Reconstructed Phylogeny and Zoogeography of
the genera and subgenera of the Selenophori Group
(Insecta: Coleoptera: Carabidae: Harpalini: Harpalina)

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Abstract

This paper is the second in a series on the classification, reconstructed phylogeny and zoogeography of the supra-specific taxa of the subtribe Harpalina (Carabidae: Harpalini). It discusses the reconstructed phylogeny and zoogeography of the Selenophori group.

Figures 1-3 present a proposed phylogeny for the group, reconstructed according to generally accepted cladistic principles.

Analysis of the contemporary zoogeography of the group shows that most taxa are adapted to tropical or subtropical climates. Distributions of selenophorines agree with the six faunal regions of Sclater (1858) and Wallace (1876). The Neotropical, Ethiopian and Oriental Regions are centers of taxonomic diversity for both supra-specific taxa and species. The Oriental and Neotropical Regions have the most diverse faunas on islands. Distributions of selenophorines suggests that the adults of some species are moderately vagile.

Past changes in climates and in land configurations probably produced great variations in environmental selection pressures on selenophorines. The overall geographical range of the group has probably been greatly reduced as climates cooled. Selenophorines probably originated in the Late Cretaceous on the combined continent of Africa and South America. The opening of the Atlantic Ocean apparently split the *Parophonus* branch, today found in both the New and Old World. The dispersal of some selenophorines from the Ethiopian into the Oriental Region may have been via rafting on India as it moved from Africa to union with Asia. The nearly total submergence of the Indo-Australian Archipelago in the Miocene means that land has been available for colonization comparatively recently, suggesting that the selenophorines there are more recently evolved than those on the Asian mainland. Development of the fauna of the Indo-Australian Archipelago probably resulted from dispersals across limited water gaps, dispersals across extensive land bridges from the Asian mainland to Australia during Pleistocene glaciations, and repeated episodes of vicariance caused by Pleistocene sea level changes. Lack of suitable tropical habitats and lack of time for dispersal probably prevented selenophorines from extensively colonizing Australia.

Evolution of selenophorines in the New World probably resulted from vicariance due to extensive changes and shifts in climates and habitats in South America from approximately the Miocene onward. The ancestors of four genera may have evolved adaptations for burrowing in response to widespread dry habitats during the Miocene. Ancestors of supra-specific groups apparently twice moved northward across water gaps between North America and South America before the Pliocene establishment of the Middle American land bridge.

A test of the hypothesis for the historical zoogeography of selenophorines via Popper's criteria fails to falsify it.

Key Terms

Carabidae, climatic adaptations, Coleoptera, continental drift, dispersal, evolution, Harpalina, Harpalini, Insecta, reconstructed phylogeny, Selenophori group, selenophorines, vicariance, zoogeographic regions, zoogeography.

Introduction

This paper is the second in a projected series on the classification, reconstructed phylogeny, and zoogeography of the supra-specific taxa of the subtribe Harpalina (tribe Harpalini). It treats the reconstructed phylogeny and zoogeography of the 25 genera and subgenera of the Selenophori group. Classification of the selenophorines is covered in Noonan (1985), the first paper in the forthcoming series. Morphological terms are as discussed in Noonan (1985). Methods of cladistic analysis are those described by Wiley (1981).

The Selenophori group is part of the tribe Harpalini, a tribe of beetles with approximately 238 genera and subgenera and 2,000 species. The tribe occurs on all continents except Antarctica and is found on many islands. Adults of harpalines are abundant in nature and are excellent organisms for testing hypotheses about evolution and zoogeography (Noonan, 1979). Although many groups of harpalines are widespread, most studies of their classification, phylogeny and zoogeography have been only regional in scope. The present paper treats all of the genera and subgenera of the Selenophori group. My hope is that this worldwide treatment of supraspecific categories will be of heuristic interest in itself and also will provide an essential framework for organizing work at the specific and infraspecific level.

Character States in the Postulated Ancestor of Selenophorines

Comparisons within Carabidae suggest that character states of the ancestor of selenophorines included: (1) body form not excessively narrow, stout, large or small; (2) glabrous or nearly glabrous dorsum; (3) mandibles normal, not elongate or projected far beyond apex of labrum; (4) glabrous paraglossae; (5) ligular sclerite with two distal ventral setae and lacking dorsal setae; and (6) clypeal apex not deeply emarginate medially.

These six character states occur within many subgroups of Harpalini and within many other tribes of the family Carabidae. The assumption is that it is most parsimonious to assume that these six states arose in the ancestor of Carabidae rather than repeatedly in many different groups of Carabidae. Current data about the phylogeny of the tribes of Carabidae do not permit specifying the sister group of the tribe Harpalini. It therefore is not practical to use the out-group method of analysis in its most rigorous expression.

The ancestor of selenophorines probably had a short stout peg-like seta (Fig. 34 in Noonan, 1985) on the venter of stylomere 2 of the ovipositor. Many species of selenophorines in the Old World and (Habu, 1973) many species of the subtribe Stenolophina (tribe Harpalini) in at least Japan (not surveyed elsewhere) have a short stout peg-like seta on the venter of stylomere 2 of the ovipositor. Females of some species of the subtribe Anisodactylina (tribe Harpalini) have a vestigial seta in the normal position of the peg-like one. The peg-like setae in some Stenolophina and selenophorines appear to be homologous character states; the vestigial setae in some anisodactylines may be a modification of this feature. Thus, the hypothetical ancestor of the tribe Harpalini probably had such a peg-like seta, and this seta, or modifications of it, shows up in various taxa of the subtribes Harpalina, Stenolophina and Anisodactylina.

Polarity of Character States Used to Reconstruct the Phylogeny

This section discusses characters and polarity of such used in reconstructing phylogenies shown in figures 1, 2 and 3. Letters correspond to those used to identify character states in these figures. Apomorphic and plesiomorphic states are denoted by upper and lower case letters respectively. Double letters indicate different aspects of plesiomorphic or apomorphic states which are not part of a homologous transformation series; letters with a superscript """" mark denote states forming part of a homologous transformation series.

The sister groups of tribe Harpalini, subtribe Harpalina, and the Selenophori group are not known. It thus is not possible to determine polarity of character states by use of the out-group method in its most rigorous expression. When a worker is faced with lack of data about sister groups of a taxon being studied, he has two basic choices: (1) declaring that it is impractical to reconstruct a phylogeny of the group being studied because of the difficulty in determining the polarity of character states; or (2) providing a reconstructed phylogeny based on the available data. The sister groups of most tribes and subtribes of Carabidae are not known. These groups will not be known until workers revise the genera and subgenera of these taxa. To be meaningful, such revisions should be based on reconstructed phylogenies as can best be postulated on the basis of available data. If workers selected the first choice listed above, there never would be cladistic based revisions of the genera and subgenera of tribes. This would mean that the sister groups of tribes and subtribes would never be elucidated. I have elected the second choice.

Since the sister group of Selenophori is not known, I have adopted the operating hypothesis that character states widespread among other Carabidae and/or other harpalines are plesiomorphic for selenophorines. It is more parsimonious to assume that the widespread distribution of such states is due to plesiomorphy rather than to the apomorphic convergent evolution of the states in many different groups. I am aware of the possible dangers (Watrous and Wheeler, 1981) of such an approach. Once sister group relationships are known, the postulated character states can be tested via methods such as out-group analysis.

Polarities are determined by comparisons within the family Carabidae for states: a, A; b, B; c; E, EE; f, F; h, H; j, J; k, K; n, N; r, R; s, S; t, T; v, V; w, W. Determination of polarities is via comparisons in tribe Harpalini for states: C, CC; d, D; g, G; m, M, M'; o, O; p, P; q, Q; u, U.

See below for description of all character states and for notes on states not determined by above comparisons.

Body form. (states a, A).

a. Body not excessively wide or narrow. *A.* Body narrow, subcylindrical to cylindrical in form.

Pubescence, Punctuation and Setation. (states b, B, B', B", c, C, CC, d, D, E, EE, f, F, g, G).

b. Dorsum generally glabrous. *B.* Dorsum with at least all of elytra densely pubescent. *B'.* Elytra with dense punctures, pubescence absent from such punctures on elytral disc in most or all species of a lineage. *B".* Most of the elytral dorsal pubescence and punctuation secondarily lost. On the basis of out-group comparisons within the selenophorines the state B' is considered for the *Siopelus* stock to be a secondary loss of the setae present in each puncture of the stock's ancestor. Loss of setae from the punctures appears, presumably by convergence, in some species of three other

lineages and seems to be part of an evolutionary trend toward secondary loss of the elytral pubescence and punctuation. Among taxa outside this stock, males of six species of *Parophonus* and of *Athrostictus dispar* have apparently secondarily lost such setae from punctures on the inner elytral intervals but retained the dense punctures; females have dense elytral pubescence. All elytral intervals of *Kareya erebia* have dense punctures each with a seta; in other species of this genus the inner elytral intervals all have dense prominent punctures, but many or all of these punctures lack setae. Loss of setae and punctures (B") from the dorsum of the elytra of New World taxa other than *Athrostictus* and *Neoaulacoryssus* is similarly presumed to be a secondary loss. Assumption that the ancestor of these latter taxa had dorsal pubescence on the elytra is supported by: presence of pubescence on outer elytral intervals in some species of *Selenophorus*; non-setigerous punctures on dorsum of elytra in some species of *Selenophorus*; and the presence of setae on all but the median portion of most intervals in one unidentified species of *Selenophorus* seen from Brazil. The most parsimonious assumption is that various types of elytral pubescence and punctuation found in *Selenophorus* represent retention of plesiomorphic states rather than evolution of new states.

C. Ligular sclerite with two long distal ventral setae and lacking other setae. *C*. Ligular sclerite with dorsal setae in addition to the two long distal setae on venter. *CC*. Ligular sclerite with 2 short distal ventral setae in addition to the two long setae.

d. Pronotum with only 1 seta at each side, situated at approximate midpoint. *D*. Pronotum also with 1 to 4 mid-length setae at each anterior angle and one such seta at each posterior angle.

E. Elytral intervals 3, 5, and 7 each with rows of setigerous punctures; such punctures associated or not with interneurs 2, 5, and 7 respectively. *EE*. Such punctures confluent with interneurs 2, 5, and 7 respectively in all but a few species of a stock or lineage. The presence or absence of rows of setigerous punctures along the disc of the third elytral interval (and in some taxa also along intervals 5 and 7) have been used by various authors (Noonan, 1985) to classify taxa as members or non members of the Selenophori group. For this paper I postulate that the ancestor of the selenophorines evolved the apomorphic feature of a row of setigerous punctures along the third interval and possibly along the fifth and seventh intervals. This presumed apomorphy provides the basis for considering the selenophorines a monophyletic group. A few taxa in other groups of harpalines and non-harpalines do have such rows of setigerous punctures on one or more of the odd intervals of the elytra. Parsimony suggests that there has been convergent evolution of the rows rather than numerous instances of loss of such punctures derived from an ancestral Carabidae. The odd intervals of the elytra are innervated by nerves (Jeannel, 1941), and various groups have probably acquired rows of setigerous punctures for sensory purposes.

f. Elytral interneurs lacking prominent non-setigerous punctures along entire lengths. *F*. Interneurs with prominent non-setigerous punctures along entire length.

g. Stylomeres 2 of ovipositor each with ventral short peg-like seta (Fig. 34 in Noonan, 1985). *G*. Stylomeres 2 lacking such peg-like seta (seta absent or replaced a thin long seta). Polarities determined as explained under section on "Character states in the postulated ancestor of selenophorines."

Head. (states, h, H, i, I, j, J, k, K, l, L, m, M, M', n, N)

h. Clypeal apex normal, not deeply emarginate medially and not exposing labral

base medially. *H*. Clypeal apex deeply emarginate medially, exposing labral base in emargination.

i. Clypeo-ocular prolongations varying within lineage from absent to present. *I*. Clypeo-ocular prolongations absent from all members of a lineage. Polarities are determined as discussed under "Reconstructed phylogeny for genera and subgenera of selenophorines."

j. Frontal foveae unmodified. *J*. Frontal foveae each an elongate deep pit near epistomal suture and with a complete deep sulcus prolonged or not onto clypeus and each with clypeo-prolongation to eye and with deep groove extended from junction of each clypeo-ocular prolongation and eye to base of mandible (Fig. 1 in Noonan, 1985).

k. Genae unmodified. *K*. Genae each with preocular sulcus for reception of antennal scape in repose.

l. Mental tooth varying from absent to present within lineage. *L*. Mental tooth absent from all species of lineage. Polarities determined by analysis given in section on "Reconstructed phylogeny for genera and subgenera of selenophorines."

m. Mandibles unmodified. *M*. Mandibles moderately elongate, with apices moderately projected beyond labral apex when in repose. *M'*. Mandibles prominently elongate, apices more projected beyond labral apex when in repose.

n. Antennomeres not modified. *N*. Antennomeres 4 to 11 markedly enlarged and with maximum widths greater than maximum widths of apices of front tibiae.

Pronotum. (states o, O, P, q, Q)

o. Shape average, not elongate. *O*. Form very elongate.

p. Anterior bead incomplete, absent medially or complete in a few species of group. *P*. In all species of group anterior bead complete, not absent medially.

q. Posterior angles average, not broadly rounded. *Q*. Posterior angles broadly rounded.

Legs. (states r, R, s, S).

r. Front tibiae not modified. *R*. Front tibiae expanded and with outer distal margins each crenulate (Fig. 35 in Noonan, 1985).

s. Front tarsi of females not enlarged. *S*. Front tarsi of females enlarged.

Elytra. (states t, T, u, U, UU).

t. Elytra not modified. *T*. Posterior portion of each elytron with intervals 7 and 8 joined into a raised longitudinal ridge extended from interval 8 to suture and formed by dorsum of disc sloped over prominent concave inflexion of distal portion of elytron (Figs. 24 and 25 in Noonan, 1985).

u. Intervals and interneurs unmodified. *U*. Intervals with 2 to 4 prominent regular to irregular shaped non-setigerous punctures per interval width; interval surfaces between punctures raised in many species into longitudinal ridges; in many species sides of intervals 1 to 8 each with ridge and interneurs deep and prominent (Fig. 26 in Noonan, 1985). *UU*. Intervals 1 to 8 or 1 to 9 with prominent elongate punctures, each with very fine short seta; some areas between the punctures joined into irregular elevated chains; interneurs prominent, wide, and deep (Fig. 27 in Noonan, 1985). While adults with U and UU look superficially similar, examination under a microscope demonstrates that the two states are different. Adults with state U lack a seta from each puncture and have punctures which are circular to irregular in shape. Adults with state UU have the punctures elongate, each with a very fine and short seta.

Abdomen. (states v, V).

v. Apex of sixth sternum of females unmodified. *V.* Apex of sixth sternum of females thickened or with median plate-like area (Figs. 28 and 31 in Noonan, 1985).

Ovipositor. (states w, W).

w. Stylomeres 2 unmodified. *W.* Stylomeres 2 each doubled (Fig. 37 in Noonan, 1985).

Reconstructed Phylogeny for Genera and Subgenera of Selenophorines

This section discusses the character changes postulated to have taken place during the evolution of selenophorines, topological features of the phylogenetic diagrams, and uncertainties about some cladistic relationships. Figures 1-3 illustrate the proposed reconstructed phylogeny for selenophorines.

Evolution probably was as follows. The ancestral selenophorines diverged early in their evolution into two major groups, *Parophonus* and *Xenodochus* branches (Fig. 1). The ancestor of the former evolved dense dorsal pubescence on at least the elytra. Separation of Africa and South America presumably split this branch and led to the ancestor isolated in South America evolving the three apomorphies characterizing the taxa of the New World. Data do not permit clarification of the precise cladistic relationships of the four major subgroups of the *Parophonus* branch.

The extant Old World forms of the *Parophonus* branch are restricted to the Oriental and/or Ethiopian Regions, and evolution of taxa presumably occurred in past tropical portions of Africa and Eurasia. *Parophonus*, *Pseudohyparpalus*, and *Pseudodiachipteryx* are grouped together on the basis of chorology since no synapomorphies unite them. Species of *Parophonus* are most numerous in the Ethiopian Region, and those of *Pseudohyparpalus* and *Pseudodiachipteryx* are endemic to that region. There are no apparent synapomorphies for all species of *Parophonus*; its species are united only by similar habitus and the lack of synapomorphies which would suggest placing them into different groups. The *Siopelus* stock contains two supra-specific taxa united by the apomorphic loss of setae from the punctures of the elytra.

Members of the *Dioryche* stock share the apomorphic state of loss of the peg-like seta from stylomere 2 of the ovipositor. *Kareya* and *Dioryche* share the apomorphy of deeply emarginate clypeal apex with labral base exposed in the emargination. Most species of these genera have also secondarily lost all or much of the pubescence from the elytral disc. The other three taxa of the stock are united only by the synapomorphy uniting the *Dioryche* stock. Data do not permit resolving the trichotomy shown for the three lineages of the stock. *Ophoniscus* and *Afromizonus* share the apomorphy of dorsal setae on the ligular sclerite. This synapomorphy is the reason for retaining *Afromizonus* within the Selenophori group. Adults of *Afromizonus* lack rows of setigerous punctures on the third elytral interval, presumably due to secondary loss.

The ancestor of the *Parophonus* branch isolated in South America by the opening of the Atlantic Ocean gave rise to 10 groups in the New World (Fig. 2).

The species of these taxa share three states suggesting common ancestry: (1) the mentum lacks a median tooth (L); (2) stylomere 2 of the ovipositor lacks a ventral peg-like seta (G); and (3) the frontal foveae of the head lack clypeo-ocular prolongations (I). (The only known specimen of an undescribed species of *Trichopselaphus* has a mental tooth and lacks rows of setae on the third elytral intervals [G. E. Ball,

pers. comm.], presumably due to reversion to plesiomorphic states.)

Among Old World genera and subgenera presence or absence of a mental tooth varies among most genera and subgenera and is usually not a stable enough character state for use in defining supra-specific taxa. Similarly among Old World taxa presence or absence of clypeo-ocular prolongations is not stable enough for defining lineages of genera. Absence of a mental tooth and of clypeo-ocular prolongations among all New World selenophorines (except the undescribed species of *Trichopselaphus*) suggests that these structures were either not present or were lost from the ancestor of the selenophorines of the New World. Absence of these structures among ten New World supra-specific groups and approximately 261 species is probably due to some genetic mechanism, possibly epistatic homeostasis, which "fixed" certain loci among these taxa, in contrast to the situation in selenophorines of the Old World. Such "fixation" is here regarded as a synapomorphy.

Species of the eight supra-specific groups which evolved after *Athrostictus* and *Neoaulacoryssus* share the state of the rows of setigerous punctures on elytral intervals 3, 5, and 7 being confluent with interneurs 2, 5, and 7 respectively in apparently all species except *Selenophorus fatuus* and *Discoderus cordicollis*. In Old World selenophorines the rows of setigerous punctures on elytral intervals 3, 5, and 7 are confluent or not with interneurs 2, 5, and 7 respectively. The association of the rows of setigerous punctures with interneurs 2, 5, and 7 presumably became "fixed" in the ancestor of the eight groups. The "fixation" of these punctures (possibly a form of epistatic homeostasis) with the interneurs among eight groups and more than 200 species can be considered as a synapomorphy when compared to variability shown among taxa of the Old World. For the above reasons I believe that the selenophorines of the New World form a monophyletic group defined by three synapomorphies.

The ancestor of this group of New World taxa early gave rise to the *Athrostictus* and *Selenophorus* stocks. The ancestor of the former stock retained the plesiomorphic state of the elytral setigerous punctures not fixed on the interneurs. The ancestor of the *Selenophorus* stock secondarily lost most dorsal pubescence and evolved the apomorphic state of setigerous punctures fixed on the elytral interneurs. (The two species known to have punctures not so fixed presumably have reverted to an earlier ancestral state.) The *Selenophorus* stock gave rise to genus *Selenophorus* with the nominate subgenus and subgenus *Celiamorphus*. There are no apparent synapomorphies defining this genus; rather it is composed of species lacking the synapomorphies characterizing the other six genera of the *Selenophorus* stock. *Selenophorus* thus probably represents a group of species not greatly differentiated (in terms of features delineating supra-specific taxa) from the ancestor of the stock. *Celiamorphus* is retained within *Selenophorus* both because its species seem relatively generalized in mode of life, as are those in the nominate subgenus, and also because a phylogenetic study at the species level may indicate that *Celiamorphus* should be made congeneric with the nominate subgenus. *Amblygnathus* and *Neodiachipteryx* presumably evolved from *Selenophorus*-like species.

The remaining four genera in the New World arose from an ancestor which evolved a narrow body form as an adaptation for a burrowing mode of life. *Trichopselaphus* and *Stenomorphus* share the apomorphy of dorsal setae on the ligula and are treated as sister genera. *Stenomorphus* shares with *Anisocnemus* the apomorphies of genae each with a preocular sulcus (for reception of the antennae in repose) and pronotum

with a complete anterior bead (presumably strengthens pronotum against stresses of burrowing). Both of these apomorphies seem to be adaptations for burrowing and are more probable to evolve independently than is the apomorphy of dorsal setae on the ligular sclerite. Furthermore, *Anisocnemus* shares with *Discoderus* the apomorphy of females with the apex of the sixth abdominal sternum thickened or plate-like medially.

The *Xenodochus* branch gave rise (Fig. 3) to the *Xenodochus* stock characterized by loss of peg-like seta from stylomere 2 of the ovipositor. It also gave rise to the *Oxycentrus* stock characterized by adults with mandibles slightly to considerably longer (apices of both mandibles projected beyond apex of labrum when in repose) than in typical selenophorines. *Hyphaereon*, with adults bearing moderately long mandibles, seems to form an intergrade towards adults of *Oxycentrus* with their more elongate mandibles. *Phyrometus* and *Xenodochus* do not share synapomorphies within the *Xenodochus* branch. Their association is due to joint occurrence of species in tropical Africa and lack of the apomorphies characterizing *Prakasha*.

Some species of *Xenodochus* and *Oxycentrus* lack rows of setigerous punctures on the disc of the third elytral interval. Some species of *Hyphaereon* have only 3 setigerous setae on the disc of this interval. The lack of rows of setigerous punctures in some species of these three genera is assumed to be a secondary loss or a reversion to the plesiomorphic state for Harpalini.

Evolutionary Trends and Homoplasies Among the Selenophorines

The most notable evolutionary trends are: (1) "fixation" in the ancestor of New World selenophorines of the states of, mental tooth absent, peg-like seta absent from stylomere 2 of ovipositor, and clypeo-ocular prolongations absent from head; (2) "fixation" of character state of rows of setigerous punctures confluent with elytral interneurs 2, 5, and 7 in the ancestor of eight New World groups which evolved after *Athrostictus* and *Neoaulacoryssus*; and (3) independent acquisitions of morphological adaptations, presumably for a burrowing mode of life.

The first two trends are discussed in the section "Reconstructed phylogeny for genera and subgenera of selenophorines."

Apparent modifications for burrowing appear in adults of six groups. Subcylindrical to cylindrical shaped bodies presumably facilitate movement in burrows and have evolved independently in the ancestor of *Oxycentrus* and that of the four New World genera with adults adapted for burrowing. The state of pronotum with anterior bead complete evolved independently in the ancestor of *Oxycentrus*, that of *Anisocnemus*, that of *Stenomorphus*, and in isolated species of various other groups. Presumably, a complete bead strengthens the pronotum for stresses encountered while burrowing. The elongate pronota of *Oxycentrus* and *Stenomorphus* probably provide room for powerful muscles used while burrowing. Apparent adaptations of the front tibiae for moving dirt include the additional apical spines present in most species of *Discoderus*, and the expanded front tibiae with strikingly crenulate outer margins in *Anisocnemus*. The preocular sulci of *Stenomorphus* and *Anisocnemus* apparently assist adults in laying their antennae against the body while burrowing.

Notable homoplasies in addition to those mentioned above include: (1) the independent loss in three lineages of the peg-like seta from stylomere 2 of the ovipositor; (2) the loss of most elytral pubescence in three lineages; (3) the similar appearing

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(but different, see descriptions) elytra of *Pseudodiachipteryx* and *Neodiachipteryx*; (4) the deeply emarginate clypeal apices of *Amblygnathus*, and those evolved by the ancestor of *Kareya*, and *Dioryche*; (5) the evolution of distal dorsal setae on the ligular sclerite once in the Old World and once in the New; and (6) the acquisition of a plate-like or thickened median area on the apex of the sixth abdominal sternum of females of *Praskasha* and the ancestor of *Anisocnemus* and *Discoderus*.

Zoogeography

Introduction

This section discusses the zoogeography of extant taxa and the postulated historical zoogeography of selenophorines. For convenience genera and subgenera are treated as equivalents in several discussions and termed "groups".

Distribution Patterns of Extant Selenophorines

Analysis of zoogeographic regions. Sclater (1858) proposed the six major faunal regions (Nearctic, Neotropical, Palaearctic, Ethiopian, Oriental, and Australian) on the basis of bird distributions. Wallace (1876) examined and further defined them by study of vertebrates and some invertebrates such as land Mollusca.

Notable suggested alterations of the zoogeographic regions include those of Heilprin, Kuschel, Flessa and Smith. Heilprin (1887) combined the northern regions, Palaearctic and Nearctic, into a Holarctic Region on the basis of vertebrates shared by the two areas. Kuschel (1963) discussed arguments for treating southern South America, southern Africa, Antarctica, and the Australian area as a distinct "Austral Region". Flessa (1981) concluded from cluster and regression analyses of the distribution of terrestrial mammal genera that the living mammal faunas form only three geographically coherent groups, a Western Hemisphere group, an Australia—New Guinea cluster, and an Eurasia — Africa group. In contrast, Smith (1983) concluded that a phenetic analysis suggests four regions for mammals: (1) North America north of Mexico and temperate Eurasia except for lands around the Mediterranean; (2) Mexico, Middle and South America; (3) temperate lands around the Mediterranean, Africa and tropical Asia; and (4) Australia, New Guinea, New Zealand various Australian islands, Madagascar and Caribbean islands. Workers have not had sufficient time to examine Flessa's or Smith's conclusions. However zoologists in general have not agreed with the views of Heilprin and Kuschel.

Analyses reconfirming the six zoogeographic regions include those of Darlington, Hewer, and Noonan. Darlington (1957) extensively examined the regions in terms of vertebrate distributions and reconfirmed them except that he preferred to treat Madagascar separately from the Ethiopian Region. Hewer (1969) discussed and reconfirmed the six zoogeographic regions on the basis of their vertebrates. Noonan (1973) used anisodactyline Carabidae to analyze the six faunal regions, rejected the modifications proposed by Heilprin and Kuschel and in general reconfirmed the definitions of Sclater and Wallace. Udvardy (1969) provided a synopsis of major ideas concerning faunal regions.

Most analyses of the six major faunal regions have been based on vertebrates —
however most species of animals are invertebrates. I believe that workers revising
previously little understood groups should analyze the regional divisions suggested
by the distribution of included taxa. Such analyses enable biogeographers to consider
possible changes in the major faunal regions as suggested by distributional data
from many different groups, including invertebrates. Below I analyze the distribu-
tions of taxa of selenophorines in terms of the six major faunal regions.

Table 1 gives the distribution of taxa by the six major zoogeographic regions and
also by three areas each composed of more than one zoogeographic region. Figure 4
provides a map showing the geographical distribution of selenophorines.

The limited temperate faunas of the Nearctic and Palaearctic Regions share no groups.

The Palaearctic Region has no endemic groups. It shares *Parophonus* with the
Ethiopian and Oriental Regions and *Oxycentrus* with the Oriental Region alone; one
species of the Ethiopian *Aulacoryssus* occurs in Africa and on the Cape Verde Islands
of the Palaearctic Region.

Table 1 shows that the Nearctic and Neotropical Regions share five groups, with
the Neotropical having five endemic groups and the Nearctic none. Only four species
can be clearly recorded as present in both regions, but revisionary studies by G. E.
Ball on North and Middle American species may change this. In terms of groups
the Nearctic seems to be a subtraction pattern extension of the Neotropical; however
it appears to have a small but distinct fauna of temperate adapted species.

The Oriental Region with its total of nine groups, four of which are endemic, and
82 species appears to be a discrete area with its own distinct fauna of selenophorines.
Data on the distributions of mainland Oriental groups and species of selenophorines
demonstrate only limited sharing of groups or species with the southern part of the
Palaearctic Region. Only two of the nine groups found in the Oriental Region also
occur in the Palaearctic Region.

The distributions of groups of selenophorines clearly indicate that the Ethiopian
Region consists of the continent of Africa south of the Sahara and of Madagascar.
The only selenophorines in Africa north of the Sahara are species of *Parophonus*.
Only *Parophonus* is shared by the Palaearctic and Ethiopian Regions. Madagascar
shares five groups and four species with Africa south of the Sahara (Table 2). Three
of the groups (*Paraphonus*, *Siopelus*, and *Xenodochus*) also occur in the Orient, but
share no species with that region. The lack of endemic groups in Madagascar argues
against separate status for the island as proposed by Darlington (1957), but the
presence of 11 endemic species in Madagascar suggests that at least some species
level evolution has occurred there. The island seems best treated as a subregion of
the Ethiopian, as done by Wallace (1876). Africa south of the Sahara and Madagascar
constitute a region with nine groups, five of which are endemic, and 122 species.
This region also has 35.7 percent of all groups endemic to only one zoogeographic region.

Climatic adaptations. Most taxa are adapted to tropical or subtropical climates,
and most of the few species present in temperate areas occur in warm temperate
portions of these. Examination of the geographical distributions of species given by
Antoine (1959), Basilewsky (1950), Csiki (1932), Darlington, (1968), and various
papers describing new taxa indicate that there is a general subtraction pattern of
species and of supra-specific taxa from tropical to temperate areas.

Data of table 1 show that the Nearctic and Palaearctic Regions contain 70 and 15
endemic species respectively. Most of those in the former occur in warm portions of

Mexico or the southern United States. Most of the 14 Palaearctic species of *Parophonus* are restricted to warm temperate lands adjacent to the Mediterranean. The Nearctic and Palaearctic Regions contain five and two supra-specific taxa respectively (table 1). None of these groups are endemic to the temperate Nearctic or Palaearctic Regions. All of these groups have large concentrations of species in tropical areas of other zoogeographical regions.

Centers of taxonomic diversity. Table 1 indicates that the Neotropical, Ethiopian, and Oriental Regions are centers of taxonomic diversity with 185, 122, and 82 endemic species respectively and 10, 9 and 9 groups respectively. Table 1 also indicates that centers of taxonomic diversity in these regions are predominately mainland in the first two but also on islands in the Oriental Region. The Indo-Australian Archipelago, including New Guinea, itself may be considered a distinct center of taxonomic diversity with 4 groups and 31 species. (Table 2).

Occurrence of species on islands. Table 1 outlines the distribution by numbers of species on mainland and island areas within the six major zoogeographic regions and combinations of such regions. Table 2 indicates the occurrence of species on the main islands of the world and also depicts sharing of species by island and mainland areas. Table 3 summarizes occurrence of species on islands by group, genus or subgenus. The Oriental and Neotropical Regions have the most diverse faunas on islands. Seven groups and 36 species occur on islands in the Neotropical Region, and five groups and 40 species are on islands in the Oriental Region. The Neotropical Region has genus *Neodiachipteryx*, the only group endemic to islands. The Ethiopian Region ranks third with five groups and 19 species on islands.

Vagility of adults. Analysis of tables 1-3 suggests that selenophorines have some species with moderately vagile adults. Of a total of 484 species, 28 or 5.7 per cent occur on both mainlands and islands. Lower sea levels during past glacial periods may have permitted direct land connections to some islands, such as in the Indo-Australian Archipelago but not to many others (Madagascar, for example; see references about past land configurations given in section on "Geographical history of the selenophorines"). Data about the geographical distributions of most selenophorine species are limited; however many genera and subgenera include species with extensive geographical ranges such as tropical portions of Africa or the Americas and mainland and island areas of the Oriental Region.

Geographical History of the Selenophorines

Analysis of the past zoogeography of selenophorines is best approached by first outlining pertinent past geological and climatic conditions.

Africa, South America, Madagascar, India, Australia, Antarctica and various other lands formed the supercontinent of Gondwanaland until the Cretaceous (Dietz and Holden, 1970; Axelrod and Raven, 1978). The South Atlantic gradually formed and began to split South America from Africa. Separation of the continents began in the south and moved northward, with the northern coasts in contact until approximately Late Cretaceous (Dietz and Holden, 1970). Eastern North America and Europe were connected until the Eocene or perhaps as late as the Miocene (Dawson and West, 1982; West and Dawson, 1978).

Axelrod and Raven (1978) summarized data about past geological and climatic events for Africa, Madagascar, India and associated lands. Madagascar remained connected with Africa into the Mid Cretaceous, was situated approximately 15 de-

grees N of its present area, against Tanzania and Kenya, and was then part of the now largely submerged Mascarene Plateau which connected with India on the east into Late Cretaceous. This Malagasy-Mascarene subcontinent provided a route for Cretaceous dinosaurs common to Africa-India-Madagascar and other regions, as well as for rich angiosperm floras of Madagascar and the Seychelles which have numerous relicts. Separation of Madagascar from Africa and India occurred between Middle and Late Cretaceous. India separated from the Malagasy-Mascarene subcontinent in early Paleocene, moved rapidly north and met the Asian landmass by Middle Eocene. In the Paleocene until the separation of India there probably was a commonality of tropical rain forest taxa in Africa and India, a relation evident today in the numerous genera of related taxa of plants still common to these areas.

Africa did not complete its union with Eurasia until Middle Miocene. The continental movements that brought northeast Africa-Arabia against south-central Eurasia closed the Tethys Sea and ended a long-persistent latitudinal circulation system which had brought warm moist climate into the entire Mediterranean region and southern Asia. Closing of the Tethys Sea together with geological changes elsewhere in the world resulted in increasing aridity in mediterranean and other lands. With the closing of the Tethys Sea there was, for the first time, a broad intermingling of Eurasian and African mammalian faunas.

Distributions of plant fossils of the tropical rain forest type suggest that in the Cretaceous there was a broad central tropical geoflora, flanked by temperate floras to the north and south. Floras north and south of the Tethys Sea show significant differences, suggesting importance of this seaway as a barrier.

The present distributions of biomes and topographic relief in Africa is relatively recent. North Africa was predominately covered with lowland rain forest until approximately the Oligocene-Miocene when savanna-woodlands began to spread across northern and southern areas of the continent. By the Late Miocene and Early Pliocene sclerophyll woodland had occupied much of extreme northern Africa, savanna woodland occurred to the south, and lowland rain forest covered much of western and central Africa. Deserts did not develop in Africa until after Early Pliocene. From Late Cretaceous into Early Tertiary Africa had little topographic relief. Climatic belts were broad in extent. Geological uplift commenced in the Late Oligocene-Early Miocene along with volcanism. These processes provided greater topographic diversity. Rain forest taxa began to invade higher colder zones in the highlands while savannas began to spread more widely at the expense of rain forest.

Moreau (1966) summarized data about recent geological and climatic events in Africa. In the Pleistocene there were dramatic climatic shifts accompanied by striking changes in habitats. During glacial periods lower limits of montane biomes shifted down from the present approximately 1500 m to 500 m, resulting in montane biomes forming an essentially continuous block from Ethiopia to Angola and southern Africa. Lowland biomes now in much of Africa were limited to the middle of the Congo basin, to another patch in the Sudan and to a rim all round the coast, which reached its greatest width of some 320 kilometers in Mozambique and in Kenya and Somalia. Climatic changes during the Pleistocene resulted in the Sahara Desert at times being greatly curtailed in size, with Mediterranean scrub and dry woodland or other types of plant formations replacing it during moister periods. During such moister regimes there was no important barrier to north-south movement of many vertebrates, such as now posed by the Sahara.

Data about past geological and climatic events in the Orient seem primarily restricted to those about continental movements or about events of the Late Tertiary or Pleistocene. During the Cretaceous and most of the Paleocene, Asia was tectonically stable; most of the present large-scale tectonics which produced the present relief in Asia began in approximately the Oligocene as a result of the India-Eurasia collision, which apparently created the Himalaya (Molnar and Tapponnier, 1975).

Ninkovich and Donn (1976) summarized data about volcanic history of the Indo-Australian Archipelago; much of it was formed in the early Tertiary; during the Middle Miocene most of it was submerged; a volcanic phase began in the Late Miocene and in some areas such as westernmost Java and Sumatra apparently continued until the Late Pleistocene. I infer (not stated by authors) that considerable portions of the archipelago were again above water by Late Tertiary, if not earlier. Raven and Axelrod (1972) concluded that most of New Guinea was submerged until the Miocene.

Sartono (1973) discussed migration routes of vertebrates in southeast Asia and concluded that they originated in Asia and migrated during the Pleistocene into the Indo-Australian Archipelago. Such migration was apparently facilitated by an interaction between orogenic uplift in the Archipelago and a worldwide lowering of sea-level in the Pleistocene. Many areas of the Archipelago emerged above sea-level, and a land bridge extended from Asia to New Guinea and Australia (except for the South China Sea which apparently remained as a large body of water inside the bridge) and also embraced the Philippines and Formosa along with most present islands of the Archipelago. Biswas (1973) concluded that there were three, or possibly four, drops in sea-level in the South China Sea, with the most recent approximately 11,000 years ago during the Wisconsin/Wurm glacial period.

Noonan (1981) summarized data about past events in South America. Before the Eocene or Miocene, tropical climates predominated across all of South America except for Patagonia with a subtropical or warm temperate regime. Climate cooled after the Miocene, and non-tropical habitats became more widespread. In the Pliocene and Pleistocene, uplift of the Andes produced a barrier to east-west dispersal of lowland organisms and favored development of coastal desert along western portions of the continent. 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. 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. After separation of Africa and South America the latter was an island continent until the Pliocene establishment of a land bridge with Middle America. Considerable climatic variation occurred during the Pleistocene. During drier warmer periods lowland forest habitats and Andean grasslands contracted into isolated refugia where organisms underwent differentiation. When climates became moister and cooler, such habitats expanded out from the refugia and each became essentially continuous.

Data in MacFadden (1981), Malfait and Dinkelman (1972), and Rosen (1975) suggest that some islands in the Caribbean date back to lands which arose in approximately the Eocene where Middle America presently occurs and migrated eastward. Apparently there were not any subsequent continuous land bridges between Caribbean islands and mainland North or South America.

Frakes (1979) summarized data about past world climates. In general, the Triassic,

Jurassic and Cretaceous Periods had climates much warmer and less latitudinally zoned than now. In the Early Tertiary the global climates had already begun a long and irregular deterioration. By Eocene however fossil floras suggesting warm and wet climates still occurred at paleolatitudes of more than 70 degrees N in Grinnell Land and elsewhere in the present Canadian and European Arctic. Climates cooled rapidly from approximately Eocene-Oligocene onward.

What can one conclude from the above history of changes in continental position, climates and habitats? Two general conclusions are that selenophorines encountered great variations in environmental selection pressures during their evolution and that the overall geographic range of the group has probably been greatly reduced as climates cooled. More specific biogeographical conclusions are described below.

Selenophorines probably originated in the Cretaceous on the combined continent of Africa and South America (Fig. 6). Origin in the Late Permian-Triassic, before Gondwanaland began to fragment, would probably have allowed selenophorines to have reached Australia via broad land connections (Fig. 5) with Africa and South America. Origin after the separation of Africa and South America would require dispersals across water barriers.

The opening of the Atlantic apparently split the *Parophonus* branch. Origin in the formerly tropical and subtropical lands of the Northern Hemisphere seems unlikely. Such origin would require crossing of the Tethys Sea for ancestral forms of the *Parophonus* branch to reach the Africa-South America land mass. In the New World, if the ancestor of groups now there gave rise in North America to most extant genera and subgenera, then there is the problem of how members of these taxa reached South America to produce the large fauna there. Development of this fauna since the Pliocene establishment of land connections between North and South America requires a more rapid evolution of taxa than normally assumed for Carabidae.

Multiple southward crossings of the Tethys Sea by members of extant supra-specific taxa are less parsimonious than a single vicariance caused by separation of Africa and South America and also contradict generally accepted patterns of dispersal for Neotropical Carabidae (Allen and Ball, 1980, for species of *Loxandrus*; Ball, 1975, for species of *Phloeoxena*; Ball, 1978, for species of *Trichopselaphus*; Ball and Shpeley, 1983, for eucheiloid Pericalina; Noonan, 1973 and 1981, for species of *Anisotarsus*; and Shpeley and Ball, 1978, for species of *Anisocnemus*). Multiple southward crossings of the Tethys Sea in the New World also contradict Ball's (1978) conclusion that "the general evolutionary-geographical pattern of selenophorines has been one of dispersals northward through Middle America terminating in temperate parts of North America." It also does not seem likely that the ancestral stock of the groups in the New World could have dispersed from North America to South America without evolving taxa which would remain extant in tropical and subtropical portions of Mexico. Assumption that all or part of the groups now there so originated, brings one back to the requirement of multiple crossings of the Tethys.

Dispersal of members of the *Paraphonus* and *Xenodochus* branches into the Orient may have been by a combination of: (1) rafting to the Orient of forms isolated in India after it separated from the Malagasy-Mascarene subcontinent in the Paleocene and began moving toward Asia (Fig. 7); (2) dispersal across the Tethys (Fig. 7); and (3) dispersal across land connections after the Tethys Sea closed in the Miocene (Fig. 8).

Problems are associated with the second and third alternatives. Dispersal across

the Tethys Sea requires crossing what was once a considerable barrier to the spread of terrestrial organisms. Extension of the selenophorines to the Orient after the Middle Miocene closure of the Tethys Sea avoids the problem of water crossings but raises the problem of migrations through lowlands with habitats possibly too arid due to decrease in precipitation with closure of the Tethys.

The distribution of groups suggests that dispersals between Africa and Asia have not been relatively recent. The Ethiopian and Oriental Regions share no species and only three groups (*Parophonus*, *Siopelus*, and *Xenodochus*). If dispersal had been relatively recent, there probably would be shared species. If there had been multiple dispersals over time, then there probably would be more shared groups.

Possibly there was a single vicariance-dispersal event caused by the movements of India. The shared groups, representing 60 percent of all groups on Madagascar, occur in mainland Africa, Madagascar, and India. The Paleocene separation of India from Africa and the Malagasy-Mascarene subcontinent may have resulted in vicariance of some selenophorines. Because of the northward movement of India and Eocene collision with Asia, the vicariance, if it occurred, was accompanied by dispersal. If dinosaurs and tropical rain forest plants were able to disperse across Africa, India and Madagascar via the Malagasy-Mascerene lands, then probably so could selenophorines. The sharing of groups thus may be due to the movements of India, as apparently is the sharing of numerous genera of related taxa of plants still common to these areas.

Data do not, however, permit selecting between the three possible alternatives of vicariance-rafting via India, dispersal across the Tethys, or dispersal across land after closure of Tethys. More information is needed about habitats occupied by extant species, about species ranges, and about shifts in habitat over time.

The nearly total submergence of the Indo-Australian Archipelago in the Miocene suggests that the selenophorines there have developed more recently than those of the Asian mainland. Development of the Indo-Australian fauna is probably a result of a complex mixture of: dispersal across limited water gaps; dispersal across the extensive land bridges from the Asian mainland to Australia during Pleistocene glaciations; and repeated episodes of vicariance caused by rising sea levels during Pleistocene interglacials or by possible past submergence of land.

The absence of selenophorines from Australia is probably due to the mostly temperate climate there and lack of time for selenophorines to disperse from the Indo-Australian Archipelago into Australia. The northern edge of Australia came into contact with tropical habitats only relatively recently (Raven and Axelrod, 1972), and habitats suitable for selenophorines probably have not been abundant on the continent. Suitable tropical habitats on the land bridges probably would have been sparse (or even absent) during the Pleistocene glacial periods when the Indo-Australian land bridges were present. If suitable habitats were present on the land bridges, such habitats probably became scarcer or disappeared in a subtraction like pattern with increased latitude south of the equator. In time, selenophorines may reach Australia as suggested by the presence of five species of *Hyphaereon* in New Guinea.

Evolution of the New World groups probably occurred primarily as a result of vicariance due to extensive changes and shifts in climates and habitats in South America from approximately the Miocene onward. If, as seems likely, burrowing by adults is an adaptation to seek out moisture, then evolution of the four genera (*Anisocnemus*, *Discoderus*, *Stenomorphus*, and *Trichopselaphus*) with burrowing

adults may have been related to the occurrence in the Miocene of savannas and woodlands in northern South America and even in much of Amazonia, areas where rain forests now predominate. Evolution of the sister genera *Trichopselaphus* and *Stenomorphus* and the sister genera *Discoderus* and *Anisocnemus* probably proceeded by the ancestor of each sister pair of genera crossing from South to North America before the Pliocene establishment of direct land connections. Populations of the ancestor of *Trichopselaphus* and *Stenomorphus* isolated in North America gave rise to *Stenomorphus*: similarly isolated populations of the ancestor of the other two genera gave rise to *Discoderus*. Evidence for this scenario includes: absence of *Discoderus* from South America; apparent concentration of species of *Stenomorphus* in tropical portions of North and Middle America; and the conclusions of Ball (1978) and Shpeley and Ball (1978) that the ancestors of *Trichopselaphus* and *Anisocnemus* probably arose in South America.

Caribbean island species of predominantly mainland groups may have been present on the proto-Antilles which were apparently rafted eastward in approximately the Eocene, could be the result of dispersal across water, or could be the result of both rafting on the proto-Antilles and overwater dispersal. Knowledge of the sister group relationships of all species in the groups may resolve the origin of the Caribbean forms.

The monobasic genus *Neodiachipteryx* is known only from Hispaniola. It does not show any close cladistic relationships to other selenophorine groups and has highly modified elytra. This genus thus quite possibly was isolated in Hispaniola as a result of vicariance as suggested by Rosen (1975) for various other terrestrial animals.

Testing of Hypothesis for Historical Zoogeography

This section evaluates the hypothesis, as advocated by Noonan (1979) for biogeographical studies, in terms of Popper's four criteria for scientific hypotheses (explanatory power, internal consistency, potential for falsification and predictive power).

The hypothesis explains the present biogeographical patterns of selenophorines.

It is internally consistent; no part of it contradicts another.

The hypothesis for the historical zoogeography is based on a postulated reconstructed phylogeny which in itself has an inherent potential for falsification. The gathering of new data results in new tests of the reconstructed phylogeny. New data might, for example, result in redetermination of polarity of character states or might reveal important but previously unperceived synapomorphies.

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

First, Old World genera of the *Xenodochus* branch which are postulated to have evolved after separation of Africa and South America will not be found in South America or if so found will have dispersal patterns suggesting recent dispersal across the Atlantic.

Second, further study of Australian Carabidae will not result in discovery of a temperate adapted fauna of selenophorines there. The group is postulated to have arisen in tropical areas and to be in the process of dispersing from tropical Asia to New Guinea and tropical portions of Australia via the Indo-Australian Archipelago.

Concluding Remarks

Selenophorines are a complex group of carabids. Despite their presence in all six major faunal regions, selenophorines have not been studied on a world wide basis before my previous work (Noonan, 1985) on their generic and subgeneric level classification. The present paper has presented a world wide analysis of the reconstructed phylogeny and zoogeography of the genera and subgenera of selenophorines. I hope that these two papers will stimulate further study of these interesting beetles.

Acknowledgments

Table 1. Distribution by numbers of species endemic to mainland and/or island areas in one or more zoogeographic regions.

Regions	Nr.	Nt.	Pa.	Et.	Or.	Au.	Nr. + Nt.	Et. + Pa.
Parophonus			14	28	16			
Pseudohyparpalus				14				
Pseudodiachipteryx				1				
Siopelus				56	5			
Aulacoryssus				11				1
Harpathaumas				1				
Ophoniscus					3			
Afromizonus				3				
Kareya					4			
Dioryche					13			
Athrostictus		16						
Neoaulacoryssus		2						
Selenophorus	31	133						
Celiamorphus	9	5					1	
Neodiachipteryx		1						
Amblygnathus	4	11						
Trichopselaphus		6						
Stenomorphus	3	6					1	
Discoderus	23	3					2	
Anisocnemus		2						
Phyrometus				1				
Xenodochus				7	3			
Prakasha					1			
Hyphaereon					20	5		
Oxycentrus			1		17			
T. # GROUPS	5	10	2	9	9	1	3	1
T. # END SP.	70	185	15	122	82	5	4	1
AVERAGE # END. SP. PER GROUP	14.0	18.5	7.5	13.6	9.1	5.0	1.3	1.0
# END. GROUPS	0	5	0	5	4	0	0	0
T. # GROUPS END. TO A REGION IN WORLD	14							
% of T. WORLD'S END. GROUPS	0	35.7	0	35.7	28.6	0	0	0
T. # GROUPS IN WORLD	25							
% OF WORLD'S GROUPS IN REGION	20.0	40.0	8.0	36.0	36.0	4.0	12.0	4.0*
T. # SP. ON ISL.	0	36	1	19	40	5	1	1

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Table 1. Distribution by numbers of species endemic to mainland and/or island areas in one or more zoogeographic regions (continued).

Regions	Nr.	Nt.	Pa.	Et.	Or.	Au.	Nr. + Nt.	Et. + Pa.
T. # SP. END. TO ISLANDS	0	29	1	14	26	5	0	0
T. # GROUPS ON ISL.	0	7	1	5	5	1	1	1
T. # GROUPS END. TO ISLANDS	0	1	0	0	0	0	0	0
% T. SP. ON ISL.	0	19.5	6.7	15.6	48.8	100	25.0	100
% T. SP. END. TO ISL.	0	15.7	0	11.5	31.7	100	0	0
% ISL. SP. END. TO ISLANDS		80.6	0	73.7	65.0	100	0	0
AV. # MAIN. SP. PER GROUP	14.0	17.3	7.5	12.0	6.2	0	1.3	1.0
AV. # ISL. SP. PER ISLAND GROUP	0	5.1	1.0	3.8	8.0	5.0	1.0	1.0
T. # SP. IN WORLD	484							
AV. # SP. PER GROUP IN WORLD	19.36							

*Note: Since some groups occur in more than 1 region, the values in this line sum to more than 100%

Key to abbreviations (Table 1).

AV.	= average
Au.	= Australian Region
END.	= endemic
Et.	= Ethiopian Region
GROUP	= supra-specific taxa (on), genus or subgenus
ISL.	= islands
MAIN.	= mainlands
Nr.	= Nearctic Region
Nr. + Nt.	= Nearctic & Neotropical Regions combined
Nt.	= Neotropical Region
Or.	= Oriental Region
Pa.	= Palaearctic Region
SP.	= species
T.	= total
#	= number
%	= percent

Table 2. Occurrence of species of genera and subgenera on islands or both on islands and mainlands. (Dashed lines connect island or mainland areas shared by one or more species.)

Mainland areas (m) or islands (i)

taxa	mNt	Car	mEt	iMad	iE of Et	mOri	iCey	iInA	iJap	mPa	other
Parophonus											
				3							1 For.
m. + isl.			1	1	1						& Ryuk.
m. + isl.						2	2				
m. + isl.						1	1	1			
m. + isl.						2		2			
Pseudohyparpalus											
				2							
m. + isl.			1		1						
Siopelus											
				3							
islands shared				3	3						
Aulacoryssus											
				2							
m. + isl.			1						1		C. Ver.
m. + isl.			3	3	3						
Dioryche											
m. + isl.						5	5				
m. + isl.						2		2			
Athrostictus											
		1									
Selenophorus											
islands only		22									2 Gal.
m. + isl.	5	5									
Celiamorphus											
m. + isl.	1	1									1 Fla.
Neodiachipteryx											
		1									
Amblygnathus											
		3									
Stenomorphus											
		2									
Discoderus											
m. + isl.	1	1									
Xenodochus											
				1		1					
Hyphaereon											
						4	13				1 Ryuk.
m. + isl.						1	1				
m. + isl.						1		1			
Oxycentrus											
								12			
m. + isl.									1	1	

Table 2. Occurrence of species of genera and subgenera on islands or both on islands and mainlands. (continued; dashed lines connect island or mainland areas shared by one or more species.)

Mainland areas (m) or islands (i)

taxa	mNt	Car	mEt	iMad	iE of Et	mOri	iCey	iIn A	iJap	mPa	other
T. # SP. ON ISL		36		18	8		14	31	1		1 C. Ver. 2 Gal. 1 Ryuk. 1 For.& Ryuk.
T. SP. END TO ISL.		29		11	0		5	25	0		2 Gal. 1 Ryuk. 1 For.& Ryuk.
T. # GROUPS		7		5	4		4	4	1		1 C. Ver. 1 Gal. 2 Ryuk. 1 For. & Ryuk.

Key to abbreviations (Table 2)

AV.	= average
C. Ver.	= Cape Verde Islands
END.	= endemic
Fla.	= Florida
For.	= Formosa
Gal.	= Galapagos Islands
GROUP	= supra-specific taxa (on), genus or subgenus
iCar	= Caribbean Islands
iCey	= Ceylon
iE of E	= islands east of Africa, other than Madagascar
iMad	= Madagascar
iInd A	= islands of the Indo-Australian Archipelago
ISL.	= islands
Jap	= japan
m.	= mainland
mEt	= mainland portions of the Ethiopian Region
mNt	= mainland portions of the Neotropical Region
mOri	= mainland portions of the Oriental Region
mPa	= mainland portions of the Palaearctic Region
Ryuk.	= Ryukyu Islands
SP.	= species
T.	= total
#	= number

Table 3. Distribution of species by supra-specific taxa in relation to islands.

	T.# sp.	T.# sp. on isl.	% sp. on isl	# sp. on m + isl.	%sp. on m + isl.	#sp. on only isl.	%T. sp. only on isl.	%isl. sp. end. isl.
Parophonus	58	10	17.2	6	10.3	4	6.9	40.0
Pseudohyparpalus	14	3	21.4	1	7.1	2	14.3	66.7
Pseudodiachipteryx	1	0	0	0	0	0	0	0
Siopelus	61	6	9.8	0	0	6	9.8	100
Aulacoryssus	12	6	50.0	4	33.3	2	16.7	33.3
Harpathaumas	1	0	0	0	0	0	0	0
Ophoniscus	3	0	0	0	0	0	0	0
Afromizonus	3	0	0	0	0	0	0	0
Kareya	4	0	0	0	0	0	0	0
Dioryche	13	7	53.8	7	53.8	0	0	0
Athrostictus	16	1	6.3	0	0	1	6.3	100
Neoaulacoryssus	2	0	0	0	0	0	0	0
Selenophorus	164	29	17.7	5	3.0	24	14.6	82.8
Celiamorphus	15	1	6.7	1	6.7	0	0	0
Neodiachipteryx	1	1	100	0	0	1	100	100
Amblygnathus	15	3	20.0	0	0	3	20.0	100
Trichopselaphus	6	0	0	0	0	0	0	0
Stenomorphus	10	2	20.0	0	0	2	20.0	100
Discoderus	28	1	3.6	1	3.6	0	0	0
Anisocnemus	2	0	0	0	0	0	0	0
Phyrometus	1	0	0	0	0	0	0	0
Xenodochus	10	2	20.0	0	0	2	20.0	100
Prakasha	1	0	0	0	0	0	0	0
Hyphaereon	25	20	80.0	2	8.0	18	72.0	90.0
Oxycentrus	18	13	72.2	1	5.6	12	66.6	92.3

Key to abbreviations (Table 3)

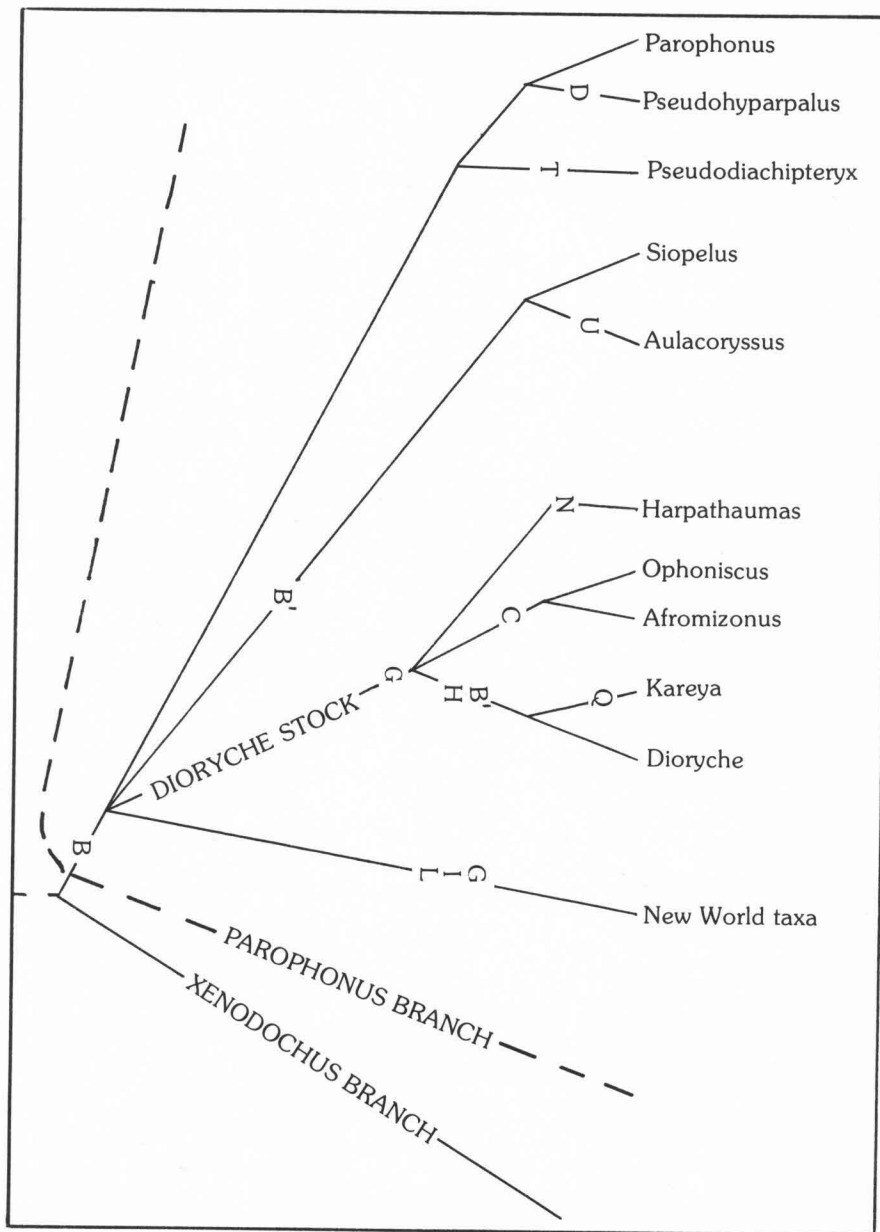|	
end.	= endemic to
isl.	= islands
m	= mainland areas
sp.	= species
T.	= total
%	= percent
#	= number

Figure 1. Reconstructed phylogeny of the genera and subgenera of the *Parophonus* branch in the Old World and the origin of the two other main lineages of the Selenophori Group.
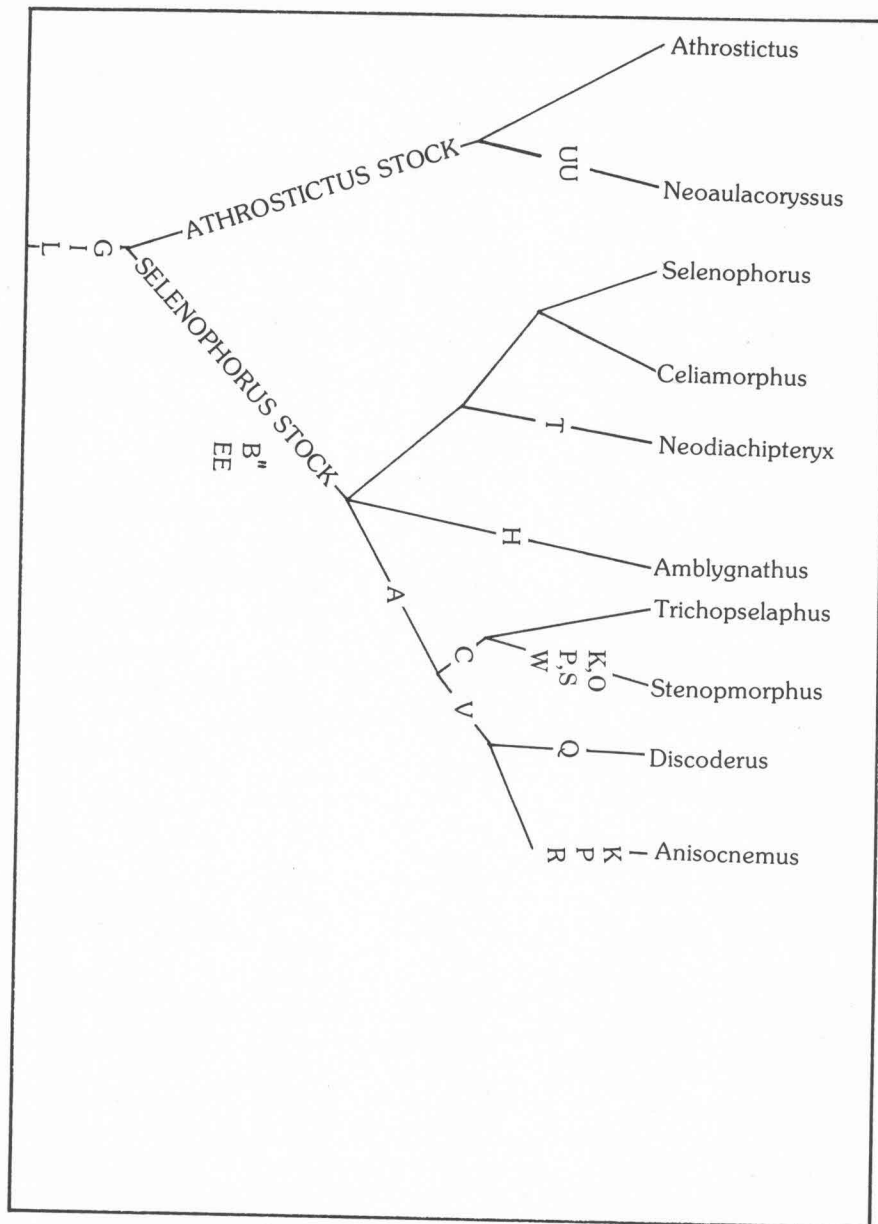
Figure 2. Reconstructed phylogeny of the genera and subgenera of the *Parophonus* branch in the New World.
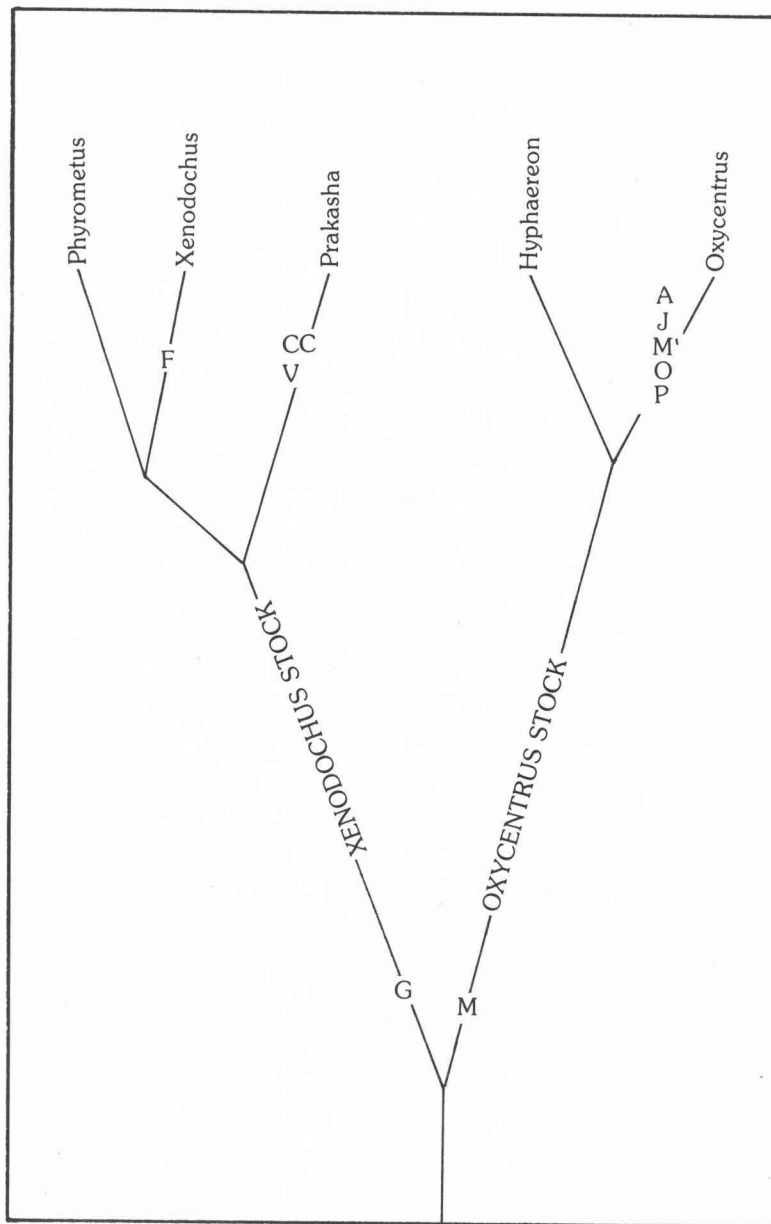
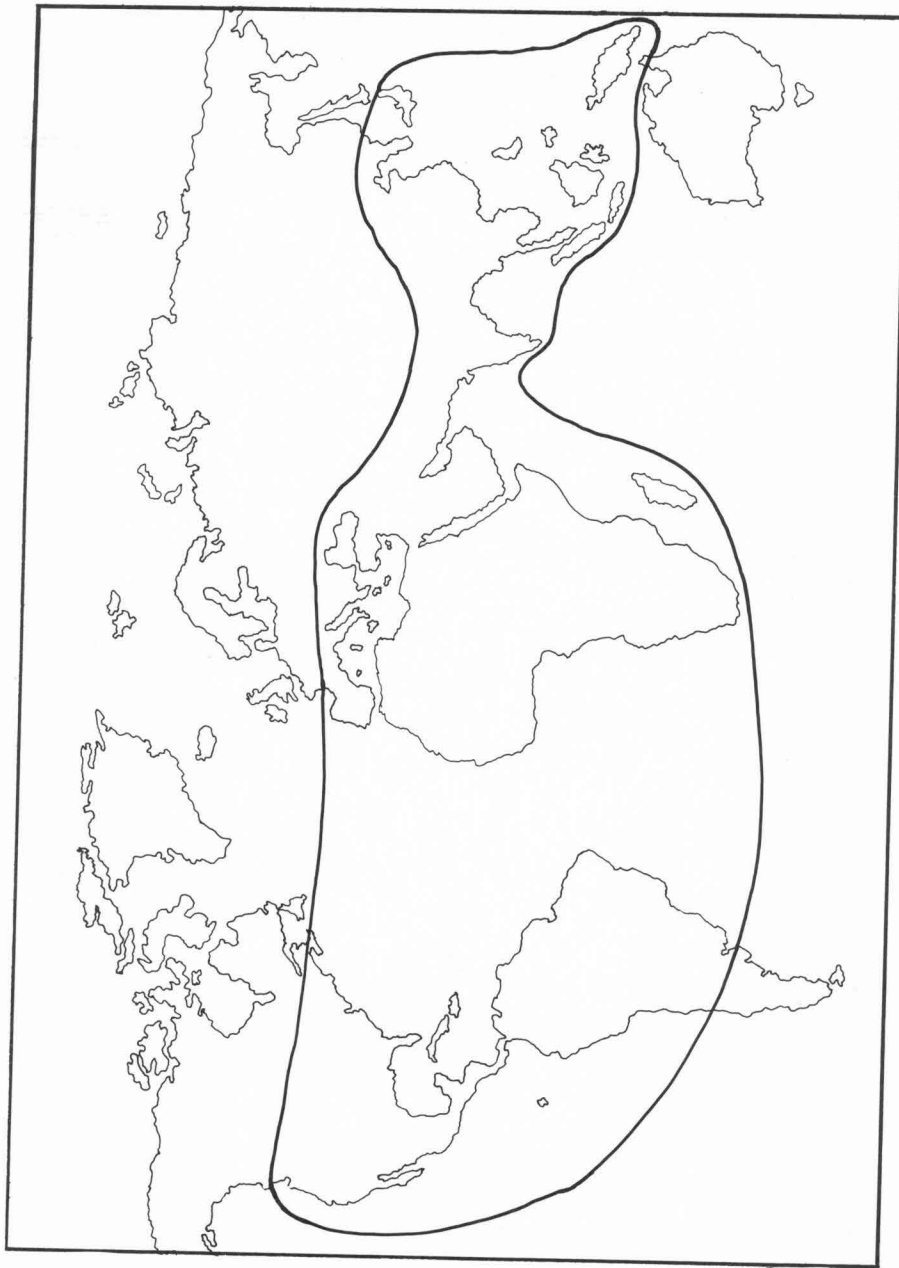**Figure 3.** Reconstructed phylogeny of the genera and subgenera of the *Xenodochus* branch.

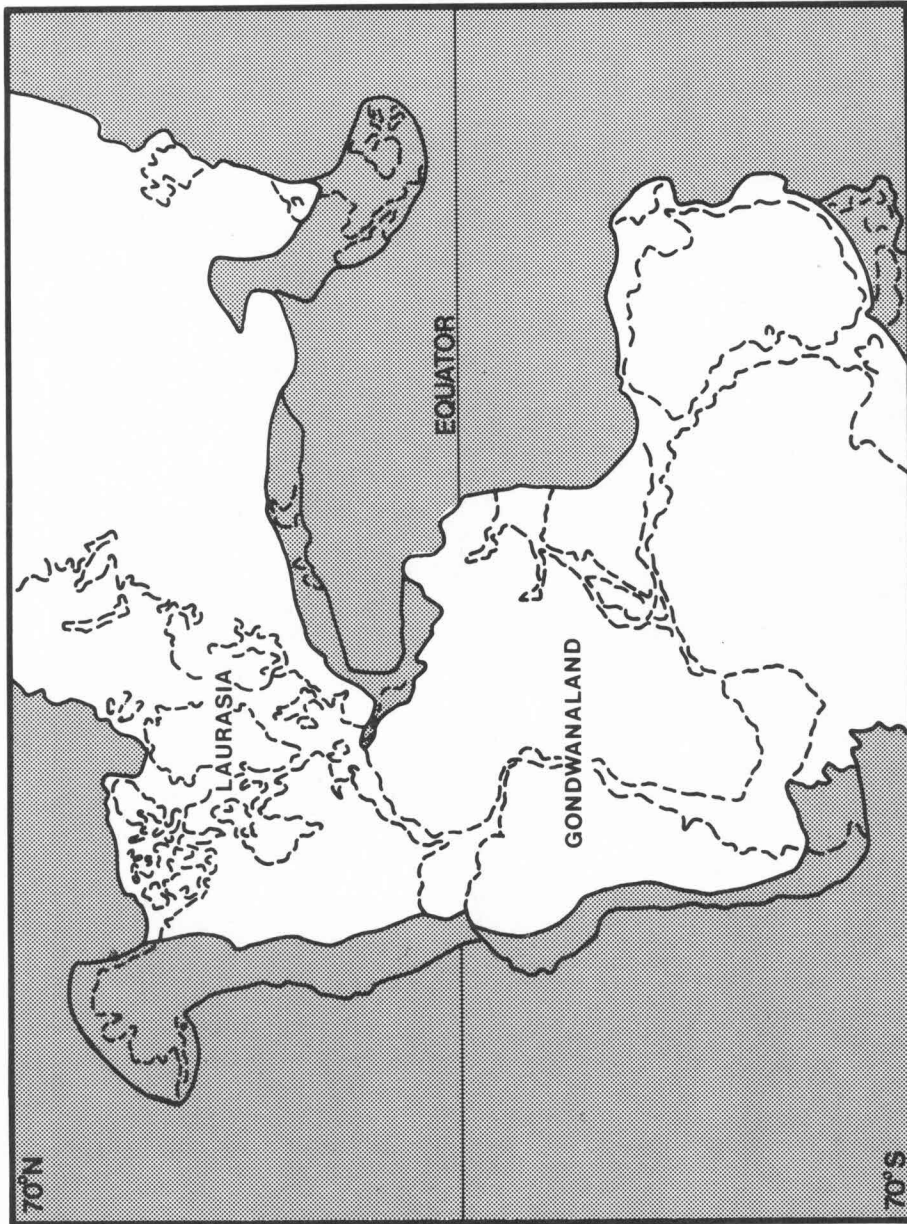**Figure 4.** Geographical distribution of extant selenophorines. (Group occurs inside the heavy solid lines.)

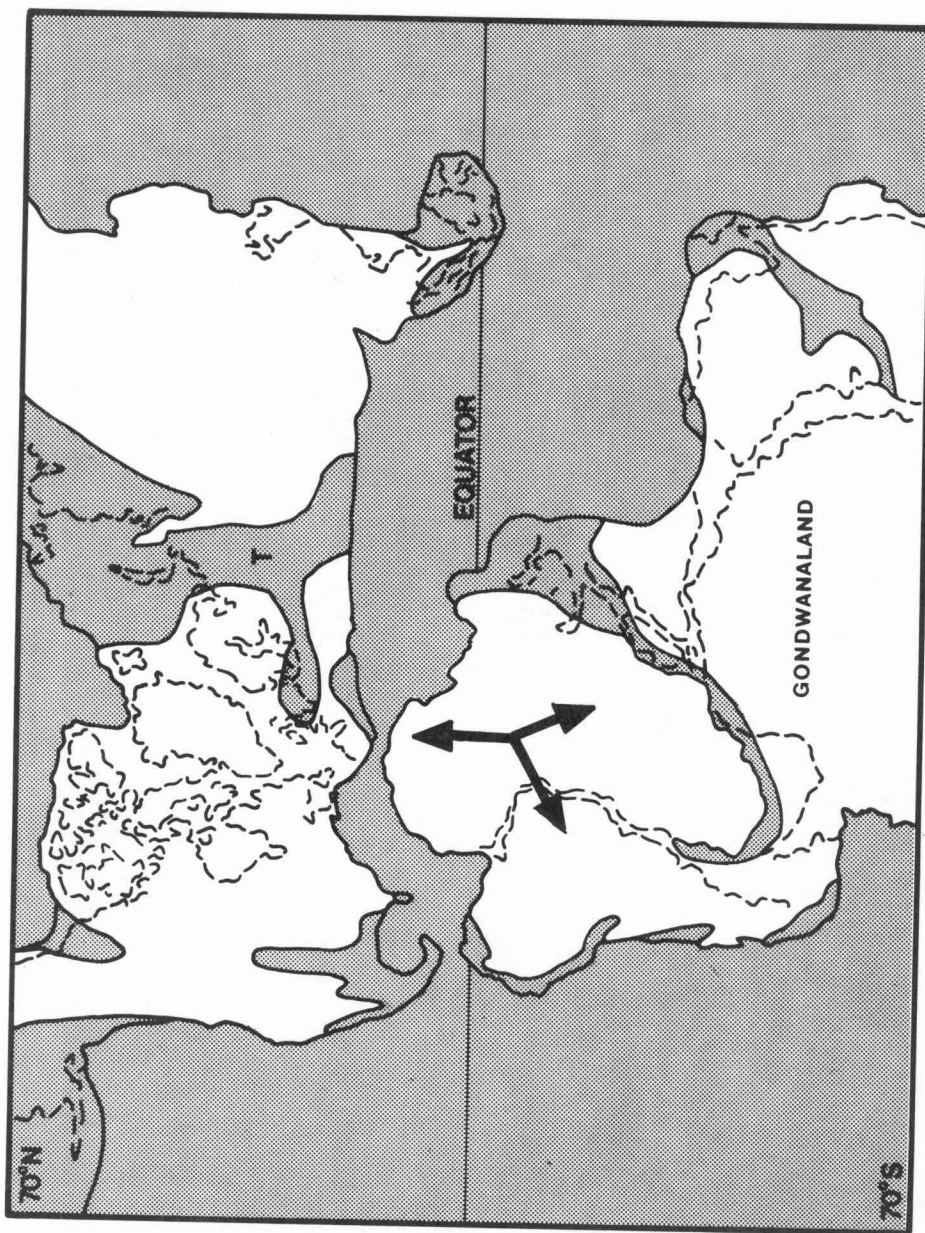**Figure 5.** Map showing land configurations of the Late Permian-Triassic.

Figure 6. Map showing land configurations of the Early Cretaceous and the postulated origin and initial dispersals of selenophorines.
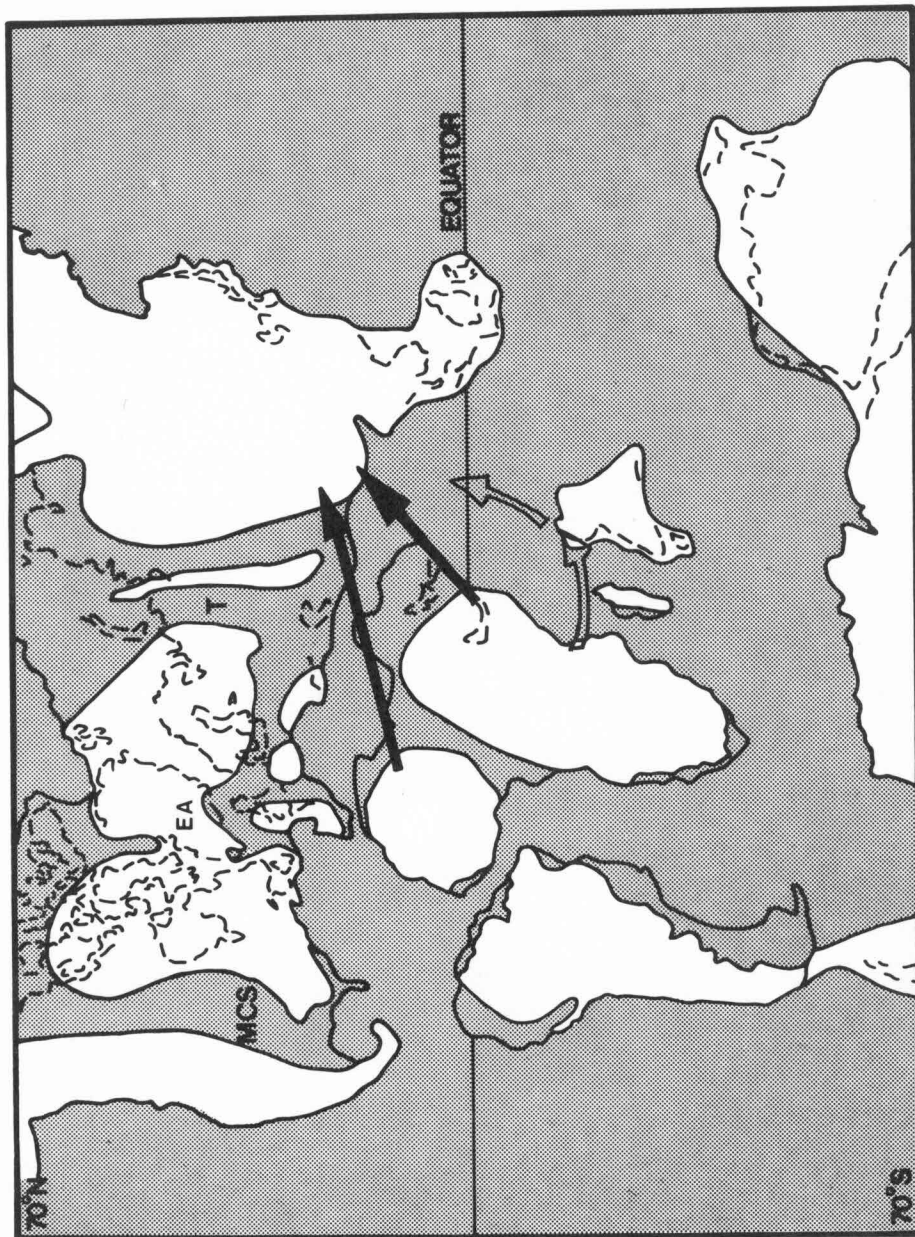
Figure 7. Map showing land configurations of the Late Cretaceous and possible movements of selenophorines. Solid arrows denote possible, but unlikely, dispersals across the Tethys Sea from Africa to Asia. Hollow arrows denote approximate path of India after it separated from Africa and began moving towards Asia. Selenophorines on India may have been rafted to Asia.
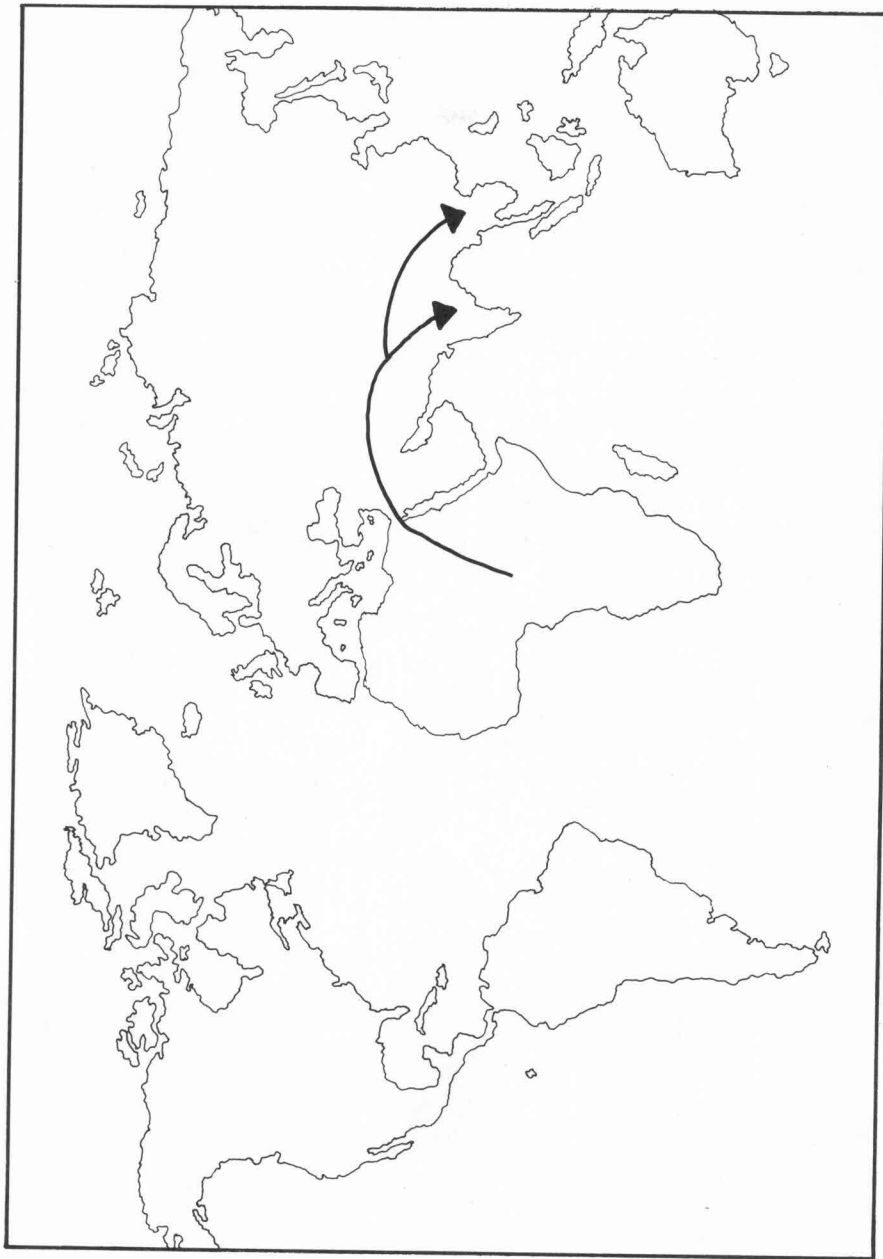
Figure 8. Map showing present land configurations and possible dispersals of selenophorines from Africa to Asia after Miocene closure of the Tethys Sea.

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