotypic, thick and prominent (Figs. 1, 2, Part I). This classification is based on: in New World, beads thin in all but the four species of the *mexicana* stock; most or all species of Australian *Anisotarsus* and most species of subgenera *Notiobia* and *Diatypus* with beads thin; and most other Anisodactylina with beads thin.

Character 6. Color of dorsum. Three states: plesiotypic, all members of species with pronotum and/or elytra having brassy, bronzish, cupreous, or green coloration; intermediate apotypic, some members of species with plesiotypic state and others with different coloration such as black; apotypic, all members of species greenish or bluish black or black. This classification is based on in-group comparisions of South American *Anisotarsus*. All specimens of *N. tucumana* and *N. praeclara* and many *N. latiuscula, N. cupripennis, N. schnusei, N. chalcites,* and *N. peruviana* have the pronotum and/or elytra as in the plesiotypic state. All members of *N. aguilarorum* are black to greenish black.

Character 7. Pillow of stout spines beneath left flap of ostium of median lobe. Two states: plesiotypic, absent (Figs. 29-32, 34-35, 38, Part I); apotypic, present (Figs. 33, 36, 37, Part I). Such a pillow is present only in *N. cupripennis* and *N. schnusei* of New World *Anisotarsus*; it is not known for any Australian *Anisotarsus* or any species of subgenera *Notiobia* and *Diatypus*, and is absent from most members of subtribe Anisodactylina.

Character 8. Distal field(s) of internal sac of median lobe. Two states: plesiotypic, field single (Fig. 33, Part I); apotypic, fields two and confluent (Figs. 36, 37, Part I). Each of the two confluent fields in *N. schnusei* appear to be approximately the size of the single field in *N. cupripennis*. The hypothesis is that the field doubled during evolution of *N. schnusei*. *Notiobia latiuscula* is the only other South American *Anisotarsus* with two distal fields, and these fields are not closely situated.

Character 9. Posterio-lateral setae on sternum six of males. Two states: plesiotypic, present; apotypic, absent. These setae are present in males of all South American species except *N. aguilarorum*. Noonan (1973) regarded the presence of the setae as apotypic. However their presence in all South American species but *N. aguilarorum* (some of whose females also lack them) suggests, that for South American forms, the plesiotypic state is setae present. The lack of such setae in the two North American species of the *mexicana* stock presumably results from apotypic loss by their common ancestor. Of the eleven North American species of the *tucumana* branch, all specimens of two species and some specimens of three others have such setae. All specimens of the remaining six species lack them. Independent loss of setae seems more probably than independent acquisition.

Reconstructed phylogeny.

Figure 1 presents the reconstructed phylogeny for evolution of the South American species, including the *tucumana* branch and *mexicana* stock which together contain three of the South American species and all 11 of the North American ones (see Noonan, 1973, for a revision of the North American species). The *tucumana* branch is characterized by the plesiotypic state for character two. The eleven diverse members in North America may have originated from more than one northwards dispersal. *Notiobia tucumana* is probably the sole South American survivor of the branch rather than the sister group of the eleven North American species. The *cupripennis* and *peruviana* branches are characterized by apotypic loss of the large spine on the internal sac. Such loss could have occurred independently, and the *cupripennis* stock, *mexicana* stock and *peruviana* branch might not form a monophyletic unit.

The *cupripennis* stock is defined by the plesiotypic state of character five. While the stock might therefore be para- or polyphyletic, I believe it is probably monophyletic. All four species share a similar general habitus. Many specimens of *N. latiuscula* can be distinguished from *N. cupripennis* and *N. schnusei* only by examination of the median lobe or its internal sac. The only consistent morphological differences between specimens of *N. cupripennis* and *N. schnusei* are the double distal field of the internal sac in the latter. The total morphological variation of the four species is approximately equal to that in *N. peruviana.* Species of the *cupripennis* stock are probably descendants from a single once widespread species which underwent vicariance and geographical differentiation similar to that now occurring in *N. peruviana* (see section on geographical differentiation).

The species of the *peruviana* branch share no synapomorphies and are grouped together on the basis of adaptation to Andean habitats and possible scenario of evolution via vacariance of a once widespread species.

Hypothesis for historical zoogeography.

Detailed examination of the South American forms and correlation of their character states with those of North American species cause slight modifications of prior (Noonan, 1973) hypotheses for evolution of *Anisotarsus* within the Americas. This section therefore refers also to the evolution of the two major North American groups.

Ancestral *Anisotarsus* presumably arose (Noonan, 1973) in southern South America, adapted to climates there, and probably were there restricted until the Miocene. Fossil floras and faunas suggest that, before Eocene or Miocene, southern Patagonia had a warm temperate or subtropical climate while the rest of the continent was tropical (Haffer, 1969; Kuschel, 1969; Patterson and Pascual, 1972; Webb, 1978). Until approximately the Miocene southern Patagonia had warm woodlands; savannas and grasses originated in South America from early in the Tertiary (Patterson and Pascual, 1972). The savannas and woodlands in temperate southern South America probably provided favorable *Anisotarsus* habitats as such plant formations now do for many populations of *N. chalcites* and *N. cupripennis.* Authors do not agree completely as to exact timing of uplift for the complex array of mountains comprising the Andes but apparently (Simpson, 1979): elevations above 2000 m were produced during the middle and later part of the Pliocene in the eastern Andes of Colombia; and the Andes of Bolivia, Ecuador, Peru, and western Colombia reached their present elevations after the end of the Tertiary. I postulate that the Andes were not a suitable northwards dispersal route for *Anisotarsus* until Miocene or Pliocene.

As climate cooled in the Miocene, *Anisotarsus* probably spread northward across southern South America. This dispersal would have been favored: by climatic cooling in the Miocene; and by northern South America having a drier climate and much less extensive lowland forests (than now) during at least part of the Miocene and early to late Pliocene (Haffer, 1974; Langenheim, Lee, & Martin, 1973). At some time from approximately Miocene to Pliocene, *Anisotarsus* diverged into the *tucumana* and *cupripennis* branches. The former branch dispersed northward via the Andes, during probably the Pliocene (see discussion below of northward extension), crossed Central America, and gave rise to all North American species except *N. mexicana* and *N. lamprota.* The *tucumana* branch may once have ranged over much of temperate southern South America. If so, the *cupripennis* branch displaced it from most of its South American range, with *N. tucumana* being the sole survivor of the *tucumana* branch in South America.

The *cupripennis* branch diverged into the *cupripennis* and *mexicana* stocks (*N. chalcites* and *N. praeclara* representing the latter in South America).

Speciation of the *cupripennis* stock probably proceeded due to Pliocene and Pleistocene geological and climatic changes vicariating species ranges and producing new selection pressures.

The *cupripennis* stock was presumably adapted to warm temperate habitats as are its four extant species. Pliocene rise of the Andes presumably divided it into eastern and western components. The present coastal desert extending from Ecuador to northern Chile apparently developed as a result of final Andean uplift during approximately Pliocene and Pleistocene (Duellman and Veloso, 1977; Garner, 1959; Jeannel, 1967; Simpson, 1979; Solbrig, 1976); the desert in Peru and Chile seems recently established and has a fauna rather poor in well adapted desert forms (Haffer, 1967; Schmidt and Walker, 1943). (However, the desert has many endemic plants, *B. Simpson, in litt.*) Increasing aridity and increasing cold, to the south, probably pushed the western component into a narrow warm temperate band between the present humid coastal rain-forests to the north, the arid desert to the south, and the Andes. The western component today is represented only by *N. aguilarorum,* known from only a small area in northern Peru and adapted to xeric warm temperate areas from approximately 1400 to 2600 m in the western Andes.

Pleistocene events presumably fostered differentiation of *N. latiuscula, N. cupripennis,* and *N. schnusei* by vicariance of an ancestral species with a range similar to the aggregate range (Fig. 2) of these three species. During one or more Pleistocene interglacial periods the ocean may have extended as far inland (B. Vuilleumier, 1971) as in Figure 3. Possibly the sea to the south, east, and west and forests to the north isolated populations in what is now Uruguay; these isolated populations presumably differentiated into *N. latiuscula,* a species still restricted to Uruguay and northeastern Argentina. Alternatively, the inland extension of the ocean may have been less than that shown in Figure 3 (B. Simpson, 1979 & *in litt*). Ocean and forest barriers might still have isolated populations ancestral to *N. latiuscula* or unknown barriers may have been important.

Evolution of *N. cupripennis* and *N. schnusei* probably proceeded as follows. Their ancestor was adapted to a wide range of lowland warm temperate habitats as *N. cupripennis* is today in part. The ancestor either evolved adaptations to Andean habitats and invaded the Andes or else had occupied pre Andean areas of Bolivia and southern Peru and gradually adapted to Andean habitats as the mountains assumed their present heights in the Pliocene.

Glacial events of the Pleistocene presumably induced vicariance and thus allowed allopatric speciation. Before the first of probably three glacial periods preglacial Lake Ballivan existed in the area of present-day Titicaca with a level at least 40 meters higher than that of today (Ahfeld, 1956). Subsequently, Lake Minchin covered the whole central and southern part of the Altiplano, with its maximum height obtained during the last interglacial period (Ahfeld, 1956; Kessler, 1962). During glacial periods Lake Minchin and extensive glaciation of the Cordillera Real (east of La Paz) probably isolated populations to the north on the Altiplano as apparently done (Simpson, 1975) for many Altiplano plants. Probably the Andean populations gave rise to *N. schnusei* and the lowland ones to *N. cupripennis.* Subsequent retreat of the lakes and glaciers and climatic warming let these two forms become parapatric.

The ancestor of the *mexicana* stock was probably adapted to subtropical or warm temperate habitats as are today many populations of *N. chalcites,* possibly all populations of *N. praeclara,* many populations of *N. mexicana,* and all those of *N. lamprota.* The *mexicana* stock dispersed northward through South America and into Central and North America during probably the Miocene or Pliocene and less probably during the Pleistocene (see discussion below on such extension). It gave rise there to *N. mexicana* and *N. lamprota. Notiobia praeclara,* know only from Andes or Colombia, may be a remnant of the northward dispersal.

The three species of the *peruviana* branch were presumably produced as a result of events accompanying Pliocene uplift of the Andes. Both *N. bradytoides* and *N. moffetti* are restricted to Andean habitats. The latter species has a small geographical range restricted to the edge of the Río Santa Valley, Peru, an area of probable geographical differentiation for *Anisotarsus* and other organisms (see section on geographical differentiation). Possibly, both *N. bradytoides* and *N. moffetti* are descendants of a once widespread species. As discussed in the section on geographical differentiation, *N. peruviana* may represent a similar widespread species now undergoing geographical differentiation.

Extension of Anisotarsus from South America to Central America.

The ancestor of the North and Central American species of the *tucumana* branch probably crossed during Miocene or Pliocene. In North and Central America the branch contains eleven species and occurs from subtropical habitats in Central America and Mexico to cool temperate ones in the United States and southeastern Canada. Several of the North American lineages and species lack synapotypies and possibly are forms phylogenetically isolated by past extinctions. Average morphological variation among North American species is considerable. The sole South American member of the branch, *N. tucumana,* has a small possibly relictual geographical distribution and has two apotypies unique within *Anisotarsus.* Considerable time was probably necessary for shift in North America from warm temperate to cool temperate adaptations, evolution of the varied North American fauna, accumulation of apotypic character states by *N. tucumana,* and extinction of any other South American species (assuming such species did exist) of the branch.

During at least part of the Miocene and early to late Pliocene northern South America had a much drier climate and less extensive lowland forests than now (Haffer, 1974; Langenheim, Lee, Martin, 1973). The Humboldt Current apparently reached as far north as the Caribbean Sea. The Andes were still low lying and permitted the strong drying influence of the Humboldt Current to reach far inland to the east. Lowland tropical forests were probably not continuous to the west coast due to aridity, and large sections of Amazonia and other now forested lowlands had semi-arid climates and savanna type vegetation.

The drier climate and reduced areas of lowland forests in northern South America probably enabled the *tucumana* branch to migrate to the northern tip of South America. Crossing into Central America may have been simultaneous with establishment of a continuous Central American land bridge or may have occurred across scattered islands present before closure (Lloyd, 1963; Malfait and Dinkelman, 1972) of the bridge. The diverse nature of the North American species and the lack of synapotypies for many lineages suggest, but in no way prove, that the branch may have crossed more than once.

A Pliocene crossing agrees with Haffer's (1974) suggestion that North American non forest mammals (such as horses, deer, camels) appeared almost suddenly in South America in late Pliocene due to establishment of the land bridge, low relief of the Andes, and the still restricted distribution of lowland forests. Possibly, (Haffer, 1974) the greatest exchange of northern and southern non forest faunas through northwestern Colombia occurred in the late Pliocene prior to the final Andean uplift and expansion of tropical lowland forests. (However, see Hershkovitz, 1972, for a view disputing the biogeographical importance to mammals of the closing in late Pliocene of the narrow Central American sea channels.)

In my 1973 paper I postulate northward extension of the *mexicana* stock after Pliocene establishment of land connections between Central and South America. Recent comments by G. E. Ball (*in litt*) cause me to reconsider this hypothesis, and I here discuss first arguments for a Pleistocene crossing and secondly, as suggested by Ball, for a Miocene or Pliocene crossing before establishment of continuous land connections.

The *mexicana* stock appears more recently evolved and more recently arrived in Central and North America than does the *tucumana* branch. North and Central America contain only *N. lamprota* and *N. mexicana;* both species share three synapotypies. The former species is restricted to subtropical to warm temperature habitats in southern Mexico while *N. mexicana* extends from Central America into warm temperate habitats of the southwestern United States. The *mexicana* stock thus appears to be at an earlier stage of evolution and northward dispersal within North America.

Recent workers (major summaries in Haffer, 1979, and B. Vuilleumier, 1971; also see references cited in this paper in introduction to "Evolution in refugia of the Andes of Ecuador and Peru and the lomas of the Peruvian desert") have postulated periodic expansion and contraction in South America of tropical lowland forests due to alternating humid and dry periods during the Pleistocene, with maximum aridity at least once reducing the now extensive tropical lowland forests to refugia isolated by savannas and the open plant communities. Prell and Hays (1976) summarize evidence for arid climates extending from northern South America to at least southern Mexico during peak Pleistocene glaciation; Webb (1978) summarizes evidence for a corridor of savanna through Central America in the Plio-Pleistocene. The *mexicana* stock probably crossed into Central and then North America during one of the arid periods when forests were reduced. Indirect support for such crossing comes from the present distribution of *N. aguilarorum* and *N. peruviana* in western Peru. The former species has been taken from semi-desert habitats at altitudes of 1490 to 2520 m and may occur in southern Ecuador or extreme northern Peru down to sea level. Populations of *N. peruviana* occur not only in the Andes but also at elevations from approximately 200 to 800 meters in lomas in the western desert of Peru. With more moisture the western lowlands of Peru, including the xeric areas inhabited by *N. aguilarorum* and the lomas with *N. peruviana,* would support tropical forests (as do areas immediately east of the Andes) with unsuitable habitats for *Anisotarsus.*

Extension of the *mexicana* stock into Central America after the last Pleistocene dry period (approximately 13000 to 21000 years B.P., van der Hammen, 1974; possibly as recent as 6500 years B.P., Hester, 1966)is unlikely. Such extension would require migration through more than 500 kilometers of tropical mostly lowland forest in northwestern Colombia and southern Panama to reach the non-forested highlands north of the Panama Canal and would conflict with speciation patterns cited below for other Carabidae.

The argument for a Miocene or Pliocene northward extension is that the site of the vicariance event that led to evolution of lineages in North and Central America and in South America is near the places where the ranges of the two vicars proximate. The northernmost range of the South American vicar is Colombia, with *N. praeclara*. The known range of *N. lamprota* is northern Nuclear Central America (see Noonan, 1973). One can infer that differentiation of the North and Central American species occurred in Nuclear Central America when this area was only indirectly connected to South America via island archipelagoes of Lower Central America in the Miocene and early Pliocene (Lloyd, 1963; Malfait and Dinkelman, 1972). After establishment of land connections between Central and South America, *N. mexicana* may have become widespread. Thus, its present wide range would not be evidence of recent arrival from South America, and the site of vicariance between South American and North and Central American species would have been the waterways of Lower Central America.

Which hypothesis is correct? When did the *mexicana* stock move into Central and North America? Arguments for a Pleistocene crossing assume that the *mexicana* stock has not undergone extensive diversification in North and Central America due to lack of time. But the genetic potentials and evolutionary rates of the *mexicana* stock and *tucumana* branch may be quite different. Possibly the species of the *mexicana* branch in North and Central America lack the potential for adapting to habitats, such as cooler climates, exploited by species of the *tucumana* branch. Elsewhere in this paper I assume different rates of evolution for groups of *Anisotarsus*: a Pliocene or Pleistocene origin for five species; a Pleistocene origin for three species; and a Pleistocene origin for infraspecific forms of *N. peruviana*. A Miocene or Pliocene extension of the *mexicana* stock agrees with crossings hypothesized for other Carabidae with similar distribution patterns (Ball, 1975 for species of *Phloeoxena;* Ball, 1978 for species of *Trichopselaphus;* and Shpeley and Ball, 1978 for species of *Anisocnemus*). And a Miocene or Pliocene extension of the *mexicana* stock could still have been after that of the *tucumana* branch, thus allowing the latter branch more time for diversification. I now regard a Miocene or Pliocene crossing of the *mexicana* stock as more probable than Pleistocene but can not rule out more recent crossing.

Taxon pulses and ecological distribution of taxa of Anisotarsus in South America.

Allen and Ball (1980) summarize Darlington's theories of taxon cycles for Carabidae (presented in a 1957 book and a series of papers with the latest in 1971) and Erwin's (1979) extension of these ideas and replacement of the term "cycle" with "pulse." One of the general pulses cited by Darlington and Erwin (diagramed in Fig. 4 of Erwin, 1979) was shift from waterside generalists to upland specialists and then to high altitude super specialists. How does this hypothesized pulse correspond to data for *Anisotarsus*?

The predominantly temperate lowland forms such as *N. cupripennis, N. chalcites,* and *N. latiuscula* seem to be "generalists" in grasslands away from the waterside. Andean forms such as *N. schnusei* and *N. peruviana* are montane "generalists." *Notiobia aguilarorum* appears to have specialized in adaptations to xeric habitats in the lower northwestern Andes of Peru. *Notiobia bradytoides* appears specialized or restricted to mesic Andean habitats in the Andes of Ecuador and northern Peru, and *N. moffetti* is a high elevation "super specialist."

The taxon pulse for South American *Anisotarsus* probably started with ancestral *Anisotarsus* adapted as generalists to temperate lowland grasslands and savannas. These generalists dispersed throughout such lowland habitats. Subsequently, with the rise of the Andes, elements of the *cupripennis* stock, *mexicana* stock, and *peruviana* branch adapted to Andean habitats, probably first as generalists since such habitats are similar to those of the temperate lowlands. The Andean species have not greatly diversified due perhaps to recency of origin of these mountains. *Notiobia peruviana* is the most generalized (in terms of diversified habitats occupied) of the Andean forms (and possibly of all South American *Anisotarsus,* see discussion of geographical differentiation of *N. peruviana),* and populations of it may be adapting to local habitats in a complex manner partly determined by climatic cycles. The most specialized of the Andean forms is *N. moffetti,* apparently restricted to a small area above 3700 m in Peru; this may be the first high altitude super specialist of the group. With time, other forms (such as populations of *N. peruviana* in core area III; see discussion of geographical differentiation of this species) may differentiate and become "super specialists" restricted to high elevations.

The taxon pulse concept thus seems applicable to South American *Anisotarsus,* with the provision that the generalists are adapted to grasslands rather than to waterside habitats. Other Harpalini such as *Harpalus* may show taxon pulses similar to that for *Anisotarsus.* For many Harpalini, grasslands may produce the generalists.

Rates of speciation

If the postulated phylogeny and historical zoogeography are correct, species belong to three groups according to probable time of origin: (1) age uncertain; (2) origin during Pliocene and/or Pleistocene; and (3) origin during Pleistocene.

The first group includes only *N. tucumana,* the sole South American survivor of the *tucumana* branch.

The second group includes: *N. aguilarorum; N. bradytoides; N. chalcites; N. peruviana;* and *N. praeclara.* Populations isolated to the west of the Andes by Andean uplift (probably isolated in Pliocene) presumably evolved during Pliocene or Pleistocene into *N. aguilarorum. Notiobia bradytoides* occurs in Andean habitats from approximately 2000 to 3800 m but is most common at elevations between approximately

2200 and 2600 m. Data from various studies (summarized by Simpson, 1975, 1979) do not give absolute elevations reached during the Pliocene and Pleistocene but suggest existence of areas in Ecuador of approximately 2000 m in the Pliocene. Thus *N. bradytoides* could have originated in Pliocene and/or Pleistocene. Geographical differentiation of populations of *N. peruviana* apparently dates back to at least approximately mid Pleistocene (see section on "Hypothesis for geographical differentiation of *N. peruviana* during climatic cycles"). The species occurs over a wide variety of habitats and elevations and may have originated in the Pliocene or Pleistocene during events accompanying Andean uplift or early Pleistocene climatic changes.

Migration northward of the *mexicana* stock (probably during Pliocene or Pleistocene climatic and habitat changes) may have led to evolution of *N. praeclara* and *N. chalcites*.

The remaining four species probably evolved during the Pleistocene. Vicariance caused by Pleistocene events presumably isolated populations that gave rise to *N. latiuscula, N. schnusei,* and *N. cupripennis,* with the latter probably representing a significant part of the gene pool and range of the common ancestor. *Notiobia moffetti* is restricted to high Andean habitats around the southern end of the Río Santa Valley in Peru. Final Andean uplift of the Cordillera Blanca and Negra, forming the eastern and western sides of this Valley respectively, was between the first and second major Pleistocene ice advances (Simpson, 1975). Although this species occurs below the upper limits of these Cordillera, its high Andean habitats probably did not appear until early Pleistocene.

LaBrecque *et al* (1977) date the Pleistocene as starting two million years B.P. and the Pliocene as extending from five to two million years B.P. Thus the maximum speciation time for the second group is within approximately five million years and that for the third is within approximately two million years. Origin of *N. latiuscula* presumably could have not been more recent than the last interglacial, Sangamon dated as extending from 400,000 to 200,000 years B.P. by Erichson and Wollin (1970). *Notiobia schnusei* could not have originated earlier than the Wisconsin Glacial Period, dated as extending from 200,000 to approximately 10,000 years B.P. by Erichson and Wollin (1970).

How do speciation rates postulated for *Anisotarsus* compare with those estimated for other Carabidae?

Estimates of speciation rates for Carabidae include: three million years estimated by Whitehead (1972) as an average time between cladistic dichotomies and consistent with respective phylogenetic and zoogeographic reconstructions of *Schizogenius* (by Whitehead), *Brachinus* (phylogeny and zoogeography by Erwin, 1970), and *Evarthrus* (phylogeny and zoogeography by Ball and Freitag, 1969); before Pleistocene for initial speciation in *Nebria trifaria* group (Erwin and Ball, 1972); within Pleistocene, for *elevatus* group of subgenus *Scaphinotus* of genus *Scaphinotus* (Ball, 1965) and for most or all

Nearctic species of *Calathus* (Ball and Nègre, 1972); within approximately 1.8 million years or less for at least five species pairs of *Nebria* (Kavanaugh, 1979a); within 450,000 years or less for at least five species pairs of *Nebria* (Kavanaugh, 1979a); more than 90,000 years (no maximum limit set) for subgenus *Cryobius* of genus *Pterostichus* (Ball, 1966a); and within the last 9,000 to 14,000 years for at least three species pairs of *Nebria* (Kavanaugh, 1979a).

Kavanaugh (1979a) notes that evolutionary theory predicts variation in speciation rate within and between groups. He also summarizes data from the fosil record suggesting slow speciation rates for Carabidae. There is little fossil evidence of morphological evolution among insects during the Upper half of the Quarternary. Some extant species of Carabidae apparently are represented in the few Pliocene (or Miocene?) fossil assemblages studied.

Kavanaugh notes the conflict between the slow speciation rates suggested by data from the fossil record and the faster ones suggested by study of some extant *Scaphinotus* and *Nebria*. He also notes that fossil assemblages studied to date are from lowland areas and that *Brachinus, Evarthrus* and *Schizogenius* primarily occupy such lowland habitats while species of the subgenus *Scaphinotus* west of the Great Plains and many *Nebria* are montane in distribution. Thus he concludes that: lowland forms might have a more uniform slower rate and montane forms more variable ones; or data from lowland fossil faunas may not be applicable to montane organisms.

Speciation rates of *Anisotarsus* show no correlation with geographical distribution of forms in lowland or montane habitats. The lowland dwelling *N. latiuscula* and the montane *N. moffetti* and *N. schnusei* apparently evolved in the Pleistocene. The montane dwelling *N. bradytoides* and *N. praeclara* apparently evolved in Pleistocene and/or Pliocene as did *N. aguilarorum,* found at low elevations along the western Andes, and *N. peruviana* found in both coastal lomas and in the Andes.

The present study of *Anisotarsus* suggests a model for speciation whereby data from the fossil record might lead to overestimation of the time required for speciation.

Speciation in the *cupripennis* branch apparently has proceeded by fragmentation or vicariance of once more widespread forms. The four resulting species have similar general habitus. In fact, external characters are so similar in *N. latiuscula, N. cupripennis,* and *N. schnusei* that without locality data all specimens of *N. latiuscula* and *N. schnusei* and many of *N. cupripennis* can be distinguished from one another only by dissection of the male genitalia or by association of females with males so dissected. *Notiobia cupripennis,* presumably the descendant with the largest component of the former ancestral geographical range and gene pool, has more external character variation than do either *N. latiuscula* or *N. schnusei.*

When a fossil is found, it frequently is first compared with extant species. A fossil of the common ancestor of *N. latiuscula, N. cupripennis* and *N. schnusei* might be classified as *N. cupripennis* (or less likely as one of the two other less widespread species) on the basis of external morphological features and occurrence in the present range of *N. cupripennis.* The conclusion would be that the species to which the fossil was assigned is at least as old as the fossil. In reality the species would be much younger since the fossil would represent one of the common ancestors. The common ancestor of *N. cupripennis* and *N. schnusei* presumably arose in the Pleistocene as presumably did these species. But the common ancestor of these two species and *N. latiuscula* might have originated much earlier and not differentiated until Pleistocene events fragmented its range.

A paleontologist would hopefully recognize the external similarity of the extant species and only conclude that the fossil was closely related to one or to all of them. But what if the fossil was found before the systematics of these species had been elucidated? Before van Emden's 1953 paper describing *N. latiuscula* and *N. schnusei,* the fossil would have been classified as *N. cupripennis.* And what if in time all but one of the three similar appearing extant species became extinct? (Extinction is certainly a common phenomenon.) The paleontologist would have no reason not to classify the fossil as conspecific with the sole extant form.

If other groups of Carabidae have speciated by vicariance and one or more descendants externally resembles an ancestor, then the fossil record may yield overestimations of time for speciation. The mode of speciation needs to be examined for other groups via reconstructed phylogenies and historical zoogeographies. It is interesting to note that, as described in the section on evolution in refugia, *N. peruviana* is apparently undergoing geographical differentiation via periods of vicariance. This species is thus apparently at an early stage of the vicariance process which presumably produced speciation in the *cupripennis* branch.

Testing of the Hypothesis for Historical Zoogeography of *Anisotarsus*

Noonan (1979) suggests that biogeographic studies on Carabidae meet Popper's four criteria for scientific hypotheses (explanatory power, internal consistency, potential for falsification, and predictive power). Does the hypothesis meet these criteria?

As demonstrated above, the hypothesis does explain the observed geographical distribution of extant species and species groups.

The hypothesis is internally consistent. No part of it contradicts another.

Potential for falsification is inherent in the postulated reconstructed phylogeny on which the overall hypothesis for historical zoogeography is based. As new data are gathered, assumptions used in reconstructing the phylogeny are tested. New data might, for example, result in different interpretation of whether given character states are plesiotypic or apotypic.

Potential for falsification and predictive power are also illustrated by the following potentially falsifiable predictions formulated from deductive analysis of the overall hypothesis.

First, the hypothesis is itself dependent on the reconstructed phylogeny being a reasonably accurate representation (although probably simplified due to extinction) of the actual course of evolution. Therefore, any new taxa which are discovered will fit at least moderately well into the already postulated phylogeny.

Second, data from future geological studies will confirm the postulated past climates and habitats.

Third, conclusions formulated in the hypothesis will not contradict those formulated from study of *Anisotarsus* of other regions of the world or those formulated by study of closely related subgenera and genera. This prediction has been partly verified. The hypothesis presented here for the South American species is consistent with that previously (Noonan, 1973, 1979) formulated for species of Central and North America. Conclusions in the hypothesis presented here are consistent with conclusions derived (Noonan, 1973, 1974, 1979) from study of other subgenera and genera of the subtribe Anisodactylina to which *Anisotarsus* belongs.

Evolution In Refugia of the Andes of Ecuador and Peru and the Lomas of the Peruvian Desert

INTRODUCTION

During approximately the last decade workers have concluded that the tropics of Central and South America have not always been stable and that Pleistocene and post Pleistocene climatic and habitat changes have greatly influenced the contemporary geographical distribution and diversity of tropical organisms. Most studies of effects of postulated Pleistocene or other past changes are based on vertebrates, plants, or Lepidoptera. Notable works discussing Pleistocene changes, refugia and/or centers of differentiation include: Brown (1975, 1977a, 1977b, 1977c; 1979); Brown and Ab'Saber (1979); Brown Sheppard and Turner (1974); Dixon (1979); Dorst (1976); Duellman (1972, 1978, 1979); Duellman and Crump (1974); Duellman and Veloso (1977); Echternacht (1971); Fairbridge (1976); Fitzpatrick (1976); Flenley (1979); Forere (1976); Gallardo (1965, 1972, 1979): Haffer (1969, 1974, 1978, 1979); Heyer (1973); Hoogmoed (1973, 1979); Jackson (1978); Langenheim, Lee and Martin (1973); Lynch (1979) Meggers (1975, 1977); Müller (1973); Myers (1973, 1974); Papavero (1975); Prance (1973, 1978);

Schreiber (1978); Silverstone (1975); Simpson (1975, 1979); Simpson and Haffer (1978); Spassky *et al* (1971); Turner (1976, 1977); Val (1976); van der Hammen (1972a, 1972b, 1974); Vanzolini (1973); Vanzolini and Williams (1970); B. Vuilleumier (1971); F. Vuilleumier (1969); Webb (1978); Whitehead (1976); Wilcox and Papavero (1975); and Winge (1973). Haffer (1979) summarizes studies of refugia in the tropical lowlands of South America; B. Vuilleumier (1971) summarizes Pleistocene changes in South America; Simpson and Haffer (1978) sumarize studies of refugia in the Amazon forest biota; and Simpson (1979) summarizes information on Quaternary biogeography of the Andes.

Most of these studies are limited to or concentrate on forms in the moist tropical lowlands. It seems logical that climatic and habitat changes in the moist tropical lowlands should be accompanied by changes affecting organisms in the Andes in tropical South America and in the lomas of the tropical coastal desert of Peru. The present study attempts to elucidate the effects, if any, of such changes in these Andean and desert regions.

METHODS AND PRIMARY TEST SPECIES

The method of analysis follows that of Vanzolini and Williams (1970). The fundamental idea is to study the geographical differentiation of each character separately. Examination of the character states of each character establishes for many characters a geographical distribution with certain areas having relatively uniform values or states for the character. When several characters exhibit agreement as to areas of relative uniformity in states, this suggests that well integrated genomes have evolved in these areas. Such evolution of presumably well-integrated genomes logically would occur during periods when organisms in the areas were isolated and their gene pools not disrupted by gene flow. The areas of relative uniformity will not always be completely coterminous for the different characters. Coadjusted character complexes built up in isolation would suffer some disorganization when they meet similarly coadjusted character complexes of other areas. Whenever such disorganization occurs, the several character states probably have independent or partially independent fates regulated by gene flow and local selection. Thus, the analysis searches for a superposition of polygons of roughly similar, but not necessarily identical, shape. Each area of maximum overlap of these polygons is termed a "core area". Each such core area is a place with maximal uniformity in character states and is where differentiation presumably occurred during a period of isolation. The location and pecularities of the core areas and intervening transition regions provide a much firmer basis for analysis than the often employed method of looking for differences between so called "populations". (Recognition of "populations" of *N. peruviana* collected during the expedition is a function of intervals at which I left the jeep to collect along a given transect.) Differences can always be found between "populations", whether by qualitative or quantitative methods. Recognition of such differences leads to recognition of subspecies, morphs, or "populations" but often contributes little to an understanding of how geographical differentiation arose.

Because of the importance of core areas and transition regions in analysis of geographical differentiation (Vanzolini and Williams, 1970), I believe they should be exhaustively analyzed and abundantly documented. This has resulted in many pages of analysis, tables, and maps. These data and analyses are necessary to enable fellow scientists to judge for themselves the accuracy and import of my conclusions.

Notiobia peruviana Dejean is an ideal study species for elucidation of core areas in the Andes of Ecuador and Peru and the lomas of the coastal desert of Peru. This species of beetle belongs to the family Carabidae, many of whose extant species are well suited to study of present and past refugia and geographical differentiation. Notable such studies using extant Carabidae include: Allen and Ball (1980); Ball (1956, 1963, 1965, 1966a, 1966b, 1969, 1975, 1976, 1978); Ball and Freitag (1969); Ball and Nègre (1972); Darlington (1943, 1971); Erwin (1970); Erwin and Ball (1972); Freitag (1979); Goulet (1974); Kavanaugh (1979a, 1979b); Lindroth (1963, 1965, 1968, 1969a, 1969b, 1969c, 1970, 1979); Noonan (1973, 1975); and Whitehead (1972). *Notiobia peruviana* has a wide geographical and altitudinal distribution, occurring from the coastal lomas near sea level to elevations above 4100 m and is present throughout a variety of grassland habitats in the Andes of Ecuador and Peru. Adults are abundant and readily collected and studied in many Andean and coastal loma habitats. Adults exhibit complex patterns of geographical differentiation at the infraspecific level. Kavanaugh (1979a) noted that analysis of refugia and geographical differentiation by study of infraspecific forms may be more productive than analysis of specific level forms since: the latter can not provide phenotypic markers reflecting intergradation following secondary contact between different infraspecific forms; and past vicariance patterns are more likely to be obscured at the specific level. Lastly, *N. peruviana* is abundant in pastures and other areas disturbed by man. The extensive alteration by man of the Andes thus probably has had less deleterious effect on *N. peruviana* than on many more specialized or habitat restricted species.

Analysis of geographical differentiation of *N. peruviana* is done by first considering separately the geographical differentiation of 11 characters and afterwards comparing the resulting geographical patterns. The sexes are studied separately since preliminary work suggested that some characters, such as elytral microsculpture, might have different geographical patterns for each sex.

Information on topography is based primarily on two maps: Ecuador, compilado por el Instituto Geográfico Militar (Sección Geográfica), scale 1:1 000 000, obtained from the Instituto Geográfico Militar, Quito, Ecuador; and Republica del Peru 1973, Mapa fisico politico, elaborado por el Instituto Geográfico Militar del Peru, scale 1:1 000 000, available from the Instituto Geográfico Militar del Peru, Lima, Peru. The map of Peru was supplemented with maps for four departments from the Instituto Geográfico Militar, Lima, Peru: Departamento de Ancash 1976 mapa fisico politico, scale 1:400 000; Departamento de Apurimac 1973 mapa fisico politico, scale 1:350 000; Departamento de La Libertad 1976 mapa fisico politico, scale 1:420 000; and Departamento de Lima 1968 mapa fisico politico, scale 1:500 000. Useful topographic information on Peru was also found in the road maps of the Touring y Automovil Club del Peru, Lima, Peru including eleven "Hoja de Ruta" and various regional maps. In the text "Ecuadorian Maps" denotes the one map used for Ecuador and "Peruvian Maps" denotes one or more of the Peruvian maps.

MATERIAL EXAMINED AND THE TRANSECTS

Data presented for the analysis of geographical differentiation are based on 13,989 adult specimens, 206 males and 212 females borrowed from other museums and 6783 males and 6788 females collected by me and my assistants in the Ecuadorian and Peruvian Andes and Peruvian coastal lomas from 19 October 1978 through 7 April 1979. Specimens were collected and studied along north to south and east to west transects in the Andes and north to south transects in the coastal lomas of the Peruvian desert. Vehicle breakdowns, washed out roads, and other logistic problems prevented access to certain regions such as southern Ecuador. Specimens borrowed from other museums provide samples from these regions.

I examined an additional 544 specimens from other museums prior to this study. These additional specimens were useful in planning the expedition but represent smaller, less completely documented samples. Data from these specimens agree with conclusions reported in this study, and these additional specimens are not used for analysis of geographical differentiation.

I follow Vanzolini and Williams (1970) in grouping the studied specimens into sites according to three orders of stringency: (1) a single well-defined locality; (2) an apparently homogeneous group of adjacent localities; (3) a group of not so close but still ecologically homogeneous localities. The three types of sites, especially the second and third, of course overlap. For some sites sample sizes are small. These sites can not be combined because of criteria two and three. It is essential however to include them because they extend or confirm geographical patterns made evident by the larger samples.

Figure 5 illustrates the locations of the 95 sites used in the analysis. Eleven of the sites (1, 11, 12, 14, 15-18, 59, 78, 87) are based on borrowed material. The remainder are based on specimens collected during the expedition alluded to above. Most specimens collected during this expedition were taken during the day from beneath rocks and other debris on the ground. Each collecting locality visited during the expedition was less than approximately one kilometer in diameter. Sites 56-59 were located in coastal lomas (56-58 visited in December and January when grass absent due to dry season and grazing by cattle); the other sites were located in grassy Andean habitats.

The Appendix describes the eight transects into which topography and logistics grouped the sample sites and also gives location and elevation for these sites.

For convenience in discussion the term "Central Valley" is applied to a valley in the Andes of southern Peru. It extends southward from the Junin Plateau and the mining town of La Oroya to Abancay at the Río Apurimac. (Complete description in the appendix.)

CHARACTERS USED

The analysis is based on 17 qualitative and three quantitative characters.

Color of the dorsal surface of the body. This character provides states very useful in analysis of geographical differentiation. Although each state or color class is part of the single character of color of dorsal surface, I found (after several preliminary analyses) it best to treat each state separately. Each such state yields information important for analysis of geographical differentiation. Four color classes or states (I-IV) are useful for analysis. A fifth (V) class includes a heterogeneous assemblage of at least three other color classes. The scattered geographical distribution and rarity of each of these three or more included classes make them unsuitable for analysis of geographical differentiation. Class I includes specimens with head and pronotum green to dark green and elytra bronze to bronzish, brassy green or green. Class II includes specimens with the dorsum blackish green, blackish bluish green, to greenish, bluish, or purplish black. (A preliminary attempt to categorize these specimens into more restrictive subgroups failed because of numerous specimens with dorsal color intermediate between such subgroups or colors of different parts of dorsum belonging to different subgroups. Class III includes specimens with head and pronotum greenish blue to purple and elytra green to bluish green; the elytra contrast in color with forebody. Class IV includes specimens with head and pronotum green to dark green and elytra purple.

Color of scapes. Two color types are recognized, black, and colors other than black. Specimens with black scapes have both such articles black. Those with scapes colored otherwise have colors varying (in some specimens independently for each article) from reddish yellow to deep brown.

Ocellate puncture between bases of elytral striae one and two. Most specimens have an ocellate puncture on each elytron between the bases of striae one and two. When a scutellar stria is present, this puncture is near it. Some specimens lack such punctures on one or both elytra.

Elytral microsculpture. Microsculpture on the elytral disc (portion of elytra not sloped downwards at sides or posterior apex) grades from a prominent isodiametric mesh to weak or apparently absent. An initial attempt to group specimens into several subgroups failed because slightly different gradations in different parts of the elytral disc of some specimens make such classification impractical.

Therefore, I recognize two character states: microsculpture present and moderate to prominent; microsculpture indistinct (apparently absent or weak if present).

Length of hind wings. Specimens either have long wings (presumably suitable for flight) or short (presumably not suitable for flight) ones. Long winged forms have large folded hind wings with normal veination. Short winged forms mostly have vestigial hind wings, but in the coastal lomas many short winged forms have hind wings approaching those found in macropterous forms.

Number of setae on the fourth abdominal sternum. Specimens outside the Río Santa Valley (sites 43-55, Ancash Department, Peru) have generally glabrous abdominal sterna, with sterna four, five and six each averaging at most five or six short fine setae situated anteriorly near the intersegmental membranes. Specimens in the Río Santa Valley grade from having generally glabrous abdominal sterna in the northern end of the Valley to having 20 or more setae per sternum at the southern end. The more numerous setae on specimens from the southern end of the Valley are longer and thicker than the few setae found on specimens elsewhere. It is difficult to measure setal lengths and impractical to measure their thickness. Sub-sampling would not suffice since there is considerable variation at even the southern end of the Valley in setal number and size among specimens from a given site. Therefore, the number of setae per fourth abdominal sternum serves as an index of change in pubescence inside the Río Santa Valley.

Relative length of the apex of the median lobe of the male genitalia. This consists of the maximum length of the apex divided by its maximum width. Figure 4 illustrates measurement of these dimensions.

Proximal field of the internal sac of the median lobe of the male genitalia. The everted internal sacs have microtrichia of various sizes and degrees of sclerotization. These microtrichia vary proximally from small and weakly sclerotized, as elsewhere on most of the internal sac, to enlarged and more heavily sclerotized and forming a proximal field of armature. The proximal field thus varies from absent to present but indistinct, to prominent (variation illustrated in Part I, Figs. 29-31). Eversion of internal sacs is too time consuming to do for all males used in analysis. Data reported for the proximal field are based on: eversion and examination of internal sacs from approximately 300 males throughout the range of the species; examination of the proximal field area, when feasible, through the walls of the median lobes of partially teneral males;

and examination of part of the internal sac by slightly lifting the ostium in some freshly killed specimens.

THE DATA

DORSAL BODY COLOR CLASS I

Tables 1 and 2 list the percents of male and female specimens in this color class at each site.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are 100 except for 88.9, 93.6 and 50.0 at sites 11, 13, and 16 respectively.

Cajamarca Transect (sites 20-33). Percents are above 80.0 in the north (sites 20-26) and decrease southward.

Otuzco Transect (sites 34-42). Only site 37 (N=one) has a percent of 100. Percents elsewhere range from 0 to 83.3.

Río Santa Valley Transect (sites 43-55). Percents are zero except for 8.3 at site 45.

Coastal Lomas (sites 56-59). Percents are zero.

Huanuco-Tarma Transect (sites 60-75). There are two sharply different groups. Percents at the 14 most northern sites (60-73) are equal to or greater than 55, with nine being 100. Those in the two most southern sites (74 and 75 with percents of 3.3 and 27.3 respectively) are below 28.0 but above zero.

Lima-Tarma Transect (sites 76-78). Site 76 (closest to the southern end of the Huanuco-Tarma Transect) has 30.0 percent; the other two sites have zero.

Central and Southern Andes of Peru Transect (sites 79-95). Percents are in two groups. Those in the Central Valley (sites 79-87) range from zero to 100, with an increase southward. Percents in the Cuzco region (sites 88-95) are more uniform and greater than 60.

The general geographical pattern (Fig. 6).

Percents are high in areas A, C and D and mostly zero in B. The Andes of Ecuador and northern Peru are A (sites 1-26), with percents of 100 at all but six sites. Area C (sites 60-73) extends southward from Huanuco, Peru onto the Junin Plateau; percents are equal to or greater than 55.0, with nine of them being 100. The southeastern Andean highlands around Cuzco constitute D (sites 88-95) with percents above 60 (three sites with percents of 100). Area B (sites 43-59, 77, 78) is the Andes of northcentral Peru, the coastal lomas, and the Río Rímac Valley as far eastwards as site 77 (78.4 km southwest of La Oroya); percents are zero except for 8.3 at site 45. Transition region T1 (sites 27-42), lies in northern Peru between A and B. The southern edge of the Junin Plateau and the Central Valley of central and southern Peru are transition region T2 (sites 74-76, 79-87). Along the southern margin of the Junin Plateau percents decrease southward and southwestward from those of C towards the mostly zero percents of B. Southeastward of approximately sites 82 or 84 percents increase irregularly towards those of D.

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are generally large, but there is moderate variation between sites. Percents at eight sites are 100, at two are between 90.0 and 100, at three are between 50.0 and 60.0, and at three sites are zero (latter three sites each with samples of two or less).

Cajamarca Transect (sites 20-33). Percents in the northern part are generally high, above 80.0 at seven sites; those south of site 30 are lower and range from 69.2 to 77.5.

Otuzco Transect (sites 34-42). Site 37 (N=one) has a percent of 100. Elsewhere percents range from 3.7 to 76.0 and are comparable to those of the southern end of the Cajamarca Transect.

Río Santa Valley Transect (sites 43-55). Percents are zero except for 3.8 and 2.6 at sites 44 and 45 respectively.

Coastal Lomas (sites 56-59). Percents are zero.

Huanuco-Tarma Transect (sites 60-75). There are two groups. Percents at the 14 most northern sites (60-73) are greater than 50.0, with nine being 100. Those in the two most southern sites (74 and 75) are below 22.0 but greater than zero.

Lima-Tarma Transect (sites 76-78). Percents decrease westward from 23.1 at site 76 to zero at site 78.

Central and Southern Andes of Peru Transect (sites 79-95). Percents are in two groups. Those in the Central Valley (sites 79-87) range from zero to 100, with an increase southward. Percents in the Cuzco region (sites 88-95) are more uniform and greater than 54.5.

The general geographical pattern (Fig. 6).

Percents are high in areas A, C, and D and zero or low in B. The Andes of Ecuador and northern Peru are A (sites 1-29) with percents at 12 sites of 100, at four between 90.0 and 100, at one between 80.0 and 90.0, at one between 70.0 and 80.0, at three between 50.0 and 60.0, and at three of zero (latter three sites each with sample sizes of two or less). Area C is the same geographically as for males; percents are equal to or greater than 50.0, with nine being 100. Area D is the same geographically as for males; percents are above 50 (three sites with 100). Area B (sites 43-59, 78) comprises the Andes of northcentral Peru, the coastal lomas, and the Río Rímac Valley as far eastward as site 78 (Matacuna). Percents are zero except for 3.8 and 2.6 at sites 44 and 45 respectively. Transition region T1 (sites 30-42), lies in northern Peru between A and B. The southern edge of the Junin Plateau, eastern edge of the Río Rímac Valley, and the Central Valley are transition region T2 (sites 74-77, 79-87). Along the southern margin of the Junin Plateau percents decrease southward and southwestward from those of C towards the mostly zero ones of B. The 100 percent at site 85 suggests that south of approximately site 84 there is an irregular transition towards the high values of D.

Comparison of the sexes.

Overall, percents for females are slightly lower; 28 sites have lower percents for females and 14 have higher ones. The general geographical patterns differ in only minor details not warranting separate maps.

DORSAL BODY COLOR CLASS II

Tables 1 and 2 list percents of male and female specimens in this color class at each site.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are zero except for 50.0 at site 16.

Cajamarca Transect (sites (20-33). Percents are generally low but increase irregularly southward.

Otuzco Transect (sites 34-42). Percents range from zero to 100. Percents at two sites are zero, at four are between 1.0 and 20.0, at one are 83.2 and at one are 100.

Río Santa Valley Transect (sites 43-55). The percents are in two groups. Those at the five most northern sites (43-47) increase irregularly southward and range from 35.7 to 97.6. Those elsewhere are 100.

Coastal Lomas (sites 56-59). Percents range from 75.0 to 87.1.

Huanuco-Tarma Transect (sites 60-75). Percents are in two groups. Percents at the 14 most northern sites (60-73) are zero except for 39.9, 11.1 and 2.1 at sites 60, 64 and 70 respectively. Percents in the two most southern sites are 46.8 and 12.1 at sites 74 and 75 respectively.

Lima-Tarma Transect (sites 76-78). Percents show an irregular transition between the moderate percents of the southern end of the Huanuco-Tarma Transect and the high ones of the Coastal Lomas Transect.

Central and Southern Andes of Peru Transect (sites 79-95). In the northern part of the Central Valley percents decrease southward to zero or generally low values.

The general geographical pattern (Fig. 7).

Percents are low in areas A, C, and E and high in B and D. The Andes of Ecuador and northern Peru comprise A (sites 1-20), with percents zero except for 50.0 at site 16. Area C (sites 60-73) extends southward from Huanuco, Peru onto the Junin Plateau; percents are zero except for 39.9, 11.1 and 2.1 at sites 60, 64 and 70 respectively. Area E (sites 82-95) consists of highlands around Cuzco in the southeastern Andes of Peru, and all but the extreme northern end of the Central Valley in Peru; percents are zero except for 40.0, 1.0, and 0.2 at sites 87, 90, and 92 respectively. The southern end of the Río Santa Valley, Peru is B (sites 48-55) with percents of 100. The coastal lomas and approximately the western half of the Río Rímac Valley are D (sites 56-59, 78), with percents from 75.0 to 87.1. Transition region T1 (sites 21-47) extends along the Andes of north central Peru and into the northern end of the Río Santa Valley; percents rise irregularly southward towards those of D. Transition region T2 (sites 74-77, 79-81) extends from the southern end of the Junin Plateau southwestward into the eastern end of the Río Rímac Valley and southward into the northern end of the Central Valley;

percents grade from the high ones of D to the low ones of C and E.

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percent is 42.9 at site 19, and zero for other sites.

Cajamarca Transect (sites 20-33). Percents vary from zero to 25.0.

Otuzco Transect (sites 34-42). Percents are generally greater than those in the Cajamarca Transect.

Río Santa Valley Transect (sites 43-55). Percents are in two groups. Those at the five most northern sites (43-47) range from 50.0 to 94.1 and increase irregularly southward. Those elsewhere are 100.

Coastal Lomas (sites 56-59). Percents range from 87.5 to 93.0.

Huanuco-Tarma Transect (sites 60-75). Percents are in two groups. Those at the 14 most northern sites (60-73) are zero at ten sites and less than 6.0 at the others except for the 41.2 at site 60. Percents at the two most southern sites, 74 and 75, are higher, 46.4 and 9.1 respectively.

Lima-Tarma Transect (sites 76-78). Percents show an irregular transition between the moderate values of the southern end of the Huanuco-Tarma Transect and the high ones of the Coastal Lomas Transect.

Central and Southern Andes of Peru Transect (sites 79-95). In the northern part of the Central Valley percents decrease southward to zero or generally low values. South of site 83 only three sites have percents greater than zero. The 100 percent for site 87 is based on a single female.

The general geographical pattern (Fig. 8).

Percents are low in areas A, C, and E and high in B and D. The Andes of Ecuador and extreme northern Peru are A (sites 1-18), with percents of zero. Area C (sites 60-73) is the same geographically as in males; percents are zero except for 41.2, 5.3 and 2.2 at sites 60, 68, and 70. Area E (sites 84-95) consists of highlands around Cuzco in the Southeastern Andes of Peru, and all but the northern portion of the Central Valley; percents are zero except for 100, 0.9 and 0.2 at sites 87, 90 and 92 respectively (N=one at site 87). The southern end of the Río Santa Valley, Peru is B (sites 48-55), with percents of 100. The coastal lomas and approximately the western half of the Río Rímac Valley are D (sites 56-59, 78), with percents from 78.6 to 93.0. Transition region T1 (sites 19-47) extends along the Andes of north central Peru and into the northern end of the Río Santa Valley. In the Río Santa Valley percents rise southward towards 100, characteristic of B. Percents elsewhere in T1 are generally intermediate between the zero values of A and the 78.6 to 93.0 values of D. Transition region T2 (sites 74-77, 79-83) extends from the southern end of the Junin Plateau southwestward into the eastern end of the Río Rímac Valley and southward into the northern end of the Central Valley; percents grade from the high ones of D to the low ones of C and E.

Comparison of the sexes.

Overall, percents for females are slightly higher; 26 sites have higher percents for females and 14 have lower ones. Areas B, C, and D are identical in both sexes. Areas A, E, T1, T2 have slightly different boundaries.

DORSAL BODY COLOR CLASS III

Tables 1 and 2 list the percents of male and female specimens in this color class at each site.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are zero except for 6.4 at site 13.

Cajamarca Transect (sites 20-33). Percents are zero at the first nine sites and vary from zero to ten elsewhere.

Otuzco Transect (sites 34-42). Percents increase irregularly southward to 63.8.

Río Santa Valley Transect (sites 43-55). Percents are in two groups. Those at the five most northern sites (43-47) vary from 2.4 to 57.1 and decrease southward except for the value of 50.0 at site 47. Percents elsewhere are zero.

Coastal Lomas (sites 56-59). Percents range from 2.1 to 25.0.

Huanuco-Tarma Transect (sites 60-75). There are two groups. Percents in ten of the 14 most northern sites (60-73) are zero and elsewhere vary from 5.1 to 33.3 (latter percent at site 67, N=three). Percents in the two most southern sites are higher, 48.7 and 60.6 at sites 74 and 75 respectively.

Lima-Tarma Transect (sites 76-78). Percents are equal to or above 50 at the two most eastern sites (76, 77) and 17.2 at the most western (78).

Central and Southern Andes of Peru Transect (sites 79-95). Percents are in two groups. Those in the southern part of the Central Valley and western edge of the Cuzco highlands (sites 85-88) are zero except for 100 at site 86. Percents elsewhere are roughly similar to those of the Coastal Lomas and the southern end of the Huanuco-Tarma Transect.

The general geographical pattern (Fig. 9).

There are four areas, A, C, D, and E, of zero or low percents and one area, B, of percents mostly between 10 and 60. Area A (sites 1-29), Andes of Ecuador and northern Peru, and area D (sites 48-55), southern end of Río Santa Valley, Peru, have percents of zero except for 6.4 at site 13. Area C (sites 60-73) extends southward from Huanuco onto the Junin Plateau; percents are zero at ten sites and elsewhere are less than 12 except for 33.3 at site 67. Area E (sites 85-88) southern part of Central Valley and western edge of Cuzco highlands, has percents of zero except for 100 at site 86. Area B (sites 38-42, 56-59, 74-84, 89-95) includes the coastal lomas and most of the Peruvian Andes. Transition region T1 (sites 30-37) lies between A and B; percents vary from zero to ten. Transition region T2 (sites 43-47) lies in the northern end of the Río

Santa Valley, Peru; percents decrease irregularly southward towards the zero values of D.

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are zero except for 100 at sites 9 and 16 (N=two or less at both sites) and 6.1 at site 13.

Cajamarca Transect (sites 20-33). Percents are zero at the first nine sites with females and range from 0.5 to 7.7 in the three most southern sites.

Otuzco Transect (sites 34-42). Percents are zero at the first four sites and range from zero to 56.3 elsewhere.

Río Santa Valley Transect (sites 43-55). There are two groups. Percents at the five most northern sites range from 4.3 to 44.7 and decrease irregularly southward. Those elsewhere are zero.

Coastal Lomas (sites 56-59). Percents range from 2.0 to 14.3.

Huanuco-Tarma Transect (sites 60-75). There are two groups. Percents in the 14 most northern sites (60-73) are zero except for 4.5 and 8.3 at sites 60 and 64. Percents in the two most southern sites, 74 and 75, are 47.9 and 69.7 respectively.

Lima-Tarma Transect (sites 76-78). Percents are greater than 60 in the two most eastern sites (76, 77) and 15.0 at the most western (78).

Central and Southern Andes of Peru Transect (sites 79-95). Percents are in two groups. Those in the southern part of the Central Valley and western edge of the Cuzco highlands (sites 85-89) are zero except for 100 at site 86. Percents elsewhere are roughly similar to those of the coastal lomas and the southern end of the Huanuco-Tarma Transect.

The general geographical pattern (Fig. 9).

There are four areas, A, C, D, and E, of zero or low percents and one area, B, of percents mostly between 10 and 70. Area A (sites 1-30), Andes of Ecuador and northern Peru, and area D (sites 48-55) have percents of zero except for 100 at sites 9 and 16 (N=two or less at both sites) and 6.1 at site 13. Area C is the same geographically as for males; percents are zero except for 4.5 and 8.3 at sites 60 and 64 respectively. Area E (sites 85-89) comprises the southern part of the Central Valley and western edge of the Cuzco highlands, Peru; percents are zero except for 100 at site 86. Area B (sites 38-42, 56-59, 74-84, 90-95) includes the coastal lomas and most of the Peruvian Andes. Transition region T1 (sites 31-37) lies between A and B; percents range from zero to 7.7. Transition region T2 (sites 43-47) lies in the northern end of the Río Santa Valley, Peru; percents decrease irregularly southward towards the zero values of D.

Comparison of the sexes.

Overall, percents for females are slightly less; 27 sites have smaller percents for females and 11 have larger. Geographical areas C and D and transition region T2 are identical. Differences in the boundaries of the remaining areas and T2 are minor, not requiring a separate map for each sex.

DORSAL BODY COLOR CLASS IV.

Tables 1 and 2 list the percents of male and female specimens in this color class at each site with such specimens.

Males.

Data from the transects and general geographical pattern (Fig. 10).

Percents are greater than zero at only two coastal loma sites, suggesting Area C (sites 56, 57).

Females.

Data from the transects and general geographical pattern (Fig. 10).

Percents are greater than zero in all four of the coastal lomas and also at site 60 near Huanuco, suggesting area A (sites 56-59) for the coastal lomas and B (site 60) for the Huanuco region.

Comparison of the sexes.

Females of this color class occur over a wider area than do males. Since all percents for both sexes are low, additional sampling may show that males of this color class occur in all of the coastal lomas and possibly also at site 60.

COLOR OF SCAPES

Table 3 lists the percents of specimens with black scapes at each site.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are 100.

Cajamarca Transect (sites 20-33). Percents are 100 except for 97.1 and zero at sites 24 and 26 respectively.

Otuzco Transect (sites 34-42). Percents decrease southward.

Río Santa Valley Transect (sites 43-55). Percents are zero at eight sites, 100 at site 55 (N=one), and range from 2.8 to 4.0 in the others.

Coastal Lomas (sites 56-59). Percents vary from zero to 24.6.

Huanuco-Tarma Transect (sites 60-75). There is a central area (sites 65-68) with percents more than 88. Percents decrease northward and southward from there to 2.6 at site 60 and zero at site 71 respectively.

Lima-Tarma Transect (sites 76-78) and Central and Southern Andes of Peru Transect (sites 79-95). Percents are zero.

The general geographical pattern (Fig. 11).

Percents are high in areas A and C and low in B and D. The Andes of Ecuador and northern Peru are A (sites 1-35), with percents of 100 except for 97.1 at site 24 and zero at site 26. Area C (sites 65-68) is the northern edge of the Junin Plateau (elevations from 2550 to 3400 m), with percents greater than 88. Area B (sites 43-55) consists of the Río Santa Valley, Peru, with percents zero at eight sites, 100 at one, and ranging from 2.8 to 4.0 elsewhere. The southern most coastal lomas, the Central Valley, and the southern Andes of Peru are D (sites 59, 71-95). Transition region T1 (sites 36-42, 56-58, 60-64, 69-70) consists of the northern three coastal lomas and much of the central and north central Andes of Peru.

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are 100.

Cajamarca Transect (sites 20-33). Percents are 100 except for 98.0 and 98.3 at sites 22 and 24 respectively.

Otuzco Transect (sites 34-42). Percents decrease southward.

Río Santa Valley Transect (sites 43-55). Percents are zero except for 2.6, 3.8, 3.6 and 3.7 at sites 43, 44, 51, and 53 respectively.

Coastal Lomas (sites (56-59). Percents in the northern most three lomas range from 1.8 to 4.5 and are zero in the most southern loma.

Huanuco-Tarma Transect (sites 60-75). Percents decrease north and south from a small central area (sites 66-68) with values greater than 84.

Lima-Tarma Transect (sites 76-78) and Central and Southern Andes of Peru Transect (sites 79-85). Percents are zero.

The general geographical pattern (Fig. 11).

Percents are high in areas A and C and zero or low in B and D. The Andes of Ecuador and northern Peru are A (sites 1-36) with percents of 100 except for 98.0 and 98.3 at sites 22 and 24 respectively. Area C (sites 66-68) is a small region on the northern edge of the Junin Plateau (elevations from 2820 to 3400 m) with percents of 100 at two sites and 84.2 at one. The Río Santa Valley, Peru is B (sites 43-55); percents are zero at all but four sites with values from 2.6 to 3.8. The southern most coastal loma, Central Valley, and the southern Andes of Peru are D (sites 59, 71-95) with percents of zero. Transition region T1 (sites 37-42, 56-58, 60-65, 69-70) includes the northern three coastal lomas and much of the central and north central Andes of Peru.

Comparison of the sexes.

Overall, the sexes have generally equal percents of specimens with scapes black in color; percents for females are larger at ten sites and smaller at twelve. The general geographical patterns are so similar that a single map suffices for both sexes.

OCELLATE PUNCTURES BETWEEN BASES OF ELYTRAL STRIAE ONE AND TWO

Less than 0.1 percent of specimens from sites 1-63 and 71-94 lack an ocellate puncture on either elytron between the bases of striae 1 and 2. Table 4 shows that 100 percent of all males and females from sites 71, 72, and 73 lack such punctures on both elytra. These sites constitute a small geographical area A (Fig. 12) in both sexes. Variation at sites 64-70 suggests transition region T1 for both sexes.

ELYTRAL MICROSCULPTURE

Table 5 lists the percents of specimens with weak or apparently absent microsculpture on the disc of the elytra.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19) and Cajamarca Transect (sites 20-33). Percents are zero except for 100 and 7.1 at sites 26 and 28 respectively (N=one at site 26).

Otuzco Transect (sites 34-42). Percents are zero in the northern end (sites 34-37) and vary from 25.5 to 96.1 in the southern (sites 38-42).

Río Santa Valley Transect (sites 43-55). Percents increase irregularly southward in sites 42-47 and are 100 in sites 48-55.

Coastal Lomas (sites 56-59). Percents range from 8.8 to 75.0.

Huanuco-Tarma Transect (sites 60-75). Percents are 76.4 and 84.9 in the two most southern sites (74 and 75 respectively) and zero elsewhere.

Lima-Tarma Transect (sites 76-78). Percents range from 17.2 to 100.

Central and Southern Andes of Peru Transect (sites 79-95). Percents range from zero to 100, with those at only four sites being less than 50.0.

The general geographical pattern (Fig. 13).

Areas A and D have percents mostly zero. The Andes of Ecuador and northern Peru are A (sites 1-37), with percents zero except for 100 and 7.1 at sites 26 and 28 respectively. Area D (sites 60-73) extends from Huanuco onto the Junin Plateau, with percents zero. The southern part of the Río Santa Valley, Peru is C (sites 48-55), with percents 100. Area B (sites 56-59, 74-95) includes the coastal lomas and much of the Peruvian Andes; percents are greater than zero at all sites except 88 and mostly range between 20 and 100. Transition region T1 (38-42) occurs between A and B; percents increase from zero to 96.1. The northern part of the Río Santa Valley is transition region T2 (sites 43-47); percents increase from those of B to the uniform values of 100 in C.

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19) and Cajamarca Transect (sites 20-33). Percents are zero.

Otuzco Transect (sites 34-42). Percents are zero in sites 34-37 and zero to 55.6 elsewhere.

Río Santa Valley Transect (sites 43-55). Percents in the northern end (sites 43-48) increase irregularly southward; percents in the southern end (sites 49-54) are 100.

Coastal Lomas (sites 56-59). Percents range from 3.1 to 10.4.

Huanuco-Tarma Transect (sites 60-75). Percents are 31.2 and 42.4 at the two most southern sites (74 and 75 respectively), and zero elsewhere.

Lima-Tarma Transect (sites 76-78). Percents range from zero to 53.8.

Central and Southern Andes of Peru Transect (sites 79-95). Percents are in two groups. Those in the northern end of the Central Valley and the highlands around Cuzco (sites 79-82, 90-95) range from zero to 60.0. Those in the middle and southern parts of the Central Valley and the western edge of the highlands around Cuzco (sites 83-89) are zero except for 33.3 at site 85.

The general geographical pattern (Fig. 14).

Percents are mostly zero in areas A, D, E, mostly between ten and 60 in B, and all 100 in C. Areas A and D are the same geographically as for males and have percents of zero. Area E (sites 83-89) consists of the mid and southern parts of the Central Valley and has percents of zero except for 33.3 at site 85. Area B (sites 56-59, 74-82, 90-95) has the same external boundaries as in males but internally contains area E. The southern part of the Río Santa Valley, Peru (sites 49-55) is C. Transition region T1 (sites 38-42) occurs between A and B. The northern end of the Río Santa Valley (sites 43-48) is transition region T2.

Comparison of the sexes.

The general geographical patterns are similar except for the occurrence of area E in females. Many female Carabidae have more prominent microsculpture than do males, and moderate to prominent isodiametric microsculpture on the disc of the elytra is plesiotypic for *Anisotarsus.* Females apparently are more likely to retain the plesiotypic state than are males. The occurrence of E for females suggests it once also existed for males but was lost through evolution or introgression with populations whose specimens had the apotypic state of microsculpture weak or apparently absent.

LENGTH OF HIND WINGS

Table 6 lists the percents of specimens with long hind wings at each site.

Males.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are 100 except for 97.4 and 59.1 at sites 14 and 18 respectively.

Cajamarca Transect (sites 20-33). Percents decrease irregularly southward.

Otuzco Transect (sites 34-42). Percents are zero except for 4.3 and 24.5 at sites 40 and 41 respectively.

Río Santa Valley Transect (sites 43-55). Percents are zero.

Coastal Lomas (sites 56-59). Percents are 5.0 and 75.0 at sites 57 and 59 and zero elsewhere.

Huanuco-Tarma Transect (sites 60-75), Lima-Tarma Transect (sites 76-78), and Central and Southern Andes of Peru Transect (sites 79-95). Percents are zero.

The general geographical pattern (Fig. 15).

Percents are 100 in area A except for 97.4 at site 14 and are zero in B. The Andes of Ecuador north of the east-west extended highlands between Cuenca and Loja are A (sites 1-17), and the Andes of most of Peru are B (sites 43-55, 60-95). Transition region T1 (sites 18-42) occurs between A and B. Percents are zero at two of the coastal lomas and vary from 5.0 to 75.0 at the others. The coastal lomas thus seem best treated as a region of character instability, transition region T2 (sites 56-59).

Females.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Percents are 100 except for 96.9 and 58.5 at sites 14 and 18 respectively.

Cajamarca Transect (sites 20-33). Percents decrease irregularly southward.

Otuzco Transect (sites 34-42). Percents are zero except for 100, 6.8 and 22.3 at sites 39, 40 and 41 respectively.

Río Santa Valley Transect (sites 43-55). Percents are zero.

Coastal Lomas (sites 56-59). Percents are 2.5 and 85.7 at sites 57 and 59 and zero elsewhere.

Huanuco-Tarma Transect (sites 60-75), Lima-Tarma Transect (sites 76-78), and Central and Southern Andes of Peru Transect (sites 79-95). Percents are zero.

The general geographical pattern (Fig. 15).

Percents are 100 in area A except for 96.9 at site 14 and are zero in B. The Andes of Ecuador north of the east-west extended highlands between Cuenca and Loja are A (sites 1-17), and the Andes of most of Peru are B (sites 43-55, 60-95). Transition region T1 (sites 18-42) occurs between A and B. Percents are zero at two of the coastal lomas and vary from 2.5 to 85.7 at the others. The coastal lomas thus seem best treated as a region of character instability, transition region T2 (sites 56-59).

Comparison of the sexes.
There are no noteworthy differences.

NUMBER OF SETAE ON THE FOURTH ABDOMINAL STERNUM

Table 7 shows that for both sexes the number of setae increase southward in the Río Santa Valley with approximately doubling of the mean number of setae between sites 46 to 47. For both sexes, sites 47 through 55 are area A (Fig. 16); most specimens have 19 or more setae on the fourth abdominal sternum. As noted in the discussion of the characters used in the analysis, the size of each seta generally increases with the number of such setae. There are no noteworthy differences between the sexes.

RELATIVE LENGTH OF THE APEX OF THE MEDIAN LOBE OF THE MALE GENITALIA

Table 8 lists the means, standard deviations, and ranges at each site for the ratio of maximum length of the apex/maximum width.

Data from the transects.
Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Most means are between 0.700 and 0.799. Five means are between 0.700 and 0.799, two between 0.600 and 0.699, one between 0.500 and 0.599, and one between 0.800 and 0.899.

Cajamarca Transect (sites 20-33). Means are larger than one except for 0.913 at site 21. Only two sites, 21 and 32, have ranges extending below 1.00.

Otuzco Transect (sites 34-42). Means and ranges decrease irregularly southward.

Río Santa Valley Transect (sites 43-55). Five means are between 0.700 and 0.799, four between 0.800 and 0.899, and two between 0.600 and 0.699.

Coastal Lomas (sites 56-59). Means vary from 0.551 to 0.591.

Huanuco-Tarma Transect (sites 60-75). Samples are in three groups. Those at the northern end of the transect (sites 60-67) have means larger than 0.900. Samples from the southern end (sites 74 and 75) have means less than 0.600. Means at the intervening sites decrease southward.

Lima-Tarma Transect (sites 76-78). Means vary from 0.556 to 0.760.

Central and Southern Andes of Peru Transect (sites 79-85). This is the only transect with means less than 0.500. Means are generally small; five are between 0.400 and 0.499; seven between 0.500 and 0.599, and one between 0.600 and 0.699.

The general geographical pattern (Fig. 17).
Two areas, B and D, have all means larger than 0.900. The Andes of Cajamarca Department, Peru are area B (sites 20-33), with means greater than one except for 0.913 at site 21. Area D (sites 60-67) extends from Huanuco onto the northern edge of the Junin Plateau (elevations

from 2000 to 3200 m). The Andes of Ecuador and extreme northern Peru are A (sites 1-19), with means mostly between 0.700 and 0.799. The Andes of north central Peru are C (sites 38-55); eight means are between 0.700 and 0.799, five between 0.800 and 0.899, and three between 0.600 and 0.699. Area E (sites 56-59, 79-95) comprises the coastal lomas and the Andes of central and southern Peru. Means are generally small; twelve are between 0.500 and 0.599, five between 0.400 and 0.499, and one between 0.600 and 0.699. Means in transition regions T1 (sites 34-37) and T2 (sites 68-78) decrease southward.

PROXIMAL FIELD OF THE INTERNAL SAC OF THE MEDIAN LOBE OF THE MALE GENITALIA

Table 9 indicates general trends for field absent, indistinct, moderate, or prominent.

Data from the transects.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Internal sacs lack a proximal field.

Cajamarca Transect (sites 20-33). The southern part of this transect appears to be an irregular transition towards the state of having a proximal field. Site 24 has some males with a prominent field, and site 32 has some males with an indistinct field.

Otuzco Transect (sites 34-42). Males from the northern sites (35-38) lack a field; those from south of site 40 have indistinct or moderate fields.

Río Santa Valley Transect (sites 43-55). Males from the northern end of the Valley (sites 43-46) have prominent fields. In the Huaraz area (sites 47-48) there is a transition towards field absent or indistinct. Males from the southern end of the Valley (sites 49-55) lack fields.

Coastal Lomas (sites 56-59). Males have prominent fields.

Huanuco-Tarma Transect (sites 60-75). Males from the northern end of the transect (sites 60-73) lack fields. There is a sharp transition in the southern end of the transect (sites 74, 75) to males with prominent fields.

Lima-Tarma Transect (sites 76-78). Except for those at site 76 all males have fields.

Central and Southern Andes of Peru Transect (sites 79-95). There are three groups. The northwestern part (sites 79-86) has males with a prominent field. Site 87 has some males with moderate and some with prominent fields. The southeastern part (sites 88-95) has males with a moderate field.

The general geographical pattern (Fig. 18).

Males from areas D and B have moderate and prominent fields respectively while those of A, C, and E have no fields. The Andes around Cuzco in southeastern Peru are D (sites 88-95). The coastal lomas and most of the Andes of central and southern Peru are area B (sites 43-46, 56-59, 75, 78-86). The Andes of Ecuador and northern Peru are A (sites 1-23). Area C (sites 60-73) extends from Huanuco southward onto the Junin Plateau. The southern end of the Río Santa Valley, Peru is area E (sites 49-55). Transition regions T1 (sites 24-42), T2 (sites 47-48), and

T4 (site 87) are between A and B, B and E, and B and D respectively. Region T3 (sites 74, 76-77) may be part of a former transition region between C and B.

ANALYSIS OF THE DATA

THE SIX CORE AREAS

Inspection of Figs. 6-18 indicates six areas of consistent difference. The precise borders of each area differ for each character, but for each area there is a residual polygon shaped core area common to several characters. The overall pattern is thus six core areas (Fig. 19), each separately definable in terms of the characters studied. Each core area is a place of maximum character state uniformity.

The analysis below examines each core area for each character and separately for each sex according to whether the area is:

A. Internally homogeneous and clearly delimited from adjacent areas.
B. As a special case of A, has values unique to it or one other area, and/or shares values with other areas.
C. Internally homogeneous but continuous with all or part of one or more adjacent areas.
D. Internally heterogeneous.
E. Other analysis as warranted.

Figure 20 summarizes points A-C for all six core areas and table 10 summarizes the distribution of character states in the core areas.

Core area I. The Andes of Ecuador and northern Peru

A. Internally homogeneous and clearly delimited in values for 11 characters (in both sexes, high percents for dorsal body color class I and scapes black, and zero or low percents for dorsal body color classes II and III, and elytral microsculpture indistinct or absent; and in males, proximal field of internal sac absent).

B. Shares unique values for four characters with core area III (in both sexes, high percents for scapes black and zero percents for elytral microsculpture indistinct or absent). Also shares values with core areas: II (values for three characters: in both sexes, mostly zero percents for dorsal body color class III; and in males proximal field of internal sac absent); III (values for eleven characters: in both sexes, high percents for dorsal body color class I and scapes black, zero or low percents for dorsal body color classes II and III, and zero percents for elytral microsculpture indistinct or absent; and in males, proximal field of internal sac absent); V (values for one character: in females, mostly zero percents for elytral microsculpture indistinct or absent); VI (values for four characters: in both sexes, high percents for dorsal body color class I and mostly zero or near zero percents for dorsal body color class II).

C. Not internally homogeneous and continuous with adjacent areas.

D. Internally heterogeneous in values for the single character of relative length of the apex of the male median lobe.

E. For the relative length of the apex of the male median lobe the northern portion of core area I has means equivalent to those of core area II while the southern portion shares uniquely high means with core area III.

This core area is generally homogeneous internally and clearly delimited.

Core area II. The southern part of Río Santa Valley, Peru

A. Internally homogeneous and clearly delimited in values for nine characters (in both sexes, high and zero percents for dorsal body color classes II and III respectively, high percents for elytral microsculpture indistinct or absent, and numerous setae on fourth abdominal sternum; and in males, proximal field of internal sac absent.

B. Has unique values for two characters (in both sexes, numerous setae on fourth abdominal sternum). Shares values with core areas: I (values for three characters: in both sexes, mostly zero percents for dorsal body color class III; and in males, proximal field of internal sac absent); III (values for three characters: in both sexes, zero percents for dorsal body color class III; and in males, proximal field of internal sac absent); IV (values for two characters: in both sexes, percents between 75 and 93 for dorsal body color class II in core area IV and thus roughly equivalent to those of 100 at all sites in core area II).

C. Internally homogeneous but continuous with: core area IV and the intervening Andes of north central Peru in values for two characters (in both sexes, mostly zero percents for dorsal body color class I); Andes of north central Peru in values for one character (relative length of the apex of the male median lobe); core areas III, V, VI, and the Andes of north central Peru in values for two characters (in both sexes, zero percents for long hind wings).

D. Heterogeneous in values for two characters (in both sexes, varied percents with black scapes).

Core area II is clearly very homogeneous and well delimited.

Core area III. Huanuco region at 2000m southward onto the Junin Plateau, with elevations up to slightly above 4000m

A. Internally homogeneous and clearly delimited in values for 14 characters (in both sexes, high percents for dorsal body color class I, zero or low percents for dorsal body color classes II and III; high percents for scapes black; 100 percent for ocellate punctures absent between elytral striae one and two, and zero percents for elytral microsculpture indistinct or absent; in males, proximal field of internal sac absent and means greater than 0.900 for relative length of apex of median lobe.

B. Has unique values for two characters (in both sexes, 100 percent of specimens lacking ocellate punctures between bases of elytral striae one and two). Shares unique values with core area I for four characters (in both sexes, high percents for scapes black and zero percents for elytral microsculpture indistinct or absent). Also shares values with core areas: I (values for eleven characters: in both sexes, high percents for dorsal body color class I and scapes black, zero or low percents for dorsal body color classes II and III; and zero percents for elytral microsculpture indistinct or absent; and in males, proximal field of internal sac absent); II (values for three characters: in both sexes, zero or low percents for dorsal body color class III; and in males, proximal field of internal sac absent); V (values for five characters: in both sexes, mostly zero percents for dorsal body color classes II and III; and in females, zero percents for elytral microsculpture indistinct or absent); VI (values for four characters: in both sexes, high percents for dorsal body color class I and zero or low percents for dorsal body color class II).

C. Internally homogeneous but continuous with core areas II, V and VI and the Andes of north central Peru in values for two characters (in both sexes, zero percents for hind wings long).

D. Heterogeneous in values for zero characters.

E. Uniquely shares with the southern part of core area I means larger than 0.900 for the relative length of the apex of the male median lobe.

Core area III is very homogeneous and clearly delimited.

Core area IV. Coastal lomas of Peru

A. Internally homogeneous and clearly delimited in values for three characters (in both sexes, percents between 75 to 93 for dorsal body color II; and in females, percents between 0.5 and 7.1 for dorsal body color class IV.

B. Has values unique to it and site 60 (of core area III) for one character (in females, percents above zero for dorsal body color class IV). Shares values with core areas: II (values for two characters: in both sexes, percents between 75 and 93 for dorsal body color class II in core area IV and thus roughly equivalent to those of 100 at all sites in core area II).

C. Internally homogeneous but continuous with: Andes of north central Peru (values for six characters: in both sexes, mostly zero percents for dorsal body color class I, and intermediate percents for dorsal body color class III; and in males, proximal field of internal sac present, and intermediate percents for elytral microsculpture indistinct or absent); core area II (values for two characters: in both sexes, percents mostly zero for dorsal body color class I); core area V (values for three characters: in males, proximal field of internal sac prominent, low means for relative length of apex of median lobe, and intermediate percents for elytral microsculpture indistinct or absent); core area VI (values for five characters: in both sexes, intermediate percents for elytral microsculpture indistinct or absent and percents mostly between 10 and 70 for dorsal body color class III; in males, low means for relative length of apex of median lobe).

D. Internally heterogeneous in values for five characters (in both sexes, scapes black and hind wings long; in males, dorsal body color class IV).

Core area IV is less internally homogeneous and less clearly delimited than the previous ones.

Core area V. Central Valley in the Andes of central and southern Peru

A. Internally homogeneous and clearly delimited in values for three characters (in both sexes, mostly low percents for dorsal body color class III; and in females, percents at all but one site zero for elytral microsculpture indistinct or absent).

B. Shares values with core areas: I (values for one character: in females, mostly zero percents for elytral microsculpture indistinct or absent; III (values for five characters: in both sexes, mostly zero percents for dorsal body color classes II and III; and in females, zero percents for elytral microsculpture indistinct or absent).

C. Internally homogeneous but continuous with core areas: II (values for two characters: in both sexes, zero percents for hind wings long); III (values for two characters: in both sexes, zero percents for hind wings long); IV (values for three characters: in males, proximal field of internal sac prominent, low means for relative length of apex of median lobe, percents mostly above zero but less than 100 for elytral microsculpture indistinct or absent); VI (values for eight characters: in both sexes, percents zero or low for dorsal body class II and zero for scapes black and for hind wings long; and in males, low means for relative length of apex of median lobe, and percents above zero but less than 100 for elytral microsculpture indistinct or absent).

D. Internally heterogeneous in values for two characters (in both sexes, percents for dorsal body color class I).

This core area probably has been genetically "swamped" in the past. It merits recognition since it is internally homogeneous and clearly delimited in values for three characters, and tables 1, 2, and 5 suggest past internal homogeneity and clear demarcation in values for another three characters. The geographical distribution of values for percents of dorsal body color class I (tables 1 and 2) suggests that core area V once had zero values. In males four of the six sites from 81-86 have zero percents while in females five of the seven sites from 81-87 have zero percents. In males the percents for elytral microsculpture indistinct or absent may once have been zero. Values in table 5 drop from 100 in site 86 to 20.0 in site 87; site 88, at the western edge of core area VI, has zero percent.

Core area VI. Andean highlands around Cuzco in southeastern Peru

A. Internally homogeneous and clearly delimited in values for three characters (in both sexes, high percents for dorsal body color class I; in males, proximal field of internal sac moderate.

B. Shares values with core areas: I (values for four characters: in both sexes, percents moderately high to 100 for dorsal body color class I, and mostly zero or near zero for dorsal body color class II); III (values for four characters: in both sexes, high percents for dorsal body color class I and zero or low percents for dorsal body color class II).

C. Internally homogeneous and continuous with core areas: II, III and V (values for two characters: in both sexes, percents zero for hind wings long); IV (values for two characters: in both sexes, percents mostly between 10 and 70 for dorsal body color class III); IV and V (values for two characters: in males percents above zero but less than 100 for elytral microsculpture indistinct or absent, and means low for length of apex of median lobe); IV (values for five characters: in both sexes, intermediate percents for elytral microsculpture indistinct or absent, and percents mostly between 10 and 70 for dorsal body color class III; in males, low means for relative length of apex of median lobe); V (values for eight characters: in both sexes, percents zero or low for dorsal body color class II, percents zero for scapes black and for hind wings long; and in males, low means for relative length of apex of median lobe, and percents above zero but less than 100 for elytral microsculpture indistinct or absent).

D. Internally heterogeneous in values for no characters.

This core area is homogeneous internally and clearly delimited in values for three characters. In the past it has probably been continuous with all or parts of core areas IV and V, been connected with core areas I and III, and isolated at other times.

INTERGRADATION BETWEEN CORE AREAS

The preceding analysis of the core areas shows that the relationships between them vary greatly. In some instances this is due to small samples or lack of them (ie. no samples from eastern Andes between core areas I, III and VI, no samples from western Andes of southern Peru, and few samples from western Andes of central Peru). For most instances differences in relationships are likely due to present or past geographical distance or barriers between the core areas. An analysis of the intergradation between core areas is a prerequisite for formulation of a scenario for evolution of the present patterns of geographical differentiation.

Intergradation of core area I with others is restricted to that between it and core area II and between it and two or more of the southern core areas (IV, V, and VI). Intergradation between core areas I and II involves values for the two characters of dorsal body color class II in both sexes and occurs primarily in the northern part of the Río Santa Valley, Peru and to a lesser extent in the western Andes between this Valley and core area I. Intergradation in values for eight characters (in both sexes, dorsal body color classes I and III, elytral microsculpture, and in males, relative length of apex of median lobe, and proximal field of internal sac) occurs between core area I and the three southern core areas in relatively narrow transition regions in the Andes of northern Peru. Similar intergradation occurs in values for six characters (in both sexes, dorsal body color class II, color of scapes and length of hind wings) in broad transition regions embracing much of the Andes of central and northern Peru and the coastal lomas.

Intergradation between core area II and other areas is restricted to: that between it and all other areas (values for two characters: in both sexes, number of setae on fourth abdominal sternum); between it and core area I (values for two characters discussed above); and between it and two or more of the three southern (IV, V, VI) core areas (values for five characters: in both sexes, dorsal body color class III and elytral microsculpture; and in males, proximal field of internal sac). Intergradation between core area II and the southern three core areas occurs in the northern part of the Río Santa Valley where values change from those characteristic of the southern core areas and the Andes of central and north central Peru to those of core area II.

Intergradation between core area III and others is restricted to that: between it and all others (values for two characters: in both sexes, occellate punctures between striae one and two); and between it and the three southern core areas (IV, V, VI) (values for six characters: in both sexes, dorsal body color classes I and II; and in males, proximal field of internal sac and relative length of apex of median lobe). This intergradation occurs along: (1) the northern edge of the Junin Plateau in values for two characters (in both sexes, ocellate punctures between striae one and two); (2) the southern edge of the Junin Plateau and the entire Central Valley in values for two characters (in both sexes, dorsal body color class I); (3) the southern edge of the Junin Plateau and northern end of the Central Valley in values for three characters (in both sexes, dorsal body color class II; and in males, proximal field of the internal sac); and (4) the southern end of the Junin Plateau, northern part of the Central Valley and all but western edge of the Río Rímac Valley in values for one character (in males, relative length of the apex of the median lobe).

Intergradation between core areas IV, V and VI occurs in (1) the Río Rímac Valley and northern part of the Central Valley in values for two characters (in both sexes, dorsal body color class II); and (2) in the entire Central Valley in values for two characters (in both sexes, dorsal body color class I).

The major transitional regions, and presumed present or past regions of genetic interchange, are: (1) the western Andes of northern, north central, and central Peru, and the northern part of the Río Santa Valley, Peru; (2) the Río Rímac Valley; and (3) the southern edge of the Junin Plateau together with all or at least the northern part of the Central Valley.

GEOGRAPHY, TOPOGRAPHY AND CLIMATE OF THE CORE AREAS AND MAJOR TRANSITION REGIONS

This section discusses the present geographical limits of the core areas (Fig. 19) and major transitional regions, present or potential barriers between them, and the internal climate and topography of each.

A brief summary of climatic conditions and major plant formations to the east and west of the Andes is appropriate since these are both a barrier to *Anisotarsus* and a significant part of present geographical boundaries. East of the Andes below approximately 1800m moist tropical climates and dense forests extend from Colombia into Bolivia (Johnson, 1976). Similar environments extend west of the Andes from Colombia south to the Gulf of Guayaquil where there is a sharp transition to savannas. These savannas become drier southward in Ecuador and grade into a desert which extends along the entire Peruvian coast and rarely receives rain except in portions near the Ecuadorian border (Sick, 1969; Troll, 1968; Weber, 1969). Moist climates, forests, and deserts are barriers to *Anisotarsus* (pers. obs. during expedition).

Core area I. This consists of the Andes of Ecuador and northern Peru. Moist climates and forests to the east and northwest and deserts to the southwest form its eastern and western boundaries. (Possibly *N. peruviana* extend into part of the savannas near the Gulf of Guayaquil; collecting is needed to test for such an extension.) The area's northern boundaries are in the Andes of northern Ecuador or southern Colombia. Colombian specimens are not known, but four days of collecting by two persons yielded ten specimens near Ibarra, approximately 50-55 kilometers south of the Colombian border. Specimens seemed rare in northern Ecuador, and populations were small and scattered. Possibly, the species has recently moved northward into northern Ecuador and is still poorly adapted to environments there. The southern boundary varies slightly according to the character being evaluated but generally is in Cajamarca or La Libertad Departments of northern Peru.

The southern boundary corresponds approximately to an extensive low lying area of the Andes in northern Peru termed by various authors the "Huancabamba Depression", "northern Peru low", and "Río Marañon Valley." This area (Fig. 21) includes: two of the most biogeographically important (Tuttle, 1970; F. Vuilleumier, 1969) trans Andean passes; an extensive area in northern Cajamarca Department, Peru with maximum elevations below 3000 m; and complexly dissected highlands (above 3000 m) in central and southern Cajamarca Department. Abra de Porculla at 5° 50' S, 79° 30' W occurs in Piura Department between the headwaters of the Río Piura and Río Huancabamba. Above 2000 m (maximum elevation 2145 m according to Peruvian maps) the Abra is only approximately five kilometers wide. Habitats are xeric on both sides of it below 2000 m (pers. obs.), and *N. peruviana* were found only above this elevation. The second pass is located at 6° 32' S, 78° 49' W in Cajamarca Department between the headwaters of the Río Chotano and Río Chancay. Above 2000 m (maximum elevation less than 3000 m according to Peruvian maps and equal to or less than 2438 m according to Tuttle, 1970) it is only approximately five kilometers wide, and environments are xeric below approximately 2000 m (Tuttle, 1970). The Andes of Peru south of Cajamarca Department have extensive, continuous highlands above 3000 m. Such highlands are less extensive and more dissected in the southern and discontinuous in the northern portions of Cajamarca Department.

The internal topography of all but the southern portion of core area I is simple compared to that of much of the Peruvian Andes. Within Ecuador and extreme northern Peru the Andes consist of two clearly formed north-south extended mountain chains with a central valley between them. Within Ecuador transverse east-west extended mountain chains or "nudas" of varied elevations divide the central valley into ten basins at elevations of approximately 2500-3000 m (Johnson, 1976; Sick, 1969; Ecuadorian and Peruvian maps; South American Handbook; pers. obs.). In all of Peru except the extreme north, the topography is complex (Peruvian maps and pers. obs). Elevations with *N. peruviana* range from 1620 (one specimen from site 25) to 3210 m (eight specimens from 24.4 km west of Cajamarca, part of site 20). Most specimens occur at elevations between approximately 2200 and 2900 m.

Data from Johnson (1976) suggest an overall climatic regime of less seasonal variation than that in the Andes south of the area. In Ecuador there are generally two periods of maximum precipitation grouped around the months of April and October, with considerable precipitation still falling in the intervening months. There is thus no pronounced dry season. Seasonal variation in day length and temperature is slight. The climate at the southern boundary of the area shows a shift toward greater seasonal variation. Climates at the cities of Quito, Cajamarca, and Cuzco typify those respectively of most of core area I, the southern boundary of this area, and the extreme southern species limits in southern Peru. Total mean monthly precipitation for the months of June, July and August (approximately the driest period of the year) at these three cities total respectively, 99 mm or 8.9 percent of the mean annual precipitation, 24 mm or 3.4 percent of the mean annual precipitation, and 13 mm or 1.7 percent of the mean annual precipitation. Annual maximum and minimum temperature extremes at these cities are respectively, 28°C and 2°C, 29°C and 0°C, and 27°C and −4°C.

The overall climatic regime for core area I is only a general pattern (Johnson, 1976). Each of the ten montane basins in Ecuador as well as different regions of northern Peru has its own climatic peculiarities. Temperatures vary greatly with altitude. Wide variations in precipitation occur, with some sheltered locations being quite dry. Within Ecuador the central valley is generally moist north of the equator but at approximately 2° S becomes dry and desert like at lower elevations. In northern Peru some low lying localities, such as Abra de Porculla (2148 m) depend primarily on fog for moisture while higher ones receive moderate precipitation (pers. obs. of general climatic patterns, persistent fog at Abra de Porculla and rich growth of epiphytes on cacti there).

Present or potential internal barriers to dispersal are the transverse nudas in Ecuador and the deep river valleys near Abra de Porculla.

Core area II. This is the southern portion of the Río Santa Valley, Ancash Department, Peru. The Valley extends southeastward from approximately 8° 40' S, 77° 54' W to 10° 5' S, 77° 16' W, has elevations increasing southward from less than 2000 m at the northern end to 4000 m at the southern, varies from 15 to 25 kilometers in width in the northern half and Huaraz region, and narrows southward from Huaraz to approximately five kilometers wide near the southern end. The Cordillera Blanca, Cordillera Negra, and highlands south of the Valley have minimal elevations over 4000 m. The northern boundary of core area II is at or slightly north of the town of Huaraz. The mountain chains to the east and west and the highlands to the south form the remaining boundaries because *N. peruviana* apparently does not occur in this region at elevations over approximately 3800 m. (Thirteen days of intensive collecting in the Valley showed that the highest elevation with specimens was 3720 m at site 55, where one specimen was found.) Elevations with specimens range from approximately 3000 to 3720 m.

There are no direct climatic data for localities within this area. An elevation-temperature table and general information in Johnson (1976) suggest: a mean annual precipitation of approximately 700 mm, with about 80 percent of this falling in November through April; and mean annual temperatures of 6° to 13° C.

There are no internal barriers to dispersal. The Cordillera Blanca has hanging glaciers (pers. obs.) part of which periodically fall into the Valley (South American Handbook). Possibly these glaciers were once larger, also present on the Cordillera Negra and might have fallen into the narrow Valley and blocked it.

Core area III. This extends from midlands (ca. 2000 m) around Huanuco southward up onto the high (maximum elevation with specimens 4120 m at site 73) Junin Plateau as far south as approximately the town of Junin. Moist forests form the eastern boundaries of the area. Sampling is needed to determine the exact northern and western boundaries. Precipitation in the Andes of central Peru generally decreases westward (Johnson, 1976); lack of moisture may be a barrier to the west on the Plateau or in the Andes below it. Discontinuous areas of grassland occur along the eastern Andes above the moist forests below (Weber, 1969). Possibly the core area once extended northward along such grassy areas to a point opposite Cajamarca Department, Peru.

Fieldwork indicated that the southern boundary of the area occurs approximately 12 kilometers north of the town of Junin at elevations slightly more than 4100 m. Two days of collecting on the Junin Plateau yielded no *Anisotarsus* from just south of the town of Junin to approximately 17.7 kilometers northwest of Tarma. Intensive grazing by cattle and sheep may explain this apparent absence. Grass there lacked seeds and often appeared to have been recently cropped. Carabids other than *Anisotarsus* were moderately abundant. In collecting sites on the Junin Plateau north of the town of Junin, *N. peruviana* were most abundant or restricted to places where the grass had seeds. *Anisotarsus* adults collected on the Junin Plateau were very agile and readily climbed over hands and other objects; possibly they climb into the grass and eat seeds as an important part of their diet. Alternatively, unknown unfavorable climatic factors may occur between Junin and Tarma.

Barriers to dispersal within core area III are those climatic and other environmental factors induced by the approximately 2000 m increase in elevation from the north to the south. Climate changes from semi-arid and moderately warm around Huanuco (measured annual average precipitation of 320 mm, Johnson, 1976; approximate mean annual temperature of 17°C estimated from elevation-temperature table in Johnson, 1976) to cold and moderately moist on the Junin Plateau (Cerro de Pasco with measured annual average precipitation of 882 mm, Johnson, 1976; approximate mean annual temperature of 6°C estimated from elevation-temperature table in Johnson, 1976).

Core area IV. This consists of lomas isolated, in the coastal desert of Peru, on slopes at elevations between approximately 100 and 800 m and from approximately 8° S near Trujillo to approximately 16° S near Chala (Johnson, 1976; and pers. obs.).

The lomas result from dense fog, almost continuously present from May to October. This fog (termed "garu") is due to inland marine air being lifted orographically and produces an almost continuous drizzle in the contact zone of clouds with the slopes of the lomas. The total precipitation during May to October can be 100 to 200 mm, and this moisture together with greatly reduced evaporation loss supports the growth of vegetation. This vegetation itself catches moisture, and once it has started growing, the soil receives additional water. During May to October the lomas stand out on the landscapes as isolated zones of intensely green pastures with cattle grazing between completely desertic landscapes below and above, corresponding respectively to the lower and upper limits of cloud or fog. In November and December clouds disappear, and the landscape of the lomas changes almost completely back to that found elsewhere in the desert (Johnson, 1976, and pers. obs.).

The coastal desert around the lomas is extremely dry but only moderately warm. Except approximately every 25 to 50 years during the "El Niño" phenomenon, the average mean annual precipitation of the desert around the lomas varies from approximately 13 to 35 mm and the average annual mean temperatures from approximately 19° to 21° C. During the infrequent "El Niños" the coastal waters warm, coastal desert temperatures may increase as much as 3° C, and rainfall may total nearly 400 mm (Johnson, 1976).

For at least part of the year the lomas thus constitute islands of mesic environment isolated by desert from one another and from the Andes. *Notiobia peruviana* and various pterostichine Carabidae are common under debris in the lomas during the periods of fog and during the remainder of the year retreat to pockets beneath large boulders (P. Aguilar, pers. comm., and pers. obs.).

Core area V. This consists of the Central Valley in central and southern Peru and extends southeastward from the vicinity of La Oroya in Junin Department to the Río Apurimac Valley near Abancay in Apurimac Department. Elevations are between 3000 and 4000 m with that at most places being close to 3000 m (Peruvian maps). Highlands above 4000 m form continuous boundaries to the north, west and northeast. Southeastward the boundary consists of discontinuous highlands above 4000 m, moist lowland forests, and the Río Apurimac Valley.

The Río Apurimac Valley has a hot, moderately arid climate, presumably preventing or significantly lessening dispersal between core areas V and VI. Elevations within the Valley are slightly less than 2000 m (Peruvian maps). The mean annual temperature is probably approximately 17° C (estimated from elevation-temperature table in Johnson, 1976). On 31 March 1978 the expedition visited the Apurimac River via the road from Cuzco to Abancay. The altimeter measured 1960 m, the countryside had vegetation suggesting a hot, moderately xeric climate, and the air temperature (not measured) felt notably warmer than that near Cuzco on the same day. Collecting by two persons on the same day from Cuzco to the River yielded no *Anisotarsus* below 3250 m (site 88). Labels on the six museum specimens from site 87 (Abancay) state 2460 m.

Climatic data are scanty for core area V. Inferences from these data and sources discussed below suggest the climate is moderate in temperature and precipitation. During the year November 1968 to October 1969 there were 107 and 151 days of precipitation at La Oroya and Jajua respectively (Johnson, 1976). Observations during an expedition transect from La Oroya to Huanucayo in early March 1978 revealed an area intensively farmed. The few undisturbed places had green grass. Much of Peru's wheat comes from the Central Valley (South American Handbook); crops such as wheat suggest a moderate climate. General discussions and an elevation-temperature table in Johnson (1976) suggest: annual mean precipitation of approximately 700 mm at most localities, with approximately 80 percent of this falling November through April; and approximate mean annual temperatures ranging from 6° C at 4000 m to 13° C at 3000 m. Since most localities appear to have elevations close to 3000 m, the predominant mean annual temperature is probably close to 13° C.

There apparently are no internal barriers to dispersal.

Core area VI. This consists of Andean highlands around Cuzco. Boundaries are the Río Apurimac Valley to the northwest, warm moist tropical lowland forests to the northeast and east, and apparently xeric habitats to the west and south. On 30 March 1978 we collected from Cuzco to 75.8 kilometers southeast of Cuzco along the road to Puno. Beyond 45.6 kilometers southeast of Cuzco the countryside became drier, we could not find *Anisotarsus,* and the Peruvian driver said the countryside became progressively drier towards Sicuani to the southeast. Precipitation in the Andes decreases sharply southward of 15° S, and to the west the desert reaches progressively higher into the mountains (Johnson, 1976). The southern boundary is probably between 46 kilometers southeast of Cuzco and the town of Puno; the southwestern boundary probably is in western portions of Cuzco or eastern portions of Arequipa Departments. Elevations with *N. peruviana* range from 2920m to 3700 m.

Climatic data for Cuzco (Johnson, 1976) suggest a moderate climate for core area VI, with most precipitation (81 percent during the period 1954 to 1970) concentrated in November through March. For 1954 through 1970 the mean annual precipitation was 750 mm, and the mean annual maximum and minimum temperatures were 20° and 5° C respectively.

There are apparently no significant barriers to internal dispersal.

Transition region comprised of the Andes of northern, north central, and central Peru. Since it is a transition region, its boundaries are those of the adjacent core areas. Elevations with *Anisotarsus* vary from approximately 2000 to 3000 m.

There are no climatic data for the region. General comments on Andean climates and an elevation-temperature table in Johnson (1976) suggest most localities with *N. peruviana* have: mean annual precipitation of approximately 700 mm, with approximately 70 to 80 percent of this falling in November through April; and mean annual temperatures from approximately 17° to 13° C for elevations of 2000 to 3000 m respectively.

There are apparently no significant barriers to internal dispersal.

Transition region in northern end of Río Santa Valley, Peru. This small region is open to the coastal lowlands and western Andes in the north, bounded to the south by core area II, and to the east and west by mountain chains above 4000 m. Elevations with *Anisotarsus* range from 2430 to approximately 2900 m.

There are no climatic data for the region. General comments on Andean climates and an elevation-temperature table in Johnson (1976) suggest for sites with *N. peruviana:* mean annual precipitation of approximately 700 mm, with approximately 80 percent falling in November through April; and mean annual temperatures from approximately 16° to 13° C for elevations of 2500 to 3000 m respectively.

There are no discernable internal barriers to dispersal.

Río Rimac Valley transition region. The Río Rimac originates in the Andes at elevations above 4000 m and flows westward to the ocean at Lima (Peruvian maps). The transition region consists of the Río Rimac Valley below elevations of 4000 m and extends eastward from the Lima area to within approximately 15 to 20 kilometers of the western most extension of the Central Valley (Peruvian maps). *Anisotarsus* probably are absent from this intervening area. Elevations with *Anisotarsus* in the transition region and the Central Valley range from 2400 to 3820 m and from 2460 to 3720 m respectively. At least part of the intervening area has elevations slightly over 4800 m (Hastenrath, 1967; Peruvian Maps; and altimeter measurements on 1 March 1978). The climatic snowline at the latitude of Lima lies at about 5000 m, with a glacier tongue descending in the intervening area to approximately 4700 m (Hastenrath, 1967). Collecting on 1 and 11 March 1978 yielded no *Anisotarsus* from this intervening area.

Climate presumably varies from dry and warm at Lima (for 1961-1970 mean annual precipitation of 10 mm and mean annual minimum and maximum temperatures of 16° and 22° C respectively, Johnson, 1976) to cooler and moister at the eastern end of the Valley (from general discussion of Andean climates and elevation-temperature table in Johnson, 1976, estimated mean annual precipitation around 700 mm and mean annual temperature approximately 6° C at 4000 m). The lower limits for rain during the Andean rainy season of November through March are approximately 1000 m (Weberbauer, 1945).

There apparently are no barriers to internal dispersal other than climatic and vegetational changes associated with elevation changes within this region.

Transition region of southern edge of Junin Plateau and northern part of Central Valley. This region is bounded in the north by core area III, in the east by moist tropical lowland forests, and in the west by the Río Rimac Valley, and in the south by all but the northern portions of core area V. Elevations with *Anisotarsus* range from 3510 to 3820 m.

Climatic data are few. Discussions for core area V suggest the transition region has a mean annual precipitation of approximately 700 mm. The elevation-temperature table in Johnson (1976) suggests approximate mean annual temperatures of 9° C for 3500 m and 6° C for 4000 m.

There are no apparent topographic or climatic barriers to internal dispersal.

HYPOTHESIS FOR GEOGRAPHICAL DIFFERENTIATION OF *N. PERUVIANA* DURING CLIMATIC CYCLES

General outline of the hypothesis.

The previous analysis establishes that there are six geographical core areas with relatively uniform values for the character states. The hypothesis is that a series of drier-warmer and wetter-cooler phases altered the potency of present or potential barriers within the Ecuadorian and Peruvian Andes and Peruvian coastal lomas and caused cycles of contraction and expansion of these core areas. During each contraction the core areas became refugia where isolated populations diverged in one or more character states. With expansion of the core areas, their different forms came into secondary geographical contact, and varying degrees of introgression occurred. Some forms survived and expanded their ranges while others perished. These cycles of contraction and expansion resulted in the production and dispersal of new forms and produced the present pattern of geographical differentiation.

Drier-warmer phases resulted in populations shifting into higher regions of the Andes in search of moisture. Pronounced aridity at the Abra de Porculla, the pass between the headwaters of the Río Chotano and Río Chancay, and possibly in other regions of the Huancabamba Depression, produced barriers to north-south dispersal, isolated core area I, and also isolated populations in the highlands between the two passes. Populations probably were also isolated in the dissected highlands of Cajamarca Department. If the coastal fogs were reduced, the coastal lomas disappeared. Populations in them dispersed eastwards into the Andes or perished. The Río Rimac Valley served as a route into the Andes. Xeric conditions isolated populations at the higher elevations of core areas II, III, and VI. Core area V was more isolated by the Río Apurimac from core area VI but probably also received an influx of populations from the coastal lomas of IV at the onset of an arid period.

Wetter-cooler phases resulted in *Anisotarsus* shifting downward in the Andes into newly developed favorable habitats. These new habitats, although partially dissected by topographic variations, were essentially continuous. Dispersal between the core areas was maximized. As a result of climatic changes a corridor of grassland or semi-arid regions developed along the eastern Andes (where there are now moist forests) and facilitated dispersal between core areas VI and III and the southern part of I. The Abra de Porculla and the pass between the headwaters of the Río Chotano and Río Chancay did not bar north-south dispersal. Such dispersal genetically swamped forms that evolved between the passes or in the adjacent dissected highlands in a prior drier period; or such forms spread north and/or south. Central and northern Ecuador (now apparently marginal for *N. peruviana)* possibly became too moist for the species to survive. Populations in the other core areas expanded and came into secondary contact with those of other core areas or intervening regions. The coastal lomas of core area IV expanded greatly in size and possibly became continuous with core area V via a route such as the Río Rimac Valley.

Associations of character states.

Vanzolini and Williams (1970) used statistics to check for correlations between pairs of 11 quantitative characters. In the present study all but three characters are qualitative, and two of the three quantitative characters (for both sexes, number of setae on fourth sternum of abdomen) shows noteworthy variation only within part of the geographical range of *N. peruviana.* Percents shown in tables 1-6 are derived by simple "yes," "no" scoring of each specimen for each character state. Formal statistical tests are therefore not necessary to indicate correlations or associations of character states. Inspection of specimens reveals that no two or more character states are associated over the entire range of the species. Associations are limited to parts of the range, apparently because character states arose independently at different times or in different areas during the contraction and expansion cycles of the core areas.

Approximately 98 percent of all males and 99 percent of all females with scapes black in color also belong to dorsal body color class I. The converse is not true. All dorsal body color class I specimens of core areas V and VI and approximately 95 percent of both sexes from core area III have the scapes colored other than black. In core areas I and III all specimens have the elytral microsculpture moderate to prominent, and approximately 99 percent and 5 percent respectively of specimens from these core areas have the scapes black in color. Probably specimens with scapes black in color originated in core area I and later dispersed to core area III.

All specimens from core area II belong to dorsal body color class II, have elytral microsculpture indistinct, and have numerous setae on the abdominal sterna. The latter character state is restricted to core area II, the other two occur elsewhere. Probably the latter state originated in core area II after the previous two states were represented there.

Sequence of geographical differentiation.

Since there are no known fossils, this sequence is inferred from study of extant forms. The discussion is best prefaced with an analysis of the geographical origin and general dispersal patterns for the species. Data from three sources suggest an origin in or near southern Peru and subsequent dispersal northward. From analysis of the supra specific taxa of the subtribe Anisodactylina (to which *Anisotarsus* belongs) Noonan (1973) concluded that *Anisotarsus* evolved in temperate southern South America and later dispersed northward via the emergent Andes. Analysis, elsewhere in the present paper, of the evolution of the South American species of this subgenus supports this conclusion, as does analysis of the geographical distribution of brachypterous versus macropterous *N. peruviana.*

The macropterous condition is plesiotypic among most Carabidae (Darlington, 1943). It also is apparently plesiotypic among South American species of *Anisotarsus* since six are entirely macropterous, two brachypterous, and two (including *N. peruviana)* dimorphic. In dimorphic species of Carabidae the regions with a preponderance of brachypterous forms represent old centers for a species (Lindroth, 1979). In *N. peruviana* the brachypterous forms are, except for the coastal lomas, dominant in southern and central Peru and almost totally absent from northern parts of core area I in Ecuador. Thus, the species has apparently been in southern and central Peru for a relatively long period and only relatively recently invaded (or reinvaded) northern Ecuador.

Darlington (1943) suggested a model whereby brachypterous forms are most numerous in relatively stable regions where flight is least needed to maintain ranges; macropterous forms are favored by scattered unstable populations arranged in a checkerboard fasion. Six months of field work suggested that: *N. peruviana* are abundant in the Andes of southern and central Peru; and populations form and merge there into a large continuous area, dissected by complex topography, but without the isolated checkerboard distribution described by Darlington. Thus, this part of the Andes consists of a series of generally favorable macrohabitats within which *N. peruviana* are able to select nearly continuous and favorable microhabitats. One way for the species to be so well adapted to conditions there is for it to have originated in this area.

Work in central and northern Ecuador suggested that *N. peruviana* is not as well adapted to the generally wetter conditions there and exists in smaller populations scattered in the checkerboard fashion. A relatively recent entry to this area might explain the lesser adaptations to conditions there.

The coastal lomas of core area IV provide a check on the applicability of Darlington's model to the species. The coastal lomas are isolated favorable habitats arranged in the pattern of a checkerboard and are the only region of southern or central Peru with macropterous forms.

Values for 20 (nine separately for each sex and two for males) characters define the six core areas. The sequence of origin, from old to recent, of the states of these characters was probably: dorsal body color class III as ancestral state; sequential origin of dorsal body color classes I, II and IV; evolution of elytral discal microsculpture indistinct or absent; evolution of black color for scapes; acquisition of the proximal field of the internal sac; acquisition of numerous setae on abdominal sterna of specimens in core area II; loss of ocellate puncture between bases of elytral striae one and two; changes in the length of the apex of the male median lobe. Brachyptery presumably evolved in the Andes of southern or central Peru after the species became well adapted to habitats there. Subsequently, macropterous forms became concentrated in recently invaded areas or in regions with scattered isolated populations.

The ancestral dorsal body color was probably that of class III. This class occurs within all specimens of *N. tucumana* and *N. praeclara*, two presumed relatively old species. The geographical distribution of this color combination for *N. peruviana* suggests a former occurrence over most or all of the species range with subsequent localized replacements by other color forms. Specimens of color class III occur within area B (Fig. 9) at percents mostly between 10 and 70, are absent from E (most of core area V) except for site 86 with percent of 100, absent from C and D (core areas III and II respectively), and absent from A (core area I) except at two sites. Replacement by more recently evolved color forms probably produced this irregular, disjunct geographical distribution.

Dorsal body color class I may be second in age to that of class III. Among other South American species of *Anisotarsus* some specimens of *N. chalcites* and *N. schnusei* and most specimens of *N. latiuscula* and *N. cupripennis* have this color combination. For *N. peruviana* the high percents of class I in core areas I, III, and VI suggest that forms with it are primarily adapted to: climates with mean annual precipitations of approximately 700 mm; mean annual temperatures between 17° and 6° C; and elevations mostly between 2000 and 4000 m. Specimens of this color class are absent from and presumably not adapted to the xeric coastal lomas of core region IV. Probably class I originated in core area VI during a period of contraction of the cores. Subsequently, it dispersed by gene flow northward through the Andes to core areas V, III, and I. It may also have reached core area II and been later displaced there.

Dorsal body color class II occurs at: 100 percents in core area II; percents greater than 74 in core area IV; and varied percents at scattered sites in the Andes of north central Peru and core area V. It is nearly absent from core areas I and III. Its scattered geographical distribution outside of core areas II and IV may be due to origin in xeric adapted specimens inhabiting dry habitats such as those of the coastal lomas or the western Andes of Peru. During a slightly drier period than now, such xeric habitats presumably spread over much of the Andes except for highlands such as core areas VI and III, and the generally more mesic core area I. Members of class II presumably dispersed eastward across the Andes via the Río Rimac Valley and northern part of the Central Valley and reached semi-arid habitats such as that now at site 60. The slightly drier climate may also have facilitated spread of these xeric adapted specimens throughout much of the Andes of Peru and into core area II. The present disjunct pattern was then obtained through a combination of increased aridity followed by wetter-cooler climates.

A potential major objection to this scenario is posed by specimens of core area II being clearly adapted to mesic habitats. Possibly, specimens of class II entered the Río Santa Valley via its xeric northern end, underwent partial adaptation to mesic conditions, became isolated in the Valley by increasing aridity, and finally became completely adapted to the generally mesic environments of core area II.

Specimens of dorsal body color class IV also may have originated in xeric habitats. Males of this color class occur in only two of the coastal lomas; females occur in all four coastal lomas and at the semi-arid site 60. The geographical disjunctions of the coastal lomas and site 60 suggest that during a past drier phase there was dispersal between the coastal lomas and the now semi-arid region around site 60. Subsequent moderation of the climate produced the disjunct distribution.

It is not possible with the available data to determine whether class II or IV evolved first. The low frequency of the latter class and its very disjunct distribution can reflect either relatively early origin and subsequent replacement by specimens of class II or origin and dispersal during a recent drier phase, with specimens of class IV starting to displace those of class II.

Most specimens of Harpalini and of *Anisotarsus* (except those of *N. moffetti*) in particular have an ocellate puncture on each elytron near the scutellar stria between the base of striae one and two. At all sites but 71 through 73, less than 0.1 percent of *N. peruviana* lack such punctures from both elytra. Absence of such punctures in this species is thus apotypic. The small geographical area (A of Fig. 12) where specimens lack this puncture suggests recent origin.

The state of elytral discal microsculpture weak or apparently absent is probably apotypic within *N. peruviana*. Moderate to prominent isodiametric mesh on the elytral disc is the plesiotypic state in most Carabidae. Among South American *Anisotarsus* only *N. praeclara* has all specimens with such microsculpture indistinct and irregular. A few specimens of *N. moffetti* have microsculpture indistinct, but most have a prominent isodiametric mesh. The microsculpture of *N. peruviana* grades from a prominent isodiametric mesh to indistinct or apparently absent. The elytral discal microsculpture of all other South American *Anisotarsus* is prominent and isodiametric.

The generally wide distribution (areas B and C of Figs. 13, 14) within Peru of reduced elytral discal microsculpture obscures geographical origin of this state but suggests age sufficient for dispersal of specimens with it through most of Peru. Core area II is the only place where all specimens have reduced microsculpture. This may be due to origin of the character state there. Alternatively, all specimens there may have secondarily acquired the state during past contraction of the core areas.

The distribution of this character state in core area V may partly elucidate its origin in time and place. Females with this character state are absent from area E (southern part of core area V). Table 5 shows a suggestion for males of a former area E once free of the character state. Female Carabidae, including *Anisotarsus,* tend to have more prominent dorsal microsculpture. Thus, females may be slower to acquire the apotypic state of reduced microsculpture. The present lack of females and presumed past lack of males with the apotypic state suggests recent origin or origin geographically remote from E; the apotypic state is still in the process of being acquired by specimens in core area V. Core area II's most southern end is approximately 180 kilometers away from a narrow northern extension of core area V.

The state of scapes black in color is probably apotypic within *N. peruviana.* No South American species of *Anisotarsus* has all specimens with this state. Four species, including *N. peruviana,* have some specimens with scapes black and some specimens with other colors. Six other species lack any specimens with scapes black.

The geographical distribution of specimens with scapes black suggests that this state evolved in either core areas I or III. It is absent from core areas V and VI and the northern part of the Río Santa Valley, and it occurs at varying percentages in a wide region (T1 of Fig. 11) embracing core area II, the Andes of central Peru and the three most northern coastal lomas of core area IV.

An origin in core area I is more probable than in core area III. The geographical distribution of this state throughout core area I and along the northern edge of the Junin Plateau of core area III suggests specimens with it are adapted primarily to moderate temperatures and mean annual precipitation of approximately 700 or more mm. During all climatic phases portions of core area I probably have more moderate temperatures and precipitation than all of core area III. The small size of core area III for the character state suggests that specimens with it are adapted to environments in only part of the area. In contrast, specimens with this state occur throughout core area I.

Probably the state originated during a past drier period in the highlands between Abra de Porculla and the pass between the headwaters of the Río Chotano and Río Chancay or in the dissected or discontinuous highlands near these passes. During a subsequent wetter phase specimens with this state spread north into Ecuador and south, via formerly continuous grasslands along the eastern Andes, into core area III. Return to a climate like the present isolated specimens with this character state along the northern edge of the Junin Plateau in core area III. Origin in Ecuador is unlikely since climate in much of Ecuador was probably too moist for *N. peruviana*.

The presence of a proximal field on the internal sac of the male median lobe is apparently an apotypic character state for *N. peruviana*. Proximal fields occur in all males of *N. tucumana*, *N. cupripennis* and *N. schnusei* and some of *N. peruviana* but differ in location and structure between species or species groups; probably such fields are homologous only within each species or species group.

The wide geographical distribution (areas D and B of Fig. 18) of males with this field obscures its geographical origin and suggests age sufficient for specimens with it to disperse through B and D and become adapted to xeric habitats from near sea level to more mesic Andean ones up to elevations of approximately 3500 m. Probably, the proximal field evolved in a series of grades from absent to: present but lightly sclerotized with small microtrichia; present and with moderate sized and moderately sclerotized microtrichia; and present and with large, prominently sclerotized microtrichia. These grades occur today in populations of the four transition regions; the intermediate grade of moderate sized, moderately sclerotized microtrichia apparently occurs in all males of core area VI (D). Possibly, the proximal field originated in D and became established in the intermediate grade among all males there. Males with this intermediate grade may have dispersed into B during a wetter climatic phase. During a subsequent drier phase, D became geographically isolated from B; males in B evolved the more prominent grade of field and dispersed throughout that area but not into D. Other scenarios are possible.

A moderately long median lobe apex is the plesiotypic state among South American species of *Anisotarsus*. The geographical distributions of male *N. peruviana* with plesiotypic moderately long apices, apotypic very long apices, and apotypic short apices suggest that changes in length of the apices occurred relatively recently. Specimens with the presumed plesiotypic state occur in areas C and A (Fig. 17). Specimens with apotypic very long apices (means of lengths/widths greater than 0.900) occur in B and D.

Area B consists of the region between Abra de Porculla and the pass between the headwaters of the Río Chotano and Río Chancay together with the discontinuous or much dissected highlands (above 3000 m) of Cajamarca Department. During a past drier period populations were probably isolated between the passes or in the highlands. Evolution in these isolated populations presumably resulted in a change from the plesiotypic moderately elongate apex to the apotypic very long form. Subsequently, as climate moderated, area B was connected via a grassland corridor along the eastern Andes to D (core area III), and introgression in D resulted in males there acquiring the very long apices. Recency of origin in area B is suggested by males all with plesiotypic moderately elongate apices in A and C to the north and south respectively of B. There has presumably not been enough time for forms with the very long apices to disperse into A or C or to be swamped by north-south dispersals between A and C.

Evolution of apotypic short apices also is probably relatively recent; specimens with such apices are restricted to southern and south central Peru. Short apices probably originated in core areas IV, V, or VI. Dispersal between these core areas during the last wetter climatic phase resulted in forms with short apices dispersing through E and to the southern parts of core area III. The dispersal to the southern parts of core area III led to transition region T2. Alternatively, this transition region may be due to continued southward dispersal from northern parts of III of males with the very long apices. Whichever is correct, short apices seem a recent development.

Development of the apotypic state of numerous setae on the abdominal sterna also seems recent, probably during the last drier phase. Specimens with the apotypic state occur only in core area II, and there is a transition region in the northern part of the Río Santa Valley from the apotypic to the plesiotypic state. If evolution had occurred in an earlier phase, forms with the apotypic state would probably have dispersed out of the Río Santa Valley. Alternatively, the forms with the apotypic state might be restricted to core area II because this is small in surface area, and forms that evolve there can not (Darlington, 1959) compete with those evolved in larger areas.

Development of the present pattern of geographical differentiation requires more than one cycle of contraction and expansion. I can specify the following hypothetical scenario based on three phases of drier-warmer and wetter-cooler climates causing three cycles of contraction and expansion respectively of the core areas.

Prologue. Dispersal of the species throughout its present range during a wetter-cooler period. Specimens all characterized by the plesiotypic states of: dorsal body color class III; scapes of colors other than black; ocellate punctures present between elytral striae one and two; elytral microsculpture a moderate to prominent isodiametric mesh; abdominal sterna lacking numerous setae; apex of male median lobe moderate in length; and internal sac of males lacking proximal field.

Contraction I. Dorsal body color class I evolves in a core area (probably in VI but possibly also in I or III); dorsal body color class II evolves in core area IV before this area is destroyed or shifts into the Andes, and specimens of this class disperse over then semi-arid, but now mesic, habitats in the Andes.

Expansion I. Specimens of dorsal body color class I spread to all core areas but IV; or if they do reach IV do not become established there or are later totally displaced by the more semi-arid adapted ones of dorsal body color class II. Specimens of dorsal body color class II become centered in core areas II and IV and scattered relictual sites.

Contraction II. Color class IV evolves in core area IV, and specimens of this color class disperse eastward through the Andes and eventually reach site 60. The state of elytral discal microsculpture reduced evolves in a core area other than I, III, or V. Scapes black in color evolves in core area I. Males in core area IV, V, or VI acquire a proximal field.

Expansion II. Specimens belonging to dorsal body color class IV become replaced by those of other color classes except in core area IV and site 60. Specimens of dorsal body color class II become replaced by those of other color classes except in core areas II and IV and various relictual sites throughout the species range. Males with a proximal field on the internal sac disperse from their source area into other regions of southern Peru. Specimens with elytral microsculpture reduced disperse from their source but do not reach core area V. Specimens with scapes black in color disperse along the eastern Andes from the southern part of core area I to core area III.

Contraction III. Males in core areas IV, V, or VI acquire short apices for median lobes. Males isolated in the southern part of the core area I (between the passes or in dissected or discontinuous highlands) acquire elongate apices for median lobes. Specimens in core area II acquire numerous setae on the abdominal sterna. Those in core area III lose the ocellate puncture between the bases of elytral striae one and two.

Expansion III. Males with elongate apices disperse to core area III. Introgression in that core area results in males with short apices invading the southern part of that core. Introgression also limits the frequency of specimens with black scapes in this core. The pattern of geographical differentiation shifts toward that of the present.

Absolute dates.

Only approximate maximum and minimum absolute dates can be postulated. The maximum period for geographic differentiation probably corresponds to the major Andean uplift which for Ecuador and Peru was approximately during the late Pliocene and Pleistocene (B. Simpson, 1975). Le Brecque *et al* (1977) assign a date of approximately two million years B.P. to the start of the Pleistocene and approximately 2.5 million years B.P. to the start of the late Pliocene.

I believe at least three complete cycles of drier-warmer and wetter-cooler climates were necessary for geographical differentiation. Hester (1966) summarizes data suggesting there have been two complete cycles from approximately 16,000 or 12,000 B.P. to present. Thus, the Wisconsin Glacial Period, starting from approximately 200,000 B.P. (Erichson and Wollin, 1970), was presumably part of the first of the two cycles recognized by Hester. The Illinoan Glacial Period from approximately 600,000 to 400,000 B.P. and the Sangamon Interglacial from approximately 400,000 to 200,000 B.P. (absolute dates from Erichson and Wollin, 1970) probably correspond to a third complete cycle. Minimum age for the present pattern of geographical differentiation is probably thus 600,000 years.

The geographical differentiation therefore probably occured during a period starting approximately two million years B.P. (maximum age based on approximate start of Pleistocene climatic changes) or as recently as 600,000 B.P. (minimum age). The taxon cycle for *Anisotarsus* (discussed earlier and also below) suggests that species such as *N. moffetti* and *N. bradytoides* evolved *before* geographical differentiation of *N. peruviana.* Such a suggestion requires at least one complete climatic cycle during the Pleistocene and supports evolution of the geographical differentiation of *N. peruviana* within the minimum 600,000 year period.

TESTING OF THE HYPOTHESIS FOR GEOGRAPHICAL DIFFERENTIATION OF *N. PERUVIANA* DURING CLIMATIC CYCLES

Noonan (1979) suggests that biogeographical studies on Carabidae meet Popper's four criteria for scientific hypotheses (explanatory power, internal consistency, potential for falsification, and predictive power). Does the above hypothesis meet these criteria?

As already demonstrated, the hypothesis explains the geographical differentiation in *N. peruviana.*

The hypothesis is internally consistent. No part of it contradicts another.

Potential for falsification and predictive power are intertwined, and the hypothesis can be tested by examining the accuracy of the following falsifiable predictions derived from a deductive examination of it: (1) geological data as they become available will support the concept of past climatic cycles in the Andes; (2) examination of the core areas will show that at least part of their boundaries correspond to potential barriers; (3) the hypothesis will agree with the taxon pulse postulated earlier for South American species of *Anisotarsus;* (4) the available data on distributions of other terrestrial organisms will show that at least some have been affected by the barriers between the core areas; (5) an alternative hypothesis that local selection causes the geographical differentiation in *N. peruviana* will not adequately explain this variation; and (6) data from studies of non morphological (eg. biochemical, behavioral, chromosomal, etc.) characters will support the hypotheses.

Geological data.

Available geological data support the hypothesis. Haffer (1974), B. Simpson (1975, 1979), van der Hammen (1974), and B. Vuilleumier (1971) summarize data indicating marked climatic fluctuations in the Andes of northern South America with accompanying pronounced changes in the vegetational cover. During the Pleistocene two or three cool or glacial phases, corresponding to those of the Northern Hemisphere, occurred in the Andes. Although the climate of the Andes was wetter during part of the cooler phases, drier conditions prevailed during the peak of glaciation. Thus, there were cycles of wetter- cooler and drier-warmer phases, with aridity characterizing the peak of the glacial periods. During part of the glacial periods, snow lines lowered by as much as 1000 m. Numerous lakes formed during wetter-cooler phases in the altiplano of Peru and Bolivia and in many other intermontane basins of the northern Andes. Temperature depressions of 7° to 8° C also occurred during these phases. The temperate Andean life zones (which *Anisotarsus* now inhabit) shifted approximately 1500 m downward (from present limits) during the wetter-cooler periods and approximately 500 m upwards (from present limits) during interglacial drier-warmer periods. These life zones thus shifted a total of approximately 2000 meters during the Pleistocene. Downward shifts resulted in extensive and nearly or completely continuous areas of temperate life zone while upward shifts produced significant dissection of this life zone.

Pronounced climatic effects in the lowlands during the Pleistocene accompanied the effects occurring in the Andes. During part of the glacial periods westerly airflow against the central Andes caused heavy snowfall, a lowering of the snow line, and a strong rain shadow east of the Andes where extensive cool-dry desert areas prevailed. Alternating drier and wetter periods probably caused the characteristic landforms along parts of the eastern and western slopes of the Andes. During the cold phases the altitudinal climatic transition from the lowlands to the cooler Andean highlands was greater than today.

The alternation of wetter and drier periods continued into post-Pleistocene and Recent times, as late as approximately 2400 B.C. Mangrove vegetation extended along the arid coast of Ecuador and Peru far south of its present limit during wetter phases dated as 5000 to 6800 B.C. and 2450 to 2650 B.C.

Hastenrath (1967) summarizes additional information about Pleistocene events in the Andes. Pliocene tectonic activity apparently continued into the Pleistocene over large parts of the Andes. However, the major part of uplift occurred prior to penultimate glaciation, and elevations during the last two glaciations were approximately those of the present. During glacial periods there were substantial snow line depressions. These depressions were greatest along the now arid Pacific region of southern Peru, suggesting a substantial increase in precipitation there. Geomorphic evidence near Arequipa and Mollendo support the asumption of a previously less arid climate. Hester (1966) summarizes data suggesting at least two complete cycles from cool and moist to warm and dry from 16,000 or 12,000 B.P. to present.

Correspondence of potential barriers to boundaries of the core areas.

The section entitled "Geography, topography, and climate of the core areas and major transitional regions" demonstrates that potential barriers correlate well with boundaries of the six core areas.

Correspondence of hypothesis with taxon pulse postulated for Anisotarsus.

Core area II is the smallest of the core areas; populations isolated there during drier-warmer periods would have relatively small gene pools and thus probably differentiate more rapidly than populations isolated in larger refugia. As noted earlier, *N. moffetti* appears to be a specialized Andean species at the end of a taxon pulse and is centered around a small area above approximately 3700 m at the southern end of core area II. Probably the species differentiated in the core area and then shifted upward (possibly due to pressure from *N. peruviana)* and became a high altitude specialist. Adults of *N. peruviana* in core area II have dorsal body color class II and are uniquely characterized by pubescent abdominal sterna. Differentiation of *N. peruviana* in this core area thus seems perhaps more rapid than in the larger core areas.

Populations of *N. peruviana* along the upper portions of core area III (above approximately 4000 m on the Junin Plateau) may be evolving toward high elevation specialization such as in *N. moffetti.* Adults from these upper elevations are small (as in *N. moffetti)* and lack (also as in *N. moffetti)* an ocellate puncture near the scutellar striae between elytral striae one and two. In time these populations may differentiate to the species level.

Data about *N. bradytoides* and *N. aguilarorum* agree with the hypothesis. *Notiobia bradytoides* seems to be specialized in or restricted to Andean habitats in core area I; probably it originated there during past climatic cycles. *Notiobia aguilarorum* appears to have specialized in adaptations to xeric habitats in the lower northwestern Andes of Peru. Its geographical distribution seems centered around lower areas of the dissected or discontinuous highlands along the southern part of core area I. Possibly its origin was by initial isolation in these highlands (as apparently was origin of the apotypic long median lobe apex in *N. peruviana)* and a subsequent shift into xeric habitats. Such a shift was possibly mandated by drier-warmer period(s) or pressure from *N. peruviana.*

Comparison with distributional data for other Andean terrestrial organisms

Terrestrial organisms other than *Anisotarsus* may have different vagility and genetic potential and thus be affected in different ways by climatic cycles. Nevertheless, at least some other groups should show evidence of having been affected by factors such as the potential barriers suggested as important in geographical differentiation of *N. peruviana.* For the grassland areas of the Andes of Ecuador, Peru, and northern Bolivia most (or perhaps all) other terrestrial organisms have apparently not been as intensively collected or studied as has *N. peruviana.* A few general comparisons can however be made.

Müller (1973) provides an interesting depiction of 40 centers of dispersal in the Neotropical Region. He bases his conclusions on the breeding cycles of vertebrates since he feels that most other organisms, except possibly Lepidoptera, are not well enough known to be used in analysis of refugia. The dispersal centers are stated by him to have presumably arisen because their faunas were isolated in them during past climatic cycles. In South America he recognizes two Andean centers above the tree line, the "North Andean centre" and the "Puna centre." The North Andean center extends south from Venezuela and the Andes of Colombia to southern Ecuador. But some mammals and birds also extend further south into the paramo of southern Peru as far as Lake Junin or else occur there as subspecies or closely related species. Therefore Müller divides the center into a "Bogota subcentre" including the high Andes of Ecuador, Colombia, and Venezuela and a "Peruvian Andes subcentre" comprising the Andes of northwestern Peru and having the character of a transition zone between the Bogota subcenter and the Puna center. The Puna center consists of the high Andes of southern Peru and northern Bolivia. Müller's conclusions suggest that vertebrates may in general be more vagile than *Anisotarsus* and therefore not as finely subdivided by climatic cycles. However, Müller mentions that the North Andean center could be subdivided further than into merely subcenters. Apparently most or all of the vertebrates used by him have not been subjected to a detailed analysis of geographical differentiation as done in this paper for *N. peruviana.* Müller notes (p. 4) that the basic distributional data are lacking for many Neotropical amphibians and reptiles and that many of the locality lists he examined had no information on the gonadial development of birds (only localities that could be proven to belong to breeding ranges are used by him). Several of the studies described below support the concept of more than two dispersal centers or refugia in the Andes for vertebrates and for plants.

In an excellent synthesis B. Vuilleumier (1971) discusses avian and plant speciation patterns for the Andes of Ecuador and Peru. Two apparent major barriers to dispersal of paramo-puna and upper montane forest plants and birds are the Upper Río Marañon Valley and northern Peru lowlands; and the Río Apurimac and Río Pampas Valleys. In his study of tyrannids, many of which occur in open Andean habitats, F. Vuilleumier (1971) concludes also that for these birds the same areas have been important barriers. These xeric barriers correspond, respectively, to the approximately southern end of core area I and the boundary between core areas V and VI for *N. peruviana.*

In a treatment of biogeographical patterns of the birds of the paramo and puna of the Andes, F. Vuilleumier (1969) concludes that the most biogeographically important of the barriers in the Andes has been the Upper Río Marañon Valley and northern Peru lowlands. For *N. peruviana* this area is also a significant barrier. Core area I is internally homogeneous and clearly delimited in values for 11 characters, second only to core area III which is homogeneous and clearly delimited in values for 14 characters.

Examination of a study by F. Vuilleumier (1968) of Andean birds of the *Asthenes flammulata* species complex shows partial correlation of species distribution with the core areas for *N. peruviana.* For the Andes of Peru Vuilleumier groups specimens into six populations primarily on the basis of whether or not certain localities appear isolated from others and thus represent potential interruptions in gene flow; and whether or not the birds from several more or less adjacent localities are morphologically uniform. His adjacent populations "I" (Cajamarca Department) and "J" (Quirivilica, La Libertad Department) are accorded separate status because of geographical variation in some characters. From his figure 2, population "I" appears to correspond to the southern end of core area I characterized in *N. peruviana* by long apices for median lobes of the male genitalia. Population "J" appears to be in what is a transition region for *N. peruviana.* Population "K" is centered on "Rock Forest" approximately 50 km west of the town of Junin, Junin Department and thus apparently corresponds to core area III. The remaining Peruvian populations occur in areas not sampled for *N. peruviana* or outside of the known species range.

Lynch (1975) reviews the 14 known species of the frog genus *Phrynopus,* with species distributed in the Andes from Colombia to western Bolivia at elevations of 1000 to 4000 m. Samples are small and he does not discuss the role of present or potential barriers in the evolution of species. Inspection of his data suggest that some of the barriers important in differentiation of *N. peruviana* have also been important for speciation in *Phrynopus.* The sister species (cladograms in his figure 19) *P. flavomaculatus* and *P. parkeri* occur respectively along the eastern Andean Cordillera in southern Ecuador and along the Andes at 3100 m in Piura Department, Peru north of the Abra de Porculla. They are thus just north of the low lying part of the Andes in northern Peru. The sister group of these species is *P. pereger* from the Andes of southcentral Peru west of the Río Apurimac. *Phrynopus simonsii* from Cajamarca Department, Peru is the sister group of five species, one from the Amazon of northern Peru and four from more southern Andean localities (more southern species: two from Cuzco Department, Peru; one from Junin Department, Peru; and 1 from La Paz Department, Bolivia). The low lying area of the Andes in northern Peru and the dissected and discontinuous highlands associated with the southern boundary of core area I for *N. peruviana* appear to have been important barriers during evolution of the above species. The Río Apurimac Valley, barrier between core areas V and VI for *N. peruviana,* may similarly be important in restricting *P. pereger* to the Andes west of this Valley.

Duellman (1979) provides an excellent review of available data about the herpetofauna of the Andes. He regards the Huancabamba Depression or low lying portion of the Andes in northwestern Peru (barrier forming approximate southern end of core area I for *N. peruviana)* as a major barrier to dispersal of montane adapted forms. In my view little more can be concluded about the importance of barriers to the evolution of the grassland montane herpetofauna in general without detailed analysis of the various taxa. Many groups appear to have at least some species adapted to tropical lowlands. The herpetofauna of the Cordillera Central in Peru is inadequately known. Apparently no group of the Andean herpetofauna has been studied in detail as done in this paper for *N. peruviana*.

In summary the data suggest that at least some vertebrates and plants may have differentiated in the Andes via refugia and barriers similar to those postulated for *N. peruviana*. Detailed analyses of vertebrates, plants, and invertebrates other than *Anisotarsus* are needed for further evaluation of the applicability of the core areas to other organisms.

Adaptations to local selection as an alternative hypothesis explaining geographical differentiation of N. peruviana.

In recent years several authors (see White, 1978 for summary) have investigated the genetics of geographical variation of wide ranging species whose individuals have moderate to low vagility. Cain and Currey (1963a, 1963b) study geographical variation in England for the snails *Cepaea nemoralis* and *C. hortensis* and are the first to recognize the so called "area effects," i.e. areas in which the genetic composition of the population is strikingly different from that in the surrounding contiguous area. They conclude that "area effect" in these snails is due to local selection (see Goodhart, 1963 for a dissenting view advocating the importance of historical factors; see Jones *et al* 1977 and White, 1978, p. 153-168, for summaries of various explanations). Endler (1977) summarizes arguments for environmental gradients as a general cause of geographical variation in organisms. A hypothesis can be proposed that the geographical variation in *N. peruviana* is due to local selection or environmental gradients rather than to historical factors such as expansion and contraction cycles *and* differentiation (under local selection) in refugia. Such a hypothesis fails to adequately explain the observed geographical patterns and has internal contradictions.

Dorsal body color class I occurs at high percents in core areas I, III, and VI. Local selection therefore must be similar despite the fact that the annual climate of VI is more seasonal than that of I and has precipitation more concentrated in a distinct rainy period. If local selection is similar in these areas, why do black antennal scapes occur only in core areas I and III? It is also contradictory for elytral discal microsculpture to be reduced in many specimens from core area VI and all specimens of core area II. Such a hypothesis does not explain why males in the southern part of core area I have apices of median lobes relatively long like those of males from the northern part of core area III and unlike the plesiotypic type in males immediately north and south of region B of figure 17. If local selection in core area VI is similar to that of I, as suggested by the geographical distribution of dorsal body color class I, then why do males in VI have apotypic relatively short apices? And why do males from the coastal lomas of core area IV also have relatively short apices when local selection in these hot dry lomas must surely be different from that in the Andes around Cuzco? If local selection is somehow similar in core areas IV and VI, then why does dorsal body color class II occur at high percents in core areas II and IV but not in VI? Why do males from Peru south of approximately 8° south have a proximal field on the internal sac except for those from core areas II and III?

Other problems with a hypothesis based on local selection could be cited.

Evaluation of the test.

The hypothesis for geographical differentiation of *N. peruviana* during past climatic cycles meets Popper's four criteria for scientific hypotheses. The hypothesis has explanatory power and is internally consistent. Four of the six potentially falsifiable predictions (correspondence with geological data, correspondence of boundaries of core areas to barriers, agreement with the taxon pulse hypothesis, and unsuitability of local selection hypothesis) have been verified here. The meager data on other Andean grassland organisms show that at least some of them have been affected by the same barriers as have *Anisotarsus*. More study is needed however of these other organisms; none apparently have been studied as intensively as *N. peruviana.* The sixth prediction, agreement of data from study of non morphological characters with the data discussed in this paper, remains to be evaluated by future studies.

CONCLUSION

Geographical differentiation or evolution apparently occurred in *N. peruviana* while populations were isolated in Andean refugia during past drier-warmer periods. Expansion of populations during wetter-cooler periods resulted in secondary contact and introgression. The differentiation probably occurred as a result of three climatic cycles during approximately the last 600,000 years. Earlier climatic cycles probably gave rise to *Anisotarsus* species such as *N. moffetti* and *N. bradytoides.*

The proposed sequence of differentiation during population contraction into refugia during drier-warmer periods and secondary contact and introgression (if reproductive isolation not complete) during wetter-cooler periods has implications for other organisms. Many terrestrial Andean grassland invertebrates, vertebrates, and plants may have evolved during such climatic cycles. The model for geographical differentiation in Andean refugia serves as a general test of the concept of refugia for tropical lowland organisms because climatic changes affecting evolution in the tropical lowlands must have been accompanied by corresponding changes and effects in the Andes. The model for Andean differentiation also extends the refugia model of evolution from the tropical lowlands up into the cool grasslands of the Andes.

Geographical differentiation in *N. peruviana* and in other *Anisotarsus* (including differentiation to the species and species group level) has apparently occurred as a result of periods of dispersal and vicariance. A separate paper will examine implications of the present study for general theories of dispersal and vicariance and other topics such as reconstruction of phylogenies.

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Appendix

Descriptions of the eight study transects and locations and elevations of the 95 sample sites.

Elevations at the Ecuadorian sites were measured by an altimeter, later found to be inaccurate. A topographic map of Ecuador facilitated determining elevations plus or minus approximately 200 meters. An accurate new altimeter measured elevations in Peru and when reset at known elevations did not vary more than plus or minus 80 meters.

Ecuadorian Transect and Abra de Porculla Sample (sites 1-19). Fieldwork in Ecuador extended south from near the Colombian border (31.4 km. N. of Ibarra) to Pelileo in central Ecuador, eastward from Quito to near the eastern edge of the Andes at 44 kilometers southeast of Quito and approximately 3900 m, and westward from Machachi to the lowlands around Santo Domingo de los Colorados. North to south, *N. peruviana* occurred in small scattered populations.

Eastward from Quito *Anisotarsus* were absent beyond approximately 30 kilometers southeast of Quito. Countryside east of there was more humid and had very dense green grass. Other Carabidae, such as Agonini, appeared to replace *Anisotarsus.* West from Machachi, *N. peruviana* was present but uncommon at site 9 located approximately 15 kilometers east of the western edge of the Andes. Habitats between site 9 and this edge appeared to receive nearly constant fog from westward moving clouds, had dense green grass and lacked *Anisotarsus.* The few habitats which could be reached along the sharp descent from the western edge of the Andes to the tropical lowlands had progressively more tropical appearing vegetation, insects associated with tropical and subtropical habitats, and lacked *Anisotarsus.*

Cajamarca Transect. (sites 20-33). This transect (Cajamarca Department, Peru) extended westward from Cajamarca along the road down from the Andes to Pacasmayo and southeastward along roads extending towards Celedín and Cajabamba. Elevations from Cajamarca to Pacasamayo ranged from 3210 m at a pass approximately 17 kilometers west of Cajamarca to sea level at Pacasmayo. Elevations with *N. peruviana* were from 3210 to 1620 m with habitats below 1620 m apparently too arid. The southeastern sampling included elevations from 3010 to 2420 m, with *Anisotarsus* present over the entire altitudinal range.

Otuzco Transect. (sites 34-42). This transect (Otuzco Province, La Libertad Department, Peru) had three subsections. The first extended east from the coastal city of Trujillo to Otuzco in the Andes with elevations from sea level to 2635 m (Otuzco). The only site with specimens was number 41 at 2540 m; habitats below this elevation appeared too arid. The second subsection extended northeast from Otuzco to Coina with elevations from approximately 3200 m (estimated, not measured) to 1500 m. Specimens were present at 3020 m, the highest elevation sampled, and absent below 2020 m, with lower elevations apparently too arid. The third subsection extended from Otuzco to the Agallpampa region with elevations from approximately 2440 to 3810 m; specimens were found at all sampled elevations.

Río Santa Valley Transect. (sites 43-55). This transect (Ancash Department, Peru) extended along a road from near the northern end of the Río Santa Valley southward through its center and into highlands over 4000 m high. Sampling sites extended from 2430 m at site 43 in the northern end of the valley to 3950 m n highlands south of the Valley. Specimens were found from 2430 m to 3720 m; elevations above 3720 m had *N. moffetti* or other carabids and appeared too moist.

Coastal Lomas. (sites 56-59). This transect extended south through four arid omas from approximately 99 kilometers north of Lima to approximately five kilometers north of Chala.

Huanuco-Tarma Transect. (sites 60-75). This extended southward along the road from Huanuco to Tarma, crossed the Junin Plateau, and traversed elevations from 1820 to approximately 4400 m. Sampling was done from 1820 to 4150 m. Elevations with specimens ranged from 2000 to 4120m. Sampling above 4120 m consisted of three brief stops. The species was abundant at 4120 m and probably occurs at higher elevations in this transect.

Lima-Tarma Transect. (sites 76-78). It extended east from Lima through the Río Rímac Valley, across highlands above 4000 m, and down to Tarma at 3050m. Sites 74 and 75 formed part of this and the Huanuco-Tarma transect.) Dense armland on all but the steepest slopes prevented sampling at elevations below

3410 m (site 75) near Tarma. Sampling in the Río Rímac Valley did not reveal specimens below or above 2400 and 3820 m respectively.

Central and southern Andes of Peru Transect. (sites 79-95). This had two sections. The first was through a valley, here termed the "Central Valley", between eastern and western Cordillera and extended south and southeastward from the region of La Oroya to Abancay at the Río Apurimac. The Junin Plateau formed the northern end of the Central Valley. North of approximately 14°S continuous eastern and western Cordillera above 4000 m formed the eastern and western boundaries; southward these Cordillera were discontinuous. Elevations ranged from approximately 2460 to 3600 m, with *Anisotarsus* present at all elevations. The second section consisted of sampling from the eastern edge of the Río Apurimac near Abancay east to Cuzco (via the road between these towns), in the Cuzco area, and southeastward from Cuzco (along the road to Puno) to 75.8 km southeast of Cuzco. Elevations ranged from 1960 to 3700 m with specimens found at or above 2920 m.

Sample Sites

(D. = department, P. = province)

Site No.	Location and Elevation
	ECUADOR (1-3 in Imbabura P.; 4-9 & 11 in Pichincha P.; 10, 12, & 13 in Cotopaxi P.)
1	Laguna Yahuarcocha, ca. 2500 m
2	12.2 & 8.3 km S Ibarra, 2900-3000 m
3	8.2 & 9 km W Cotachi, 2900 m
4	9.9 km NW Cayambe, ca. 2500 m
5	1.8 km W Cayambe, 2500 m
6	13.6 km NE Guayllabamba & Guayllabamba, 2600 m & 2200 m
7	2.2 km S Quinche, 2500 m
8	22.8 km SE Quito, 2500 m
9	7.9 km NW Machachi, 2900 m
10	34.5 km N Latacunga, 3100 m
11	10 km W entrance Parque Nacíonal Cotopaxi
12	Latacunga to Pilaló, 3700 m
13	13 km S Latacunga, 2600 m
14	10 km N Alausi, Chimborazo P., 2700 m
15	Azogues, Canar P., 2000 m
16	Cuenca and S Cuenca, Azuay P., 2000 m
17	Ona, Azuay P., 2500 m
18	Loja, Loja P., 2000 m
	PERU (19 in Piura D; 20-33 in Cajamarca D.; 34-42 in Otuzco P., La Libertad D.; 43-55 in Ancash D.; 56-58 & 76-78 in Lima D.; 59 in Arequipa D.; 60-65 in Huanuco D.; 66-71 in Pasco D.; 72-75 & 79-86 in Junin D.; 87 in Apurimac D.; 88-95 in Cuzco D.)
19	Abra de Porculla at 55.8 & 57.8 km E Olmus, 2105 m & 2070 m
20	16.9 & 24.4 km W Cajamarca, 3210 m & 2900 m
21	34.8 km W Cajamarca, 2460 m
22	41.1 km W Cajamarca, 2250 m
23	41.3 km W Cajamarca, 2240 m

24	43.5 km W Cajamarca, 2100 m
25	56.9 km W Cajamarca, 1620 m
26	12.4 km SE Cajamarca, 2780 m
27	16.3 km SE Cajamarca, 2780 m
28	17.4 km SE Cajamarca, 3010 m
29	19.7 km SE Cajamarca, 2860 m
30	28.7 km SE Cajamarca, 2720 m
31	55.6 km SE Cajamarca, 2720 m
32	59.2 km SE Cajamarca, 2540 m
33	62.9 km SE Cajamarca, 2420-2430 m
34	59.9 km NE Otuzco, 2020 m
35	59.2 km NE Otuzco, 2080 m
36	42.6 km NE Otuzco, 2800 m
37	40.8 km NE Otuzco, 2820 m
38	21.1 km NE Otuzco, 3020 m
39	17.9 km E Agallpampa, 3180 m
40	10.8 km NW Agallpampa, 2440 m
41	8.2 km NW Agallpampa, 2540 m
42	1.9 km NW Agallpampa, 2840 m
43	48.7 km NW Huaraz, 2430 m
44	46.1 km NW Huaraz, 2570 m
45	19.8 km NW Huaraz, 2830 m
46	19.0 km NW Huaraz, 2880 m
47	11.3 km NW Huaraz, 2940 m
48	Huaraz, 3091-3100 m
49	10.5 km SE Huaraz, 3180 m
50	12.9 km SE Huaraz, 3220 m
51	24.4 km SE Huaraz, 3410 m
52	29.9 km SE Huaraz, 3480 m
53	41.1 km SE Huaraz, 3660 m
54	42.4 km SE Huaraz, 3700 m
55	43.7 km SE Huaraz, 3720 m
56	Reserva Nacional de Lachay, 99 km N Lima, 380-550 m
57	Loma at Atacongo, 25.2 km S Lima, 200-400 m
58	Loma Pachacamac nr. Pachacamac, 29-32 km S Lima, 280-ca. 400 m
59	Lomas de Atiquipa, ca. 5 km N Chala, ca. 500 m
60	1.9 km NW Huanuco, 2000 m
61	24.0-24.4 km S Huanuco, 2050 m
62	31.3 km S Huanuco, 2200 m
63	34 km S Huanuco, 2260 m
64	37.1 km S Huanuco, 2380 m
65	44.7 km S Huanuco, 2550 m
66	56.1 km NE Cerro de Pasco, 2820 m
67	42.6 km NE Cerro de Pasco, 3230 m
68	36.1 km NE Cerro de Pasco, 3400 m
69	32.1 km NE Cerro de Pasco, 3520 m
70	21.6 km NE Cerro de Pasco, 3760 m
71	22.6 km NE Cerro de Pasco, 4110 m
72	13.5 km N Junin, 4120 m
73	12.5-13.4 km N Junin, 4120 m

74 18.4 km NW Tarma, 3810 m
75 10.0 km NW Tarma, 3410 m
76 69.5 km SW La Oroya, 3820 m
77 78.4 km SW La Oroya, 3300 m
78 Matacuna, 2400 m
79 24.5 km SE La Oroya, 3610 m
80 40.6 km SE La Oroya, 3510 m
81 54.0 km SE La Oroya, 3510 m
82 2.9 & 1.8 km NW Jauja, 3460 m & 3410 m
83 51.1 km NW Huancayo, 3400 m
84 42.3 km NW Huancayo, 3360 m
85 14.0 km NW Huancayo,3270 m
86 8.9 km NW Huancayo, 3250 m
87 Abancay, 2460 m
88 70.1 km W Cuzco, 3250 m
89 63.6 km W Cuzco, 3460 m
90 54.0 km W Cuzco, 3700 m
91 14.3 km NE Cuzco, 3600 m
92 Sacsayhuaman, 3 km NE Cuzco, 3500 m
93 Pisac, 2920 m
94 14.6 km SE Cuzco, 3100 m
95 45.4 km SE Cuzco, 3100 m

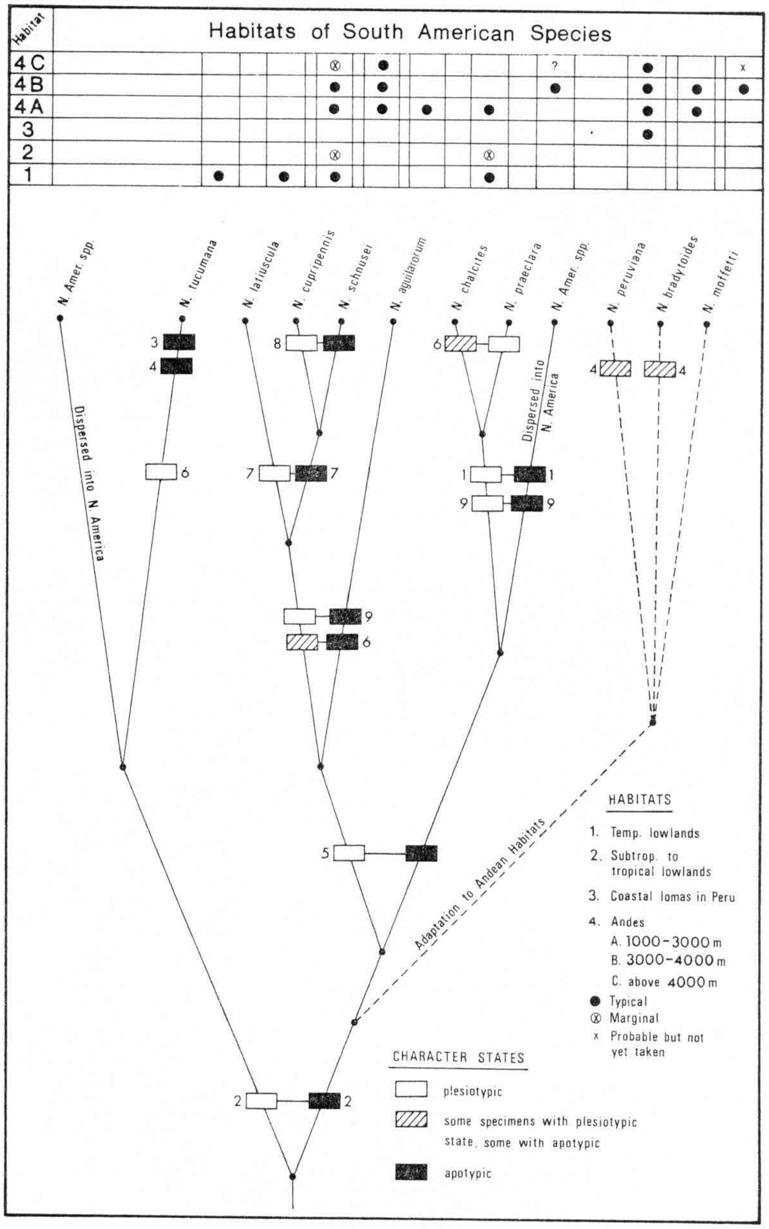
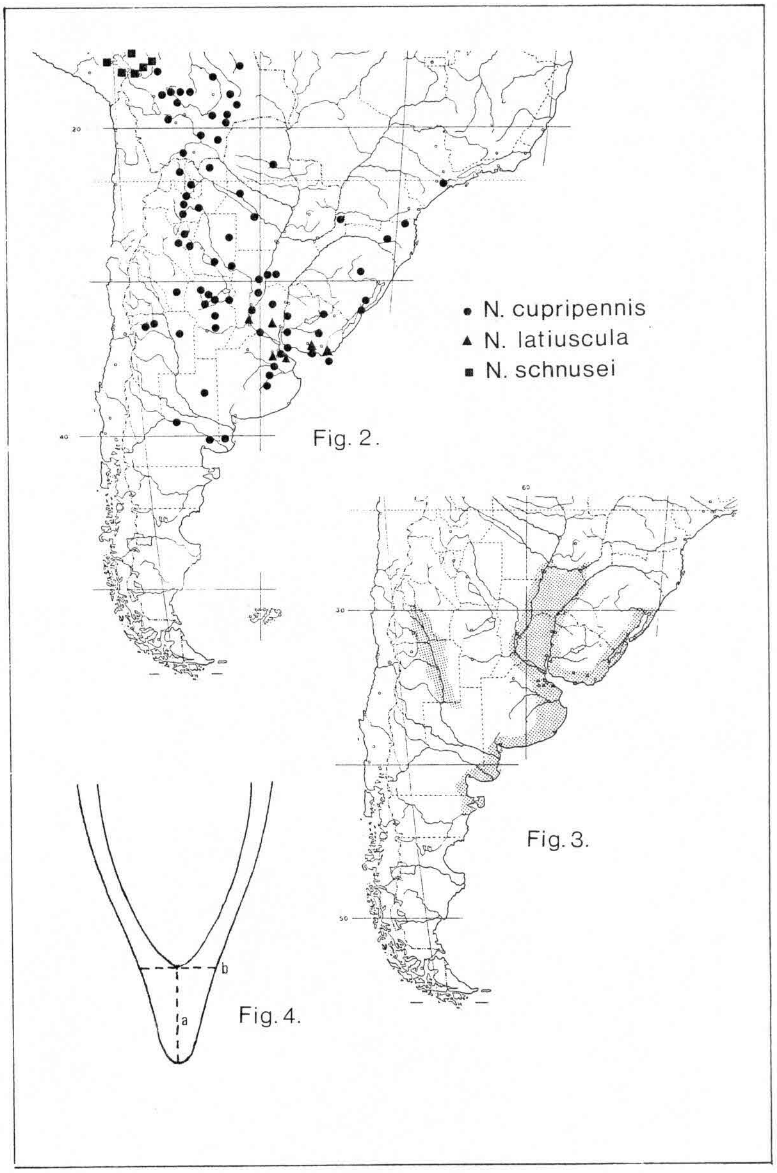


Fig. 1. Reconstructed phylogeny and habitat distribution of species of the subgenus *Anisotarsus* in South America and of the two groups that dispersed into North and Central America.



Figs. 2-4. Fig. 2. Present geographical distribution of *N. cupripennis*, *N. latiuscula*, and *N. schnusei.* Fig. 3. Map of southern South America during a Pleistocene interglacial episode showing interglacial sea transgressions and the large, inland, freshwater lake in western Argentina (redrawn from B. Vuillieumier, 1971). Fig. 4. Illustration of measurement of median lobe apex of *N. peruviana* for calculation of relative length of apex. Length was measured along line "a" and width along line "b".

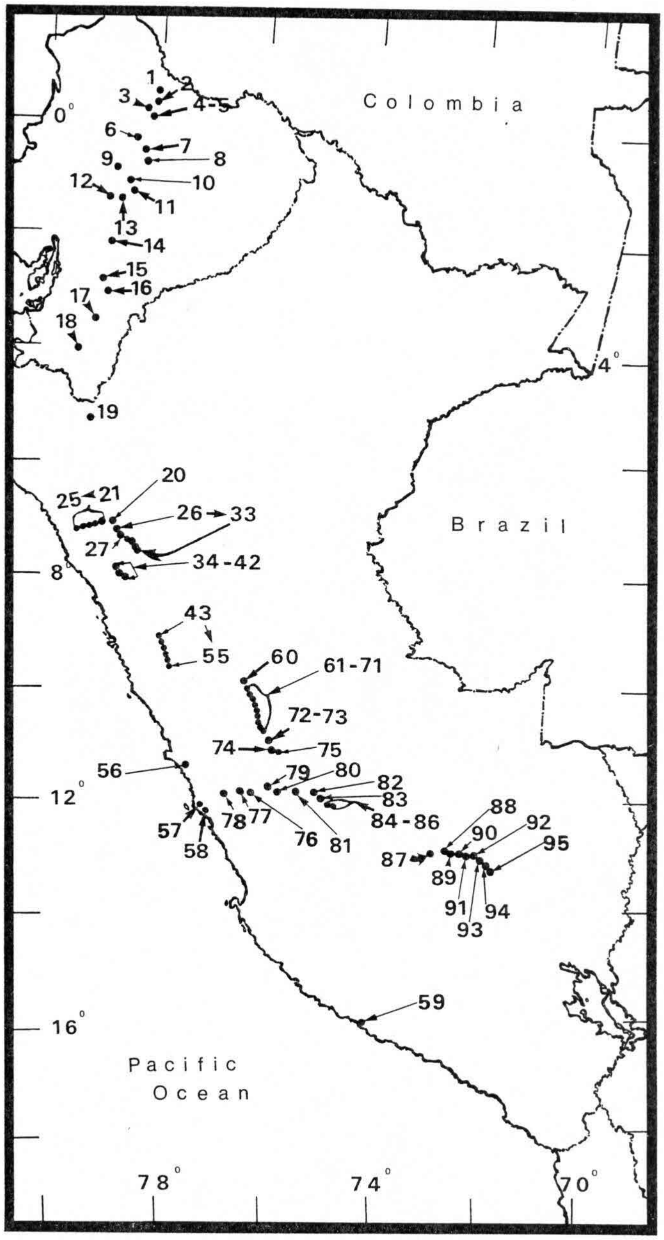


Fig. 5. Location of the 95 sampling sites used in analysis of geographical differentiation in *N. peruviana.* (See Appendix for description and exact location of individual sites.)

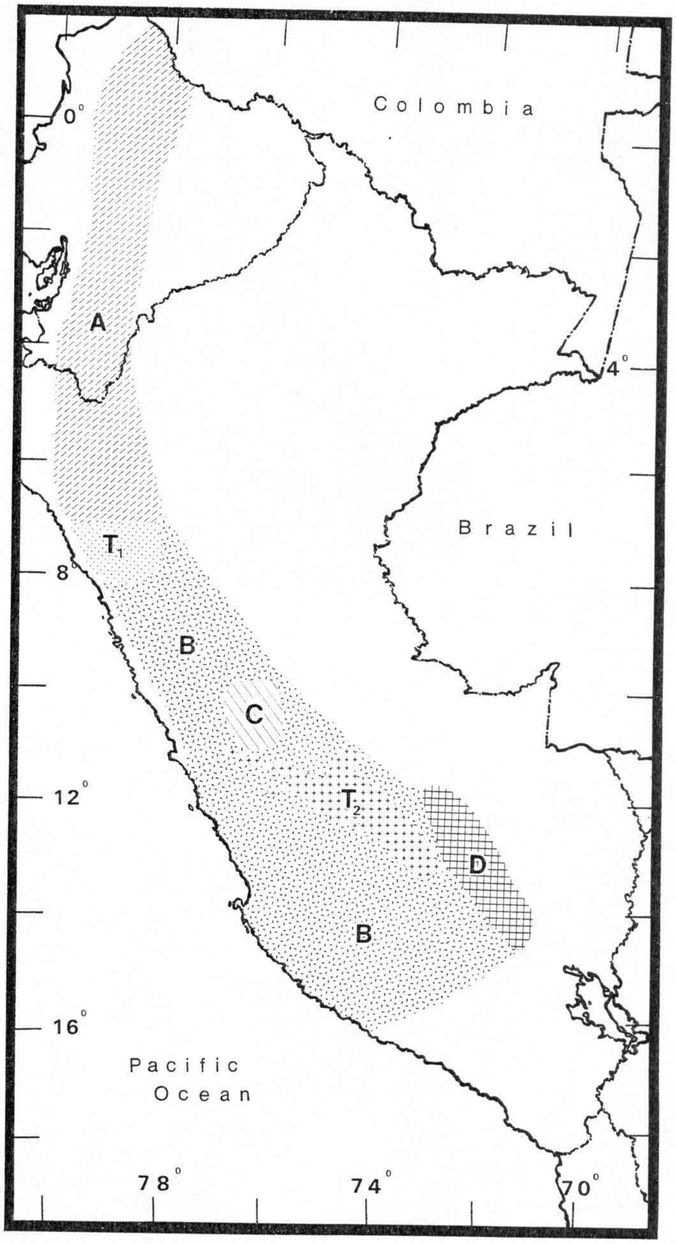


Fig. 6. General geographical pattern of areas of character state uniformity (A-D) and transition regions (T1-2) for dorsal body color class I in both sexes of *N. peruviana*.

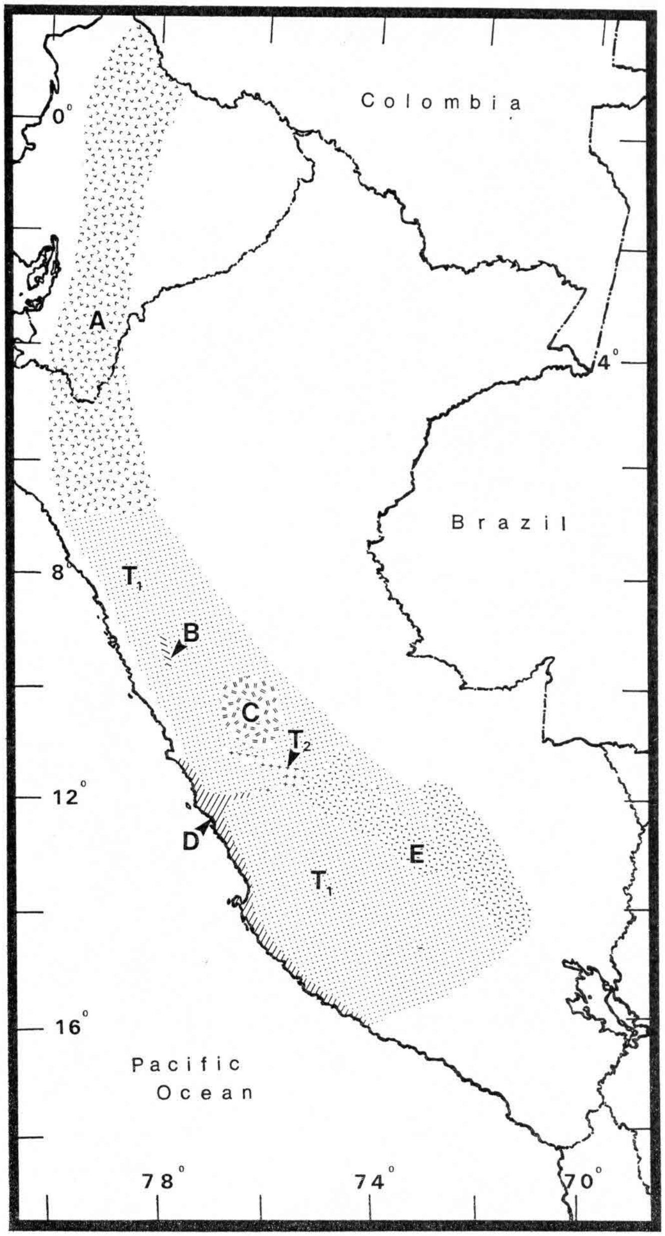


Fig. 7. General geographical pattern of areas of character state uniformity (A-E) and transition regions (T1-2) for dorsal body color class II in male *N. peruviana*.

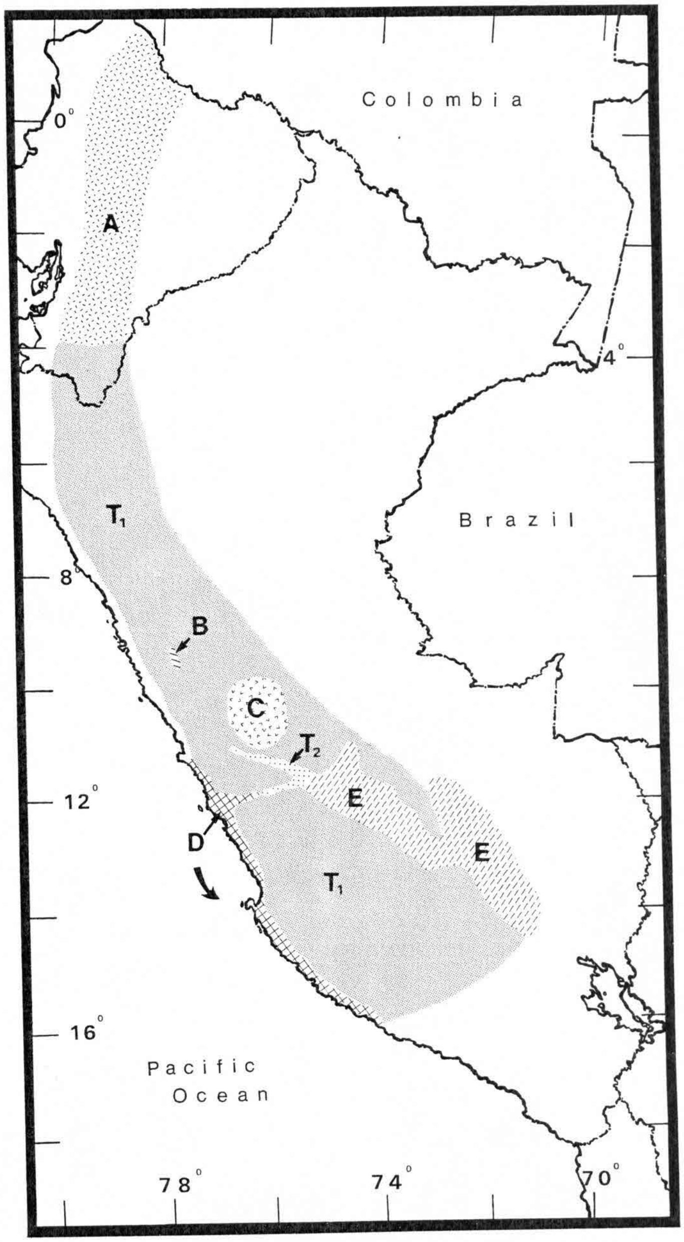


Fig. 8. General geographical pattern of areas of character state uniformity (A-E) and transition regions (T1-2) for dorsal body color class II in female *N. peruviana*.

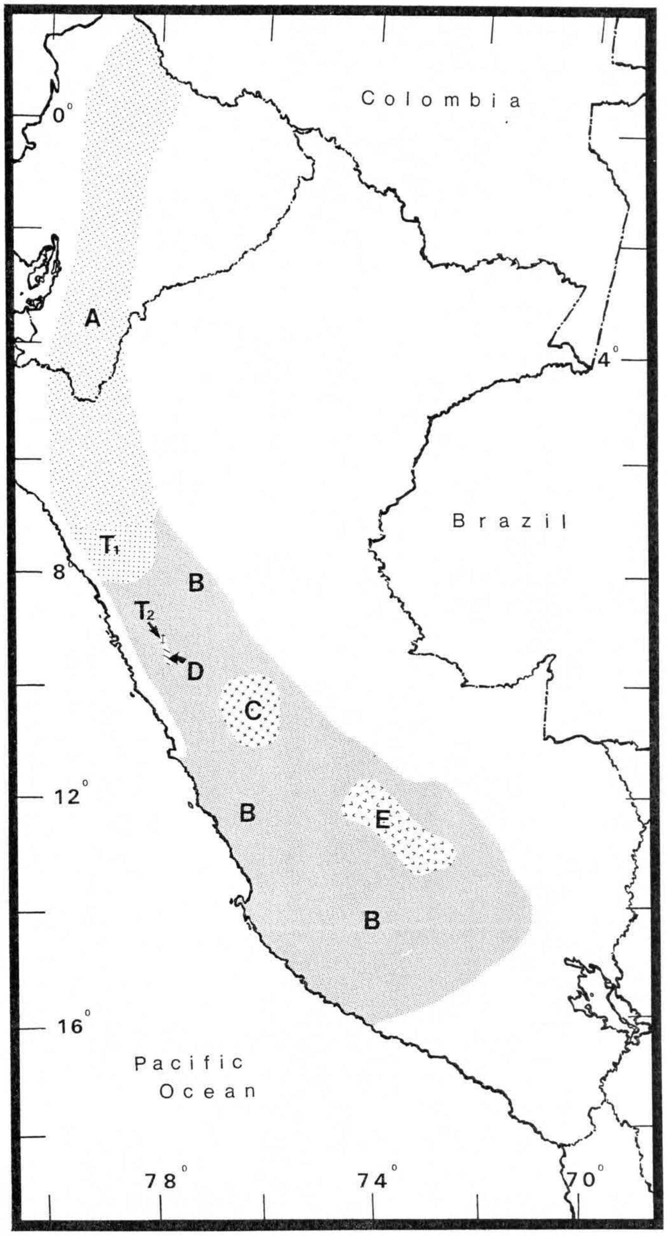


Fig. 9. General geographical pattern of areas of character state uniformity (A-E) and transition regions (T1-2) for dorsal body color class III in both sexes of *N. peruviana.*

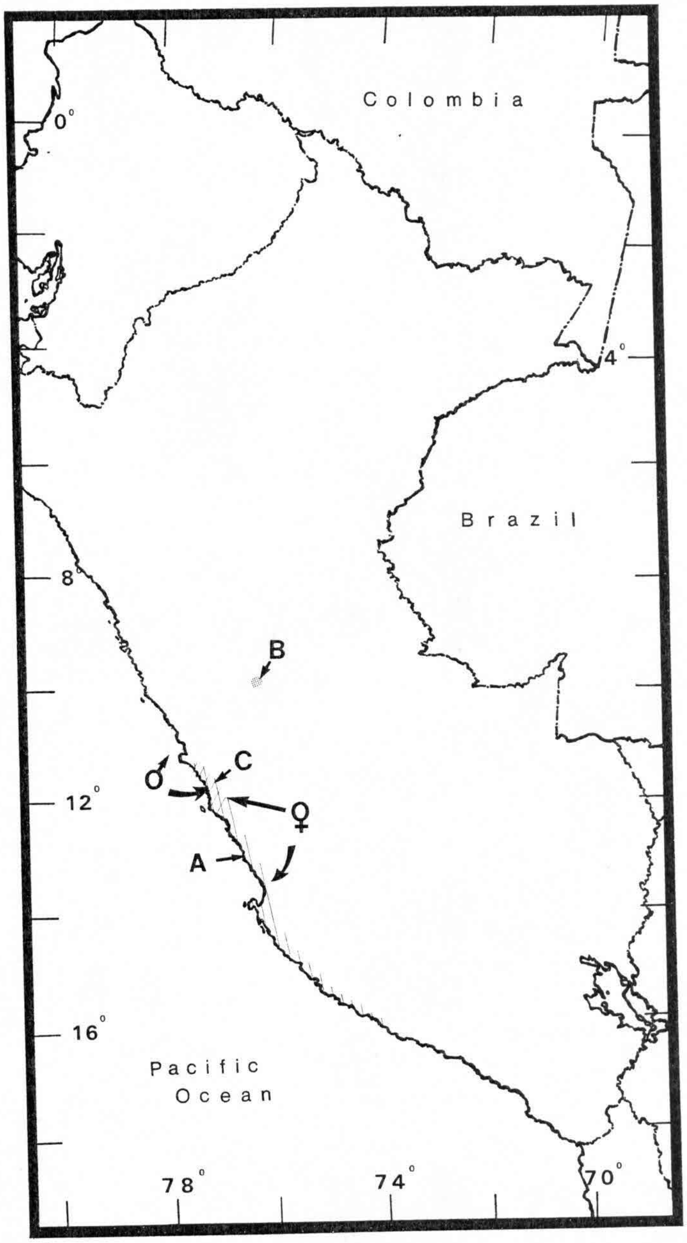


Fig. 10. General geographical pattern of areas of character state uniformity (C for males, A-C for females) for dorsal body color class IV in *N. peruviana.*

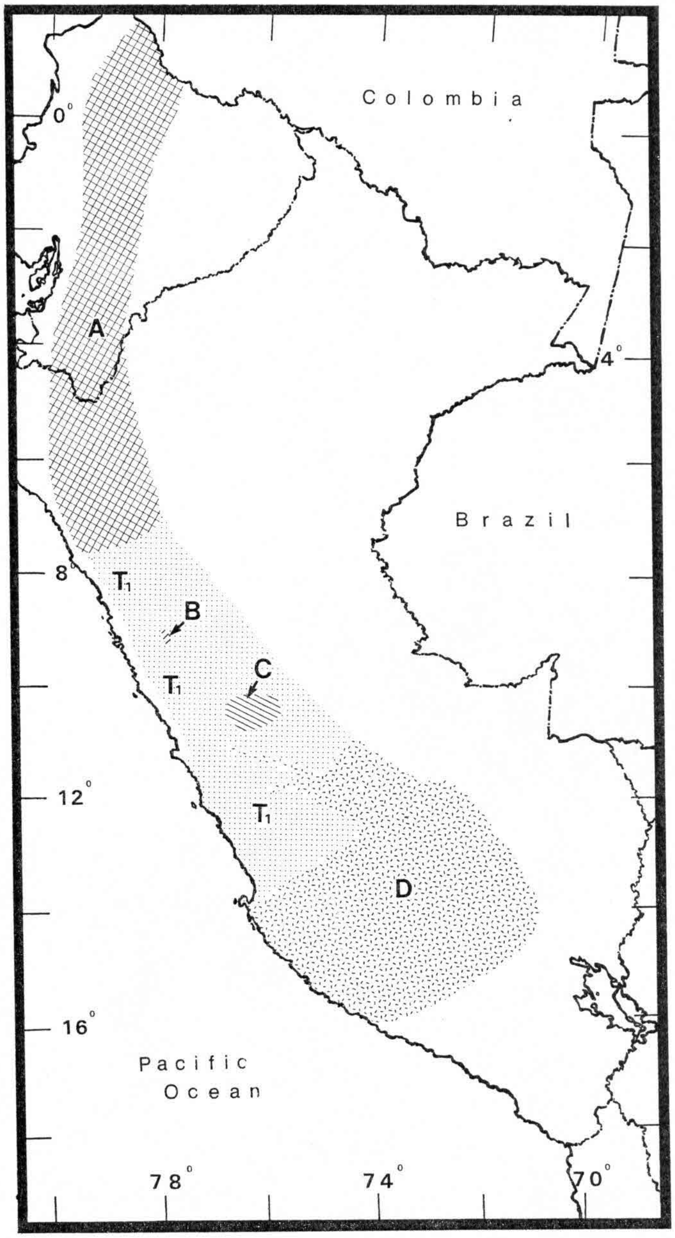


Fig. 11. General geographical pattern of areas of character state uniformity (A-D) and transition region T1 for color of scapes in both sexes of *N. peruviana.*

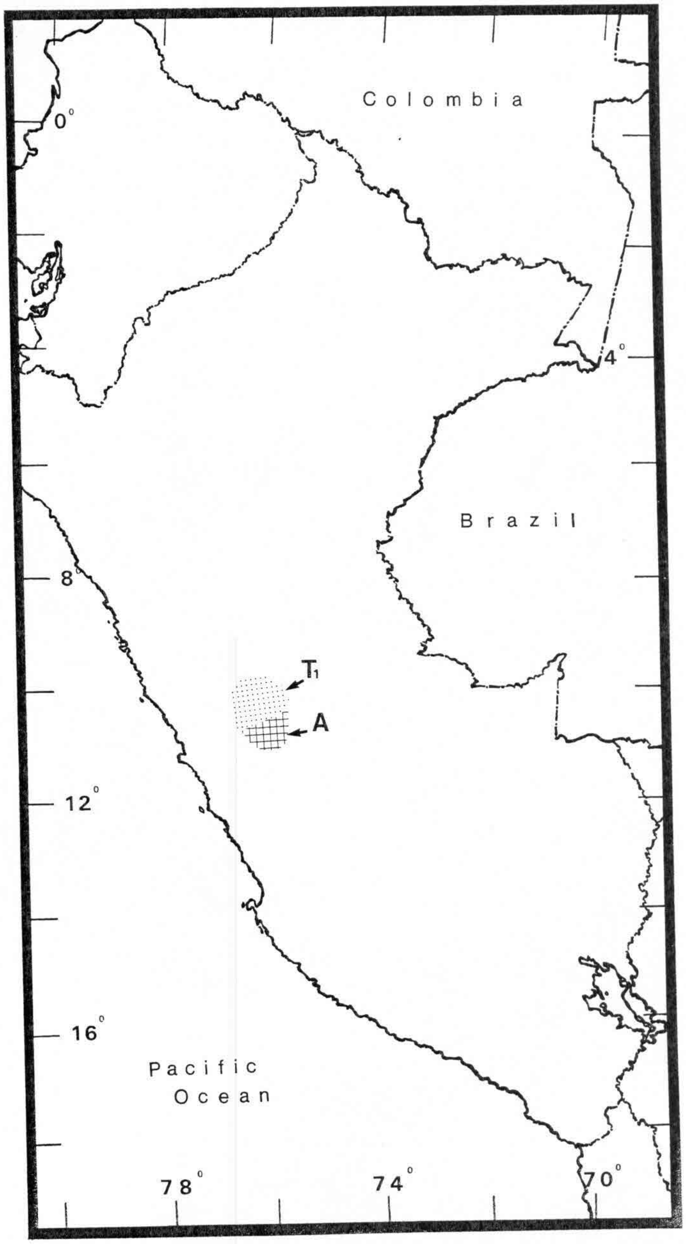


Fig. 12. General geographical pattern of area of character state uniformity (A) and transition region T1 for ocellate puncture absent between bases of elytral striae 1 and 2 in both sexes of *N. peruviana*.

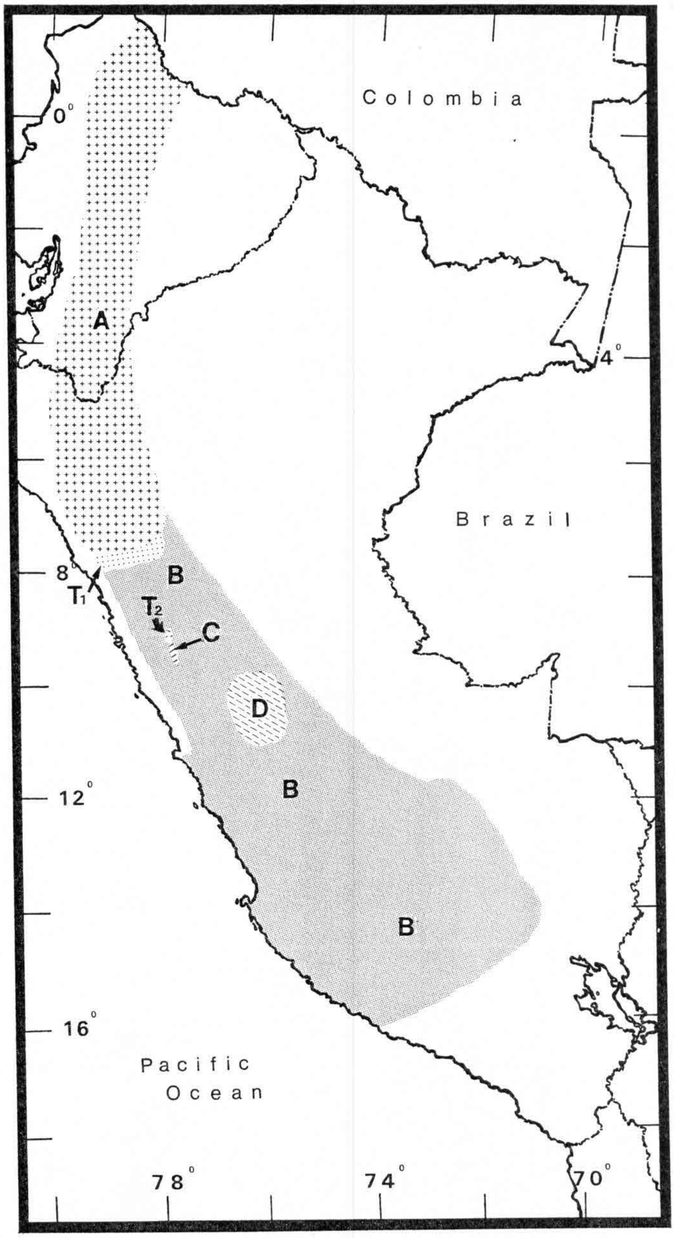


Fig. 13. General geographical pattern of areas of character state uniformity (A-D) and transition regions (T1-2) for elytral microsculpture in male *N. peruviana*.

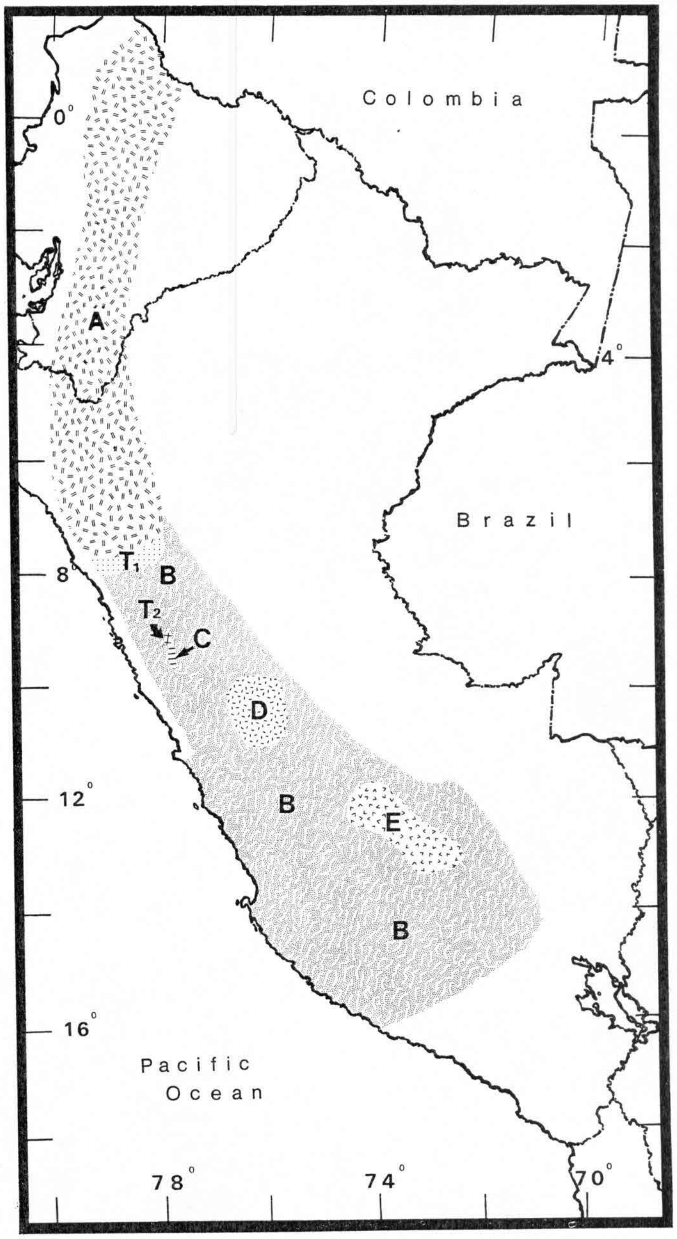


Fig. 14. General geographical pattern of areas of character state uniformity (A-E) and transition regions (T1-2) for elytral microsculpture in female *N. peruviana.*

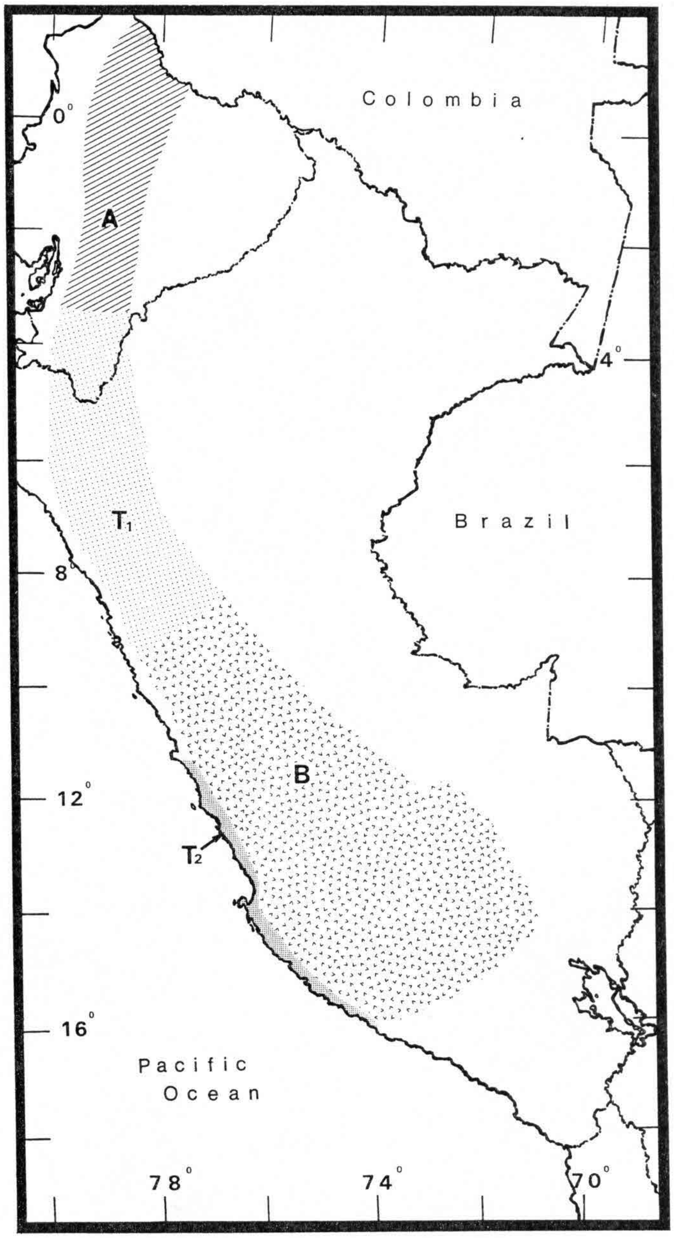


Fig. 15. General geographical pattern of areas of character state uniformity (A-B) and transition regions (T1-2) for hind wing length in both sexes of *N. peruviana*.

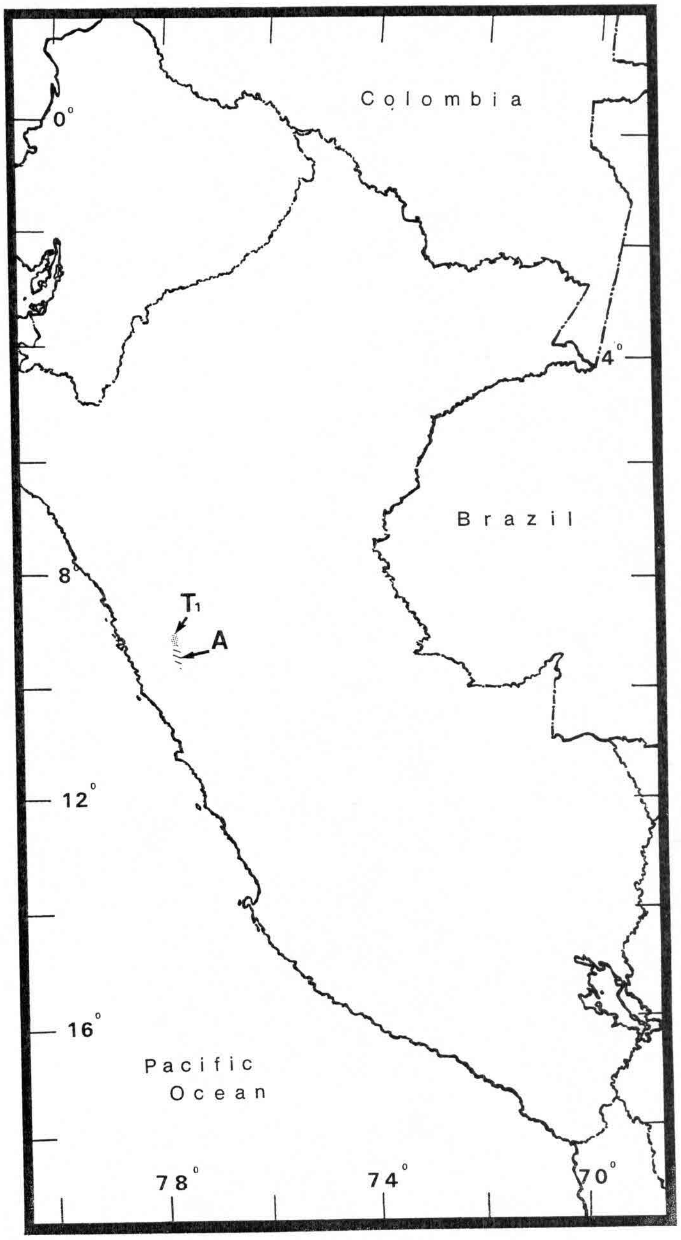


Fig. 16. General geographical pattern of area A (specimens with numerous setae on abdominal sterna) and transition region T1 for both sexes in *N. peruviana*.

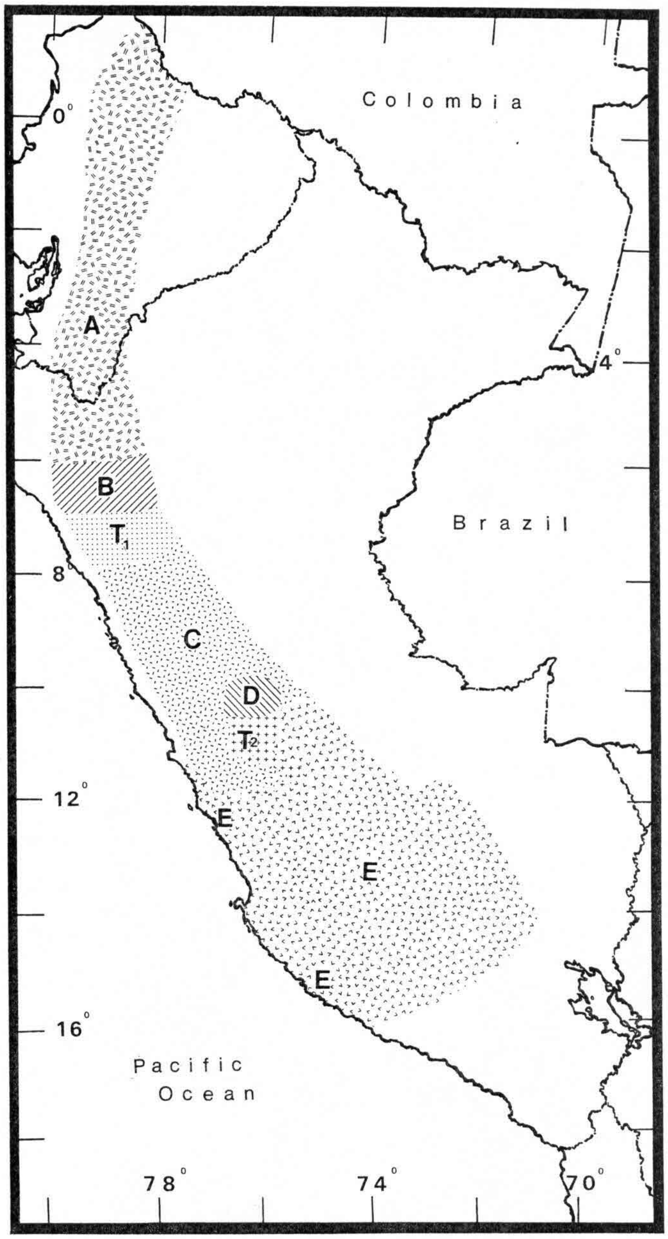


Fig. 17. General geographical pattern of areas of character state uniformity (A-E) and transition regions (T1-2) for relative length of apex of male median lobe in *N. peruviana*.

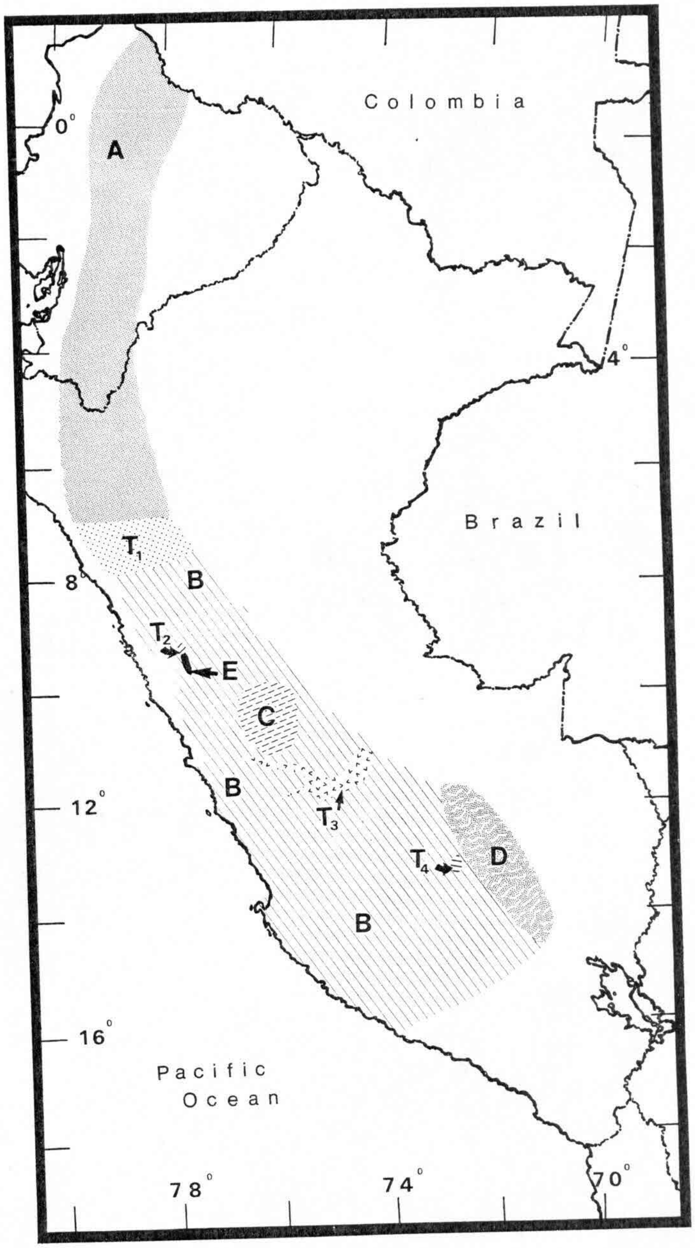


Fig. 18. General geographical pattern of areas of character state uniformity (A-D) and transition regions (T1-4) for proximal field of internal sac of male genitalia in *N. peruviana*.

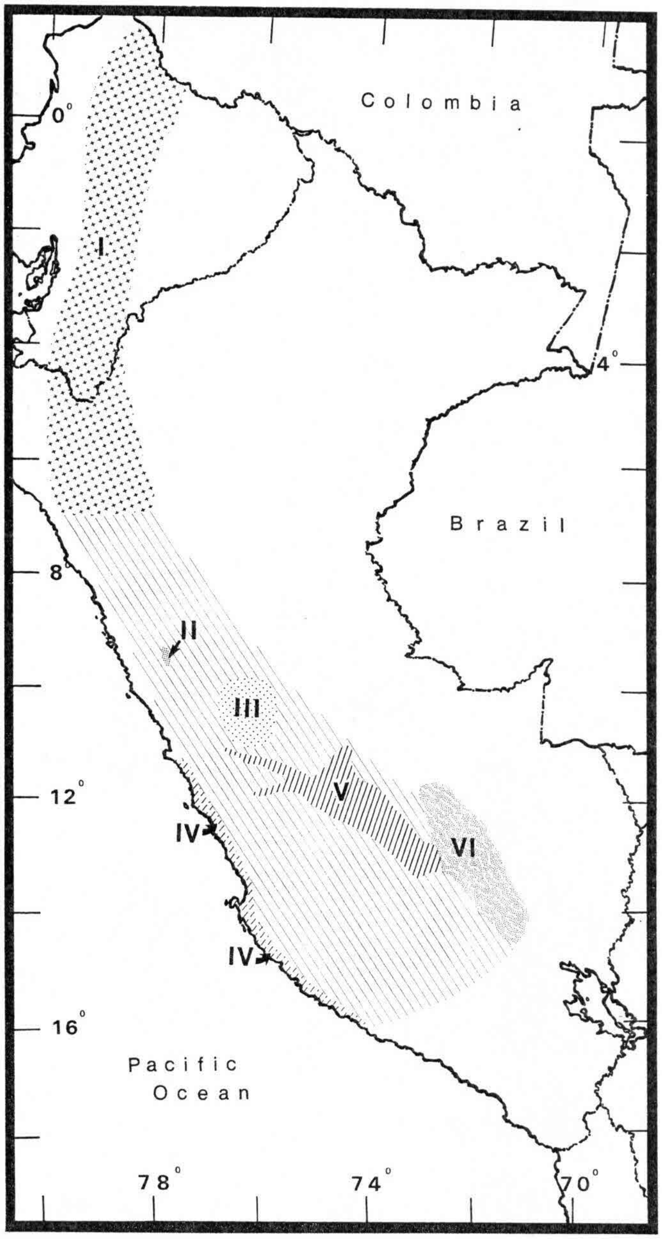


Fig. 19. The six core areas of *N. peruviana.* Slanted lines indicate approximate range of species outside these core areas.

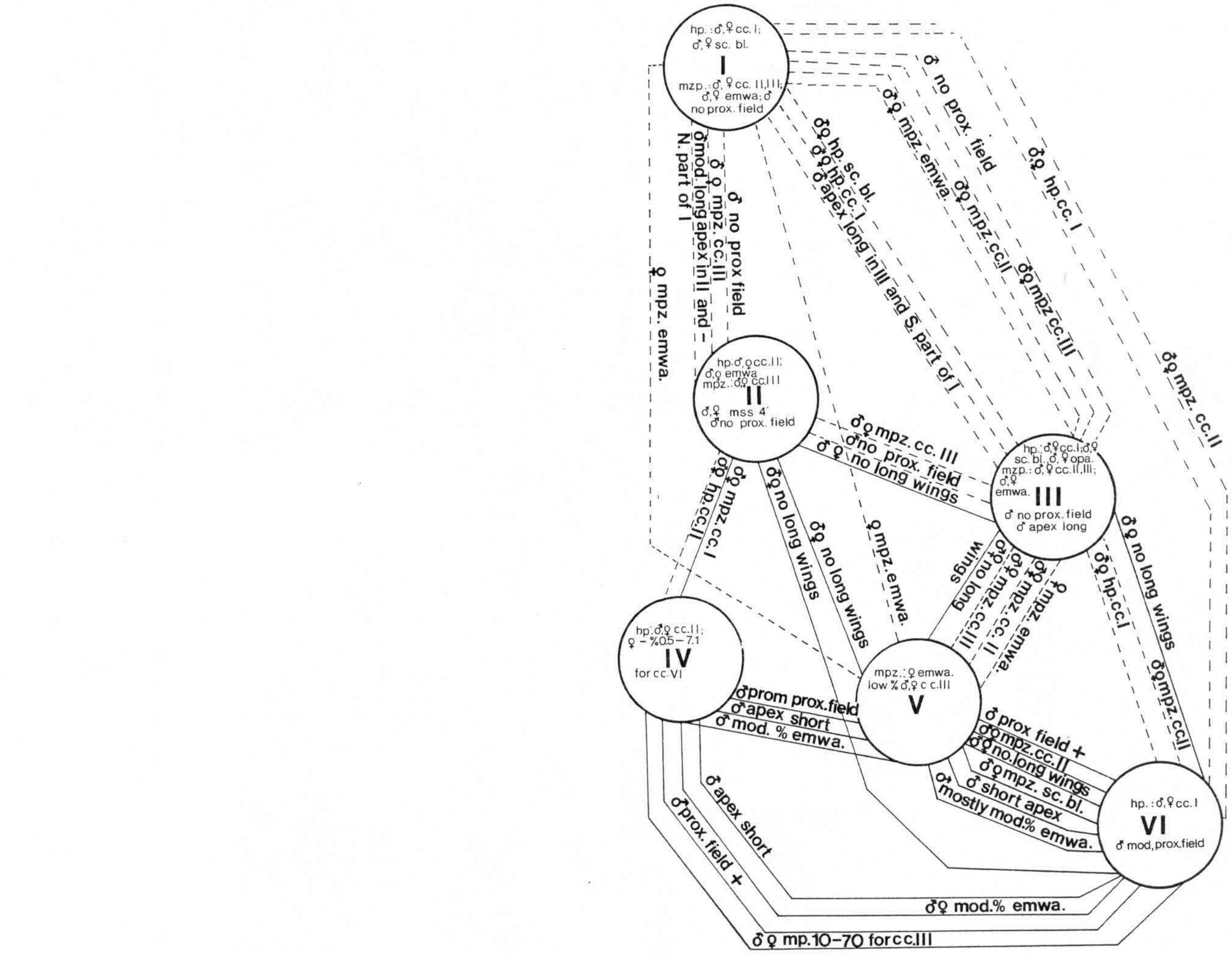


Fig. 20. Summary of analysis of six core areas. Circles represent the six core areas; the character states in each circle are those for which the corresponding core area is homogeneous and clearly delimited. Broken lines between circles denote shared character states clearly delimited for each connected core area while solid lines denote character states continuous between connected core areas. Abbreviations: apex = apex of median lobe of male genitalia, used when referring to relative length/width of such structure; cc = dorsal body color class; emwa = elytral microsculpture weak or apparently absent; hp. = high percents; mod. = moderate; mp. = most percents; mpz. = most or all percents zero; mss4. = many setae on fourth sternum of abdomen; N. = northern; opa. = ocellate punctures absent between bases of elytral striae 1 and 2; prom. = prominent; prox. field = proximal field of internal sac of median lobe of male genitalia; S. = southern; sc.bl. = scapes black in color; + = present; % = percent; ♂ = character state present in males; ♀ = character state present in females; ♂♀ = character state present in both sexes.

Fig. 21. Map illustrating topography of Andes of northwestern Peru. Slanted lines indicate areas between 2000 – 3000 m while "+" signs indicated areas above 3000 m. The letter "A" denotes Abra de Porculla while "B" indicates the pass between the Río Chotano and Río Chancay. Dissected and/or discontinuous highlands above 3000 m, referred to in text, center around the two passes. The generally low lying portion of the Andes centered around these passes is termed the "Huancabamba Depression" or "northern Peru low" by various authors.

Table 1. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Males of Population Samples of *Notiobia peruviana* Dejean.

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
1	2	100	0	0	0	0
2	4	100	0	0	0	0
3	15	100	0	0	0	0
4	1	100	0	0	0	0
5	0					
6	6	100	0	0	0	0
7	0					
8	1	100	0	0	0	0
9	1	100	0	0	0	0
10	0					
11	9	88.9	0	0	0	11.1
12	0					
13	47	93.6	0	6.4	0	0
14	38	100	0	0	0	0
15	1	100	0	0	0	0
16	2	50.0	50.0	0	0	0
17	1	100	0	0	0	0
18	115	100	0	0	0	0
19	1	100	0	0	0	0
20	3	100	0	0	0	0
21	8	87.50	12.5	0	0	0
22	27	96.3	0	0	0	3.7
23	0					
24	102	97.1	2.9	0	0	0
25	1	100	0	0	0	0
26	1	100	0	0	0	0
27	9	77.7	22.3	0	0	0
28	42	92.9	7.1	0	0	0
29	1	100	0	0	0	0
30	30	60.0	30.0	10.0	0	0
31	15	73.3	26.7	0	0	0
32	108	85.2	5.6	5.6	0	3.6
33	186	77.4	20.4	2.2	0	0
34	2	0	100	0	0	0

Table 1. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Males of Population Samples of *Notiobia peruviana* Dejean (continued).

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
35	119	11.8	83.2	0	0	5.0
36	60	83.3	11.7	1.7	0	3.3
37	1	100	0	0	0	0
38	336	63.7	0	36.3	0	0
39	0					
40	279	48.7	1.8	37.6	0	11.9
41	200	2.50	20.0	50.0	0	27.5
42	116	30.2	5.2	63.8	0	0.8
43	42	0	35.7	57.1	0	7.2
44	26	0	42.3	53.8	0	3.9
45	84	8.3	76.2	14.3	0	1.2
46	82	0	97.6	2.4	0	0
47	10	0	40.0	50.0	0	10.0
48	101	0	100	0	0	0
49	31	0	100	0	0	0
50	4	0	100	0	0	0
51	27	0	100	0	0	0
52	40	0	100	0	0	0
53	178	0	100	0	0	0
54	19	0	100	0	0	0
55	1	0	100	0	0	0
56	348	9	82.5	14.7	2.8	0
57	140	0	87.1	2.1	5.7	5.1
58	57	0	84.2	15.8	0	0
59	4	0	75.0	25.0	0	0
60	311	55.0	39.9	5.1	0	0
61	465	100	0	0	0	0
62	16	100	0	0	0	0
63	4	100	0	0	0	0
64	9	77.8	11.1	11.1	0	0
65	1	100	0	0	0	0
66	1	100	0	0	0	0
67	3	66.7	0	33.3	0	0
68	17	100	0	0	0	0

Table 1. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Males of Population Samples of *Notiobia peruviana* Dejean (concluded).

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
69	0					
70	43	97.9	2.1	0	0	0
71	14	100	0	0	0	0
72	42	100	0	0	0	0
73	621	100	0	0	0	0
74	639	3.3	46.8	48.7	0	1.2
75	33	27.3	12.1	60.6	0	0
76	10	30.0	20.0	50.0	0	0
77	12	0	0	100	0	0
78	29	0	82.8	17.2	0	0
79	99	3.0	60.6	36.4	0	0
80	0					
81	9	0	88.9	11.1	0	0
82	9	22.2	0	33.3	0	44.5
83	5	0	0	100	0	0
84	2	0	0	50.0	0	50.0
85	2	100	0	0	0	0
86	5	0	0	100	0	0
87	5	60.0	40.0	0	0	0
88	4	100	0	0	0	0
89	1	100	0	0	0	0
90	103	62.1	1.0	35.0	0	1.9
91	711	98.5	0	1.5	0	0
92	498	82.1	0.2	17.3	0	0.4
93	121	95.0	0	4.1	0	0.9
94	13	100	0	0	0	0
95	48	89.6	0	10.4	0	0

Table 2. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Females of Population Samples of *Notiobia peruviana* Dejean.

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
1	0					
2	6	100	0	0	0	0
3	36	97.2	0	0	0	2.8
4	0					
5	1	100	0	0	0	0
6	2	100	0	0	0	0
7	3	100	0	0	0	0
8	2	50.0	0	0	0	50.0
9	1	0	0	100	0	0
10	2	0	0	0	0	100
11	11	54.5	0	0	0	45.5
12	1	100	0	0	0	0
13	49	93.9	0	6.1	0	0
14	32	100	0	0	0	0
15	0					
16	2	0	0	100	0	0
17	1	100	0	0	0	0
18	130	100	0	0	0	0
19	7	57.1	42.9	0	0	0
20	7	85.7	0	0	0	14.3
21	14	78.6	21.4	0	0	0
22	49	100	0	0	0	0
23	2	100	0	0	0	0
24	117	96.6	1.7	0	0	1.7
25	0					
26	0					
27	7	100	0	0	0	0
28	39	92.3	7.7	0	0	0
29	1	100	0	0	0	0
30	16	75.0	25.0	0	0	0
31	13	69.2	23.1	7.7	0	0
32	69	73.9	15.9	2.9	0	7.3
33	191	77.5	22.0	0.5	0	0
34	2	0	100	0	0	0

Table 2. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Females of Population Samples of *Notiobia peruviana* Dejean (continued).

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
35	107	3.7	96.3	0	0	0
36	50	76.0	24.0	0	0	0
37	1	100	0	0	0	0
38	455	53.6	8.4	38.0	0	0
39	3	66.7	33.3	0	0	0
40	264	53.8	15.5	30.3	0	0.4
41	345	24.7	24.6	28.4	0	22.3
42	126	38.9	4.0	56.3	0	0.8
43	38	0	50.0	44.7	0	5.3
44	26	3.8	57.7	19.2	0	19.3
45	116	2.6	90.5	4.3	0	2.6
46	85	0	94.1	5.9	0	0
47	8	0	75.0	25.0	0	0
48	94	0	100	0	0	0
49	71	0	100	0	0	0
50	9	0	100	0	0	0
51	28	0	100	0	0	0
52	43	0	100	0	0	0
53	82	0	100	0	0	0
54	14	0	100	0	0	0
55	0					
56	393	0	80.7	13.7	5.6	0
57	200	0	93.0	2.0	1.5	3.5
58	32	0	87.5	6.3	6.2	0
59	14	0	78.6	14.3	7.1	0
60	199	53.8	41.2	4.5	0.5	0
61	351	100	0	0	0	0
62	9	100	0	0	0	0
63	5	100	0	0	0	0
64	12	91.7	0	8.3	0	0
65	0					
66	1	100	0	0	0	0
67	2	100	0	0	0	0
68	19	94.7	5.3	0	0	0

Table 2. Data About Geographical Variation of Color of the Dorsal Surface of the Body Among Females of Population Samples of *Notiobia peruviana* Dejean (concluded).

		Color Class and Percent for Each Class				
Site No.	N	Class I	Class II	Class III	Class IV	Other Classes
69	1	100	0	0	0	0
70	45	97.8	2.2	0	0	0
71	16	100	0	0	0	0
72	69	100	0	0	0	0
73	372	100	0	0	0	0
74	509	2.9	46.4	47.9	0	2.8
75	33	21.2	9.1	69.7	0	0
76	13	23.1	15.4	61.5	0	0
77	13	7.7	0	92.3	0	0
78	20	0	85.0	15.0	0	0
79	147	1.4	63.9	34.7	0	0
80	3	33.4	66.6	0	0	0
81	23	0	100	0	0	0
82	5	20.0	20.0	60.0	0	0
83	4	0	50.0	50.0	0	0
84	1	0	0	100	0	0
85	3	100	0	0	0	0
86	4	0	0	100	0	0
87	1	0	100	0	0	0
88	1	100	0	0	0	0
89	2	100	0	0	0	0
90	114	54.4	0.9	44.7	0	0
91	861	98.6	0	1.4	0	0
92	475	85.9	0.2	13.9	0	0
93	121	93.4	0	6.6	0	0
94	11	100	0	0	0	0
95	44	79.5	0	20.5	0	0

Table 3. Data About Geographical Variation of Percents of Specimens with Scapes Black Among Population Samples of *Notiobia peruviana* Dejean.

	males		females	
Site No.	N	%	N	%
1	2	100	0	
2	4	100	6	100
3	15	100	36	100
4	1	100	0	
5	0		1	100
6	6	100	2	100
7	0		3	100
8	1	100	2	100
9	1	100	1	100
10	0		2	100
11	9	100	11	100
12	0		1	100
13	47	100	49	100
14	38	100	32	100
15	1	100	0	
16	2	100	2	100
17	1	100	1	100
18	115	100	130	100
19	1	100	7	100
20	3	100	7	100
21	8	100	14	100
22	27	100	49	98.0
23	0		2	100
24	102	97.1	117	98.3
25	1	100	0	
26	1	0	0	
27	9	100	7	100
28	42	100	39	100
29	1	100	1	100
30	30	100	16	100
31	15	100	13	100
32	108	100	69	100
33	186	100	191	100
34	2	0	2	0

Table 3. Data About Geographical Variation of Percents of Specimens with Scapes Black Among Population Samples of *Notiobia peruviana* Dejean (continued).

	males		females	
Site No.	N	%	N	%
35	119	100	107	100
36	60	100	50	100
37	1	0	1	0
38	336	4.5	455	1.3
39	0		3	100
40	279	0.4	264	1.9
41	200	4.0	345	0.6
42	116	6.0	126	7.9
43	42	0	38	2.6
44	26	0	26	3.8
45	84	0	116	0
46	82	0	85	0
47	10	0	8	0
48	101	4.0	94	0
49	31	3.2	71	0
50	4	0	9	0
51	27	3.7	28	3.6
52	40	0	43	0
53	178	2.8	82	3.7
54	19	0	14	0
55	1	100	0	
56	348	6.3	393	1.8
57	140	9.3	200	4.5
58	57	24.6	32	2.8
59	4	0	14	0
60	311	2.6	199	1.0
61	465	6.9	351	3.1
62	16	12.5	9	0
63	4	0	5	0
64	9	11.1	12	25.0
65	1	100	0	
66	1	100	1	100
67	3	100	2	100
68	17	88.2	19	84.2

Table 3. Data About Geographical Variation of Percents of Specimens with Scapes Black Among Population Samples of *Notiobia peruviana* Dejean (concluded).

	males		females	
Site No.	N	%	N	%
69	0		1	0
70	43	23.3	45	31.1
71	14	0	16	0
72	42	0	69	0
73	621	0	372	0
74	639	0	509	0
75	33	0	33	0
76	10	0	13	0
77	12	0	13	0
78	29	0	20	0
79	99	0	147	0
80	0	0	3	0
81	9	0	23	0
82	9	0	5	0
83	5	0	4	0
84	2	0	1	0
85	2	0	3	0
86	5	0	4	0
87	5	0	1	0
88	4	0	1	0
89	1	0	2	0
90	103	0	114	0
91	711	0	861	0
92	498	0	475	0
93	121	0	121	0
94	13	0	11	0
95	48	0	44	0

Table 4. Data About Geographical Variation of Percents of Specimens Lacking Ocellate Puncture Between Bases of Elytral Striae 1 & 2 Among Population Samples of *Notiobia peruviana* Dejean.

Site No.	N	Left Elytron %	Right Elytron %	Both Elytra %
1-63 & 74-95		less than 0.1	less than 0.1	less than 0.1
64	9♂, 12♀	0♂, ♀	0♂, 8.3♀	0♂, ♀
65	1♂, 0♀	0♂	0♂	0♂
66	1♂, 1♀	0♂, ♀	0♂, ♀	0♂, ♀
67	3♂, 2♀	0♂, ♀	33.0♂, 50.0♀	0♂, ♀
68	17♂, 19♀	17.6♂, 0♀	11.8♂, 5.2♀	0♂, ♀
69	0♂, 1♀	0♀	0♀	0♀
70	43♂, 45♀	16.2♂, 4.4♀	9.3♂, 6.7♀	16.2♂, 22.2♀
71-73	677♂, 457♀	0♂, ♀	0♂, ♀	100♂, ♀

Table 5. Data About Geographical Variation of Percents of Specimens with Elytral Microsculpture Reduced Among Population Samples of *Notiobia peruviana* Dejean

	males		females	
Site No.	N	%	N	%
1	2	0	0	
2	4	0	6	0
3	15	0	36	0
4	1	0	0	
5	0		1	0
6	6	0	2	0
7	0		3	0
8	1	0	2	0
9	1	0	1	0
10	0		2	0
11	9	0	11	0
12	0		1	0
13	47	0	49	0
14	38	0	32	0
15	1	0	0	

Table 5. Data About Geographical Variation of Percents of Specimens with Elytral Microsculpture Reduced Among Population Samples of *Notiobia peruviana* Dejean (continued).

	males		females	
Site No.	N	%	N	%
16	2	0	2	0
17	1	0	1	0
18	115	0	130	0
19	1	0	7	0
20	3	0	7	0
21	8	0	14	0
22	27	0	49	0
23	0		2	0
24	102	0	117	0
25	1	0	0	
26	1	100	0	
27	9	0	7	0
28	42	7.1	39	0
29	1	0	1	0
30	30	0	16	0
31	15	0	13	0
32	108	0	69	0
33	186	0	191	0
34	2	0	2	0
35	119	0	107	0
36	60	0	50	0
37	1	0	1	0
38	336	96.1	455	55.6
39	0		3	0
40	279	94.4	264	27.7
41	200	25.5	345	0.9
42	116	67.2	126	16.7
43	42	9.5	38	0
44	26	11.5	26	0
45	84	90.5	116	11.2
46	82	93.9	85	5.9
47	10	50.0	8	12.5
48	101	100	94	83.0

Table 5. Data About Geographical Variation of Percents of Specimens with Elytral Microsculpture Reduced Among Population Samples of *Notiobia peruviana* Dejean (continued).

	males		females	
Site No.	N	%	N	%
49	31	100	71	100
50	4	100	9	100
51	27	100	28	100
52	40	100	43	100
53	178	100	82	100
54	19	100	14	100
55	1	100	0	
56	348	39.1	393	10.4
57	140	22.1	200	4.0
58	57	8.8	32	3.1
59	4	75.0	14	7.1
60	311	0	199	0
61	465	0	351	0
62	16	0	9	0
63	4	0	5	0
64	9	0	12	0
65	1	0	0	
66	1	0	1	0
67	3	0	2	0
68	17	0	19	0
69	0		1	0
70	43	0	45	0
71	14	0	16	0
72	42	0	69	0
73	621	0	372	0
74	639	76.4	509	31.2
75	33	84.9	33	42.4
76	10	70.0	13	38.5
77	12	100	13	53.8
78	29	17.2	20	0
79	99	48.5	147	10.9
80	0		3	0
81	9	77.8	23	4.3

Table 5. Data About Geographical Variation of Percents of Specimens with Elytral Microsculpture Reduced Among Population Samples of *Notiobia peruviana* Dejean (concluded).

	males		females	
Site No.	N	%	N	%
82	9	88.9	5	60.0
83	5	20.0	4	0
84	2	50.0	1	0
85	2	100	3	33.3
86	5	100	4	0
87	5	20.0	1	0
88	4	0	1	0
89	1	100	2	0
90	103	68.0	114	21.1
91	711	60.8	861	14.2
92	498	42.7	475	48.4
93	121	78.5	121	33.1
94	13	53.9	11	9.1
95	48	91.7	44	29.6

Table 6. Data About Geographical Variation of Percents of Specimens with Hind Wings Long Among Population Samples of *Notiobia peruviana* Dejean.

	males		females	
Site No.	N	%	N	%
1	2	100	0	100
2	4	100	6	100
3	15	100	36	100
4	1	100	0	
5	0		1	100
6	6	100	2	100
7	0		3	100
8	1	100	2	100
9	1	100	1	100
10	0		2	100
11	9	100	11	100
12	0		1	0
13	47	100	49	100

Table 6. Data About Geographical Variation of Percents of Specimens with Hind Wings Long Among Population Samples of *Notiobia peruviana* Dejean (continued).

	males		females	
Site No.	N	%	N	%
14	38	97.4	32	96.9
15	1	100	0	
16	2	100	2	100
17	1	100	1	100
18	115	59.1	130	58.5
19	1	100	7	100
20	3	0	7	0
21	8	0	14	0
22	27	96.3	49	93.9
23	0		2	0
24	102	100	117	100
25	1	100	0	
26	1	0	0	
27	9	0	7	0
28	42	0	39	0
29	1	0	1	0
30	30	0	16	0
31	15	13.3	13	23.1
32	108	5.6	69	5.7
33	186	0	191	0
34	2	0	2	0
35	119	0	107	0
36	60	0	50	0
37	1	0	1	0
38	336	0	455	0
39	0	0	3	100
40	279	4.3	264	6.8
41	200	24.5	345	22.3
42	116	0	126	0
43	42	0	38	0
44	26	0	26	0
45	84	0	116	0
46	82	0	85	0
47	10	0	8	0

Table 6. Data About Geographical Variation of Percents of Specimens with Hind Wings Long Among Population Samples of *Notiobia peruviana* Dejean (continued).

	males		females	
Site No.	N	%	N	%
48	101	0	94	0
49	31	0	71	0
50	4	0	9	0
51	27	0	28	0
52	40	0	43	0
53	178	0	82	0
54	19	0	14	0
55	1	0	0	0
56	348	0	393	0
57	140	5.0	200	2.5
58	57	0	32	0
59	4	75.0	14	85.7
60	311	0	199	0
61	465	0	351	0
62	16	0	9	0
63	4	0	5	0
64	9	0	12	0
65	1	0	0	0
66	1	0	1	0
67	3	0	2	0
68	17	0	19	0
69	0	0	1	0
70	43	0	45	0
71	14	0	16	0
72	42	0	69	0
73	621	0	372	0
74	639	0	509	0
75	33	0	33	0
76	10	0	13	0
77	12	0	13	0
78	29	0	20	0
79	99	0	147	0
80	0	0	3	0
81	9	0	23	0

Table 6. Data About Geographical Variation of Percents of Specimens with Hind Wings Long Among Population Samples of *Notiobia peruviana* Dejean (concluded).

	males		females	
Site No.	N	%	N	%
82	9	0	5	0
83	5	0	4	0
84	2	0	1	0
85	2	0	3	0
86	5	0	4	0
87	5	0	1	0
88	4	0	1	0
89	1	0	2	0
90	103	0	114	0
91	711	0	861	0
92	498	0	475	0
93	121	0	121	0
94	13	0	11	0
95	48	0	44	0

Table 7. Data About Geographical Variation of Numbers of Setae on Fourth Abdominal Sternum Among Population Samples of *Notiobia peruviana* from the Santa Valley, Peru.

	Males			Females		
Site	N	Range	Mean & Standard Deviation	N	Range	Mean & Standard Deviation
43	42	0-21	6.61±5.48	38	1-23	6.67±6.05
44	26	0-14	5.75±4.42	26	1-23	8.00±4.99
45	84	0-33	6.92±5.26	116	0-42	9.18±6.68
46	82	1-24	7.78±4.77	85	0-32	8.13±6.58
47	10	4-44	19.0 ±14.17	8	9-35	19.43±10.88
48	101	19-142	57.05±15.93	94	14-102	63.44±22.46
49	31	11-75	50.94±12.37	71	11-102	49.48±21.74
50	4	51-93	69.00±20.90	9	12-86	51.22±23.74
51	27	12-72	35.22±15.98	28	12-73	40.36±15.79
52	40	17-78	44.34±17.81	43	28-106	54.19±18.07
53	178	3-88	39.13±18.17	82	9-64	31.78±12.77
54	19	10-94	47.22±26.44	14	8-72	31.86±19.05
55	1	33				

Table 8. Data About Geographical Variation of Values for the Ratio of Length of Apex of Male Median Lobe/Maximum Width of Apex Among Population Samples of *Notiobia peruviana* Dejean.

Site	N	Mean & Standard Deviation	Range
1	2	0.813 ± 0	0
2	2	0.640 ± 0.020	0.620 – 0.660
3	7	0.710 ± 0.040	0.655 – 0.769
4	1		0.741
5	0		
6	5	0.690 ± 0.020	0.667 – 0.714
7	0		
8	1		0.767
9	1		0.750
10	0		
11	8	0.752 ± 0.073	0.666 – 0.857
12	0		
13	41	0.778 ± 0.067	0.629 – 0.889
14	35	0.710 ± 0.060	0.556 – 0.875
15	1		0.867
16	2	0.568 ± 0.060	0.526 – 0.611
17	1		0.733
18	111	0.733 ± 0.056	0.632 – 0.882
19	1		0.892
20	1		1.000
21	4	0.913 ± 0.192	0.714 – 1.176
22	19	1.192 ± 0.073	1.050 – 1.333
23	0		
24	73	1.180 ± 0.099	1.00 – 1.667
25	1		1.560
26	1		1.368
27	6	1.151 ± 0.077	1.053 – 1.235
28	36	1.299 ± 0.092	1.134 – 1.474
29	0		
30	23	1.141 ± 0.061	1.053 – 1.250
31	12	1.072 ± 0.050	1.000 – 1.176
32	84	1.077 ± 0.079	0.950 – 1.188
33	166	1.114 ± 0.087	0.894 – 1.375
34	2	0.715 ± 0.046	0.684 – 0.750

Table 8. Data About Geographical Variation of Values for the Ratio of Length of Apex of Male Median Lobe/Maximum Width of Apex Among Population Samples of *Notiobia peruviana* Dejean (continued).

Site	N	Mean & Standard Deviation	Range
35	43	0.976 ± 0.081	0.834 – 1.267
36	36	0.951 ± 0.077	0.842 – 1.134
37	0		
38	232	0.837 ± 0.077	0.667 – 1.077
39	0		
40	155	0.798 ± 0.097	0.526 – 1.333
41	154	0.652 ± 0.067	0.500 – 0.867
42	83	0.735 ± 0.082	0.526 – 0.923
43	32	0.753 ± 0.084	0.615 – 0.933
44	19	0.776 ± 0.081	0.666 – 0.933
45	71	0.757 ± 0.085	0.625 – 0.933
46	79	0.718 ± 0.073	0.466 – 0.875
47	5	0.748 ± 0.037	0.705 – 0.764
48	92	0.800 ± 0.025	0.533 – 1.00
49	24	0.629 ± 0.058	0.500 – 0.750
50	4	0.636 ± 0.037	0.588 – 0.666
51	23	0.826 ± 0.073	0.705 – 0.941
52	37	0.812 ± 0.077	0.666 – 0.937
53	156	0.728 ± 0.065	0.625 – 0.933
54	14	0.808 ± 0.074	0.625 – 0.933
55	1		0.640
56	286	0.591 ± 0.052	0.466 – 0.750
57	128	0.582 ± 0.065	0.429 – 0.786
58	53	0.563 ± 0.041	0.500 – 0.647
59	4	0.551 ± 0.040	0.500 – 0.600
60	300	0.939 ± 0.064	0.739 – 1.117
61	416	0.946 ± 0.067	0.750 – 1.166
62	15	0.949 ± 0.077	0.833 – 1.067
63	4	0.918 ± 0.119	0.778 – 1.067
64	9	0.928 ± 0.116	0.778 – 1.188
65	1		0.882
66	1		0.778
67	2	0.935 ± 0.003	0.933 – 0.938
68	16	0.878 ± 0.066	0.770 – 1.00

Table 8. Data About Geographical Variation of Values for the Ratio of Length of Apex of Male Median Lobe/Maximum Width of Apex Among Population Samples of *Notiobia peruviana* Dejean (concluded).

Site	N	Mean & Standard Deviation	Range
69	0		
70	40	0.852 ± 0.057	0.764 – 0.941
71	14	0.682 ± 0.100	0.500 – 0.786
72	35	0.682 ± 0.071	0.500 – 0.769
73	603	0.656 ± 0.058	0.444 – 1.100
74	606	0.540 ± 0.068	0.333 – 0.769
75	30	0.529 ± 0.051	0.460 – 0.625
76	6	0.760 ± 0.010	0.580 – 0.850
77	12	0.556 ± 0.082	0.400 – 0.667
78	10	0.642 ± 0.064	0.533 – 0.714
79	97	0.539 ± 0.070	0.353 – 0.692
80	0		
81	8	0.423 ± 0.555	0.333 – 0.500
82	7	0.467 ± 0.077	0.375 – 0.625
83	1		0.500
84	2	0.470 ± 0.083	0.411 – 0.529
85	2	0.594 ± 0.084	0.588 – 0.600
86	4	0.546 ± 0.072	0.471 – 0.625
87	3	0.579 ± 0.083	0.500 – 0.666
88	3	0.673 ± 0.216	0.429 – 0.842
89	1		0.529
90	89	0.511 ± 0.063	0.375 – 0.706
91	687	0.470 ± 0.067	0.333 – 1.200
92	292	0.539 ± 0.066	0.400 – 0.642
93	115	0.484 ± 0.063	0.333 – 0.647
94	9	0.533 ± 0.047	0.500 – 0.571
95	37	0.586 ± 0.064	0.500 – 0.727

Table 9. Data About Geographical Variation of Proximal Field of the Internal Sac Among Males of Population Samples of *Notiobia peruviana* Dejean.
(X = given state present in one or more males from a site.) (No males from sites 5, 7, 10, 12, 23, 39, 69, 80.)

Sites	Field Absent	Weak Field	Moderate Field	Prominent Field
1-4	x			
6	x			
8–9	x			
11	x			
13–22	x			
24	x			x
25–31	x			
32	x	x		
33–38	x			
40	x	x	x	
41			x	
42		x	x	
43–46				x
47	x	x	x	
48	x	x		
49–55	x			
56–59				x
60–68	x			
70–73	x			
74	x	x	x	x
75				x
76	x	x		
77			x	
78–79				x
81–86				x
87			x	x
88-95			x	

Table 10. Summary of Distribution of Character States of *Notiobia peruviana* Dejean in the Six Core Areas.

Character	core area I	core area II	core area III	core area IV	core area V	core area VI
% cc. I, ♂,♀	100 or ms. > 80	0	100 or ms. > 90	0	heter.	> 50
% cc. II, ♂, ♀	m. 0	100	m. 0, all < 11.2	75 – 93	heter.	0 or ms. < 1
% cc. III, ♂, ♀	m. 0	0	m. 0	2 – 25	m. 0	m. > 1 but < 50
% cc. IV, ♂	0	0	0	heter.	0	0
% cc. IV, ♀	0	0	0 except at site 60	0.5 – 7.1	0	0
% sc. bl. ♂, ♀	100	< 5	> 80	1.8 – 24.6	0	0
% opa., ♂, ♀	0	0	100	0	0	0
% emwa., ♂	0	100	0	8.8–75	0–100	> 50 at all but 1 site
% emwa., ♀	0	100	0	3.1–10.4	0 at all but 1 site	9.1–48.4
% hwl., ♂, ♀	100 in N. & tr. in S	0	0	heter.	0	0
#s4as., ♂, ♀	< 6	ms. 40 or more	< 6	< 6	< 6	< 6
means of apex.	in all but S. m. > 0.6 but all < 0.82; in S. > 0.90	0.629 – 0.826	> 0.90	0.55–0.591	< 0.60	< 0.60
prox. fl.	—	—	—	+ & prom.	+ & ms. prom.	+ & mod.

Key to Abbreviations (Table 10)

apex = relative length/width of apex of median lobe of male genitalia
cc. = dorsal body color class
emwa. = elytral microsculpture weak or absent
heter. = heterogeneous
hwl. = hind wings long
mod. = moderate
m. = most
ms. = mostly
N. = north
opa. = ocellate punctures absent between bases of elytral striae 1 and 2
prom. = prominent
prox. fl. = proximal field of internal sac of median lobe of male genitalia
S. = south
sc.bl. = scapes black in color
tr. = transitional values
+ = present
− = absent
> = greater than
< = less than
% = percent
#s4as. = number of setae on fourth sternum of abdomen
♂ = character state for males
♀ = character state for females
♂, ♀ = character state for both sexes

Information for Authors

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