TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF THE CARRION BEETLES OF LATIN AMERICA (COLEOPTERA: SILPHIDAE)

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ABSTRACT

*The species of Silphidae, excluding Agyrtidae, are reviewed for Mexico, Central America, and South America. Keys are provided for the identification of adults of six genera (*Necrodes, Heterosilpha, Oiceoptoma, Thanatophilus, Oxelytrum, Nicrophorus) *and 24 species known or suspected to occur in Mexico or southward. No new species are proposed. The following new synonymies are presented:* Silpha microps *Sharp is a junior synonym of* Oxelytrum anticola *(Guérin-Méneville) and* Hyponecrodes opacus *Portevin is a junior synonym of* Oxelytrum erythrurum *(Blanchard).*

Given for each species, as appropriate, are: synonymy, diagnosis, comments on variation, geographic distribution, seasonality, ecological data, and illustrations of important structural characteristics. Geographic distributions are mapped for all species.

Oxelytrum *is regarded as the sister genus to* Ptomaphila *of the Australian region.* Oxelytrum, *represented by eight species, probably originated and diversified during the Tertiary in South America when this continent was isolated. Two lineages of* Oxelytrum *are recognized based on adult characters. The* emarginatum *group has four species found in northern and eastern lowland and mid-elevation montane habitats, with only one species, O.* discicolle, *ranging into Central America and north to extreme southern Texas. The* lineatocolle *group has four species found in south-western coastal lowlands and low to high elevation montane habitats.*

Nearctic species of Necrodes, Oiceoptoma, Heterosilpha *and* Thanatophilus *which also occur in Latin America range no further south than the Isthmus of Tehuantepec. Only* T. graniger *is endemic, found in high elevation habitats of central and northern Mexico.*

Nicrophorus *is represented by nine species in three species groups in Latin America. All groups are of northern origin. The five species of* Nicrophorus *endemic to Latin America are all members of the* orbicollis *group. Ancestors of the three South American endemic species probably moved south along the mountain axis of Central and South America in late Cretaceous or early Tertiary time and likely diversified in the Tertiary following fragmentation of forest habitats. The two Middle American endemics are probably the result of a second, but mid-Tertiary, inter-island dispersal of a northern ancestor. The four remaining species of* Nicrophorus *represent two species groups. All of these species occur in the United States with three ranging into arid areas of central and northern Mexico; the*

fourth ranges south to El Salvador.

A classification of New World Nicrophorus *is also presented. Thirteen of the fifteen New World species are placed in four species groups based on larval and adult characters. Two species are* Incertae sedis. *A reconstructed phylogeny is presented for the New World members of each species group.*

RESUMEN

*Se revisan las especies de Silphidae, excluyendo Agyrtidae, de México, Centroamérica y Suramérica. Se proveen claves para la identificación de los adultos de los 6 géneros (*Necrodes, Heterosilpha, Oiceoptoma, Thanatophilus, Oxelytrum, Nicrophorus) *y 24 especies que se conoce o se sospecha que existen en México o hacia el sur. No se proponen nuevas especies. Se presentan, a continuación, los nuevos sinonimos:* Silpha microps *Sharp es un sinónimo reciente de* Oxelytrum anticola *(Guérin-Méneville) e* Hyponecrodes opacus *Portevin es un sinónimo reciente de* Oxelytrum erythrurum *(Blanchard).*

Se dan para cada especie, según sea apropiado: la sinonimia, el diagnóstico, comentarios sobre la variación, la frecuencia por estacion, datos ecológicos e ilustraciones de características estructurales importantes. Se presentan las distribuciones geográficas de todas las especies.

Oxelytrum *se considera el género hermano de* Ptomaphila *de la región australiana.* Oxelytrum, *representado por ocho especies, probablemente se originó y diversificó en Suramérica durante el Terciario cuando este continente se encontraba aislado. Basados en las características de los adultos, se reconocen dos linajes en* Oxelytrum. *El grupo* emarginatum *tiene 4 especies que se encuentran en hábitats montanos de baja y media altitud en el este y norte de norteamérica, con una sola especie,* O. discicolle, *que se extiende a Centroamérica y de allí hacia el norte hasta el extremo sur de Texas. El grupo* lineatocolle *tiene 4 especies que se encuentran en áreas de baja elevación en la costa suroeste y en hábitats montanos de alta y baja altitud.*

Las especies neoárticas Necrodes, Oiceoptoma, Heterosilpha *y* Thanatophilus *que también se presentan en Latinoamérica se extienden, hacia el sur, no más allá del Istmo de Tehuantepec.* T. graniger *es la única endémica, encontrándose en hábitats de alta elevación en el centro y norte de México.*

Nicrophorus *está representado por 9 especies en 3 grupos de especies. Todos los grupos tienen su origen en el norte. Las 5 especies de* Nicrophorus, *endémicas para Latinoamérica, son todas miembros del grupo* orbicallis. *Los ancestros de las 3 especies endémicas de suramérica probablemente se dispersaron al sur a través del eje montañoso de Centro y Sur América en el Cretáceo tardío o a comienzos del Terciario y, es muy posible, que se diversificaran en el Terciario, siguiendo la fragmentación de los hábitats forestales. Las dos endémicas de Mesoamérica son, probablemente, el resultado de una dispersión secundaria a través de islas, a partir de un ancestro norteño durante el Terciario medio. Las cuatro especies restantes de* Nicrophorus *representan dos grupos de especies. Todas estas especies se encuentran en los Estados Unidos con tres que se extienden hasta zonas áridas del centro y norte de México; la cuarta, se extiende, hacia el sur, hasta El Salvador.*

Se presenta también una clasificacion de Nicrophorus *para el Nuevo Mundo. Trece de las quince especies del Nuevo Mundo se agrupan en 4 grupos de especies basados en caracteres de las larvas y los adultos. Dos especies son* Incertae sedis. *Se presenta una reconstrucción filogenética para los miembros de cada grupo de especies del Nuevo Mundo.*

INTRODUCTION

The Silphidae, or carrion beetles, are the predominant beetles scavenging on dead terrestrial vertebrate remains in temperate and sub-arctic regions in the Northern Hemisphere. Silphids also occur in tropical lowlands, as well as in tropical montane and south temperate regions. However, their role in the carrion-feeding insect guild is noticeably less in tropical than in temperate regions (Cornaby, 1974; Jirón and Cartín, 1981). They are probably less abundant in lowland tropical regions because they are less able to compete with increased rates of bacterial decomposition and feeding of ants and fly larvae, and with the greater abundance of carrion scavenging vertebrates (Arnett, 1946; Janzen, 1976). Recent reviews of the silphid fauna of North America north of Mexico recognized 29 species in 8 genera (Anderson and Peck, 1985), most of which have their relationships with species in Europe and Asia. Some of these also have distributions extending south into Mexico. However, most of the Latin American (used herein to indicate all of Mexico, Central America, and South America) fauna

consists of species in the primarily South American genus *Oxelytrum* and of endemic species in the genus *Nicrophorus*. No silphids are known to occur on the islands of the Carribean.

The Latin American silphids were last revised by Portevin (1926). His liberal use of infraspecific categories, inadequately illustrated and complex keys, which also served as descriptions, and vague distributional data have led to problems in interpreting the species in Latin America. This present work attempts to alleviate these problems by reviewing and revising available knowledge about classification, distribution, and relationships of the Latin American silphid fauna.

NATURAL HISTORY

Silphid beetles are commonly called carrion beetles because of their association with dead vertebrate carcasses. Both adults and larvae of most species are scavengers and eat carrion. Based on studies of Nearctic species, silphids feed in two different ways. In the first, both adults and larvae of the sub-family Silphinae feed on comparatively large carcasses which remain exposed on the soil surface. No parental care of larvae is known. In the second, adults of the genus *Nicrophorus* feed at large and exposed carcasses, but they must also secure a comparatively small carcass and bury it for reproduction and subsequent larval maturation. Adults remain with the developing larvae and care for them until they pupate. The Oriental genus *Ptomascopus* exhibits behavior combining aspects of the life histories of both Silphinae and *Nicrophorus*, but does not exhibit the parental care of larvae typical of *Nicrophorus* (Peck, 1982). These differing methods of carrion use are also found in Palearctic Silphidae.

Detailed studies have not been made on the Neotropical species, but there is no reason to suspect that their feeding and reproductive behaviors differ. Our field observations indicate that all species of *Oxelytrum* behave as typical Silphinae in feeding and breeding primarily on large carcasses. Species of *Oxelytrum* differ from most Nearctic and Palaearctic silphines in that most are nocturnal instead of being diurnal.

Unfortunately, natural history data are few for Latin American species of *Nicrophorus* but they indicate that at least some of the species are nocturnal. There is no reason to suspect that Latin American *Nicrophorus* differ in other aspects of their natural history from Holarctic *Nicrophorus*. Rearings have not been attempted, and larvae are unknown for most species.

Anderson (1982a, 1982b) and Anderson and Peck (1985) review more detailed accounts of the natural history of silphids.

METHODS

We do not include the Agyrtidae, previously considered as part of the Silphidae, but now separated as a distinct family (Lawrence, 1982; Lawrence and Newton, 1982). The only agyrtids known from Latin America are three Mexican species of *Apteroloma* (reviewed in Bolívar and Hendrichs, 1972, who list them as *Pteroloma*).

Full synonymies for North American genera and species are given in Peck and Miller (in press). Type-species of genus-group names are in Madge (1980). Full synonymies are not given here for species which also occur in the U.S. and Canada; they are given in Peck and Miller (in press), and Anderson and Peck (1985). Full synonymies are listed only for those species limited in their distribution to Latin America. All original literature has been checked unless otherwise noted. We give the first use of a name or combination, and only references that contribute new

data. It is not our intention to give references to every use of a name in the older literature. We do not cite "aberrations" but only usage of a name as a "variety", because it may be interpreted as having subspecific rank (International Code of Zoological Nomenclature, 1974, art. 45 (e) (i)). For species that occur in the U.S. and Canada as well as Latin America, only the synonyms pertaining to material from Latin America are given. Nomina nuda are not cited. Such are listed by Portevin (1926), Hatch (1928), and Blackwelder (1944). Depositories are indicated for type material we examined. In those instances where type material was not examined we have indicated the probable depository according to Horn and Kahle (1937), and noted this with a question mark.

Keys for identification of species north of Mexico were published by Miller and Peck(1979), Peck (in press), and Anderson and Peck (1985) and should be consulted to confirm species identifications of specimens from northern Mexico. Keys presented here include only species known or likely to occur in Latin America. Keys for larvae are not presented because of lack of species descriptions. Keys to larvae of some genera and species which occur in Latin America are in Anderson and Peck (1985).

Species that may in the future be found to naturally occur in Latin America, but are not yet recorded, are mentioned below. These are excluded from the detailed species discussions and keys.

Nicrophorus americanus, N. carolinus, N. investigator, and N. tomentosus and some silphines of the southeastern United States may yet be found in Mexico because they occur in bordering states to the north. A significant component of the biota of this region does occur in temperate forests in northeastern Mexico (Martin and Harrell, 1957; Rosen, 1978). We have seen one specimen of N. sayi labelled "Mexico, N.L., Sierra de Gaucamayas, Zarogoza, 2-3.VII.69, J.M. Matthieu, M.W. Sanderson, trampa de luz negra" (SBPC) but cannot accept this single record for this far northern species as evidence of its occurrence in Mexico. Another doubtful record is one of Necrophila americana labeled "Cuepayaca" (Cuernavaca) IX-46, H. Field (FMNH).

Old records that we believe are erroneous, doubtful, or un-substantiated by recent specimens are cited in Portevin (1926), Hatch (1928), and Blackwelder (1944). We do not discuss these any further.

We have been unable to establish the identity of the names Nicrophorus quadricollis Gistel from Mexico and Necrodes pronotus Gistel (1857:94) from Brazil. The types were supposedly in the collections of the Zoological Museum in Munich (Horn and Kahle, 1937), but are now considered lost (G. Scherer, in litteris 1984).

Distributions of all species are mapped based on personal examination of specimens. Because of space limitations, full label data are not given but are available from the first author. We cite only condensed locality (under State or Department or Province names in large countries) and ecological data in alphabetical order, month (if on label) and number of specimens if more than one. Specimen repository information or literature references follow the records for each country. Obscure localities from Matthews (1888) in the Biologia Centrali Americana were verified or located in Selander and Vaurie (1962).

All drawings were prepared with a camera lucida or an ocular grid and squared paper. Measurements of length are from the anterior margin of pronotum to the elytral apex.

Phylogenies are reconstructed following Hennig (1966) and Wiley (1981). As do most systematists, we adopt the biological species concepts as outlined by Mayr (1963). Since there is no direct information available about reproductive isolation in Latin American Silphidae,

such isolation is inferred from differences in structural features, distribution, and available information about natural history. We do not attempt to recognize subspecies. Adequate population samples are not available to investigate the significance of variation in coloration such as occur in some species of *Oxelytrum* and *Nicrophorus*.

MATERIALS

We have borrowed and examined material, totaling more than 4580 specimens, from the following individuals and collections through the kindness of their owners or curators as follows:

AFNC   Alfred F. Newton, Jr. Collection, Cambridge, Mass., U.S.A.
BMNH   British Museum (Natural History), London; England; R.B. Madge.
CASC   California Academy of Sciences, San Francisco, California, U.S.A.; D.H. Kavanaugh.
CBMV   Carlos Bordon Collection, Maracay, Venezuela; C. Bordon.
CMNH   Carnegie Museum of Natural History, Pittsburg, Penn., U.S.A.; G. Ekis
CNCI   Canadian National Collection of Insects, Ottawa, Ont., Canada; A. Smetana.
FMLC   Fundacion M. Lillo, Tucuman, Argentina; R. Golbach.
FMNH   Field Museum of Natural History, Chicago, Ill., U.S.A.; H.S. Dybas.
FSCA   Florida State Collection of Arthropods, Gainesville, Fla., U.S.A.; R.E. Woodruff.
GMNH   Geneva Museum of Natural History, Geneva, Switzerland; I. Lobl.
INPA   Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; N.D. Penny.
ITMM   Instituto Technológico de Monterrey, México; Juan Contreras.
IZAV   Instituto de Zoología Agricola, Maracay, Venezuela; F. Fernandez-Yepez.
LACM   Natural History Musuem of Los Angeles County, Los Angeles, California, U.S.A.; C.L. Hogue.
LPMCN La Plata Museo de Ciencias Naturales, La Plata, Argentina; L. De Santis.
MCZC   Musuem of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.; A.F. Newton, Jr.
MHNM   Museo de Historia Natural de la Ciudad de México, México City, México; P. Reyes-Castillo.
MNHN   Museum National d'Histoire Naturelle, Paris, France; N. Berti.
MNSC   Museo Nacional de Historia Natural, Santiago, Chile; G.A. Santic.
MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil; C. Costa.
OSCU   Ohio State University, Department of Entomology, Columbus, Ohio, U.S.A.; C.A. Triplehorn.
PURC   Purdue University Entomology Collection, Lafayette, Ind., U.S.A.; R.D. Waltz.
RDCC   R.D. Cave Collection, Auburn, Ala., U.S.A.
RSAC   Robert S. Anderson Collection, Edmonton, Alta., Canada.
SDMC   San Diego Natural History Musuem, San Diego, Calif., U.S.A.; S.E. Miller.

SBPC Stewart B. Peck Collection, Ottawa, Ont., Canada.

TMMC Texas Memorial Museum Collection, University of Texas, Austin, Tx., U.S.A.; J. Reddell.

UAIC University of Arizona Insect Collection, Tuscon, Ariz., U.S.A.; F.G. Werner.

UFPB Universidade Federal do Paraná, Curitiba, Paraná, Brasil; D. Urban.

UICM University of Idaho, Department of Entomology, Moscow, Idaho, U.S.A.; W.F. Barr.

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; T.J. Spilman.

UTDZ University of Texas, Department of Zoology, Austin, Tx., U.S.A.; J. Rawlings.

No fossil silphids are known from Latin America. Churcher (1966) tentatively reported silphids among the insects found in the Talara late Pleistocene tar seeps of Peru. We examined these fossils, deposited in the Royal Ontario Museum, Toronto, Ontario, Canada, and found that they belong to other beetle families.

SYSTEMATICS

Key to Adults of Latin American Genera

1   Antenna clavate, the antennomeres gradually widening into an apical club (fig. 1); fronto-clypeal suture absent (fig. 3); abdominal tergum V lacking mid-dorsal stridulatory files: subfamily Silphinae 2

1'   Antenna with the apical four antennomeres forming an abrupt club (fig. 2); fronto-clypeal suture present (fig. 4); abdominal tergum V bearing a pair of mid-dorsal stridulatory files (hidden in many specimens by apices of truncate elytra): subfamily Nicrophorinae . . . . *Nicrophorus* Fabricius, p. 265

2   (1) Elytra with at least some reddish markings (fig. 5); pronotal postcoxal lobe short and broadly rounded (fig. 6) . . . . *Necrodes* Leach, p. 253

2'   Elytra wholly black; pronotal postcoxal lobe large, prominent (fig. 7) 3

3   (2') Elytra with ramose or branching sculpturing (fig. 9) . . . . *Heterosilpha* Portevin, p. 253

3'   Elytra lacking ramose or branching sculpturing 4

4   (3') Pronotum with two or four pairs of low, broad longitudinal costae on disc (fig. 1); widest at or before middle, lacking hairs on dorsal surface . . . . *Oxelytrum* Gistel, p. 257

4'   Pronotum lacking costae; widest behind middle, bearing at least some hairs on dorsal surface 5

5   (4') Head with a short row of long, erect hairs behind the eyes (fig. 11); elytra tricostate . . . . *Oiceoptoma* Leach, p. 254

5'   Head lacking a short row of erect hairs behind the eyes; elytra either lacking costae entirely (fig. 12) or with numerous tubercles on dorsal surface (figs. 13, 14). . . . . *Thanatophilus* Leach, p. 255

SUBFAMILY SILPHINAE

NECRODES LEACH 1815

Four species are known in this genus, one of which occurs in North America where it is widespread (Anderson and Peck, 1985; Ratcliffe, 1972). Adults are easily recognized by the key characters, large size and form of elytra (Fig. 5).

Necrodes surinamensis (Fabricius)
Figures 5, 6, 17

Silpha surinamensis Fabricius, 1775: 72. Type locality: *"in America meridianali."*. Syntypes: in Hunterian collection, University of Glasgow (Ratcliffe, 1972). Ratcliffe, 1972; Anderson and Peck, 1985.

Diagnosis.— Length 15 - 25 mm. Eyes large, separated by distance about twice width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, sparsely punctate; orbicular, widest near middle (Fig. 17). Pronotal postcoxal lobe short, broadly rounded (fig. 6). Elytra tricostate, black with red markings present in apical quarter (fig. 5), some specimens also with red markings along lateral margin near midlength. Some males with hind femora greatly expanded.

Distribution.— Because *N. surinamensis* occurs in counties bordering the Rio Grande in Texas, it most likely occurs in bordering Mexico (Ratcliffe, 1972). The species name suggests that it occurs in South America. We have seen a single specimen (MCZC) labeled "Ucayale P(eru?). Maranon R., C. Sarkady" (which seemingly means where the Ucayale and Maranon Rivers meet). In the absence of any other verifiable records, and our inability to find the species in extensive collecting in Latin America, we cannot now accept the presence of the species any farther south than possibly northern Mexico.

Ratcliffe (1972) has reviewed the natural history and distribution of the species in the United States.

HETEROSILPHA PORTEVIN 1926

Two species of this endemic North American genus are known. Among Latin American silphids, they are easily recognized by the ramose or branching sculpturing on the elytra.

Key to species

1   Males with pro- and mesotarsomeres 1-4 broadly expanded and with elytral apex not prolonged (fig. 9); females with elytral apex somewhat prolonged (fig. 8); male genitalia thicker and broader, parameres with apices thicker and down-curved (figs. 18, 19); elytra without metallic lustre

         . . . .
         . . . . *H. ramosa* (Say), p. 254

1'   Males with pro- and mesotarsomeres 1-4 not expanded; male and female elytral apices similar, not prolonged (fig. 10); male genitalia more thin and slender, parameres more narrow and straight (figs. 20, 21); elytra of some specimens with metallic lustre . . . . *H. aenescens* (Casey), p. 254

Heterosilpha ramosa (Say)
Figures 8, 9, 18, 19; Map 1

Silpha ramosa Say, 1823: 193. Type locality: "the upper Missouri (River)". Neotype: in MCZC (designated by Miller and Peck, 1979: 93). Miller and Peck, 1979; Anderson and Peck, 1985.

Diagnosis.— Length 14 - 18 mm. Eyes small, separated by distance about four times width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Elytron tricostate, wholly black, with well developed branching sculpturing (fig. 9). Males with pro- and mesotarsomeres 1-4 laterally expanded, densely pubescent beneath; females with elytral apices slightly prolonged (fig. 8). Male genital characters as in key (figs. 18, 19).

Distribution.— The species is widespread throughout much of western North America (Anderson and Peck, 1985). Its natural history in Colorado is described by Brewer and Bacon (1975). Matthews (1888: 95) reports one specimen of the species from an unspecified site in northern Sonora. Horn (1894) lists it from San Pedro Martir, Baja California. We have seen the following record: Mexico. *Baja California.* Tijuana, III, 3. FMNH.

Heterosilpha aenescens (Casey)
Figures 10, 20, 21

Silpha aenescens Casey, 1886: 171. Type locality: San Francisco, California. Lectotype: in USNM (designated by Miller and Peck, 1979: 93). Miller and Peck, 1979.
Heterosilpha aenescens (Casey), Portevin, 1926: 85.

Diagnosis.— Length 14 - 18 mm. Eyes small, separated by distance of about four times width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Elytron tricostate, wholly black but many specimens with a metallic lustre, with well developed branching sculpturing. Males with pro- and mesotarsomeres 1-4 not expanded, not densely pubescent beneath; male and female with elytral apices similar, not prolonged in female. Male genital characters as in key (figs. 20, 21).

Distribution.— The species is known from southern to northern coastal California and southern Oregon (Miller and Peck, 1979), and may occur in northwestern Mexico. We have seen records from as far south as San Diego, California and suspect it occurs in northern Baja California, Mexico.

OICEOPTOMA LEACH 1815

Three species of the Holarctic genus *Oiceoptoma* are known from North America, one of which may enter extreme northeastern Mexico. Six species in this genus are known from the Palearctic region.

Oiceoptoma rugulosum (Portevin)
Figures 11, 16, 23

Silpha inaequalis rugulosa Portevin, 1903: 333. Type locality: Savannah, Georgia. Type: in MNHN?, not seen.

Diagnosis.— Length 13 - 15 mm. Head with short row of long, erect hairs behind eyes (fig. 11). Eyes small, separated by distance about four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly moderately densely punctate;

with few blackish hairs; transverse, widest near base. Pronotal postcoxal lobe broad, with right-angled apical point. Elytron black, tricostate; some specimens with elytral intervals with transverse rugose sculpturing. Elytral humeri each with a single tooth (fig. 16). Females with elytral apices prolonged to sharp points; males with apices broadly rounded.

Taxonomic status and distribution.— The species has usually been considered conspecific with *O. inaequale*, which is widespread in both eastern Canada and the United States (Anderson and Peck, 1985). Adults of the two taxa are separated most readily by those of *O. rugulosum* having a narrow elytral epipleuron (on the posterior half the upper oblique part is subequal to the lower vertical part, fig. 23) and by those of *O. inaequale* having a wide elytral epipleuron (on the posterior half the upper oblique part is at least twice the width of the lower vertical part, fig. 22). We know *O. rugulosum* to occur from Florida to Indiana to Texas. It is probably active in winter or spring. Portevin (1903: 333; 1926) cites the species from Mexico, which is possible, but records are not known to us, and from Guiana, which is an obvious error.

THANATOPHILUS LEACH 1815

Six species of this widespread genus are known to occur in North America. Three of these occur in Latin America, from central to Northern Mexico. Although primarily a northern cold-adapted taxon, some species of *Thanatophilus* occur in southern desert grasslands and shrublands. Other than two species which occur in the grasslands of southern Africa, members of the genus are Holarctic in distribution. Where they occur at more southerly latitudes they usually do so at higher elevations.

Key to species

1   Elytra abruptly truncate, lacking costae (fig. 12) . . . .
         . . . . *T. truncatus* (Say), p. 255
1′   Elytra not abruptly truncate; tricostate and with tubercles interspersed
         between the costae (figs. 13, 14) 2
2   (1′) Head and pronotum with abundant, long yellow-grey hairs; metasternal
         hairs yellow-grey; posterior margin of abdominal sternum VII of female
         unornamented, with marginal hairs only (fig. 24) . . . .
         . . . . *T. lapponicus* (Herbst), p. 256
2′   Head and pronotum with shorter and darker hairs which do not entirely
         obscure the basal sculpture; metasternal hairs brown; posterior margin of
         abdominal sternum VII of female with numerous coarse crenulations or
         tooth-like projections (figs. 25a, 25b) . . . . *T. graniger* (Chevrolat), p. 256

Thanatophilus truncatus (Say)
Figure 12; Map 2

Silpha truncata Say, 1823: 193. Type locality: eastern Colorado. Neotype: in MCZC (designated by Peck and Miller, 1982: 154). Matthews, 1888: 95.
Philas truncata (Say), Portevin, 1903: 331.

Diagnosis.— Length 11 - 14 mm. Eyes small, separated by distance four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densly punctate; with short appressed blackish hairs over entire surface; transverse, widest near base.

Pronotal postcoxal lobe large, rounded at apex. Mesosternal hairs black. Elytra black, lacking costae, apices in both sexes abruptly truncate (fig. 12).

Natural history and distribution.— The species occurs in arid and open habitats in the southwestern United States and extends in such habitats onto the Mexican Plateau. Adults are known to be active from June to September. We have seen 76 specimens representing the following records:

MEXICO. *Chihuahua.* Pinos Altos. Santa Clara. *Coahuila.* Canon del Fuenteno, Sierra de la Madera, VII. *Districto Federal.* Mexico City. *Durango.* Durango. El Salto, 2450-2750m, VI, 27. 32 km E El Salto, 2450 m, IX, 2. Pedicena (not located), VI, 8. *Guerrero.* Chilpancingo. *Michoacan.* Rio Balsas (Rio Mescales). Tancitaro. *Nayarit.* Jesus Maria, VII, 7. La Mesa, VII, 3. *Puebla.* Puebla. *Veracruz.* Jalapa. *Zacatecas.* 40 km W Fresnillo, 2400 m, VI, 9. BMNH, CNCI, FMNH, SBPC, USNM.

Horn (1895: 227) mentions a record from "Sierra San Lazaro", Baja California. We do not know this locality. The specimen was probably destroyed in the 1905 San Francisco earthquake and fire.

Thanatophilus lapponicus (Herbst)
Figures 13, 24; Map 2

Silpha lapponica Herbst, 1793: 209, plate 52; fig. 4. Type locality: Lappland. Type: in Berlin?, not seen. Anderson and
    Peck, 1985. Not the species listed by Matthews, 1888: 96.
Thanatophilus lapponicus (Herbst), Portevin, 1926: 33.

Diagnosis.— Length 10 - 14 mm. Eyes small, separated by distance of four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; with long yellow-grey hairs variably distributed over surface; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Mesosternal hairs yellow-grey. Elytra shorter, black, tricostate, with numerous tubercules interspersed between costae (fig. 13). Females with elytral apices prolonged and rounded (fig. 13); males with apices rounded, but not prolonged. Female with posterior margin of abdominal sternum VII unornamented, with marginal hairs only (fig. 24).

Natural history and distribution.— The species is widespread in North America, especially at higher altitudes or latitudes (Anderson and Peck, 1985). Portevin (1926: 136) states that *T. californicus* Mannerheim, a synonym of *T. lapponicus*, is distributed from California, through Central America, and along the Andes to Bolivia. This is an error. Records of this species in Matthews (1888) refer to *T. graniger.*

A single Mexican record is known to us: MEXICO; *Baja California.* Tijuana, III, 5. FMNH.

Thanatophilus graniger (Chevrolat)
Figures 7, 14, 25a, 25b; Map 1

Oiceoptoma granigera Chevrolat, 1833: 1. Type locality: Mexico. Type: in MNHN?, not seen.
Silpha lapponica Herbst, misidentification of Matthews, 1888: 96.

Diagnosis.— Length 10 - 14 mm. Eyes small, separated by distance of four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; with short yellow-grey hairs variably distributed over surface; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex (fig. 7). Mesosternal hairs dark brown. Elytra longer, black, tricostate, with numerous tubercules interspersed between costae (fig. 14). Females with elytral apices prolonged and rounded (fig. 14); males with apices rounded but not prolonged. Females with posterior margin of abdominal sternum VII with numerous coarse crenulations or tooth-like projections, nearly as long as marginal hairs (figs.

25a, 25b).

Taxonomic notes, natural history and distribution.— This species has usually been considered conspecific with *T. lapponicus*, however, the female abdominal character clearly separates the two as distinct taxa.

The species is known only from the higher elevations of the Transverse Volcanic Sierra of Mexico, and Cerro Potosi in northeastern Mexico. Adults were collected during February, May, June, and November.

We have seen 38 specimens representing the following records:

MEXICO. *Districto Federal.* Mexico City. *Hidalgo.* Guerrero Mills, 5. Apan, V, 1. *Jalisco.* Sayula. *Mexico.* Salazar, 3000 m, IX, 6. *Morelos.* Km 50 Mexico to Cuernavaca Road, VIII, 2. *Nuevo Leon.* Galeana, Cerro Potosi, 3750 m, VI, 16. *Puebla.* Ciudad Serdan (San Andres Cholchicomula). *Vera Cruz.* Jalapa. Las Vigas. No locality, II. No data, 2. BMNH, ITMM, MCZC, MHNM, SBPC, USNM.

OXELYTRUM GISTEL 1848

Several generic and subgeneric names have been used for the species of *Oxelytrum.* We are unable to find enough characters which combine to form a consistent suite justifying recognition of more than a single genus.

Adults of this genus are easily recognized by tricostate elytra, lacking ramose sculpturing, a pronotal disc lacking hairs and bearing two or four low longitudinal costae (fig. 1), and a large pronotal postcoxal lobe. We recognize eight species in the genus, most of which are confined to South America. Only the very widespread *O. discicolle* enters extreme southern Texas.

Key to species

1   Eyes small, not prominently protruding, separated by distance distinctly
         greater than three times width of an eye in dorsal view (figs. 26a, 26b) 2
1'   Eyes large, prominently protruding, separated by distance about three
         times or less than width of an eye in dorsal view (figs. 1, 3) 4
2   (1) Pronotum with quadrangular reddish spot in posterolateral corner;
         pronotum and elytra with vague blue-green iridescence ....
         .... *O. biguttatum* (Philippi), p. 258
2'   Pronotum wholly black; pronotum and elytra lacking trace of iridescence 3
3   (2') Apical three antennomeres orange-yellow .... *O. apicale* (Brullé), p. 258
3'   Antenna black .... *O. anticola* (Guérin-Méneville), p. 259
4   (1') Pronotum and elytra concolorous chestnut brown to black; apical
         antennomere orange ....
         .... *O. lineatocolle* (Laporte), p. 260
4'   Pronotum with margins orange-yellow, disc mostly or partly blackish (fig.
         1); antennae various in color 5
5   (4') Elytral humeri rounded (fig. 27); pronotum with costae distinctly elevated 6
5'   Elytral humeri toothed (fig. 28); pronotum with costae present but
         indistinct 7
6   (5) Apical antennomere orange-yellow; elytra with apices emarginate, sutural
         angles sharp (fig. 32) .... *O. emarginatum* (Portevin), p. 260
6'   Apical antennomere black; elytra with apices not emarginate, the sutural
         angles evenly rounded or only slightly prolonged ....
         .... *O. erythrurum* (Blanchard), p. 261

7   (5')   Pronotum with postcoxal lobe wholly orange-yellow; pronotum with dark
             coloration confined to very middle of disc; elytral apices produced and
             blunt (Figs. 35, 36) .... *O. cayennese* (Stürm), p. 262
7'   Pronotum with postcoxal lobe wholly black; pronotum with dark coloration
             more extensive (fig. 1); elytral apices sharply pointed (figs. 37, 38) ......
             .... *O. discicolle* (Brullé), p. 263

Oxelytrum biguttatum (Philippi), NEW COMBINATION
Figures 26b, 29; Map 3

Necrodes biguttatus Philippi, 1859: 664. Type locality: Chile. Type in: MNSC; syntypes no. 2219-2220, not
   seen.
Silpha biguttula Fairmaire and Germain, 1859: 350. Type locality: Straits of Magellan. Type in: MNHN?,
   not seen.
Necrodes biguttulus (Fairmaire and Germain), Fairmaire, 1888: 27.
Hyponecrodes biguttatus (Philippi), Berg, 1901: 327. Schouteden, 1905: 199.
Paranecrodes biguttatus (Philippi), Portevin, 1921: 81. 1926: 131.
Silpha (Paranecrodes) biguttata (Philippi), Hatch, 1928: 116.

Diagnosis.— Length 12 – 19 mm. Head with eyes not prominent, separated by distance five
times width of an eye in dorsal view (fig. 26b); frontal depressions absent; occipital-frontal crest
acute. Antennae black. Pronotum black with vague blue-green iridescence, with quadrangular
reddish spot in each posterolateral corner; transverse, about 0.6 times as long as wide; posterior
angles obtusely angulate; margins not reflexed upwards; pronotal costae present but effaced.
Pronotal postcoxal lobe black. Elytra black with blue-green iridescence, elytral humeri not
toothed. Abdomen of both sexes with segment VII and apical portion of segment VIII
orange-red, otherwise black. Males with elytral apices abruptly rounded (fig. 29); in females,
slightly more prolonged and evenly rounded.

Natural history and distribution.— The species occurs in forests and open habitats in the
southern half of Chile and adjacent Argentina. Adults were collected from October to April.
We have seen 59 specimens representing the following records:

ARGENTINA. *Chubut*. No data, 1. No locality, XI. *Neuqen*. Nahuel Huapi, 2. Neuquen, III, IV, 4. Pucara, Parque
Nacional Lanin, XII, 2. *Rio Negro*. Bariloche. Gutierrez, XI. *Santa Cruz*. Lago Argentino. Lago Blanco. Valle Tunel (not
located), 2. Ventisquero Moreno, Los Glacieres, I. No data, 1. *Tierra del Fuego*. Bahia San Sebastian, Cerrillos, IV. Rio
Grande. Rio McClelland (not located). San Sebastian. Ushuaia, II. No Locality, I. No data, 2. BMNH, FMLC, FMNH,
LPMCN, USNM.

CHILE. *Aisen*. Golfo de Penas, I, 5. Laguna San Rafael, Taitao, X, XII. Puerto Cisnes, II. *Chiloe*. Palena.
Llanquihue. Frutillar, I. *Malleco*. 20 km E Manzanar, 1100m, XII, 12. Termas de Tolguaca, II. *Magallanes*. Dawson
Island. Esperanza (not located), I. Isla Navarina, XI. Isla Riesco, Mina Elena, II. Puerto Eden, XII. Punta Arenas, II.
Useless Bay. No data, 1. *Osorno*. Parque Nac. Puyehue, Antillanca Rd., 965 m, *Nothofagus* forest, XII, 3. *Valdivia*.
Corral. Enco, III. AFNC, BMNH, CNCI, MCZC, MNSC, SBPC, USNM.

Oxelytrum apicale (Brullé), NEW COMBINATION
Figures 26a, 30a, 30b; Map 4

Silpha apicalis Brullé, 1840: 74, *in* Brullé and Blanchard, 1840. Type locality: Potosi, Bolivia. Type in: MNHN?, not
   seen.
Hyponecrodes apicalis (Brullé), Kraatz, 1876: 375.
Hyponecrodes (Katanecrodes) apicalis (Brullé), Portevin, 1921: 82.
Silpha (Katanecrodes) apicalis (Brullé), Hatch, 1928: 113.

Diagnosis.— Length 9 – 11 mm. Head with eyes not prominent, separated by distance
about five times width of an eye in dorsal view (fig. 26a); frontal depressions moderately deep;
occipital-frontal crest obtuse. Apical three antennomeres orange red. Pronotum black;

transverse, about 0.75 times as long as wide; posterior angles broadly rounded; margins not reflexed upwards; pronotal costae distinctly elevated. Pronotal postcoxal lobe black. Elytra black; middle costa of some specimens effaced at basal one third; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange segment VIII in females. Males with elytral apices abruptly rounded (fig. 30a); in females very slightly prolonged immediately lateral to sutural apex and more evenly rounded (fig. 30b).

Natural history and distribution.— The species is known to us only from high and low elevation open habitats in northwestern Argentina and adjacent Bolivia. Adults were collected from November to April. We have seen 107 specimens representing the following records:

ARGENTINA. *Catamarca.* Catamarca, II. El Manchado, 3000 m, I; 4000 m, I. El Suncho Experimental Station, II, 6. Famabulasto (not located). La Cienaga, 3700 m, III, 2. Las Mansas (not located), III. Los Angeles, II. Nevados del Aconquija, Quebrada de los Cazedores, 4500 m, XI; between Ingehio and Puesto de los Ojos (not located), II. Santa Maria Puesto de los Ojos (not located), II, 5. *Cordoba.* Cordoba, 4. Pampa de Achala, II. *Jujuy.* Abra Pampa, III. *La Rioja.* Velasco, II. Mina da Esperanza (not located), II, 5. *Tucuman.* Amaicha, 2000 m, II; Quebrada Amaicha, IX. Between El Nagalar and Santa Maria, III. Infiernillo, XI, 12; XII, 33; Quebrada Honda, 3400 m. San Jose, 2500 m, IV, 2. Siambon, III. Tafi del Valle, II, 3; III, 2; XI, 8; no date, 7. Tafi Viejo, II. Trancas, San Pedro Colalao, II. No locality, 3. FMLC, GMNH, LPMCN, MZUSP.

BOLIVIA. Pongo de Quime, VI. USNM.

Oxelytrum anticola Guérin-Méneville), NEW COMBINATION
Figure 31; Map 5

Silpha anticola Guérin-Méneville, 1855: 592. Type locality: Ecuador. Type in: Brussels Museum?, not seen.
Hyponecrodes anticola (Guérin-Méneville), Kraatz, 1876: 375.
Silpha microps Sharp, 1891: 40. NEW SYNONYMY. Type locality: Quito, Ecuador, 2895 m (9500 feet). Type in BMNH, seen.
Hyponecrodes (Katanecrodes) andicola (Guérin-Méneville), Portevin, 1921: 82.
Silpha (Katanecrodes) anticola (Guérin-Méneville), Hatch, 1928: 114.
Silpha (Katanecrodes) microps (Sharp), Hatch, 1928: 114.

Diagnosis.— Length 9 – 11 mm. Head with eyes not prominent, separated by distance about five times width of an eye in dorsal view; frontal depressions moderately deep; occipital-frontal crest obtuse. Antennae black. Pronotum black; transverse, about 0.75 times as long as wide; posterior angles broadly rounded; margins not reflexed upwards; pronotal costae distinctly elevated. Pronotal postcoxal lobe black. Elytra black; middle costa of some specimens effaced at basal one-third; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange segment VIII in females. Males with elytral apices abruptly rounded (fig. 31); female apices very slightly prolonged immediately lateral to sutural apex and more evenly rounded.

Notes about synonymy.— *Silpha microps* Sharp is placed in synonymy with *O. anticola* because we find no features on the type which separate it from the description or specimens of *Oxelytrum anticola* from the same general locality.

Natural history and distribution.— The species is known mostly from high elevation open habitats in the Andean countries of Ecuador, Peru, and Bolivia. Portevin (1926) cites the species from Colombia, which is possible, but we know of no records. Adults were collected during the months of December through April and in July. We have seen 17 specimens representing the following records:

BOLIVIA. La Paz, II; El Alto, 4100 m, XII; no date, 2. Oruro, 3700 m. BMNH, USNM.

ECUADOR. Latacunga, I. Machachi, VII. Quito (at Miami in aircraft, quarantine intercept), VII. 16 km N. Quito. Mitad del Mundo, III. PURC, USNM.

PERU. Cajacey, 2650 m, IV. Carumas, 2200 m, IV. Chiquata, near Arequipa, 3100 m, II. Hlancayo (not located), III. Otoyo (not located), 4000 m. Tacana Libra (Totora)(not located), 2. BMNH, FMLC, FMNH, LPMCN, MCZC, USNM.

Oxelytrum lineatocolle (Laporte)
Figures 33, 34; Map 6

Silpha lineatocollis Laporte, (Comte de Castelnau) 1840: 5. Type locality: Chile. Type in: MNHN?, not seen. Fairmaire and Germain, 1859: 350.

Necrodes gayi Solier, 1849: 359: Type locality: Chile. Type in: MNHN?, not seen.

Hyponecrodes lineatocollis (Laporte), Kraatz, 1876: 375.

Hyponecrodes lineaticollis (Laporte), Berg, 1901: 329.

Hyponecrodes (Hyponecrodes) lineatocollis (Laporte), Portevin, 1921: 84.

Silpha (Oxelytrum) lineaticollis (Laporte), Hatch, 1928: 115.

Diagnosis.— Length 15 – 22 mm. Head with eyes prominent, separated by distance about twice width of an eye in dorsal view; frontal depressions present but shallow; occipital-frontal crest acute. Antennae black. Pronotum wholly black to dark brown; transverse, about 0.65 times as long as wide; posterior angles obtusely angulate; margins not or else very slightly reflexed upwards; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black to dark brown; costae continuous throughout; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange anterior portion of segment VIII. Males with elytral apices abruptly rounded (fig. 33); apices in female slightly more prolonged and more evenly rounded (fig. 34).

Natural history and distribution.— The species is known from central Chile and adjacent Argentina. Adults have been collected from October to July, and are associated with both open and forested habitats. We have seen 358 specimens representing the following records:

ARGENTINA. *Neuquen.* Pampa Central, III. *Patagonia.* No other data. "NW Patagonia," 300-900 m. *Rio Negro.* El Bolson, III. BMNH, LPMCN, LACM.

CHILE. *Arauco.* Caramavida, X. Cordillera Nahuelbuta, XII, 4. *Cautin.* Bellavista, Lago Villarrica, 310 m, Valdivian rainforest, XII, 13. 3 km NE Tolten, 3 m, II, 4. Volcan Villarrica, *Nothofagus* forest, 1120 m, XII, 23; 1250 m, XII, 4. *Chiloe.* Chiloe Island. *Concepcion.* Ejido Pinares, XII. Concepcion, III, 3; IV; V, 4. 6 km S San Pedro, 360 m, *Pinus* forest, XII, 101. *Curico.* El Coigo, III. *Llanquihue.* Chamiza, III. Lago Chapo, 11.7 km E Correntoso, 320 m, Valdivian rainforest, XII, 58; 13.5 km e Correntoso, 310 m, Valdivian rainforest, XII, 24. Maullin, I. Petrohue, 600 m, I, 2. *Malleco.* Malalcahuello, 6.5 km E, 1080 m, *Nothofagus* forest, XII, 8; 14 km E, 1570 m, forest, XII. Manzanar, 1100 m, XII. 15 km W Victoria, 200 m, XII, 2. *Maule.* No locality, 1. El Pantanillo, 17 km SE Constitucion, 250 m, XI. *Nuble.* Alto Trequalemu, 500 m, 20 km SE Chovellen, I; XII, 3. Las Trancas, 1400 m, 70 km E Chillan, XII. Termas de Chillan, I. 3 km NE Tolten, 3 m, II, 4. 17.5 km S Curanipe, 50 m, I, 2. *Osorno.* Parque Nacional Puyehue, 600 m, Aguas Calientes, II, 9; Antillanca Rd., 720 m, *Nothofagus* forest, XII, 3; 4.1 km NE Anticura, 430 m, Valdivian rainforest, XII, 16. 15 km W Termas de Puyehue, Rancho Mirado, 205 m, II. 7.7 km NE Termas de Puyehue, 200 m, Valdivian rainforest, XII, 206. No locality, 6. *Santiago.* Leyda, VI. Santiago. *Tarapaca.* Mocha (doubtful record). *Valdivia.* 4.1 km W Anticura, 270 m, Valdivian rainforest, XII, 44. Enco, 120 m, III. Valdivia, X, 5; XII; no date, 5. *Valparaiso.* Quillota, VII, 2. Valparaiso, 6. AFNC, BMNH, CMNH, CNCI, FMNH, GMNH, LPMCN, MNSL, MZUSP, SBPC, USNM.

Oxelytrum emarginatum (Portevin)
Figure 3; Map 7

Hyponecrodes emarginatus Portevin, 1920b: 506. Type locality: Brazil. Type in: MNHN, seen.

Hyponecrodes (Hyponecrodes) emarginatus Portevin, Portevin, 1921: 83.

Silpha (Oxelytrum) emarginata (Portevin), Hatch, 1928: 114.

Diagnosis.— Length 14 – 18 mm. Head with eyes prominent, separated by a distance of about three times the width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Apical antennomere orange. Pronotum with margins orange-red, disc black; transverse, from 0.60-0.65 times as long as wide; posterior angles obtusely angulate; margins reflexed upwards in most specimens; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced near base, middle costa effaced at basal one-third in some specimens; elytral humeri not toothed. Abdomen of males and females with segment IX and apical portion of segment VIII orange-red. Males and females with elytral hind angles abruptly rounded, apex emarginate, the sutural apices prolonged to needle-like points (fig. 32).

Variation.— One female from the Boraceia Biology Station, Salesopolis, Brazil, (MZUSP), has distinctly emarginate elytral apices but only a vaguely orange-red apical antennal segment.

Natural history and distribution.— The species is known to us only from the coastal ranges and highlands of southeastern Brazil. We have seen 11 specimens representing the following records:

BRAZIL. *Minas Gerais.* Sapucai-Mirim, Cidade Azul, 1400 m. Virginia, Faz Campos, 1500 m. *Rio de Janeiro.* Itatiaia. Rio de Janeiro. *São Paulo.* Boraceia, 850 m, X, 3; XI. Pindamonhangaba. Salesopolis, VI. Viradouro. CNCI, MNHN, MZUSP, USNM.

Oxelytrum erythrurum (Blanchard)
Map 7

Silpha erythrura Blanchard, 1840: 75, *in* Brullé and Blanchard, 1840. Type Locality: Montevideo, Uruguay. Type in: MNHN, seen.
Hyponecrodes erythrurus (Blachard), Kraatz, 1876: 376.
Hyponecrodes erythrura (Blanchard), Berg, 1901: 328.
Hyponecrodes (Hyponecrodes) erythrurus (Blanchard), Portevin, 1921: 85.
Hyponecrodes erythrurus var. *melanurus* Portevin, 1926: 129. Type locality: not given. Type in: MNHN?, not seen.
Hyponecrodes (Hyponecrodes) erythrurus var. *pygialis* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.
Hyponecrodes (Hyponecrodes) erythrurus var. *melancholicus* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.
Silpha (Oxelytrum) erythrura (Blanchard), Hatch, 1928: 114.
Hyponecrodes (Hyponecrodes) opacus Portevin, 1921: 83. NEW SYNONYMY. Type locality: Bolivia. Type in: MNHN, seen.
Hyponecrodes (Hyponecrodes) opacus var. *tristis* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.
Silpha (Oxelytrum) opaca (Portevin), Hatch, 1928: 114.

Diagnosis.— Length 10 – 19 mm. Head with eyes prominent, separated by distance about three times width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins orange-red, disc black; transverse, about 0.65 times as long as wide; posterior angles obtusely angulate; margins slightly to strongly relexed upwards in some specimens; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced at very bases, otherwose strongly raised and glabrous; elytral humeri not toothed. Males with abdominal tergum VIII and IX with basal portion orange-red to varying degree; abdominal sternum VIII entirely black. Females with abdominal segment VIII entirely yellow-orange. Elytral apices broadly and evenly rounded in male; slightly prolonged immediately laterally of sutural apices in female. Some males with posteriorly directed lateral expansions of sternite of abdominal segments V and VI, but not appearing as prominent spines as in *O. cayennensis.*

Variation and Synonymy.— The amount of orange coloration on abdominal tergum IX (in males) varies. Portevin used this in establishing varieties. We also find coloration to be related to sex of the specimens, and cannot find any coherent pattern of geographic variation. There is also individual variation in the extent to which elytral costae are effaced. This was the main character used to define *Hyponecrodes opacus* Portevin. Portevin (1921) described the species from only five specimens, supposedly from Brazil and Bolivia. Of these, we have seen only the type, a female. The only distinctive feature we see in it is that it has the second elytral costa completely effaced in the anterior half. It bears the following labels: a square hand written label "Bolivie / Standiger", a square machine printed label "Museum Paris / Coll. A. Grouvelle 1915", a square machine printed label in red type "TYPE", and an apparently recent square label "H. opacus Port". One specimen, labelled *O. opacus*, in the BMNH has narrower first elytral costae in the basal one third than does *O. erythrurum.* Specimens of *O. erythrurum*

from NW Argentina tend to have the second elytral costa more effaced. We conclude that the type of *O. opacum* is within the range of variation we have seen in *O. erythrurum*, and since we know of no other characters to separate it, consider the two names synonyms.

Natural history and distribution.— This species is widespread and apparently common in northern Argentina, Bolivia, southern Brazil, Paraguay, southeastern Peru, and Uruguay. It seemingly occurs in open and forested habitats. Adults have been collected in all months of the southern summer. We have seen 230 specimens representing the following records:

ARGENTINA. *Buenos Aires.* Ajo. Bahia Blanca, XI. Buenos Aires, I, 2; VI, 3; XI; no date, 3. Lago de Gomez, Junin, XII. Lago Monte, San Miguel del Monte, XII. Las Flores, Ciudad, X. La Plata, 23. Palermo, II; III, 4. Punta Lara, X. Rincon de Ajo, 5. San Fernando, XI, 8. Tiore (not located), II. Vitel, N of Chascomus, XI. *Catamarca.* Andalgata. El Manchado, 3000 m, I. El Rodeo, I. Los Hoyos Mesaga (not located), 1700 m, IV, 3. *Cordoba.* Alta Gracia, XI. Cordoba. *Corrientes.* Corrientes, VII. *Entre Rios.* Gualequay. Primero de Mayo, X. *Jujuy.* Digue la Cienaga, III (not located). Estero Uyto, II, 2. Sunchal, IX. *Misiones.* Iquazu, X, 3. No data, I. *Salta.* Capital, II. Coronel Moldes, II, 20. El Corralito, 15 km S Campo Quijano, II, 9. Rio Blanco, Campo Quijano, I, 11. Rosario de Lerma, II, 7. San Antonio, XI. San Lorenzo, I; XI. *Santa Fe.* Rosario, 4. Santa Fe, 3. *Tucuman.* Aguadita (not located), I, 5. Guabatal (not located), I, 2. Infiernillo, III, 6. La Higuera, IV. Parque Aconguija, XII, 2. Rio Los Sosa, 900 m, III, 2. San Pedro de Colalao, I, 3. Siambon, II, 3; III, 6; VII, 2; XII. Tacanas, I, 2; II; XII, 2. Tafi del Valle, II; XI, 16. Tafi, Taficillo, 1500 m, XI. Tucuman, Ciudad Universitaria, II; 11. Tucuman, II, 2. BMNH, CASC, FMLC, FMNH, FSCA, GMNH, LPMCN, MZUSP, SBPC, USNM.

BOLIVIA. La Paz, II. USNM.

BRAZIL. *Mato Grosso.* Maracaju. *Parana.* Curitiba, 900 m, XI. Serrinha Parana, XII, 4. *Rio Grande do Sul.* Pelotas, X; XII, 2. Rio Grande. *Santa Catarina.* No data. *São Paulo.* Sao Paulo, 2. BMNH, CMNH, MCZC, MZUSP, USNM.

PARAGUAY. *Caaguazu.* Paso Yobai (not located), X. *Cordillera.* Caacupe, X, Blacklight. FMLC, RDCC.

PERU. *Junin.* Valle Chanchamayo, 1400 m, IV. FMLC.

URUGUAY. Las Piedras, Canelones, II. Maldonado. Montevideo, II; XI; XII, 2; no date, 2. BMNH, FSCA, GMNH, USNM.

Oxelytrum cayennense (Stürm)
Figures 28, 35, 36; Map 8

Silpha cayennensis Stürm, 1826: 61. Type locality: Cayenne, French Guiana. Type in: Munich?, not seen.
Hyponecrodes cayennensis (Stürm), Kraatz, 1876: 375.
Hyponecrodes (Hyponecrodes) cayennensis (Stürm), Portevin, 1921: 85.
Oxelytrum occidentale Gistel, 1848: 190. Type locality: Brazil. Type in: probably lost.
Oxelytrum aequinoctiale Gistel, 1848: 190. Type locality: Brazil. Type in: probably lost. Madge, 1980: 357.
Silpha (Oxelytrum) cayennensis (Stürm), Hatch, 1928: 115.

Diagnosis.— Length 13 – 19 mm. Head with eyes prominent, separated by distance about two times width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins and most of disc orange-red or yellow, only very middle of disc black; transverse, about 0.6 - 0.65 times as long as wide; posterior angles obtusely angulate; margins not reflexed upwards; pronotal costae present but effaced; pronotal postcoxal lobe entirely orange yellow. Elytra black; inner two elytral costae partially to almost completely effaced from midlength to basal one-third in most specimens, otherwise elevated; elytral humeri each with a single tooth (fig. 28). Males and females with abdominal segment VIII entirely orange-red; abdominal segment VII either black or with orange-red area at middle of apical margin. Males with elytral apices obliquely truncate, sutural angle evenly rounded (fig. 35); apices in female prolonged and sinuate but not sharply pointed (fig. 36). Some males with prominent posteriorly directed lateral expansions of abdominal sternites V and VI which appear as large spines.

Variation.— Specimens vary in extent of orange color on abdominal segment VII and VIII. This was used by Portevin to establish several aberrations. There is also variation in the extent to which the elytral costae are effaced. We have not been able to observe a geographic pattern

in this variation.

Natural history and distribution.— The species occurs over much of northern and central South America. It is most frequently collected in lower to middle elevation rain forest habitats and is active in all months. We have seen 268 specimens representing the following records:

BOLIVIA. *Beni.* Ivon, II. Rosario, Lago Rogagua, X. *Santa Cruz.* Buena Vista, Ichilo, II, 3; XII: no date, 2. Rio Japacani, Santa Cruz de la Sierra, 450 m, 34. CASC, CMNH, MZUSP, USNM.

BRAZIL. *Amapa.* Rio Amapani, VII. Rio Amapai, VIII, 2. Rio Branco, Boa Vista, I. Serra do Navio, X, 5. *Amazonas.* Manaus, INPA Station, VII; X. Maues, II, 3. Reserva Ducke, 26 km ex Manaus, I; III; V, 45. Rio Purus, Hyutanaha. *Mato Grosso.* Reserva Humboldt, Bento Mascarenhas (not located). Serra do Norte (not located), III. Xavantina, gallery forest. *Minas Gerais.* Bello Horizonte, IV. Miscosa (not locaated), XI. *Para.* Cachimbo. *Rio de Janeiro.* Rio de Janeiro. *Rondonia.* V. Rondonia, 378 km S P. Velho, 387 km S P. Velho, I. *São Paulo.* Boraceia, Casa Grande, I, 2. USNM, SBP, INPA, MZUSP, MCZC, UFPB.

COLOMBIA. *Amazonas.* Leticia, rainforest, II. *Cundinamarca.* Bogota, no date, 4. *Norte de Santandar.* 35 km S Cucuta, Quebrada Honda, 700 m, V. 4. SBPC, USNM.

ECUADOR. *Manabi.* 78 km NE Chone, 450 m,, VI, 2. *Napo.* 12 km SW Tena, 500 m, VII, 21. *Pastaza.* Puyo, II, 8. 22 km SW Puyo, 900 m, VII, 5; 22 km W Puyo, II. *Pichincha.* Rio Palenque Station, 47 km S Santo Domingo, rainforest, V, 7. Tinalandia, 16 km SE Santo Domingo, lower montane rainforest 680 m, II, 2; VI, 61. SBPC, USNM.

FRENCH GUIANA. Marioni River, Duserre. Mana River, V. CMNH, USNM.

GUYANA. Bartica. Essequibo River, Morabaldi Creek; Monkey Jump. Kartabo, VIII, 2. Membaro Creek, upper Mazaruni River. Oronoque and New River Heads. BMNH, FMNH, MCZC.

PERU. *Loreto.* Estiron, Rio Ampiyachu, XI, 2. *Junin.* La Merced. Valle Chanchamayo, 800 m, I, 2. BMNH, FMLC, FMNH.

VENEZUELA. *Amazonas.* Mt. Marahuaca, N slopes, V, 9. Peraitepuy, 4. *Aragua.* Rancho Grande, N of Maracay, VI. *Zulia.* Kunana, Perija, 1100 m, Rio Negro, XII, 8. IZAV, USNM.

Oxelytrum discicolle (Brullé)
Figures 1, 3, 15, 37, 38; Map 9

Silpha discicollis Brullé, 1840: 75, *in* Brullé and Blanchard, 1840. Type locality: Altamachi River, near Cochabamba, Bolivia. Type in: MNHN?, not seen.
Hyponecrodes discicollis (Brullé), Portevin, 1905: 50.
Hyponecrodes (Hyponecrodes) discicollis (Brullé), Portevin, 1921: 85.
Silpha (Oxelytrum) discicollis (Brullé), Hatch, 1928: 115.
Necrodes analis Chevrolat, 1843: 26. Type locality: Orizaba, Mexico. Type in: MNHN?, not seen.
Hyponecrodes analis (Chevrolat), Kraatz, 1876: 376. Matthews, 1888: 95.
Hyponecrodes (Hyponecrodes) discicollis var. *elongatus* Portevin, 1921: 84. Type locality: not given. Type in: MNHN?, not seen.
Hyponecrodes (Hyponecrodes) discicollis var. *discretus* Portevin, 1921: 84. Type locality: not given. Type in: MNHN?, not seen.
Silpha (Oxelytrum) discicollis (Brullé), Hatch, 1928: 115.

Diagnosis.— Length 11 – 19 mm. Head with eyes prominent, separated by distance about twice width of an eye in dorsal view (fig. 3); frontal depressions shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins orange-red, disc black; transverse, about 0.6-0.65 times as long as wide; posterior angles obtusely angulate; margins very slightly reflexed upwards in some specimens; pronotal costae present but indistinct. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced at base in most specimens; middle costa partially to completely effaced from midlength to basal one-third in most specimens, otherwise costae elevated; elytral humeri each with a single tooth (fig. 15). Males and females with abdominal segment VIII entirely orange; tergum of abdominal segment VII with orange-red spot of variable size at apical margin, otherwise black. Males with elytral hind angles evenly rounded, sutural angles very slightly prolonged to a sharp point (fig. 37); apices in females slightly prolonged and with sutural spines very slightly longer than in males (fig. 38). Some larger males with lateral margins of abdominal sterna V and VI very slightly produced laterally.

Variation.— The extent of the orange coloration of abdominal segment VII varies within and between sexes of a single population. This variation was used by Portevin to establish aberrations. There is also variation in the extent to which the elytral costae are effaced.

Natural history and distribution.— This is the most commonly collected species of silphid in Latin America. Many adults are attracted to carrion baits, and come commonly at night to ultraviolet and other light traps. The species is distributed from southern Brazil and Paraguay, through much of central and northern South America (but not the lowlands of the Amazon Basin), through Central America, to Mexico and extreme south Texas. Adults have been collected in every month of the year, in habitats ranging from rainforest to montane cloud forest from near sea level to more than 3000 m elevation, and in open semi-arid thorn-scrub vegetation. We have seen 3096 specimens representing the following records:

ARGENTINA. *Misiones.* Cataracas de Iguazu, XI. Eldorado, XI, 2. Iguazu, III, X. FMLC, USNM.

BELIZE. Belmopan, 50 m, rainforest, VIII, 2. 6 km S. Belmopan, VIII, rainforest. SBPC.

BOLIVIA. *Cochabamba.* Alto Palmar, 800 m, X. Chaparé, 1000 m. Cochabamba. Incachaca, 2500 m, 30. *La Paz.* La Paz. Yan(aca)chi (?). *Santa Cruz.* Carahuasi, 250 km E Cochabamba, 3000 m, VII. Santa Cruz, 300 m. Parapeti, X, 4. Yanchi. CMNH, FMLC, MZUSP, USNM.

BRAZIL. *Amazonas.* Tucano, 1500 m, IV, 2. *Bahia.* Salvador, VIII. *Distrito Federal.* Brasilia. Foresta da Tijuca, VIII. *Espiritu Santo.* No data. Guarapari, 3. *Minas Gerais.* Bello Horizonte, IV. Lambari, XI. Laveras, III. Vicosa, III. Serra do Caraca, XI,13; XII, 8. Sapucai-mirim, Cda. de Azul, 1400 m, XI, 2. *Parana.* Banhados (Curitiba to Paranagua), 800 m, II, 34. Fozo do Iguazu, IX, 2; XII, 4. Guaixa (not located), XII. Jaguariaiva, I. Marumbi, II, VI. Quatro Barras, III, 3. Sao Joao, Guayra. S.J. Pinhais (not located), I, 3. *Rio de Janeiro.* Angra dos Reis, IX, 6. Rio de Janeiro, X; no date, 3. Itatiaia, II, 3. Ouro Preto. Petropolis, Km 50 Estrada Contorno, 900 m, XI. Teresopolis, XII. *Rio Grande do Sul.* Cochoeira (not located), X. *Santa Catarina.* Nova Teutonia, III, 4; no date, 11. Rio dos Autos Camayo, I. Rio dos Reis, 3. *São Paulo.* Alto da Serra, IX; 3. Anbembi (not located), 7. Barreiro, Serra do Bocaira, II. Bariero (not located), III. Barueri, I; II; III; VI; XI, 4; XII, 3. Boraceia Station, Salesopolis, 850 m, I, 2; II, 2; III; IV, 4; XII, 2; no date, 14. Campos de Jordao, 13, no date; XI. Jaba-quara, X. Consobacao (not located), II. Faz Campinas, Mogi Guacu, I, 13. Mogi das Cruzes. Iguap, 2. Jpiranga, XI. Pampeia (not located), VIII. Parana Macaba, III. Pindamonhangaba, I, 16; III; IX; X, 9. Porto Cabral, X. Paranapicaba. Piraciacaba, XII, 9. S. Bernando, 2. Santana, II, 6; VI; X; XI; XII, 4. San Jose dos Campos, IX. Opasco, I. São Paulo, 3. Tremembe, III. Ypiranaga, XI; XII, 2. CNCI, FSCA, GMNH, IZAV, MZUSP, UFPB, USNM.

COLOMBIA. Cundinamarca. Bogota, 6. Cajica, I. Sasaima, IV. *Cesar.* Valledupar, 1300 m, 2. *Guajira.* Sierra de Perija, Socorpo Mission, 1400 m, IX, 5. *Magdalena.* Campana, 26 km S Santa Marta, 1050 m, V. El Libano, 1800 m. *Meta.* E of Villavicencio, no date. 23 km NW Villavicencio, Quebrada Suumuco, 1000 m, III, 3. *Narino.* Mallama. *Norte de Santandar.* 2 mi N Chinacota, 900 m, V. 32 km S Cucuta, Quebrada Honda, 600 m, V, 2. *Putomayo.* Santa Rosa, Rio San Miguel. *Quindio.* No data. *Valle.* Km 18 Buenaventura Hwy, I. BMNH, CASC, CMNH, FMNH, FSCA, SBPC, USNM.

COSTA RICA. *Alajuela.* Poasito, Volcan Poas, 1840 m, VII, 14. *Cartago.* Irazu, 1650 m, II; 2200 m, II; 3000 m, IX, 2. Turrialba, III, 2; VIII, 2; IX, 2. *Puntarenas.* Coronado, VI; VII, 4. La Palma (1500 m?), VI. Monteverde, 1400 m, V, 4; VI, 4; VII, 2; 1500 m, II; VI, 2. 21 km NE Potrero Grande, IX, 3. 6 km N Santa Elena, 1400 m, V. *San Jose.* Carillo. San Jose, 1172 m, VIII, 6; 1200 m, I; no date, 2. 14 km N San Isidro; 1600 m, VI. CMNH, CNCI, FSLC, LACM, SBPC.

ECUADOR. *Guayas.* Guayaquil. *Loja,* 2220 m, 7. San Ramon, 27 km WSW, V, 7. *Napo.* Baeza, 2000 m, III, 20. 6 km N Baeza, 2000 m, II, 29. 17 km NE Baeza, 4 km SW Chaco, III, 32. 7 km S Baeza, 2000 m, II, 61. 125 km NW Baeza, 2000 m, III, 2. 24 km NE Baeza, 1200 m, III, 4. *Pastaza.* 1 km E Mera, 1100 m, VII. *Pichincha.* 28 km NE Alluriquin, Chiriboga Road, 1600 m, VI, 8. 3 km E Tandapi, 1300 m, VI, 25. 18 km E Tandapi, 1800 m, VI, 24. 24 km E Tandapi, 2300 m, VI, 60. 16 km E Tandapi, 2000 m, VI, 3. *Tungurahua.* Banos, 1200 m, Mera Trail, IX; 1800 m, IX, 7. 39 km E Banos, I. 6 km E Rio Negro, 1400 m, VII. 8 km E Rio Negro, 1500 m, VII, 13. CASC, SBPC.

EL SALVADOR. 16 km N Metapan, Montecristo, 1760 m, V. SBPC.

GUATEMALA. *Alta Verapaz.* Coban, VI, 2. Patal, 5 km S Tactic, 1350 m, VIII. *Chimaltenango.* Yepocapa, VIII. *Peten.* Pacomon (not located), VI, 2. SBPC.

MEXICO. *Chiapas.* 32 km N Bochil, 1700 m, VIII, 3. Cerro Tres Picos, 2000 m, 5. 8 km SW El Bosque, VI. Montebello Lagunas, VIII. Ocozocuautla, 800 m, 2. Rosario Izapa. San Cristobal de las Casas, V, 2; VIII, 5. Santa Rosa, VIII, 3. *Distrito Federal.* No data. *Durango.* 66 km SW Ciudad de Durango, 2300 m, VI, 15. *Guerrero.* 6.5 km W Miatlan, 1450 m, IX, 3. 12 km W Maystlan, Microondas, 2150 m, IX. *Hidalgo.* 4.5 km N Tlanchinol, 1600 m, VIII, 2. *Jalisco.* 9.5 km W Atenquique, 1700 m, IX, 2. 15 km SW Autlan, 1300 m, IX, 2. 19 km SW Cocula, 1750 m, IX, 2. Los Volcanes, 1650 m, near El Rincon. *Mexico.* 5 km S Temascaltepec, 2000 m, IX, 2; 9.6 km NE, 2150 m, IX, 4. 8 km SW Tenancingo, 2200 m, IX. Valle de Bravo, 1830 m, XI, 2. *Michoacan.* Morelia. Patzcuaro, IX, 2. San Jose Purua, II. Tacambaro. Tancitaro, 1850 m, VIII, 4. Urapan, VIII. *Morelos.* Cuernavaca, I; VII. No data, 2. 12 km E Cuernavaca, VII, 2. *Nayarit.* Tepic, VII, 3. *Nuevo Leon.* Allende. 29 km W Linares, Santo Rosa Canyon, 700 m, oak-thorn forest, VI,

2. Monterrey, Chipinque Mesa, 1350 m, V; VI; VII. Monte Peila, V. 21 km W Montemorelos, Cueva de Chorros de Agua, VI, 5; Chorros de Agua, VI, 291. Rayones, III, 2. *Oaxaca*. 14.5 km E El Camaron 1300 m, IX. Juquila Mixes, 1450 m, VI; VII. Oaxaca, VI; VIII. 14.5 km NE Oaxaca, 1900 m, VII, 24. 147 km N Oaxaca, V. Sierra Madre del Sur, Escondido Road Crest, VI, 28. 24 km S Sola de Vega, 1850 m, V, 5. 13.5 km S Suchixtepec, IV. 5 km N Suchixtepec, 2900 m, VI. 12 km S Valle Nacional, 900 m, V, 18. Temascal, VI. *Peubla*. Cholula. 7 km SW Huauchinango, 1700 m, VII. Villa Juarez, X. *Queretaro*. 29 km E Landa de Matamoros, 1600 m, VI, 2. 32 km W Xilitla, 1600 m, VI, 9. *San Luis Potosi*. 24 km W El Naranjo, 1100 m, VI, 2. Cueva de la Puente, 20 km S San Francisco, 3000 m, V. *Sinaloa*. 62 km NE Concordia, 1900 m, IX. El Palmito, VII, 3; 2200 m, VIII. 7 km NE La Capilla del Taxte (not located), VI, 2. *Tamaulipas*. 7 km W El Encino, III, 6. Gomez Farias, Rancho del Cielo, cloud forest, 1000 m, 1150 m, VI; VII, 19. Sotano de las Salas, I. *Veracruz*. Catemaco, V, 2. Chocaman, VII. Cordoba, I, 2; II, 3; III; VII, 3; VIII, 3; IX, 6; XII; no date, 3. 7 km N Huatusco, 1300 m, VII; VIII, 3. Jalapa, V, 2; VI, 2; VII, 2; no date, 8. Orizaba, I; XI, 3; XII, 6. Perote, V, 2. Presidio, X. Rio Metlac, near Fortin, 1000 m, VI, 2; VII, 40. Sumidero, near Fortin, 750 m, V, 6. 22.5 km S Tlapacoyan, 120 m, VII. Cueva de Tlilapan, 5 km S Orizaba, VIII. BMNH, CASC, CNCI, FMNH, ITMM, LACM MHNM, RDCC, SBPC, TMMC, USNM, UTDZ.

NICARAGUA. Chontales. BMNH.

PANAMA. *Bocas del Toro*. 20 km SE Chiriqui Grande, 900 m, VI, 7. *Chiriqui*. Boquete, IX, UV Light, 5. Boquete, Alto Lindo, VII, 2; IX, UV light, 8. 5 km W Boquete, El Salto Road, 1610 m, VI, 3. 10 km W Cerro Pando, V, 39. 2 km W Cerro Punta, 1760 m, V, 2; VI, 159. 2 km E Cerro Punta, 2200 m, VI, 37. La Fortuna Dam, 800 m, VII, 11; 1000 m, VII, 4. 4 km W Hato del Volcan, 1360 m, VI, 301. Lagunas, 5 km SW Hato del Volcan, 1360 m, VI, 273. 2 km N Santa Clara, Hartman Finca, 1200-1500 m, V, 375; VI, 41. Volcan de Chiriqui, 1200-1900 m, 4. BMNH, GMNH, SPBC, USNM.

PARAGUAY. *Alto Parana*. Puente Stroessner, VIII, 8. *Caaguazu*. Paso Yobai (not located), X. *Itapua*. Trinidad, X. *Misiones*. Loreto, VI, 5; X, 2. No location, 2. *Paraquari*. Parque Nacional Ybycui, I, 4. *Parana*. Iguazu, X. *San Pedro*. Carumbe (not located), II. FMLC, GMNH, LPMCN, RDCC.

PERU. *Cuzco*. Cuzco, VIII. Marcapata, Hacienda Cadena, VIII. *Huanuco*. N side Cerro Carpish, nr. Chinchao, 1920 m, montane rainforest, I, 2. *Junin*. Perene, 600-900 m. Valle Chanchamayo, 1400 m, I; II. *La Libertad*. Samne, 1500 m, VII. *Pasco*. Huancabamba, 3000 m, 2. *Ucayali*. Sinchono (=Fundo Chinchona), 1300 m, V. La Divisorio, 1400 m, V. AFNC, FMLC, USNM.

VENEZUELA. *Aragua*. Camp Rangel, VII. Choroni, V; Km 27, VI, 2; Km 25, III, 2; 9000 m, X, 10. Rancho Grande, N of Maracay, 1100 m, I, 2; II, 78; III, 7; IV, 4; V, 9; VI, 27; VII, 5; VIII, 26; IX, 1; X, 2; XI, 2; XII, 5; 1500 m, II, 6; 1700 m, V. *Bolivar*. El Dorado - Santa Elena, Km 107, 520 m, VIII, 10; Km 109, VIII, 3; Km 38, 160 m, VIII; Km 125, 1100 m, IX, 3. *Carabobo*. Borburato, III, 2. *Districto Federal*. Caracas, Quebrada de Catuche, VI. Caracas. El Avila, 1400 m, X. El Junquito, 1900 m, VI, 7. El Limon, 1350 m, VI, 14. Macizo, Naiguanta, IX. *Lara*. Terepaima (not located), XI. *Merida*. Merida, 5; La Pedregosa, 1800 m, IX, 4. Mucay (not located), IX. Santa Rosa, X, 2. *Miranda*. Fila de Mariche (not located), 1200 m, III. San Antonio de los Altos, 1300 m, IV; V; VII; VIII, 28; IX, 31. *Sucre*. Carripana (not located), VI. *Tachira*. San Cristobal, 1200 m, VIII, 7. 20 km NE San Cristobal, 1200 m, V, 11. 38 km NE San Cristobal, 2150 m, V, 12. *Trujillo*. Bocano, VIII, 16. *Yaracuy*. San Felipe. CMNH, CBMV, IZAV, MZUSP, SBPC, USNM.

UNITED STATES. *Texas*. Willacy County, Lyford, VI (record in Davis, 1980). This is the only known United States record.

SUBFAMILY NICROPHORINAE

NICROPHORUS FABRICIUS 1775

These large insects are commonly called burying or sexton beetles. About 85 species are known in the genus throughout the world. Most live in Europe and Asia. In the Old World, they occur only as far south as Ethiopia in Africa and in southern Asia to New Guinea and the Solomon Islands. Fifteen species live in the United States and Canada. Nine species are known in Latin America, from Mexico southward to southern Chile and Argentina.

Key to species of *Nicrophorus* in Latin America

1		Posterior lobe of metepimeron (fig. 39) with many long golden hairs 2	
1′		Posterior lobe of metepimeron with only a few dark hairs or glabrous 3	
2	(1)	Anterior face of procoxa with short hairs; elytral maculations large (figs. 2, 45, 48) . . . . *N. marginatus* Fabricius, p. 266	

Nicrophorus marginatus Fabricius
Figures 2, 4, 45, 48; Map 10

Diagnosis.— Length 15 – 22 mm. Pronotum markedly cordate, with narrow lateral margins and wide basal margin (fig. 2). Anterior face of procoxa with short black hairs. Apical four antennomeres orange-red. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibiae slightly curved. Elytron with epipleural ridge long, extending to about level of base of scutellum (figs. 45, 46); dorsal surface lacking hairs; elytron with pattern as in figures 2, 45, 48.

Natural history and distribution.— The species is widespread in open grassland, old field, and shrubby habitats from southern Canada and most of the United States into northern Mexico (Anderson and Peck, 1985). Adults have been collected throughout the summer months. We have seen the following 17 records:

MEXICO. *Coahuila.* 14 km NW Saltillo, VII. Parras. Rancho Encantada, Sierra de la Encantada, VII. *Distrito Federal.* Mexico City. *Durango.* Villa Lerdo. 32 km E El Salto, 2400 m, VI, 9. *Puebla.* Cholula, Esperanza. *Veracruz.* Jalapa. BMNH, CNCI, SBPC.

Nicrophorus guttula Motschulsky
Figures 40-44; Map 10

Necrophorus guttula Motschulsky, 1845: 53. Type locality: Sitka, Alaska. Type: in Leningrad?, not seen. Miller and Peck, 1979; Peck and Miller, 1982; Anderson and Peck, 1985

Diagnosis.— Length 14 – 20 mm. Pronotum markedly cordate, with narrow lateral margins and wide basal margin. Anterior face of procoxa with long black hairs. Apical three antennomeres orange-red or black. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescecne. Hind tibiae slightly curved. Elytron with epipleural ridge long, extending almost to level of base of scutellum (figs. 40a, 44a). Elytral pattern various, as in figures 40-44.

Taxonomic notes and distribution.— The species is widespread in dry forests and grasslands in southwestern Canada and the western United States. The more conspicuously maculate individuals were formerly called *N. hecate* Bland (Peck and Miller, 1982). Border records indicate that the species probably occurs in northwestern Mexico. We know only of the following record:

MEXICO. *Baja California.* Valle de Trinidad, Aguajito Spring, III, 3, SDMC.

Nicrophorus mexicanus Matthews
Figures 46, 54; Map 11

Necrophorus mexicanus Matthews, 1888: 91. Type locality: Mexico. Type in: BMNH, seen.

Diagnosis.— Length 14 – 18 mm. Pronotum quadrate, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescense dense, dark brown; metepimeron with small tuft of dark brown hairs. Hind tibiae straight. Elytron with epipleural ridge long, extending almost to level of base of scutellum (fig. 46); dorsal surface lacking hairs. Elytron with pattern as in figure 54.

Natural history and distribution.— The species occurs in habitats ranging from semi-arid and open thorn scrub to moist closed-canopy cloud forests in the southwestern United States, through Mexico, to Guatemala and El Salvador. Over its southern range, adults have been collected in all months of the year. Zaragoza and Pérez (1975) give a morphometric and seasonal analysis based on 436 specimens collected in black light traps over three years near Mexico City. They report *N. mexicanus* to be most abundant in October. Reproductive behavior has been studied by Halffter *et al.*(1982). We have seen 127 specimens representing the following records:

EL SALVADOR. Montecristo, 23 km N Metapan, 2300 m, cloud forest, V, 8. SBPC.
GUATEMALA. *Zacapa.* Jabah, S slope Sierra Minas, VII. FMNH.
MEXICO. *Chiapas.* 5 km W San Cristobal de las Casas, 2440 m, IX, 2. *Chihuahua.* Mesa del Huracan, 2557 m, VII, 4. Nuevo Casas Grandes, 20 km SE, Hwy 10, 1700 m, VIII. Sierra de la Catarina, 30 km SW Buenaventura, 2600 m, VIII, 9. Sierra de Choreachic, Microwave Sta. Hwy 16, 30 km W Cuauhtemoc, 2500 m, VIII. Sierra Huachinera, 30 km SW Colonia Juarez, 2200 m, VIII, 3. *Distrito Federal.* Lomas, V. Mexico City, V. No locality, III. *Durango.* 5 km W El Salto, 2745 m, VI, 15; VII, 8. 16 km W El Salto, 2745 m, VI; VII, 16; VIII. 66 km SW Durango, 2250 m, VI, 2. Ciudad de Durango, 1800 m, IV. 38 km W La Ciudad, VII, 20. 32 km E El Salto, 2400 m, VI, 5. 54 km E El Salto, 2100 m, IX, 5. *Guerrero.* 12 km W Mazatlan, 2130 m, IX, 3. *Hidalgo.* Guerrero Mills. 10 km S Tenango de Doria, 3000 m, VII, 5. *Mexico.* Ayolta. *Nuevo Leon.* Galeana, 2217 m. Iturbide, 1800 m, VII, 3. *Oaxaca.* La Parada. Sierra Madre del Sur, Escondida Road Crest, VI. 5 km N Suchixtepec, 2850 m, VI. Yolotepec. Road to Yuvila, 2430 m, VIII, oak-pine forest, 2. *Tamaulipas.* Gomez Farias, Rancho del Cielo, 2000 m, XII. *Tlaxcala.* 3 km S Apizaco, pine forest, VI, 3. BMNH, CNCI,

FMNH, LACM, MCZC, MHNM, OSUC, SBPC.

Nicrophorus nigrita Mannerheim
Map 10

Necrophorus nigrita Mannerheim, 1843: 251. Type locality: California. Type: in Helsinki?, not seen. Miller and Peck, 1979; Anderson and Peck, 1985.

Diagnosis.— Length 13 – 18 mm. Pronotum quadrate, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescense dense, dark brown; metepimeron glabrous. Hind tibiae straight. Elytron with epipleural ridge long, extending almost to level of base of scutellum; dorsal surface lacking hairs. Elytron wholly black.

Natural history and distribution.— The species occurs in drier forests on the Pacific coast from British Columbia to southern California, including the Channel Islands (Miller and Peck, 1979). Horn (1876, 1880) lists the species from Guadalupe Island, Baja California. We know of only the following Mexican records:

MEXICO. *Baja California*. Guadalupe Island, 5 (not shown on map). 10 km E El Rosario, uv light, III. MCZC, UICM.

Nicrophorus quadrimaculatus Matthews
Figures 49, 55; Map 12

Necrophorus quadrimaculatus Matthews, 1888: 93. Type locality: Guatemala. Type in: BMNH, seen.

Diagnosis.— Length 9 – 16 mm. Pronotum orbicular with wide lateral and basal margins (fig. 55). Apical three antennomeres orange-red. Metasternal pubescense moderately dense, dark brown; metepimeron with long dark brown hairs. Hind tibiae very slightly curved. Elytral epipleural ridge short (as in fig. 47); dorsal surface of elytron with long, dense hairs. Elytron with pattern as in figure 49. Metatrochanter with sharp spine.

Natural history and distribution.— The species ranges from southern Mexico to western Panama. Adults have been collected only from June to September, and only in montane pine or cloud forests. We have seen 52 specimens representing the following records:

COSTA RICA. *Puntarenas*. Monteverde, 1400 m, VI; VII, 2; IX; 1520 m, VII; 1700 m, V. No data, 2. BMNH, CMNH, LACM, SBPC.

EL SALVADOR. 16 m N Metapan, Montecristo, 1760 m, mixed pine forest, V, 2. SBPC.

GUATEMALA. *Alta Verapaz*. 6 km S Coban, 1373 m, VIII, 5. Patal, 5 km S Tactic, 1373 m, VIII. Senahu, 1098 m, VIII. *Baja Verapaz*. San Jeronimo. *Quezaltenango*. Volcan Zunil. BMNH, SBPC.

MEXICO. *Chiapas*. Lagunas de Montebello, 1373 m, VIII. 1 km SW Rizo de Oro, 834 m, VIII. SBPC.

PANAMA. *Chiriqui*. 4 km N Santa Clara, Cerro Pelota, Hartman Finca, 1200 m, V; 1500 m, V, 20; VII, 6; VIII, 5. SBPC.

Nicrophorus didymus Brullé
Figure 50; Map 13

Nicrophorus didymus Brullé, 1840: 73. *in* Brullé and Blanchard, 1840. Type locality: Altamachi River, eastern mountain slopes, Cochabamba, Bolivia. Type in: MNHN?, not seen. Berg, 1901: 326; Portevin, 1903: 331.
Nicrophorus didymus var. *peruvianus* Pic, 1917: 2. Type locality: Peru. Type in: MNHN?, not seen.
Nicrophorus flexuosus Portevin, 1924: 191. Type locality: not given. Type in: MNHN?, not seen. Hatch, 1928: 128.
Nicrophorus flexuosus var. *portevini* Pic, 1933: 6. Type locality: Merida, Venzuela. Type in: MNHN?, not seen.

Diagnosis.— Length 13 – 16 mm. Pronotum orbicular with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescense moderately dense, dark brown; metepimeron with few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to base of scutellum; dorsal surface with long and

moderately dense hairs. Metatrochanter with spine reduced or absent. Elytra with pattern as in figures 50a, 50b.

Variation.— Many elytral patterns have received varietal and aberrational names. The elytral maculations vary from two distinct bars to four distinct spots (a pair of spots forming from a color bar) on each elytron. We have not seen a pattern of geographic variation in such coloration.

Natural history and distribution.— The species occurs in middle to upper elevation Andean forests from Venezuela through Colombia, Ecuador, and Peru to Bolivia. We believe literature records for the species from Mexico, Central America, and Argentina pertain to other species. Adults have been collected during eight months of the year. We have seen 76 specimens representing the following records:

BOLIVIA. *Cochabamba.* Incachaca, 2300 m. MCNH.

COLOMBIA. *Antioquia.* Medellin. *Magdalena.* Rio Don Amo, 600 m, VII. Rio Don Diego, 36 m, VII. No other data. BMNH, CMNH.

ECUADOR. *Napo.* 7 km S Baeza, 2000 m, II, 2. El Chaco, 2000 m, II. *Province Unknown.* Mangosia River (not located), 650 m. BMNH, SBPC.

PERU. *Huanuco.* N side Cerro Carpish, near Chinchao, cloud forest, 2300 m, I, 24; 2400 m, I. *Pasco.* Oxapampa, 1800 m, I. Pozuzo (10°4'S 75°32'W). AFNC, FMLC, SBPC, USNM.

VENEZUELA. *Aragua.* Cerro Choroni, 1600 m, II. Rancho Grande, N of Maracay, 1500 m, II, 8; V; VIII, 2; XII. Maracay to Choroni, 1000 m, XII; 1300 m, XII. *Districto Federal.* Caracas, no data. Caracas, Rio Caurimare, 1000 m, V, 7. El Junquito, VI; X. El Limon, 1350 m, VI, 5. *Lara.* Cabudare, Terepaima Creek, 1200 m, I. *Tachira.* San Cristobal, 1200 m, VIII, 17. *Trujillo.* Bocono, VIII. *Zulia.* Sierra de Peria, Kunana, 1100 m, XII. BMNH, CBMV, IZAV, SBPC.

Nicrophorus chilensis Philippi
Figure 51; Map 14

Necrophorus chilensis Philippi, 1871: 293. Type locality: Santa Cruz, Curico, Chile. Type in: MNSC, holotype no. 171, not seen.

Diagnosis.— Length 13 – 16 mm. Pronotum subquadrate with wide lateral and basal margins. Apical three antennomeres black. Metasternal pubescence dense, dark brown; metepimeron glabrous. Hind tibiae straight. Elytron with epipleural ridge short, not extending to level of apex of scutellum; dorsal surface lacking hairs. Metatrochanter with sharp spine. Elytron with fasciae confluent and large, pattern as in fig. 51.

Variation.— The anterior and posterior elytral maculations of some specimens are joined and may be so large that the black area is reduced to only the extreme anterior and posterior sutural margins of the elytra.

Natural history and distribution.— The species apparently occurs in open and semi-arid areas of central Chile and adjacent Argentina (Peña, 1981), as well as in *Nothofagus* and *Arucaria* forests of Chile. Adults are seemingly active from November to March. We have seen only 19 specimens representing the following records:

ARGENTINA. *Neuquen.* Lago Tramen, 1000 m, III; XI; XII. San Martin de los Andes, XII. *Tucuman.* Tucuman (questionable location). *Locations Unknown:* "Patagonia", no data, 4. "Pampas", no data. "Salinas Chicas", no data (in Berg, 1901). LPMCN.

CHILE. *Curico.* Cordillera de Teno. *Malleco.* 6.5 km E Malalcahuello, 1080 m, *Nothofagus* forest, XII. 14 km E Malalcahuello, 1570 m, *Nothofagus* and *Aurucaria* forest, XII. Laguna Jesus-Maria and Pino Hachado (records of Peña, 1981). *Maule,* No data, 3. *Valdivia.* No data. No locality, 2. AFNC, BMNH, MNSC, SBPC.

Nicrophorus olidus Matthews
Figure 52; Map 15

Necrophorus olidus Matthews, 1888: 92. Type locality: Mexico. Type in: BMNH, seen.

Diagnosis.— Length 10 – 14 mm. Pronotum orbicular with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescense moderately dense, dark brown; metepimeron with a few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to apex of scutellum; dorsal surface with long dense hairs. Metatrochanter with sharp spine. Elytra with pattern as in figure 52.

Natural history and distribution.— The species is known only from Mexico north of the Isthmus of Tehuantepec. Adults have been collected from May to November. It occupies open forests, cloud forests, and rainforests. We do not accept Portevin's (1926) statement that the species occurs in Central America and Colombia. We have seen 267 specimens representing the following records:

MEXICO. *Durango.* 66 km SW La Ciudad de Durango, 2250 m, VI, 6. Revolcaderos, VII, 3 (location unknown). *Guerrero.* Omilteme. Xucamanatlan. *Hidalgo.* 10 km S Tenango de Doria, 3000 m, VII, 2. *Jalisco.* Ajijic, 1567 m, V, 3; XI, 2. 9.5 km W Atenquique, 1677 m, XI, 12. 13 km W Atenquique, 1799 m, IX. 15 km SW Autlan, 1312 m, IX, 30. 19 km SW Cocula, IX, 6. El Rincon, Los Volcanes, 1647 m. Cd. Guzman (L. de Zapotlan). *Mexico.* 5 km NE Temascaltepec, 1922 m, IX, 5. 9.6 km. NE Temascaltepec, 2135 m, IX, 2. Tenancingo, 2165 m, IX. *Morelia.* 12 km E Cuernavaca, VII. *Nuevo Leon.* Iturbide, 1800 m, VII, 2. 26 km W Linares, 671 m, V. *Oaxaca.* 11 km E Hautla. Juquila Mixes, XI, 4. 14.5 km NE Oaxaca, 1891 m, VIII, 7. 84 km S Oaxaca, V, 2. Sierra Madre del Sur, Escondido Road Crest, VI, 14. 24 km from Sola de Vega, 1830 m, V. Suchixtepec. 21 km S Valle Nacional, 1098 m, VII, 16; VIII, 8. 24 km S Valle Nacional, 1220 m, V. *Puebla.* 7 km SW Huachinango, 1700 m, VII, 2. Nuevo Necaxa, VII, 3. *Queretaro.* 29 km E Landa de Matamoros, 1617 m, VI, 3. 32 km W Xilitla, VI. *San Luis Potosi.* 17.5 km W El Naranjo, 960 m, VI, 25. 20 km W Xilitla, 1600 m, cloud forest, VI-VII, 3. 22.5 km W Xilitla, 1312 m, VI, 3. *Tamaulipas.* 10 km W El Encino, 2000 m, cloud forest, VII. Gomez Farias, 300 m, tropical deciduous forest, VI-VIII, 34; Rancho del Cielo, cloud forest, 1000 m, VI-VIII, 25; 1129 m, VII, 27. *Veracruz.* Cordoba. Tuxtla. 1.9 km S Huatusco, 1344 m, VIII, 2. 7 km N Huatusco, 1281 m, VIII, 3. 8 km W San Andres Tuxtla, VII.

Nicrophorus scrutator Blanchard
Figure 53; Map 14

Necrophorus scrutator Blanchard, 1840: 74, *in* Brullé and Blanchard, 1840. Type locality: Bolivia. Type in: MNMN?, not seen.

Diagnosis.— Length 17 – 22 mm. Pronotum orbicular, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence dense, dark brown; metepimeron with a few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to level of scutellar apex; dorsal surface with only a few long hairs, majority confined to lateral margins. Metatrochanter with spine reduced, broadly rounded. Elytron with pattern as in figure 53.

Variation.— A single specimen from Machu Pichu, Peru (in MZUSP) has an epipleuron with slightly more than the anterior half orange-red and the two fasciae on each elytron are confluent along the epipleural margin. This specimen also has typical brownish metasternal pubescence and the last three antennal segments are orange-red.

Natural history and distribution.— The species occurs in Peru, Bolivia and northwestern Argentina, seemingly in both open semi-arid and moist forested habitats. It is active from October to April. We have seen 40 specimens representing the following records:

ARGENTINA. *Catamarca.* Andalgala, 4. Cuesta Mina Capillas (not located), 3200 m, II. Las Estancias (not located), I. San Angelo (not located), II. *Jujuy.* Jujuy, II. Volcan. *Misiones.* No data, questionable record. *Salta.* Anta, XII. 20 km N La Caldera, El Ucumar, 780 m, I; II. Cerillos, 1200 m, X. *Tucuman.* Ciudad Universitaria, San Javier, Tucuman, II. Horco Molle, 12 km W Tucuman, 700 m, I. Infiernillo, III. Mala-Mala, 2000 m, IV. Parque Aconquija, IV. Quebrada de Lules, III, 3; XII. Rio Pueblo Viejo, 1000 m, humid forest. San Pablo, 1200 m, 2. Siambon, II; VII. Tafi Viejo. Tucuman, VI; no date, 2. Villa Nouques, V; XII. Villa P. Mont, Burrayacu. BMNH, FMLC, LPMCN, SBPC.

BOLIVIA. *Chuquisaca.* La Laguna, Neubo Mundo Mountains, XII (Brullé and Blanchard, 1840). Tiguipa, IV. *Pando.* Rio Negro, II, doubtful record. *Santa Cruz.* Valle Grande (between Chilan and Tasajos, X (Brullé and Blanchard, 1840: 74). No data, 2. BMNH, MNHN.

PERU. *Cuzco.* Machu Pichu, 2600-2800 m, VII. MZUSP.

PHYLOGENY AND ZOOGEOGRAPHY

In this section we discuss the phylogenetic and geographic relationships of the Latin American silphid fauna and propose hypotheses about its origin.

RECONSTRUCTED PHYLOGENY OF *OXELYTRUM*

Ranges of all silphines of Latin America (listed in table 1), except *Oxelytrum*, extend into Mexico from the north and terminate at or before the southern edge of the Mexican Neo-Volcanic Plateau. Of these genera, only *Heterosilpha* is endemic to North America. All other genera have the majority of their species and ranges in Eurasia. A phylogenetic analysis of these genera can best be accomplished by including the Palearactic and Oriental species and will not be attempted here.

We do, however, present a reconstructed phylogeny for all members of the wholly New World genus *Oxelytrum* (fig. 56). *Oxelytrum* is identified as a monophyletic group on the basis of possession of the derived character state of presence of coxal spines or tubercles. Two lineages, each including four species, are recognized within *Oxelytrum*. One lineage, the *lineatocolle* group, is characterized by the derived character state of a black pronotum. It is associated with western coastal lowland and Andean montane habitats. Members of the other lineage, the *emarginatum* group, share the derived character state of a pronotum with reflexed margins, and a generally very similar overall habitus. It is associated with eastern and northern montane and lowland habitats.

The character analysis uses only adult characters (table 3) and is based on out-group comparison with the silphine genus *Ptomaphila* of Australia and New Guinea. These two genera are considered to compose a monophyletic group based on their shared possession of the derived character states of long hairs on the underside of the elytra near the apical callus, and a pronotum with elevated costae. These character states appear in no other Silphinae. We interpret these two genera as otherwise comparatively primitive, of great antiquity and derived from a common Gondwanaland ancestor.

Oxelytrum characters.— Characters used are those of taxonomic value. Whether all such characters are valuable as indicators of phyogenetic relationships is questionable. Characters have not been objectively weighted. As virtually all characters have unknown biological significance, it is not known how prone they are selective pressures promoting homoplasy. Nevertheless, gross inferences have been made concerning the degree of homoplasy expected in each character (Table 3).

Character 1, pronotum–dorsal surface. Two character states have been identified. Because elevated costae are not known in other Silphinae aside from *Oxelytrum* and *Ptomaphila* this state is interpreted as apotypic and of high weight.

Character 2, elytra–undersurface. Two character states have been identified. Because long hairs in the region of the apical callus are unknown in other Silphinae this state is interpreted as apotypic and of high weight.

Character 3, elytra–apex. Two character states have been identified. An internal flange is well-developed in members of *Ptomaphila* and lacking in *Oxelytrum* species. No other Silphinae possess such a feature, considered here as apotypic, although development of similar structures do occur in other Coleoptera probably as means of locking the elytra together at the

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apex.

Character 4, head–frons. Three character states have been identified although there is variation in the degree to which the frons is swollen. In most other Silphinae, the frons is uniformly swollen while in *Oxelytrum* species a "v-shaped" swollen area (chevron) is present. *Ptomaphila* species lack any degree of swelling on the frons. Because the frons is swollen in members of Nicrophorinae, lack of or reduction in swelling is interpreted as apotypic. Tendency towards reduction in swelling could also be interpreted as further evidence of sister-group relationship between *Oxelytrum* and *Ptomaphila*.

Character 5, elytra–dorsal surface. Two character states have been identified although within species of *Oxelytrum* and other Silphinae, there is variation in the degree of elevation of costae. Presence of tubercles arranged linearly in place of costae (latter are only vaguely defined) is interpreted as apotypic. Linearly placed tubercles are lacking in all other Silphinae although tubercles interspersed between costae are known in species of *Thanatophilus*.

Character 6, elytral epipleuron–width. Two character states have been identified. Because a narrow epipleuron is found in most Silphidae this state is considered plesiotypic.

Character 7, coxae–ornamentation. Two character states have been identified: lack of any ornamentation and, presence of ornamentation as tubercles or spines. Because spines and tubercles are not known in other Silphinae, presence of these structures is considered apotypic.

Character 8, pronotum–color. Four character states have been identified. Because members of *Ptomaphilia* possess a pronotum with the margins orange-red and disc black, presence of this state in *Oxelytrum* species is considered plesiotypic. An entirely black pronotum is interpreted as apotypic. Presence of a black pronotum with the posterolateral corners orange-red is interpreted as autapotypic and derived from an entirely black pronotum. A fourth character state is represented by a reduction in the size of the central black spot on the disc. Pronota with colored margins are known in species of other silphine genera but it is not known if they represent symplesiomorphy or secondary apotypic developments. Although the sole basis for recognizing monophyly of the *lineatocolle* group, it should be emphasized that this is a character likely prone to convergence and should thus be considered accordingly.

Character 9, eyes–size. Two states have been identified. Because large eyes are found in species of *Ptomaphila*, this state is considered plesiotypic. Eye size is undoubtedly correlated with diel activity patterns. Nocturnal species have large eyes; diurnal species small eyes. Accordingly this character is extremely prone to homoplasy and should be weighted accordingly.

Character 10, pronotum–posterior angles. Two states have been identified. Because obtuse angles are known in species of *Ptomaphila* and most other Silphinae, this state is considered plesiotypic.

Character 11, female genitalia–stylus. Two states have been identified. Because aberrant scoop-like styli are unknown in any other Silphinae, they are considered apotypic. Whether the modification of the styli represents a change in oviposition habits is not known.

Character 12, coxae–ornamentation. Two states have been identified. Spines and tubercles on the coxae are not known in other Silphinae. Presence of spines is considered apotypic because they represent a likely progression from an ancestor which possessed tubercles, the plesiotypic state. Consideration of spines as apotypic is also compatible with distribution of states of character 11 and with overall similarity of members of the group being defined.

Character 13, pronotum–margins. Three states have been identified. Because flat or deflexed pronotal margins are known in other Silphinae, including *Ptomaphila*, reflexed

margins are considered apotypic. States of this character represent apparently simple changes and are probably prone to homoplasy. Distribution of states of this character is the sole basis for recognizing the monophyly of the *emarginatum* group, and the latter should be considered accordingly.

Character 14, abdominal segments of male–lateral margins. Two states have been identified although there is variation in species of *Oxelytrum* in the prominence of the lateral projections. Because lateral projections are unknown in other Silphinae, their occurrence in species of *Oxelytrum* is considered apotypic. The reduced prominence of the projections in *O. discicolle* are interpreted as secondarily reduced and autapotypic.

Character 15, elytra–humeri. Two states have been identified. Toothed humeri are known in some species of *Oiceoptoma*. However, they are not known in *Ptomaphila* or other Silphinae and thus likely represent independent developments. Presence of a tooth on the humerus in species of *Oxelytrum* is therefore considered apotypic but possibly homoplasous.

Character 16, pronotum–color. Four states have been identified. Two of these have been considered previously. A pronotum with the central black spot markedly reduced in size is considered apotypic, derived from a similarly colored pronotum with the black spot larger in size.

RECONSTRUCTED PHYLOGENY OF *NICROPHORUS*

We present here a phylogenetic analysis of the relationships of all species of *Nicrophorus* in the New World (listed in table 2), based upon both adult and, where available, larval characters (tables 4-7 and figures 57-60). Larval characters and interpretations of their polarity are from Anderson (1982a). The adult characters, habitats, and distributions of the Nearctic species are from Anderson and Peck (1985), and are interpreted for the first time here. Polarization of all larval and adult character states in *Nicrophorus* are based on out-group comparison with the Asian genus *Ptomascopus*, the only other genus in the subfamily Nicrophorinae. We also make predictions about phylogenetic affinities of some *Nicrophorus* species which are testable by the discovery and description of their larvae.

Since only New World species of *Nicrophorus* are considered, the cladograms may require subsequent modification when Old World species are included. This will be especially so if the New World component of a particular species group is found not to be monophyletic. Hatch (1927) gives a start at an evolutionary analysis, but his assignment of *Nicrophorus* species into groups was based on shared ancestral characters (symplesiomorphies) and on characters which we believe are subject to convergence. We agree with his placement of some species, but dispute others. Since we have not carefully studied many Palearctic species, we refrain from including any of these in our delimited species groups although we think that at least some Palearctic species are easily placed in our groups. We do not attempt to demonstrate relationships between species groups. This can only be reliably accomplished following examination of all *Nicrophorus* species.

The *orbicollis* group
This species group is characterized by the uniquely derived adult character states of a short elytral epipleural ridge and by most members having prominent hairs on the dorsal surface of the elytra. We place six New World species in this group and propose phylogenetic relationships as in table 4 and figure 57. Larvae of all Latin American species are undescribed.

orbicollis group characters.— Character 1, elytral epipleuron–length. Two character states have been identified. Because a long elytral epipleuron occurs in *Ptomascopus* species and Silphinae, this state is considered plesiotypic. A short epipleuron is also known in some southeast Asian species of *Nicrophorus*, however the relationships of these species to members of the *orbicollis* group have yet to be assessed.

Character 2, pronotum–shape. Four character states have been identified in *Nicrophorus* species. For *Nicrophorus*, a cordate pronotum is considered plesiotypic because this is the state which occurs in species of *Ptomascopus*. Among subquadrate, quadrate and orbicular pronta, we hypothesize the subquadrate condition as plesiotypic, directly derived from a cordate pronotum. We believe that quadrate and orbicular pronota each represent unique apomorphic states derived directly from the subquadrate state. Alternative interpretations are perhaps equally likely concerning the position in the transformation series of the orbicular pronotum. Alternatively, this state could be directly derived from the primitive cordate state. We find the former alternative to be most compatible with distribution of states of other characters.

Characters 3,5,6 elytron–vestiture of dorsal surface. Five character states concerning the nature ofthe dorsal vestiture have been identified in *Nicrophorus* species. A dorsal surface with very few or no hairs is considered plesiotypic because this state also occurs in species of *Ptomascopus*. We hypothesize increasing density of the hairs as increasing degrees of apotypy. Hairy elytra are also known in some southeast Asian species of *Nicrophorus*. However, the relationships of these species to members of the *orbicollis* group have yet to be assessed.

Character 4, metatrochanter–ornamentation. Two states have been identified in *Nicrophorus* species. Because a metatrochanter with a sharp, well-developed spine is known in other *Nicrophorus* and *Ptomascopus* a reduced, blunt spine is considered apotypic.

Character 7, elytral epipleuron-vestiture. Three character states have been identified in *Nicrophorus* species. Because an epipleuron with a few short hairs is known in *Ptomascopus* species, this state is considered plesiotypic. Occurrence of a densely hairy epipleuron is probably correlated with a densely hairy elytral dorsal surface, and is considered apotypic.

New World members of this group are associated with forested or open habitats in both North and Latin America. This species group appears to have its center of diversity in Latin America, with only one New World species being distributed north of Mexico. All species of *Nicrophorus* known from southern Central and South America belong to this group. This may indicate that the group is endemic to the New World and that the species evolved from an early lineage within *Nicrophorus*. This latter suggestion is supported by the plesiomorphic condition of larval character states of *N. orbicollis* (Anderson, 1982a).

According to Portevin (1920a, 1926), the derived character states of short epipleural ridges and hairy elytra are also known to occur (at least in part) in *N. distinctus* Grouvelle (Sulawesi(=Celebes) Islands), *P. heurni* Portevin (New Guinea), and *N. podagricus* Portevin (Borneo and Sulawesi) and also in *N. kieticus* Mroczkowski (1959) from the Solomon Islands. The relationship of these southern Indo-Malayan species to our *orbicollis* species group may be of importance for subsequent biogeographic interpretations to be discussed later.

The *defodiens* group

This species group can be defined by the uniquely derived larval character states of narrowly separated labial palpi with the basal segment ventrally unsclerotized.

defodiens group characters.— Character 1, larval labial palpi–relative position of bases. Two states have been identified. Because labial palpi with widely separated bases are known in

Ptomascopus morio, this state is considered plesiotypic.

Character 2, larval labial palpi–sclerotization of basal segment. Two states have been identified. Because labial palpi with a sclerotized ventral surface of the basal segment are known in *Ptomascopus morio*, this state is considered plesiotypic.

Character 3, pronotum–shape. See discussion of Character 2 in the *orbicollis* group.

Character 4, adult antennomeres 9,10–setosity. Two character states have been identified. Because white setae on the ventral surfaces of antennomeres 9 and 10 are not known in *Ptomascopus* species or other *Nicrophorus* species, this state is considered apotypic. Dense setae, arranged in a "figure eight" pattern are autapotypic in *N. vespilloides*.

We place three New World species in this group and their relationships are indicated in table 5 and figure 58. New World members are associated with northern Nearctic forested and swampy habitats. No species in the group is known or suspected to occur in Latin America.

The *investigator* group

This species group can presently best be defined by the uniquely derived character state of a prepupal overwintering stage. In *N. mexicanus* and *N. nigrita* there are no known overwintering stages but the species are most active in fall, winter and spring seasons suggesting descent from an ancestor with a prepupal overwintering stage. Both *N. nigrita* and *N. investigator* share the derived larval character of a sclerotized ventral apex of abdominal segment 10.

investigator group characters.— Character 1, overwintering stage. Two stages have been identified based on studies of populations at northerly latitudes. We hypothesize overwintering as an adult as plesiotypic and expect that it occurs in *Ptomascopus*. Southerly species that are fall-through-spring active are considered derived from a northern ancestor which had a prepupal overwintering stage.

Character 2, adult metasternum–vestiture. Two states have been identified. Because a uniformly pubescent metasternum is known in *Ptomascopus* species and all other *Nicrophorus* species, this state is considered plesiotypic.

Character 3, larval abdominal segment 10–ventral apex. Two states have been identified. Because an unsclerotized apex is known in *Ptomascopus* species and all other *Nicrophorus* species, this state is considered plesiotypic.

Character 4, pronotum–shape. See discussion of Character 2 in the *orbicollis* group.

Character 5, adult metasternum–color of vestiture. Two states have been identified. Because yellow pubescence is found in primitive *Nicrophorus* species, this state is deemed plesiotypic within the *investigator* group. Yellow pubescence may be apotypic for the genus *Nicrophorus* because *Ptomascopus* species possess brown pubescence. Distribution of states of this character in all *Nicrophorus* species suggests a high degree of homoplasy and cautions against its overemphasis. Distributional data on *N. mexicanus* and *N. nigrita*, and uniformity of habitus, also support a sister-species relationship between these two species.

We place five New World species in this group and their relationships are indicated in table 6 and figure 59. Larvae of *N. mexicanus* are undescribed but are expected to possess the derived character states in table 6 based upon our interpretation of its phylogenetic position with respect to other members of this group. New World members of the group are associated with open, sparsely forested, and densely forested habitats throughout North America. Within this group only *N. mexicanus* and *N. nigrita* have ranges extending into Mexico. *N. nigrita* occurs not only on the mainland of Baja California, but has dispersed 250 km to Guadelupe

Island. It has also crossed smaller water gaps to the California Channel Islands. *N. mexicanus* extends throughout the Mexican Plateau and into Guatemala. It and *N. marginatus* are the only species of *Nicrophorus* with an extensive distribution in both the United States and Latin America.

The *marginatus* group

This species group is defined by the uniquely derived adult character state of dense yellow hairs on the posterior lobe of the metepimeron and the derived larval character state of an unsclerotized base of the venter of abdominal segment 10.

marginatus group characters.— Character 1, larval abdominal segment 10–ventral base. Two character states have been identified. Because a sclerotized base occurs in *Ptomascopus* species, this state is considered plesiotypic.

Character 2, adult metepisternum, posterior lobe–pubescence. Three states have been identified in *Nicrophorus* species. Because a metepimeral lobe with a few sparse hairs is known in *Ptomascopus* species, this state is considered plesiotypic.

Character 3, larval abdominal segment 9–sternite. Two states have been identified. Because a sternite with the outer angles acute is known in *Ptomascopus morio*, this state is considered plesiotypic.

We place three New World species in this group and their relationships are shown in table 7 and figure 60. A fourth, *N. carolinus*, is tentatively placed within this group although adults lack the above derived characters and larvae are undescribed. However, we suspect that *N. carolinus* is phylogentically close to the *marginatus* group based on its overall habitus and retention of some ancestral character states, shared with members of the *marginatus* group. We predict that larvae, when described, will support these suspicions (fig. 60). New World members of the group (excluding *N. carolinus*) are primarily associated with open habitats throughout western North America. Within the group, only *N. marginatus* has a distribution which extends into the arid regions of the northern half of the Mexican Plateau.

Incertae Sedis

At present we are unable to assign the North American *N. americanus* and *N. pustulatus* to definable New World species groups. This is partly due to the fact that larvae are undescribed for both species, and that adults retain primitive states for all characters used to define the above groups. Our inability to assign these species to groups may also be because they have no other relatives in the New World, as has already been suggested for *N. americanus* by Anderson (1982c).

ZOOGEOGRAPHY AND SPECIES ORIGINS

Silphinae other than Oxelytrum.— Genera and their number of included species in North America north of Mexico are as follows: *Necrodes* (1), *Thanatophilus* (5), *Aclypea* (2), *Oiceoptoma* (3), *Heterosilpha* (2), and *Necrophila* (1). Of these, only *Heterosilpha* is endemic. We assume all but *Heterosilpha* to have originated in the Palearctic region because this is where their highest species diversity is, and where several additional related genera occur. We assume that members of these genera independently invaded North America at least five different times in the Tertiary, probably across the Bering Land Bridge, but alternatively across North Atlantic land bridges, before the opening of this ocean in the early Tertiary

(Matthews, 1979). There is no evidence that any of these silphine genera occurred in Latin America any farther south than the edge of the Mexican Plateau. In these genera, the sole endemic Latin American species, *T. graniger*, is readily interpreted as a southern isolate of *T. lapponicus* or its ancestor, which reached the uplands of the Mexican Plateau and the Transverse (or Neo) Volcanic Sierra in a cooler glacial climate, and became isolated there in a warmer interglacial.

Latin American silphid fossils are not known. Hatch (1927) reviewed the known Mesozoic and Tertiary fossils known to that time and attributed to Silphidae. They tell little about the origin of extant North American or Latin American genera. This is also true of the recent review of Russian Mesozoic beetles (Arnoldi *et al.*, 1977).

Oxelytrum.— The sister group relationship of a Latin American genus (*Oxelytrum*) and an Australian genus (*Ptomaphila*) is a pattern known in many insect and other groups (reviewed in Keast, 1973). This pattern can be best interpreted as resulting from separation of an ancestral distribution on at least part of the southern Mesozoic supercontinent of Gondwanaland following its breakup during the Cretaceous. Temperate lands remained in proximity between Australasia and South America into the Eocene (50 million years BP), some 40 million years after their separation from Africa, and 30 million years after the separation of New Zealand (Raven and Axelrod, 1975). No other closely related silphine genera occur on the other present or formerly southern main land masses of New Zealand, Africa, Madagascar, or India. We suggest that *Oxelytrum* diversified and speciated after the separation and isolation of South America from other southern land masses.

We suggest initial divergence of this *Oxelytrum* stock into two lineages; the *lineatocolle* group in more western coastal lowland habitats, and, the *emarginatum* group in more northern and eastern lowland habitats.

The *lineatocolle* group probably had an ancestral species possessing many character states similar to those of *O. lineatocolle* and may have originally occupied temperate habitats such as *Nothofagus* forests along the western coast of South America. We hypothesize that the first phase of the Andean orogeny during the late Cretaceous may have provided the earliest set of barriers allowing for the divergence of this lineage into two descendant forms. One of these is currently represented by *O. lineatocolle* in the south-central Chilean coastal lowlands and Andean slopes. The other, perhaps a more inland and higher elevation form, representing the ancestor of the remaining three species in this group, underwent subsequent divergence into (1), a more southerly cold-temperate, but lower-elevation montane form, and (2), a more northerly cold-adapted high-elevation montane form. This perhaps occurred during the second phase of Andean orogenic activity and formation of high elevation grassland habitats. The first is presently represented by *O. biguttatum* in extreme southern Chile and Argentina. The second represents the ancestor of *O. apicale* and *O. anticola* which probably inhabited the high elevation grasslands and steppes of Argentina, Bolivia, Ecuador and Peru. A possible early Pliocene or Pleistocene isolation of northern and southern forms, perhaps as a result of glacial events (Noonan, 1981), is indicatedby the descendant species, the more northerly *O. anticola* and the more southerly *O. apicale*, allopatrically distributed in these high Andean open habitats.

In the *emarginatum* group, the ancestral species probably possessed many character states similar to those of *O. emarginatum* and may have occupied the lowland forests of northern, central and eastern South America. We hypothesize isolation of a more upland form in the southern Brazilian Highlands, presently represented by *O. emarginatum*, and a widespread

northern lowland form representing the ancestor of the remaining three species in this group. This latter form diverged into southerly lowland northern lowland to middle elevation montane forms perhaps during the second phase of Andean orogeny in the mid-Tertiary. The southern lowland form is presently represented by the allopatric *O. erythrurum* and the other form represents the ancestor of the widespread, but largely allopatric, *O. discicolle* and *O. cayennense*. Divergence into these latter two species may also be due to continued Andean orogeny in the Pliocene or Pleistocene. *O. cayennense* is apparently limited to the lower montane and lowland Amazon Basin forests, while *O. discicolle* is distributed in forests of the surrounding regions at higher elevations. *O. discicolle* is the only species of *Oxelytrum* ranging into Central America and Mexico. This is probably the result of Pleistocene dispersal from montane areas of northern South America along the island-like montane habitats of Central America to Mexico. Although many recent interpretations of the evolutionary histories of Latin American taxa have emphasized the role of Pleistocene forest refugia caused by climatic changes in South and Central America (reviewed by Simpson and Haffer, 1978; Prance, 1982; Whitehead, 1976; but for an alternative view see Endler 1982) in promoting speciation we believe that species origins of all Latin American Silphidae, with the possible exception of *Thanatophilus graniger*, predate the Pleistocene.

Nicrophorinae.— The full biogeographic history of *Nicrophorus* can be presented only after the Eurasian fauna has been extensively studied. The sister genus of *Nicrophorus* is *Ptomascopus* of eastern Asia whose adults exhibit more primitive states of structural characters and have not evolved advanced parental care of the larvae, as is found in members of *Nicrophorus* (Peck, 1982). The genus *Nicrophorus* seems to be Eurasian in origin because this is where the sister genus occurs, and because more species of *Nicrophorus* occur in Eurasia (about 60) than in the New World (20). No species are known to occur in Australia or sub-Saharan Africa.

We suggest that each of the four species groups, plus *N. americanus* and *N. pustulatus*, may represent one or more ancestral invasions of North America via the Bering or North Atlantic Land Bridges during the Tertiary or Pleistocene. Only two species, *N. vespilloides* and *N. investigator*, are in both North America and Eurasia, occupying far northern localities. Both probably occurred on and moved freely across the Bering Land Bridge during low sea stands in the Pleistocene.

Somewhat more than half of the North American species live in deciduous forests of the eastern and southeastern United States. We interpret this to be suggestive of the ancestral habit. Occupation of North America by species ancestral to these can therefore date to the early Tertiary when such forests were continuous from Asia, across Beringia, to North America or alternatively from Europe, directly to eastern North America (see Matthews, 1979, 1980 for review).

Grassland and open shrub habitats seemingly started to become abundant in North America in the Miocene, as a result of the formation of large rain shadows caused by the uplift of the Rocky Mountains. We suggest that species occupying these more open and semi-arid environments are younger and more derived, or represent later ancestral invasions. Except for the *orbicollis* group, only these species of more open and arid habitats have entered northern Mexico, and most of them range no farther south than the edge of the Mexican Plateau. We suggest only a Pleistocene or Recent occupation of Mexico by these species. The single exception, *N. mexicanus*, reaches Guatemala and El Salvador.

Only the *orbicollis* group of *Nicrophorus* contains species endemic to Latin America. This group may be the earliest to enter North America from Eurasia due to its apparent primitive position with respect to other species groups, and its association primarily with hardwood forested habitats.

The basal stock of the *orbicollis* group would seem to possess character states similar to those of *N. chilensis* (fig. 57). This stock probably reached South America from North and Central American ancestors in the date Cretaceous or early Tertiary while the two areas were still connected, or by over-water dispersal as is proposed for some island-hopping mammals in the early or mid-Tertiary (Darlington, 1957; Simpson, 1980). Alternatively, arrival of the *orbicollis* group of *Nicrophorus* in South America may date from the early Pliocene, and be contemporaneous with the start of the "Great American Interchange" of faunas. At this time the Andes were considerably uplifted, but not to their present height. By late Pliocene the Panama seaway was closed and additional uplift of the Andes formed a continuous temperate Andean dispersal corridor (Haffer, 1974; Simpson, 1980).

Diversification and endemicity of Central and South American *Nicrophorus* species argues for an early rather than late entry into Central and South America. There is no evidence to suggest that *Nicrophorus* reached South America from the south, when it was part of the Gondwanaland supercontinent, although Melville (1981) discusses plant taxa with South American and Indo-Malayan affinities and interprets them as parts of a fragmented hypothesized supercontinent called Pacifica. We have not closely examined Old World relationships of the *orbicollis* group. They may lie with some southeast Asian species and may be another example of this type of distribution pattern. Alternatively, such relationships may be taken as evidence of a more widespread distribution of the members of this species group than initially thought.

After reaching South America, the *Nicrophorus* ancestor seemingly remained in forested habitats and spread down the rising Andes chain to Chile. Here, perhaps due to the later development of an arid barrier across the Andes, an isolated population now represented as *N. chilensis* was formed. The remaining northern South American ancestal stock was again split with the development of two isolated forest regions separated partly by the high Andes. We suggest that this produced *N. scrutator* on the eastern flanks, in Peru, Argentina and Bolivia, and *N. didymus* with a range generally in more northerly Andean forests.

We finally suggest that the ancestor of the remaining three species in this group was distributed throughout warm-termperate or subtropical humid forests from eastern North America, through Mexico to at least Guatemala, if not Panama. Many organisms, and especially species or species pairs in tree genera such as *Fagus* (Beech), *Liquidambar* (Sweetgum), *Cercis* (Redbud), *Carpinus* (Blue Beech), and *Ostrya* (Ironwood), show this former Tertiary distributional connection across the present broad and arid barrier formed by the Rio Grande depression (see Martin and Harrell, 1957; Rosen, 1978; Allen and Ball, 1980). The formation of this arid barrier in the late Tertiary allowed for the concurrent isolations of *N. orbicollis* in the United States, and populations in Mexico through to Panama which subsequently gave rise to the allopatric *N. olidus* in humid upland forests in Mexico north of the arid lowland barrier of the Isthmus of Tehuantepec, and *N. quadrimaculatus* in the upland forests between the Chiapas highlands and western Panama.

BIOGEOGRAPHIC SYNTHESIS

Latin American silphid species can be grouped into four categories based upon distribution (modified from Savage, 1982): 1), Widespread–A single species found throughout Middle and South America; 2), South American–Ten species endemic to South America; 3), Middle America–One species endemic to Central America, two endemic to Mexico; and 4), Extratropical North American–Ten species found largely in North America but whose ranges extend at least in part into Mexico or northern Central America.

Many entomologists do not realize that silphids are present in Latin America. This is perhaps because the necrophagous niche has been extensively exploited by Scarabaeidae possibly due to a comparative lack of large herbivores which supply the fecal material for these beetles in other areas of the world. That the silphid presence in Latin America is of great antiquity is indicated by the endemic South American assemblage of species. Of the ten South American endemics, seven belong to the genus *Oxelytrum*, and three to the *orbicollis* group of *Nicrophorus*. The presence of these two groups in South America, however, is the result of two different historical pathways.

Oxelytrum, like many South American taxa, appears to owe its presence in South America to fragmentation of the supercontinent of Gondwanaland during the Cretaceous period. Species diversification of *Oxelytrum* occurred during the Tertiary while South America was in isolation. On the other hand, endemic species of *Nicrophorus* in South America appear to be the result of southerly movement from North America into South America perhaps during the late Cretaceous or early Tertiary while the two land areas were still connected. Alternatively, dispersal to South America could have taken place during the Tertiary over the island chain that is now Central America, as proposed for angiosperms by Raven and Axelrod (1974). The former appears preferrable since the two Middle American endemic *Nicrophorus* are highly derived and have a North American sister-group and thus probably originated at some later time in the Tertiary through a second inter-island dispersal from a northern and not southern source.

Only a single species of *Oxelytrum* has dispersed from South America north into Middle America, but because no divergence has taken place between populations, it is likely that this was a Pleistocene event. No South American *Nicrophorus* have reached Middle America. The other Mexican endemic, *Thanatophilus graniger*, is readily interpreted as resulting from a Pleistocene isolation of northern ancestral form.

The ten remaining species are all extratropical North American with the greater part of their range in temperate North America, and in most instances they just range into the arid desert lands of northern Mexico. Only two species occur extensively in these arid areas, reaching as far south as the Neo-Volcanic Sierra. A third species, *Nicrophorus mexicanus*, ranges to El Salvador. Most of these species seem to be of recent origin, and probably evolved *in situ* in response to increasing aridity and cooling trends in the late Tertiary.

Thus the Latin American silphid fauna originated from a variety of sources during various time periods since the late Cretaceous. As with many Latin American taxa, South America possesses a characteristically more primitive and largely endemic assemblage of species. Central America is largely transitional with species found there either being widespread tropical or montane endemics of probable Tertiary origin and either direct North or South American ancestry. Mexico not only possesses endemics of this latter kind, but also species of more recent Pleistocene origin. A final significant portion of the fauna of Mexico is due to the

widespread nature of the distributions of species found in the arid southwestern United States.

SUGGESTIONS FOR FUTURE WORK

The present review has attempted to clarify understanding of the classification, phylogeny and zoogeography of Latin American Silphidae. We hope we have, at least in part, succeeded. During our work however, we soon came to realize that many aspects of Latin American silphids have not been well studied and warrant further attention. We think it important to outline some of the more interesting and potentially useful of these topics here in the hope that someone will find them stimulating enough to undertake.

First, we think life history studies of species of Latin American *Nicrophorus* and *Oxelytrum* should be undertaken. Not only will this provide missing basic biological information, but also other life stages including larvae, which can be subsequently used to test reconstructed phylogenies presented here by adding more characters for analysis. Second, comparative ecological studies should be undertaken to find out how silphids are interacting with other necrophagous arthropods in tropical, subtropical and south-temperate habitats and if their roles in carrion communities are similar regardless of locality. Third, patterns of color variation in some species of *Oxelytrum* and *Nicrophorus* should be examined, and the results considered within the framework of the Pleistocene forest refugium theory. These species represent needed further examples that could be used to support or discredit this now highly controversial theory. Finally, attempts should be made to provide more specimens, particularly of South American species. This will lead to increased resolution of species distributions and species chorological relationships. The latter especially, may play an important role in determining species geographic limits.

ACKNOWLEDGMENTS

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Table 1. Classification of known or possible Latin American Silphinae.

Oxelytrum Gistel
    lineatocolle group
        O. lineatocolle (Laporte)
        O. biguttatum (Philippi)
        O. apicale (Brullé)
        O. anticola Guérin-Méneville
    emarginatum group
        O. emarginatum (Portevin)
        O. erythrurum (Blanchard)
        O. cayennensis (Stürm)
        O. discicolle (Brullé)
Necrodes Leach
    N. surinamensis (Fabricius)
Thanatophilus Leach
    T. graniger (Chevrolat)
    T. lapponica (Herbst)
    T. truncata (Say)
Heterosilpha Portevin
    H. aenescens (Casey)
    H. ramosa (Say)
Oiceoptoma Leach
    O. rugulosum Portevin

Table 2. Classification of New World *Nicrophorus* species.

Nicrophorus Fabricius
 orbicollis group
   N. chilensis Philippi
   N. scrutator Blanchard
   N. didymus Brullé
   N. orbicollis Say
   N. olidus Matthews
   N. quadrimaculatus Matthews
 defodiens group
   N. sayi Laporte
   N. defodiens Mannerheim
   N. vespilloides Herbst
 investigator group
   N. tomentosus Weber
   N. hybridus Hatch and Angell
   N. investigator Zetterstedt
   N. nigrita Mannerheim
   N. mexicanus Matthews
 marginatus group
   N. marginatus Fabricius
   N. obscurus Kirby
   N. guttula Motschulsky
   N. carolinus (Linnaeus)
 Incertae sedis
   N. americanus Olivier
   N. pustulatus Herschel

Table 3. Analysis of character transformations in *Oxelytrum* - *Ptomaphila* lineage of Silphinae. Relationships only of species of *Oxelytrum* are shown in fig. 56. Species of *Ptomaphila* are not considered. Superscripts on characters indicate that we consider them to be homoplasious (1) or simple and unique (2). *Terms of Arnett 1944.

	character	plesiotypic character state	apotypic character state
1.	pronotum[2]	without elevated costae	with costae
2.	elytral undersurface[2]	lacking long hairs	with long hairs near apical callus
3.	elytral apex[2]	lacking flange	with flange
4.	head[2]	with v-shaped swollen area (chevron) on frons	lacking frontal chevron
5.	elytron[2]	tricostate	tuberculate
6.	elytral epipleuron[2]	narrow	extremely wide
7.	male coxae[2]	without tubercles or spines	with tubercles or spines
8.	pronotum[1]	margin orange red, disc black	all black
9.	eyes[1]	large size	small size
10.	pronotum[1]	posterior angles obtuse	posterior angles rounded
11.	female genital coxites[2]*	with styli small, unmodified	with styli large, scooplike
12.	male coxae[2]	with tubercles	with spines
13.	pronotum[1]	margins flat or deflexed	margin reflexed
14.	abdominal segments 4, 5[1] (of some males)	without lateral projections	with lateral projections
15.	elytra[1]	humeri not toothed	humeri each with single tooth
16.	pronotum[1]	black spot on disc large	black spot on disc reduced

Table 4. Analysis of character transformations in *orbicollis* group of species in *Nicrophorus*. Relationships of species are shown in fig. 57.

	character	plesiotypic character state	apotypic character state
1.	elytral epipleuron	long	short
2.	pronotum	subquadrate	orbicular
3.	elytron	dorsal surface glabrous, or with few short hairs	with long hairs
4.	metatrochanter	with spine sharp, well developed	with spine reduced, rounded
5.	elytron	hairs sparse	hairs dense
6.	elytron	hairs dense	hairs extremely dense, short
7.	elytral epipleuron	glabrous or with few short hairs	densely hairy

Table 5. Analysis of character transformations in the *defodiens* group of species in
Nicrophorus. Relationships of species are shown in fig. 58.

	character	plesiotypic character state	apotypic character state
1.	larval labial palpi	bases widely separated	bases narrowly separated
2.	larval labial palpi	ventral surface of basal segment sclerotized	ventral surface of basal segment unsclerotized
3.	adult pronotum	subquadrate	quadrate
4.	adult antennomeres 9, 10	lacking white setae on ventral surfaces	possessing white setae on ventral surfaces

Table 6. Analysis of character transformations in the *investigator* group of species in *Nicrophorus*. Relationships of species are shown in fig. 59.

	character	plesiotypic character state	apotypic character state
1.	overwintering stage	adult	prepupa
2.	adult metasternum	lacking bald spot	with bald spot immediately posterior to mesocoxae
3.	ventral apex larval abdominal segment 10	unsclerotized	sclerotized
4.	adult pronotum	sub-quadrate to cordate	quadrate
5.	adult metasternal pubescence	yellow	brown

Table 7. Analysis of character transformations in the *marginatus* group of species in *Nicrophorus*. Relationships of species are shown in fig. 60.

	character	plesiotypic character state	apotypic character state
1.	ventral base of larval abdominal segment 10	sclerotized	unsclerotized
2.	pubescence of adult metepimeral posterior lobe	glabrous or with few hairs	dense yellow hairs
3.	sternite of larval abdominal segment 9	outer angles acute	outer angles truncate
4.	hairs on anterior face of adult procoxae	short	long
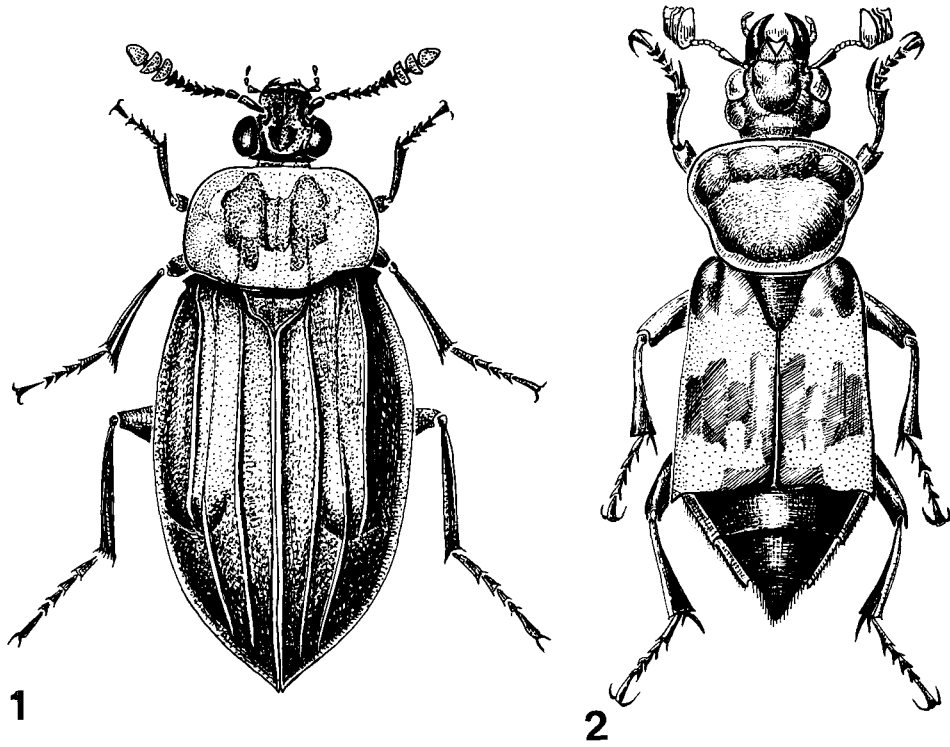
Plate 1. Figures 1, 2. Fig. 1. Habitus of *Oxelytrum discicolle*, body length 15 mm. Fig. 2. Habitus of *Nicrophorus marginatus*, body length 19 mm.

Plate 2. Figures 3-15. Fig. 3. Head of *Oxelytrum discicolle*: l, labrum; c, clypeus; f, frons. Mandibles not drawn. Fig. 4. Head of *Nicrophorus marginatus*; symbols as in fig. 3; Note nicrophorine character of very small second antennal segment. Fig. 5. Right elytra of *Necrodes surinamensis* with apical reddish markings. Fig. 6. Short and broadly rounded pronotal postcoxal lobe (p) of *Necrodes surinamensis*. Fig. 7. Longer pronotal postcoxal lobe (p) of *Thanatophilus graniger*. Fig. 8. Pointed elytral apices of female *Heterosilpha ramosa*. Fig. 9. Reticulate sculpturing and rounded elytral apices of male *Heterosilpha ramosa*. Fig. 10. Rounded elytral apices of male and female *Heterosilpha aenescens*. Fig. 11. Head of *Oiceoptoma rugulosum*. Fig. 12. Elytron of *Thanatophilus truncatus*. Fig. 13. Elytron of female *Thanatophilus lapponicus*. Fig. 14. Elytron of female *Thantophilus graniger*. Fig. 15. Elytron of female *Oxelytrum discicolle*
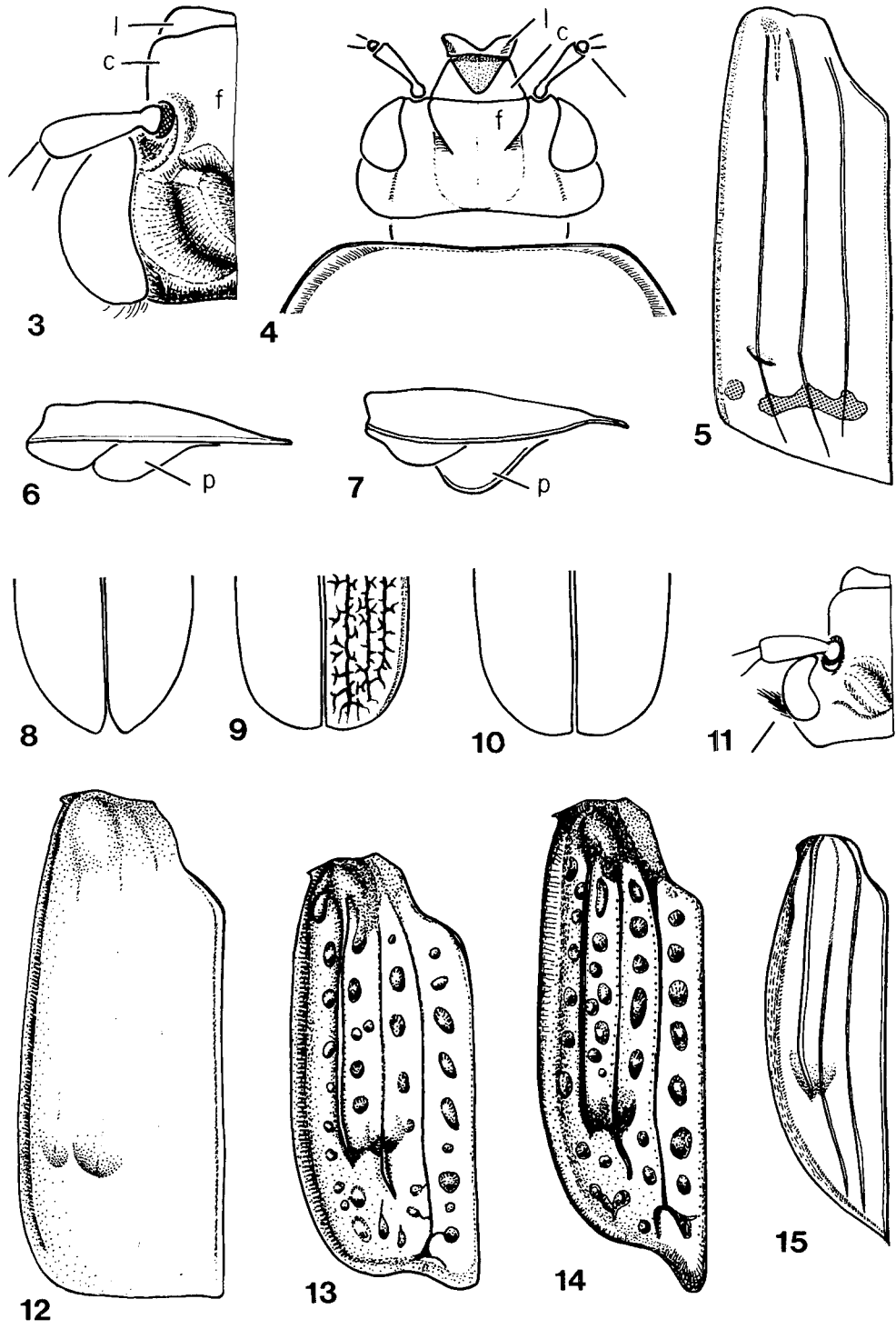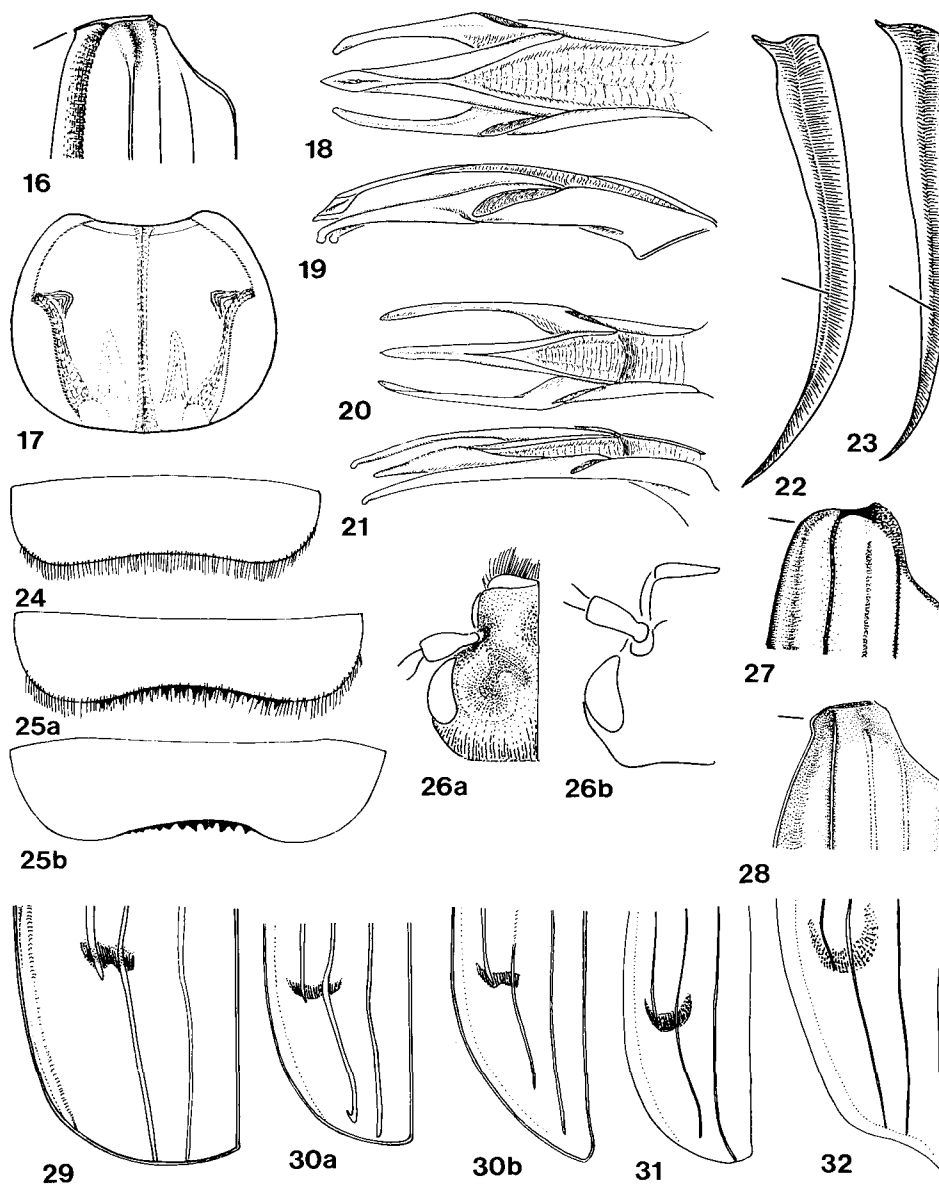
Plate 3. Figures 16-32. Fig. 16. Elytral shoulder of *Oiceoptoma rugulosum*. Fig. 17. Pronotum of *Necrodes surinamensis*. Fig. 18. Dorsal view aedeagus *Heterosilpha ramosa*. Fig. 19. Right lateral view aedeagus *Heterosilpha ramosa*. Fig. 20. Dorsal view aedeagus *Heterosilpha aenescens*. Fig. 21. Right lateral view aedeagus *Heterosilpha aenescens*. Fig. 22. Elytral epipleuron of *Oiceoptoma inaequale*. Fig. 23. Elytral epipleuron of *Oiceoptoma rugulosum*. Fig. 24. Plain posterior margin of female fifth visible abdominal sternite of *Thanatophilus lapponicus*. Fig. 25. Crenulate posterior margin of female fifth visible abdominal sternite of *Thanatophilus graniger* from (a) Cerro Potosi, Nuevo Leon, and (b) Guerrero Mills, Hidalgo. Fig. 26a. Head of *Oxelytrum apicale* Fig. 26b. Head of *Oxelytrum biguttatum*. Fig. 27. Elytral shoulder of *Oxelytrum erythrurum*. Fig. 28. Elytral shoulder of *Oxelytrum cayennense*. Fig. 29. Elytral apex male *Oxelytrum biguttatum*. Fig. 30. Elytral apex of *Oxelytrum apicale*; (a) male, (b) female. Fig. 31. Elytral apex male *Oxelytrum anticola*. Fig. 32. Elytral apex female *Oxelytrum emarginatum*.
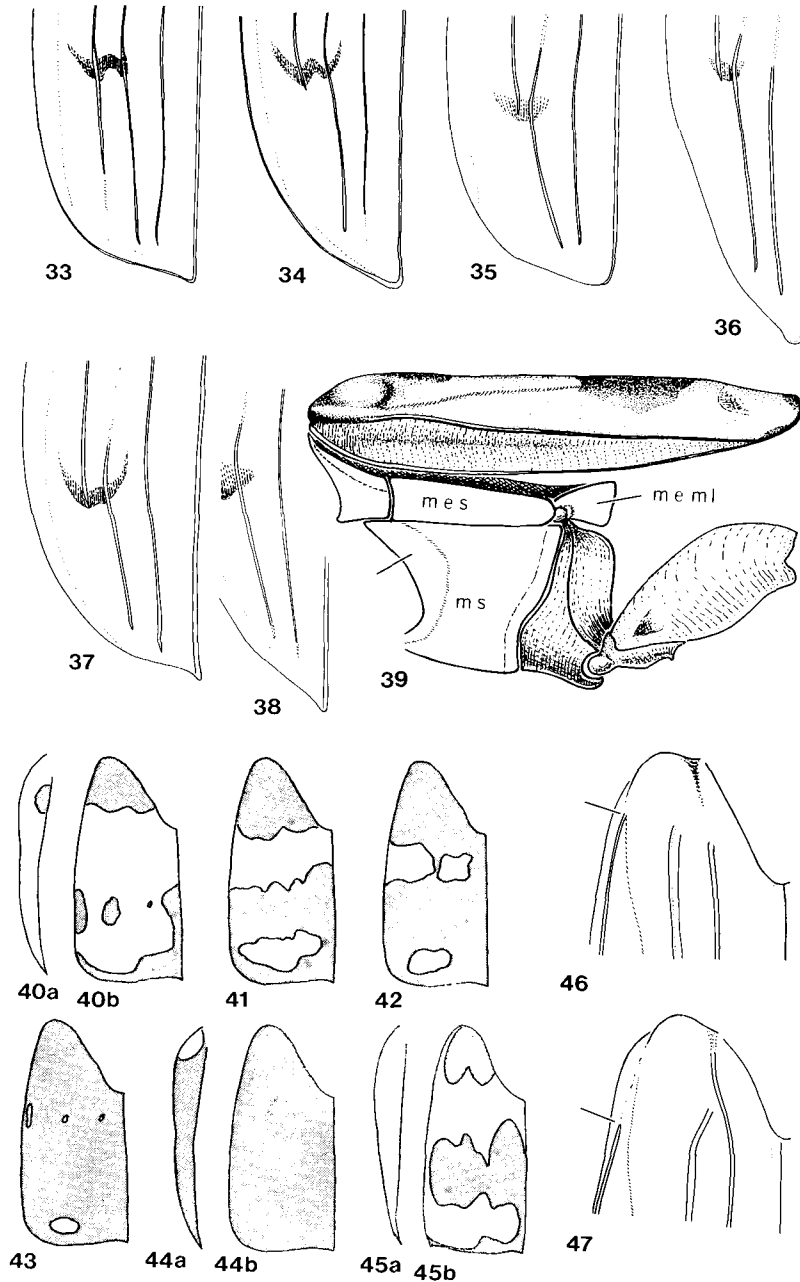
Plate 4. Figures 33-47. Fig. 33. Elytral apex male *Oxelytrum lineatocolle*. Fig. 34. Elytral apex female *Oxelytrum lineatocolle*. Fig. 35. Elytral apex male *Oxelytrum cayennense*. Fig. 36. Elytral apex female *Oxelytrum cayennense*. Fig. 37. Elytral apex male *Oxelytrum discicolle*. Fig. 38. Elytral apex female *Oxelytrum discicolle* Fig. 39. Left lateral view of elytra, epipleuron, and part of thorax of *Nicrophorus*: mes, metepisternum; meml, metepimeral lobe; ms, metasternum with anterior area which may be glabrous. Figs. 40-44. Dorsal view of elytron and lateral view of left elytral epipleuron of *Nicrophorus guttula* showing variation in size of orange-red fasciae. Fig. 45. Elytron and left epipleuron of *Nicrophorus marginatus*. Fig. 46. Long epipleural ridge, *Nicrophorus mexicanus*. Fig. 47. Short epipleural ridge, *Nicrophorus orbicollis*.
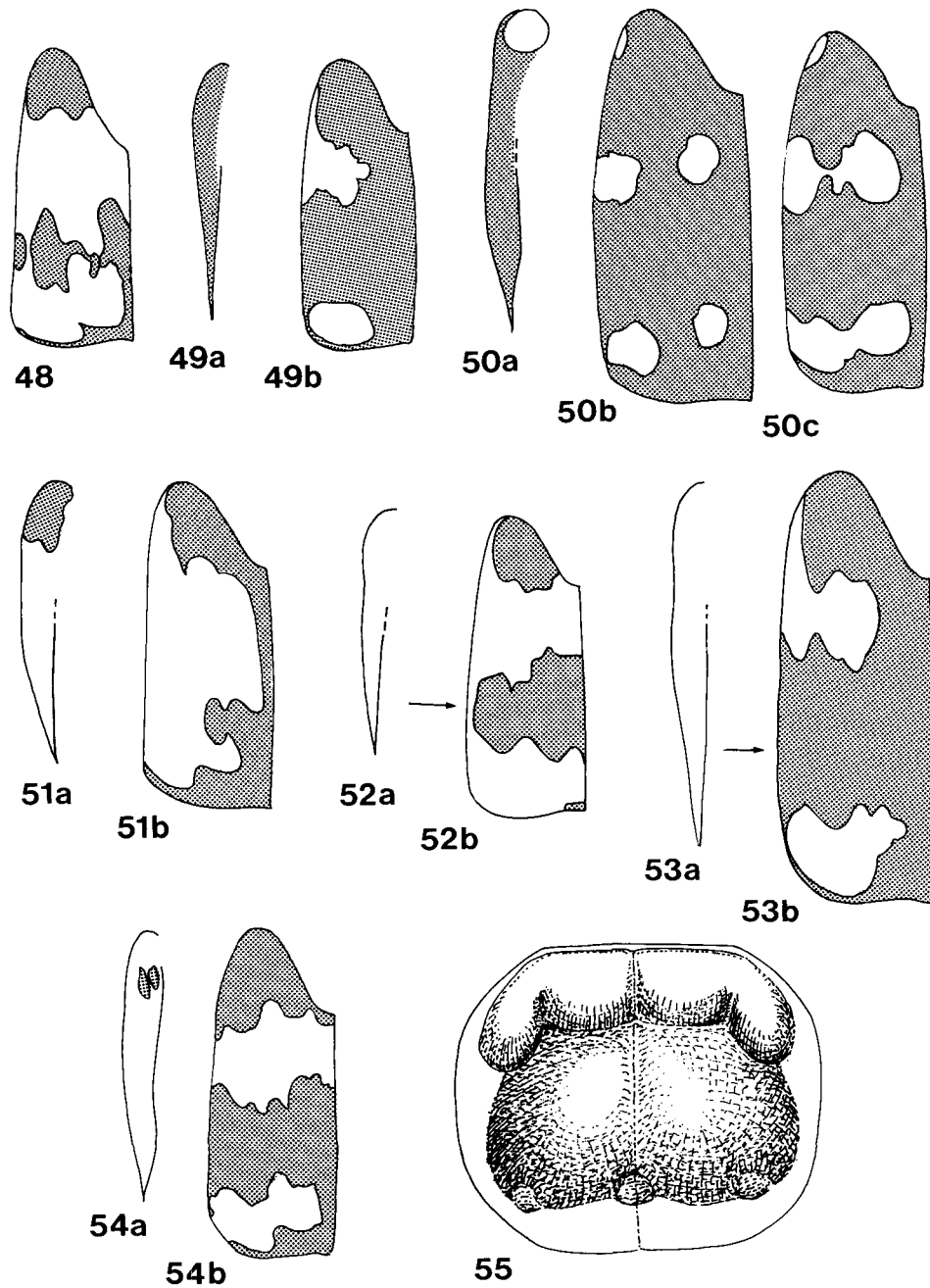
Plate 5. Figures 48-55. Fig. 48. Elytron *Nicrophorus marginatus*, Coahuila, Mexico, Fig. 49. Epipleuron and elytron, *Nicrophorus quadrimaculatus*, Chiriqui, Panama. Fig. 50. Epipleuron and elytral fasciae variation *Nicrophorus didymus*, Cerro Carpish, Huanuco, Peru. Fig. 51. Epipleuron and elytron *Nicrophorus chilensis*, Malleco, Chile. Fig. 52. Epipleuron and elytron *Nicrophorus olidus*, Jalisco, Mexico. Fig. 53. Epipleuron and elytron *Nicrophorus scrutator, Tucuman, Argentina. Fig. 54. Epipleuron and elytron Nicrophorus mexicanus*, Durango, Mexico. Fig. 55. Pronotum *Nicrophorus quadrimaculatus*, Chiiiriqui, Panama.

Ptomaphila (Aust., N.Guin.)

O. anticola (S.A.)

O. apicale (S.A.)

O. biguttatum (S.A.)

O. lineatocolle (S.A.)

O. emarginatum (S.A.)

O. erythrurum (S.A.)

O. cayennensis (S.A.)

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O. discicolle (S.A.,C.A.,
Mex.,Tex.)

Figure 56. Reconstructed phylogeny of *Oxelytrum* - *Ptomaphila* lineage of Silphidae. Numbers refer to characters in Table 3; closed circles indicate apotypic character state.

N. chilensis (S.A.)

N. scrutator (S.A.)

N. didymus (S.A.)

N. orbicollis (N.A.)

N. olidus (Mex.)

N. quadrimaculatus (C.A.)
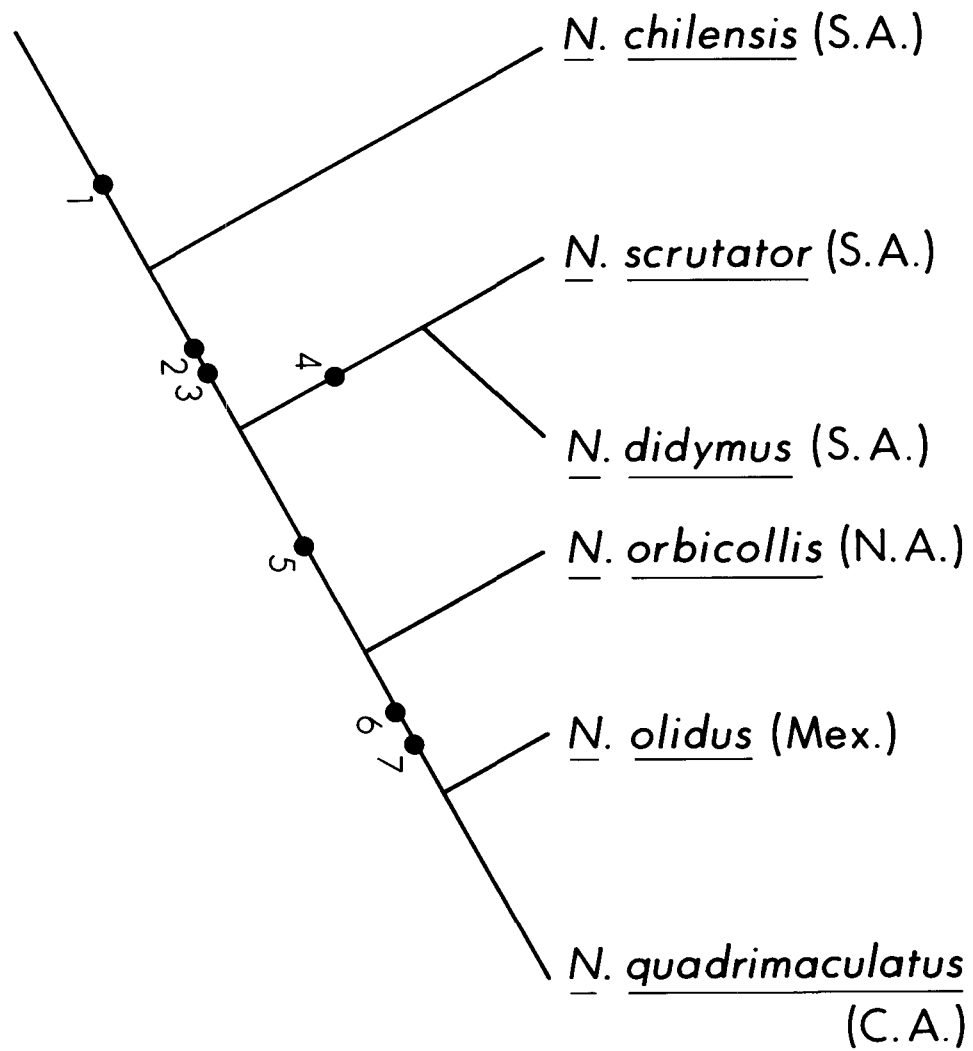
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Figure 57. Reconstructed phylogeny of species of *orbicollis* group of *Nicrophorus*. Numbers refer to characters in Table 4; closed circles indicate apotypic character state.

N. *sayi* (Nearc.)

N. *vespilloides* (Holarc.)

N. *defodiens* (Nearc.)
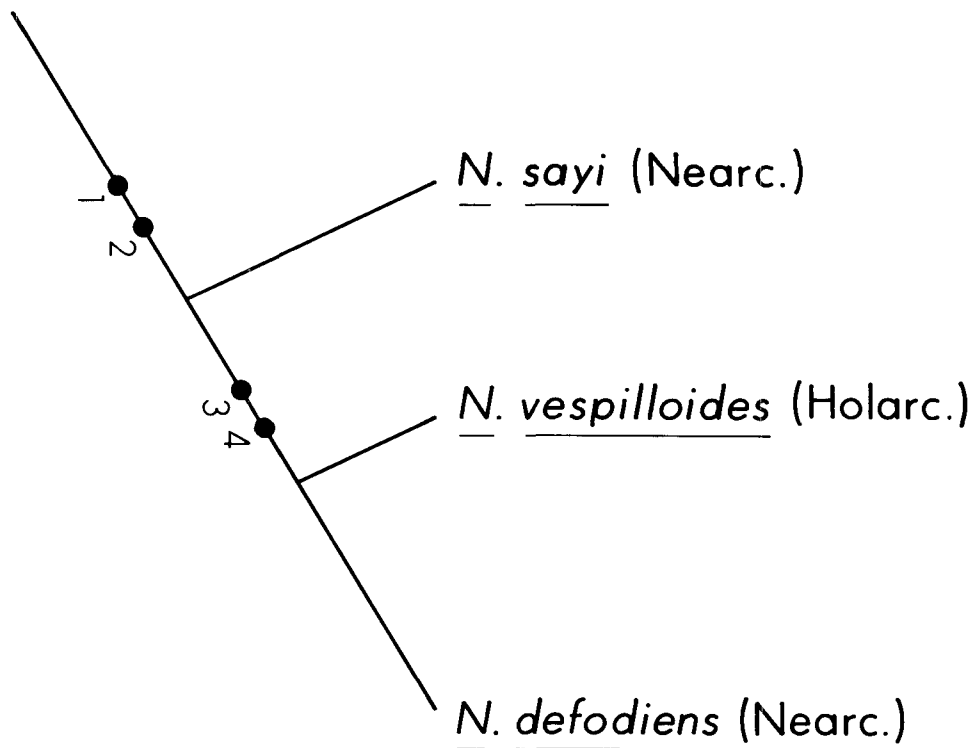
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Figure 58. Reconstructed phylogeny of species of *defodiens* group of *Nicrophorus*. Numbers refer to characters in Table 5; closed circles indicate apotypic character state.

N. *tomentosus* (Nearc.)

N. *hybridus* (Nearc.)

N. *investigator* (Holarc.)

N. *nigrita* (Nearc.)

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N. *mexicanus* (Nearc., Mex.,C.A.)
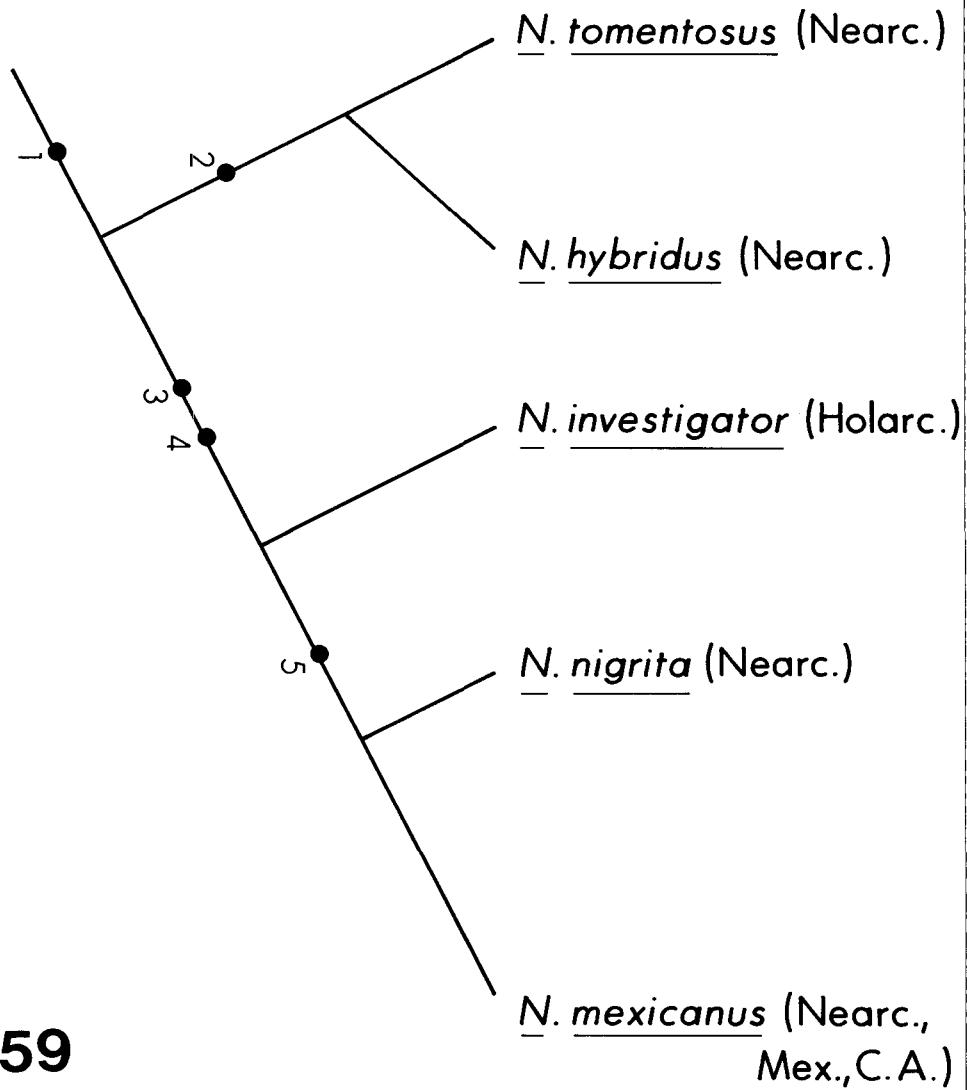
Figure 59. Reconstructed phylogeny of species of *investigator* group of *Nicrophorus*. Numbers refer to characters in Table 6; closed circles indicate apotypic character state.

N. *carolinus* (Nearc.)

N. *marginatus* (Nearc.,
Mex.)

N. *obscurus* (Nearc.)

N. *guttula* (Nearc.)

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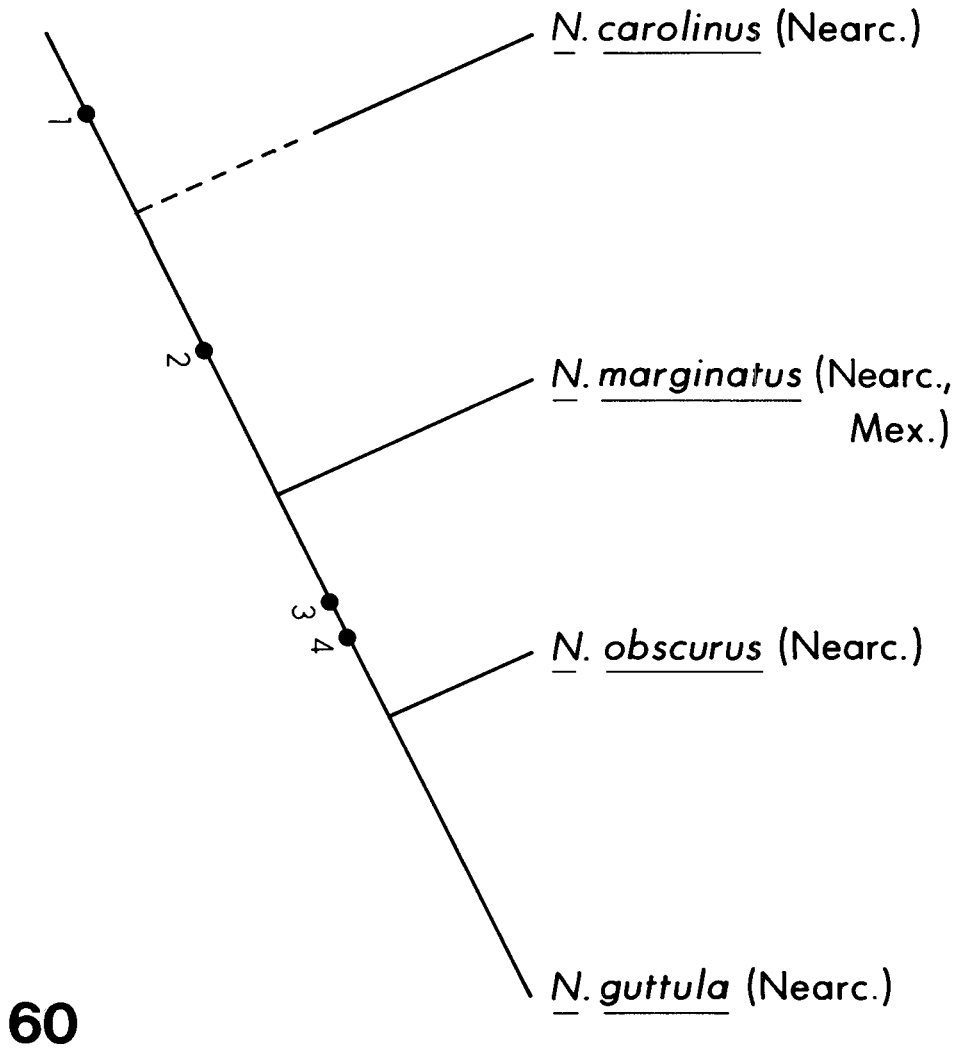
Figure 60. Reconstructed phylogeny of species of *marginatus* group of *Nicrophorus*. Numbers refer to characters in Table 7; closed circles indicate apotypic character state; dotted line indicates uncertain placement.
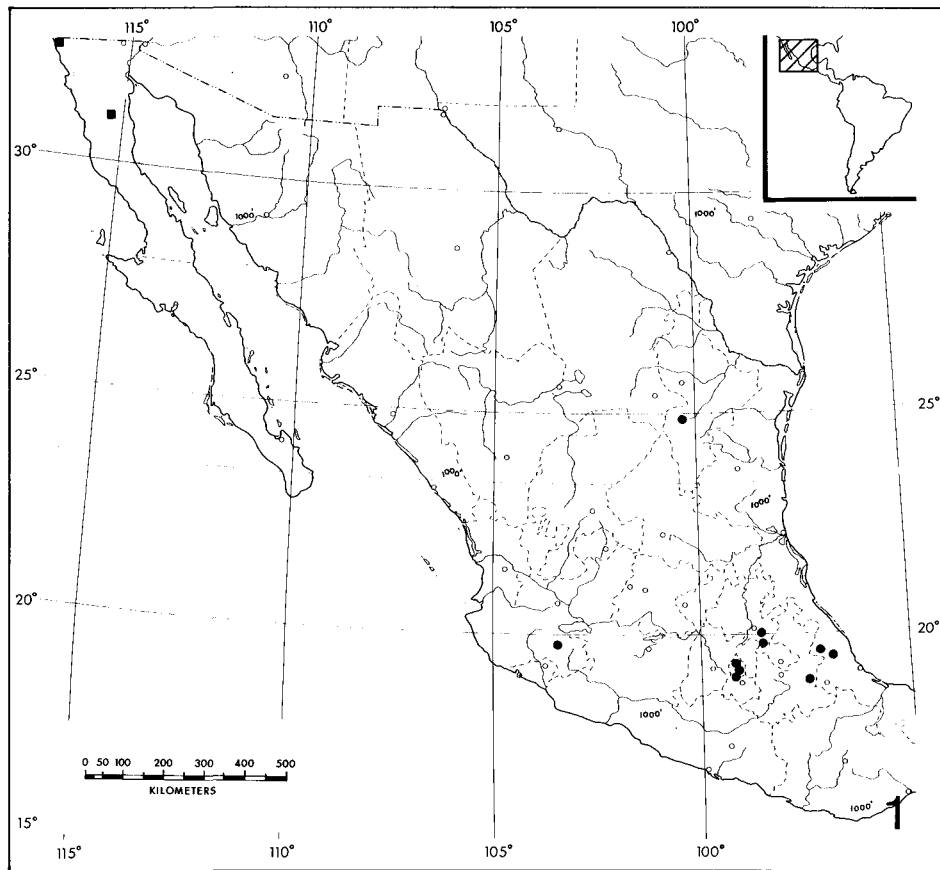
Map 1. Distribution of *Thanatophilus graniger* (black dots) and *Heterosilpha ramosa* (black squares) in Mexico.
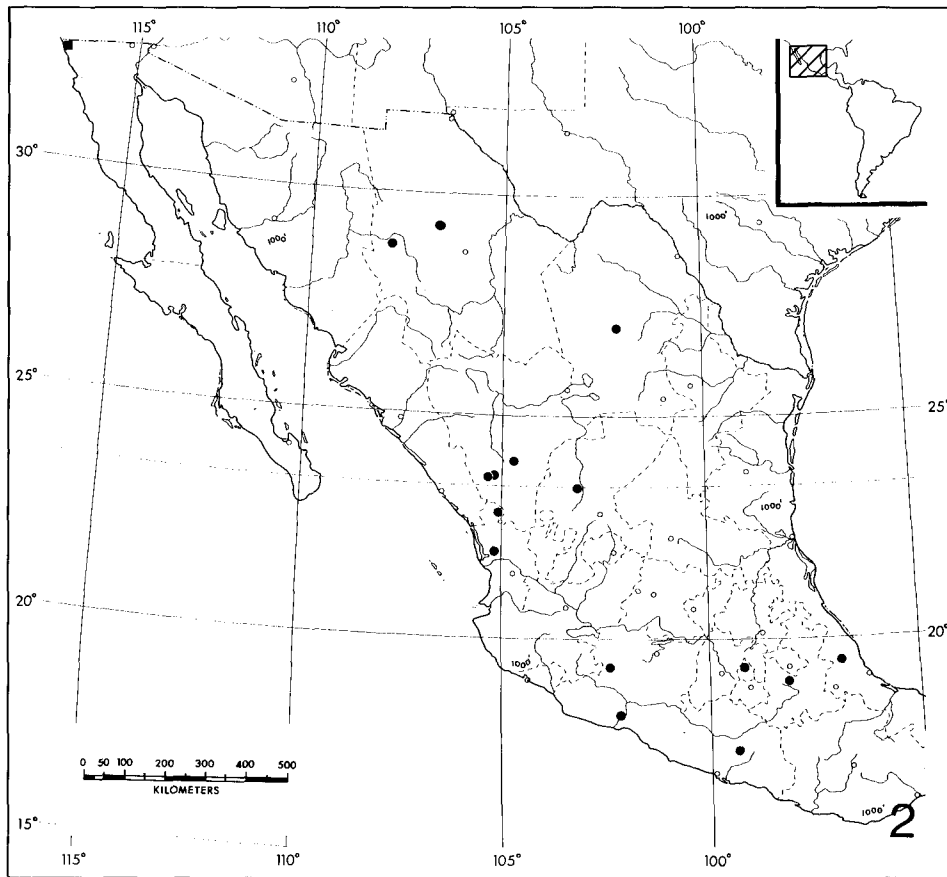
Map 2. Distribution of *Thanatophilus truncatus* (black dots) and *Thanatophilus lapponicus* (square) in Mexico.
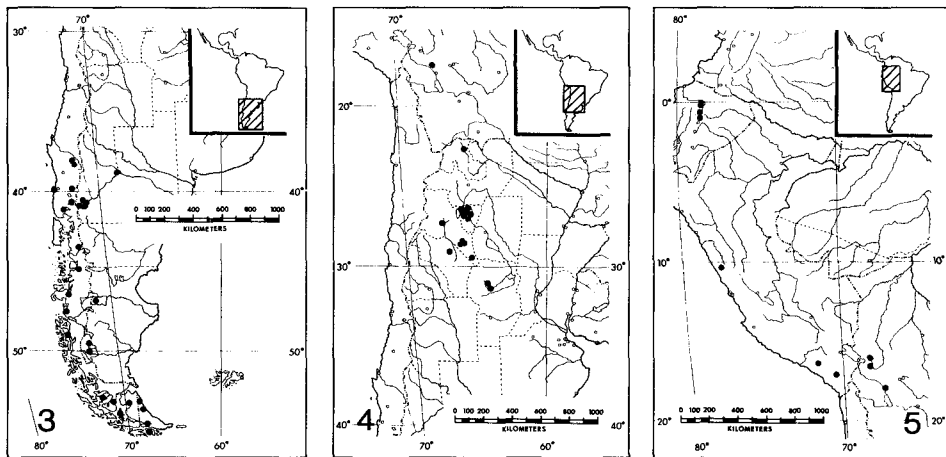
Map 3. Distribution of *Oxelytrum biguttatum* in southern South America. Map 4. Distribution of *Oxelytrum apicale* in Bolivia and northern Argentina. Map 5. Distribution of *Oxelytrum anticola* in the central and northern Andes.
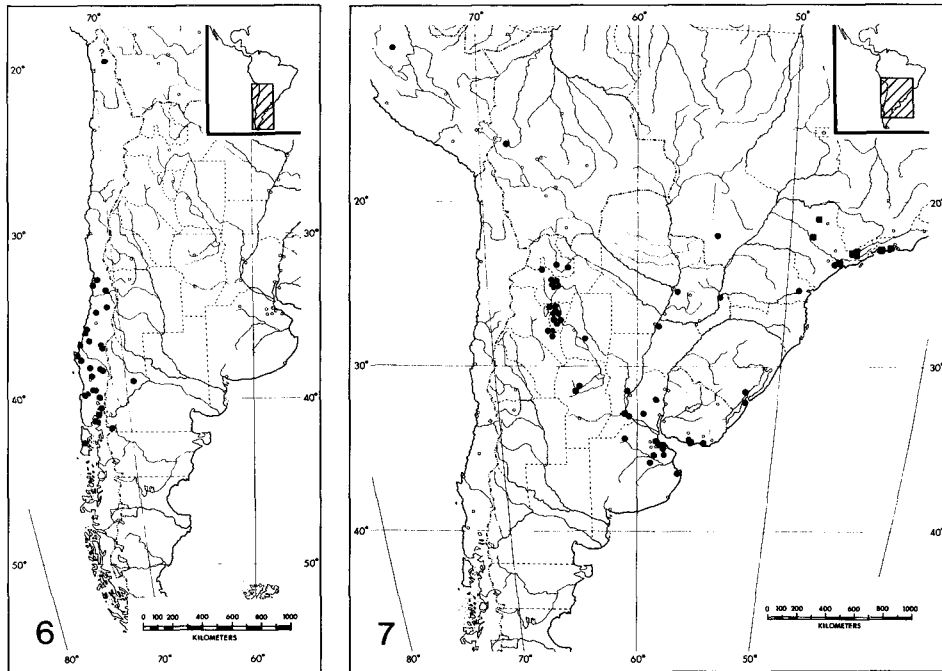
Map 6. Distribution of *Oxelytrum lineatocolle* in Chile and Argentina. Map 7. Distribution of *Oxelytrum erythrurum* from Bolivia to southern Brazil and Argentina (black dots) and *Oxelytrum emarginatum* in southeastern Brazil (black squares).
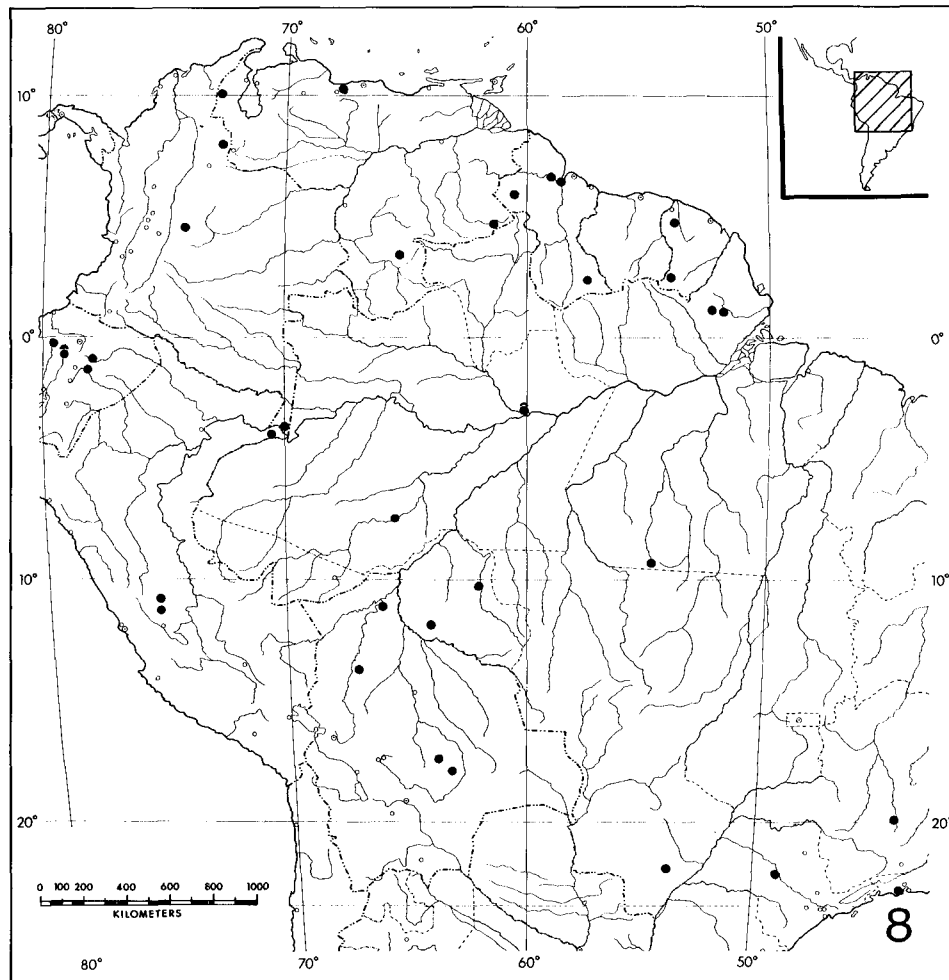
Map 8. Distribution of *Oxelytrum cayennense* in northern South America.
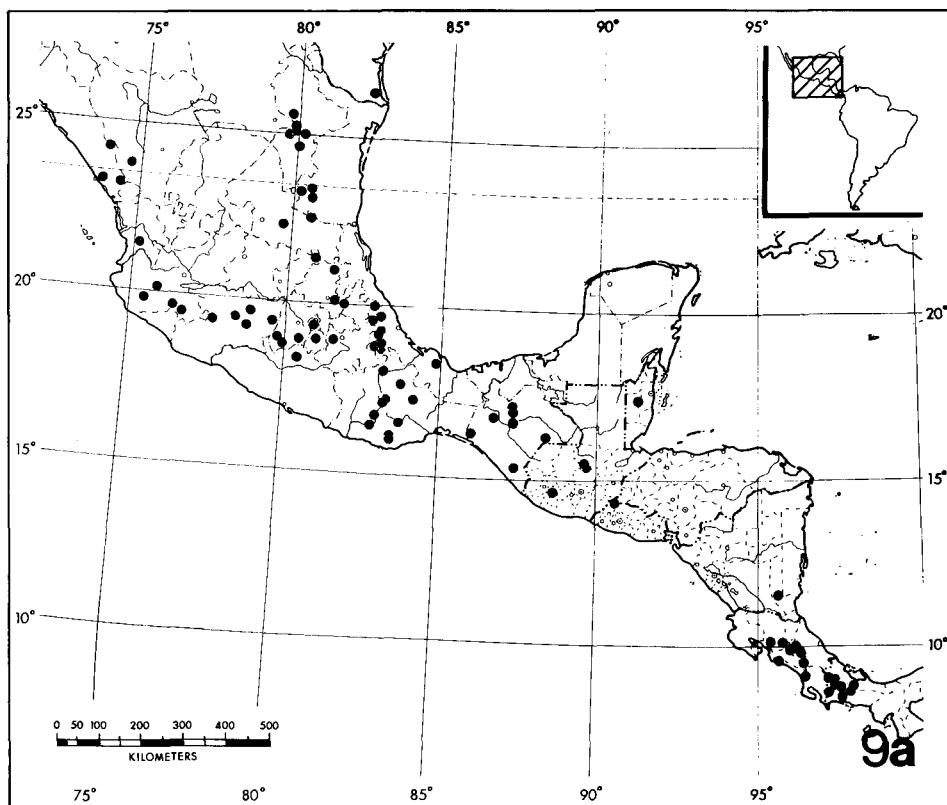
Map 9a. Distribution of *Oxelytrum discicolle* in Texas and Middle America.
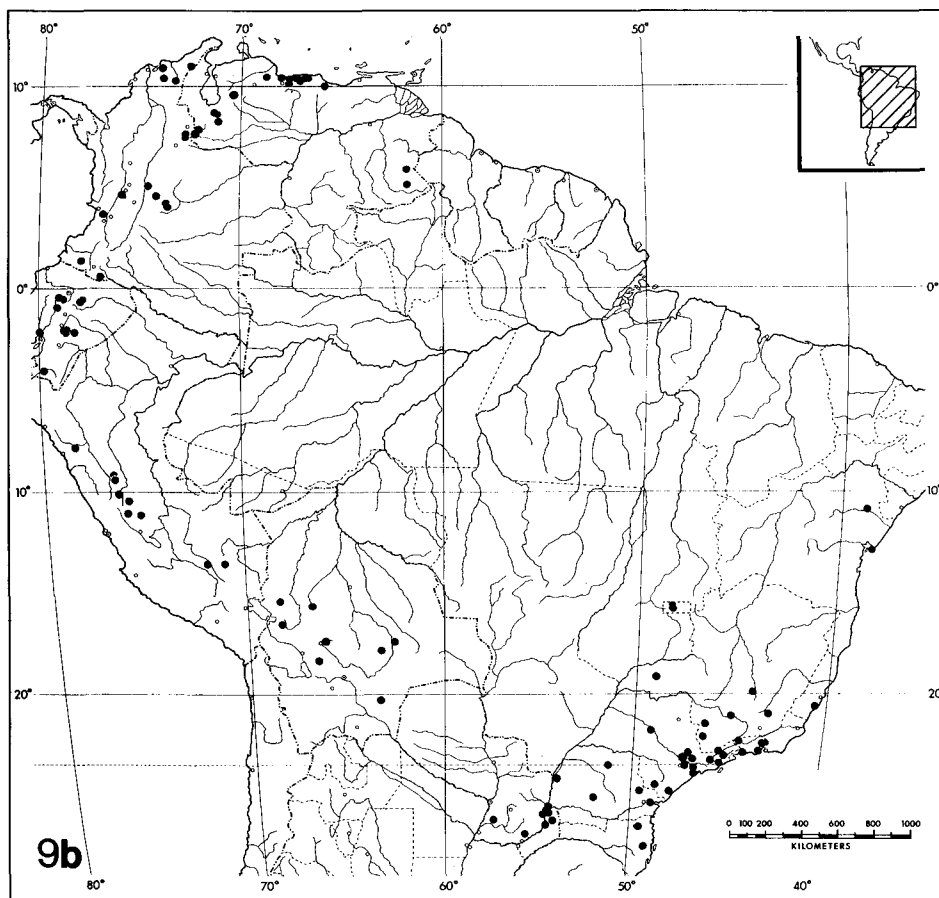
Map 9b. Distribution of *Oxelytrum discicolle* in South America.
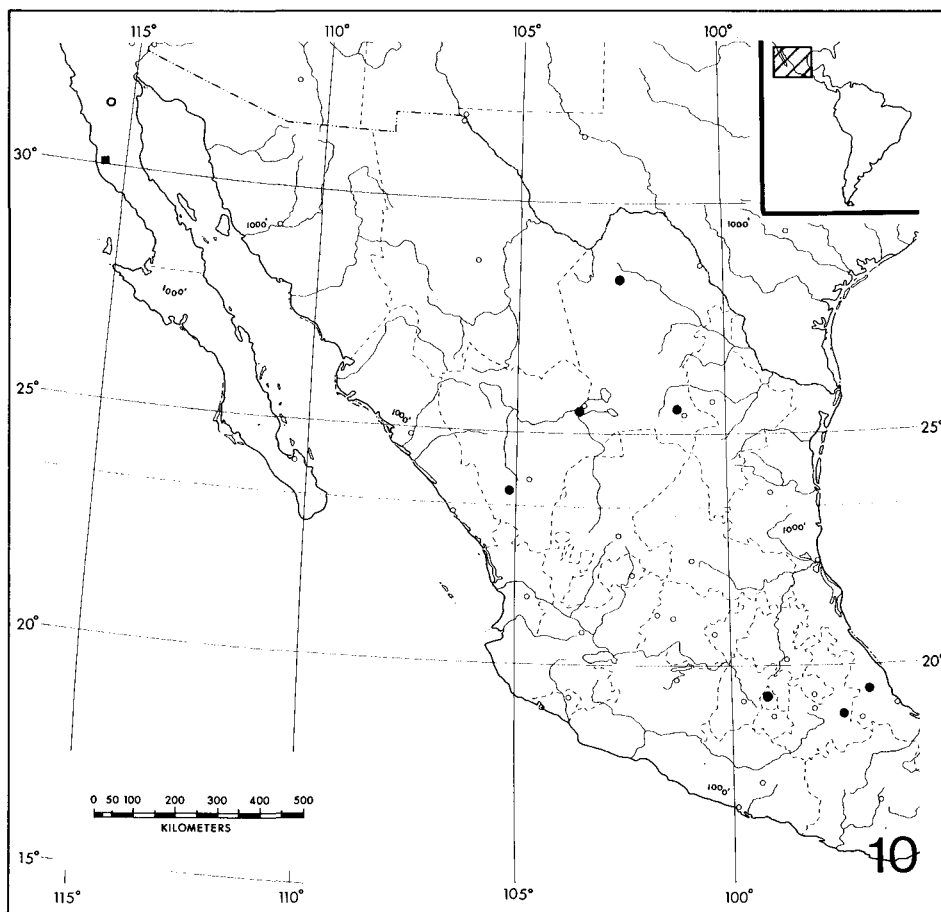
Map 10. Distribution of *Nicrophorus marginatus* (black dots), *Nicrophorus guttula* (open dot), and *Nicrophorus nigrita* (black square, Guadelupe Island record not shown) in Mexico.
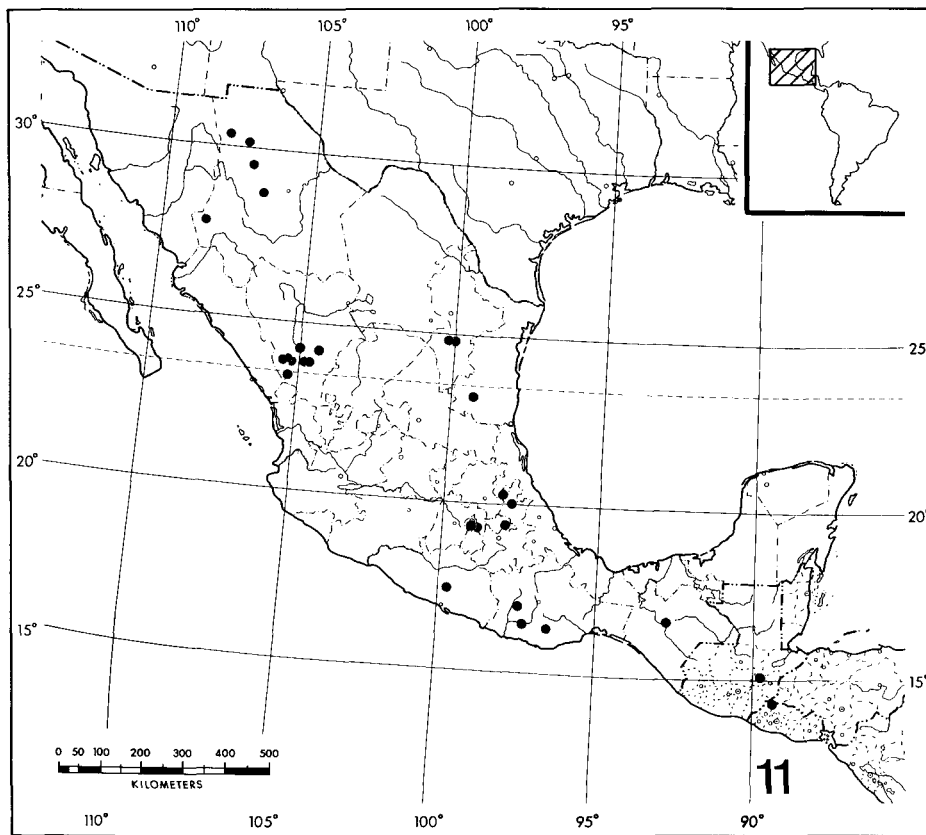
Map 11. Distribution of *Nicrophorus mexicanus* in Mexico to El Salvador.
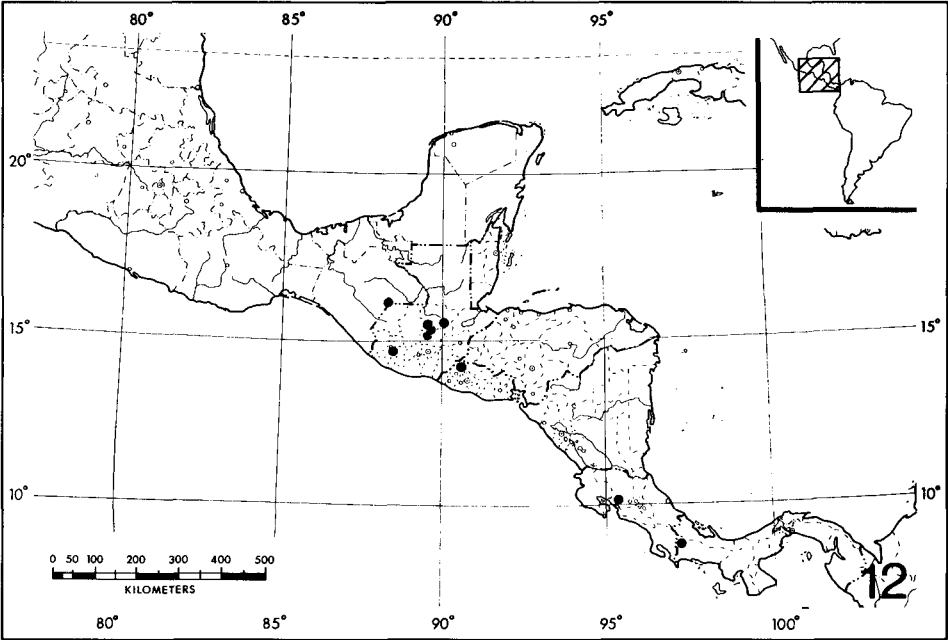
Map 12. Distribution of *Nicrophorus quadrimaculatus* in Chiapas, Mexico and Central America.
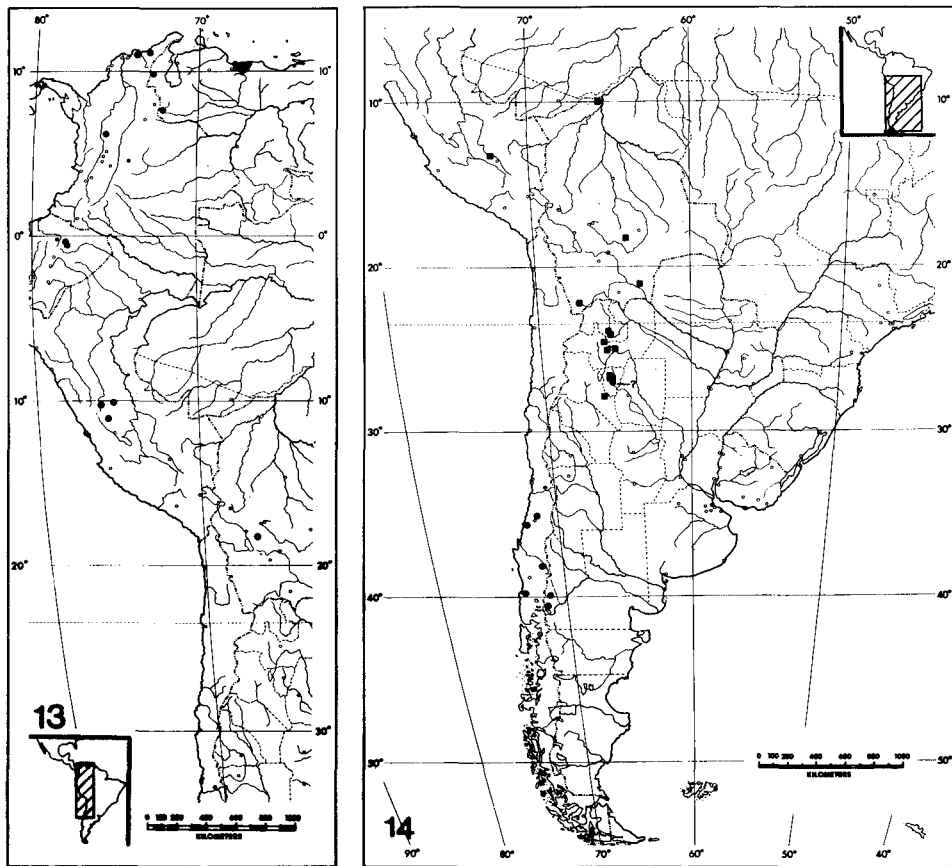
Map 13. Distribution of *Nicrophorus didymus* in northern Andean South America. Map 14. Distribution of *Nicrophorus chilensis* (Black dots) and *Nicrophorus scrutator* (black squares) in Bolivia, Argentina, and Chile. Question mark indicates anomalous record.
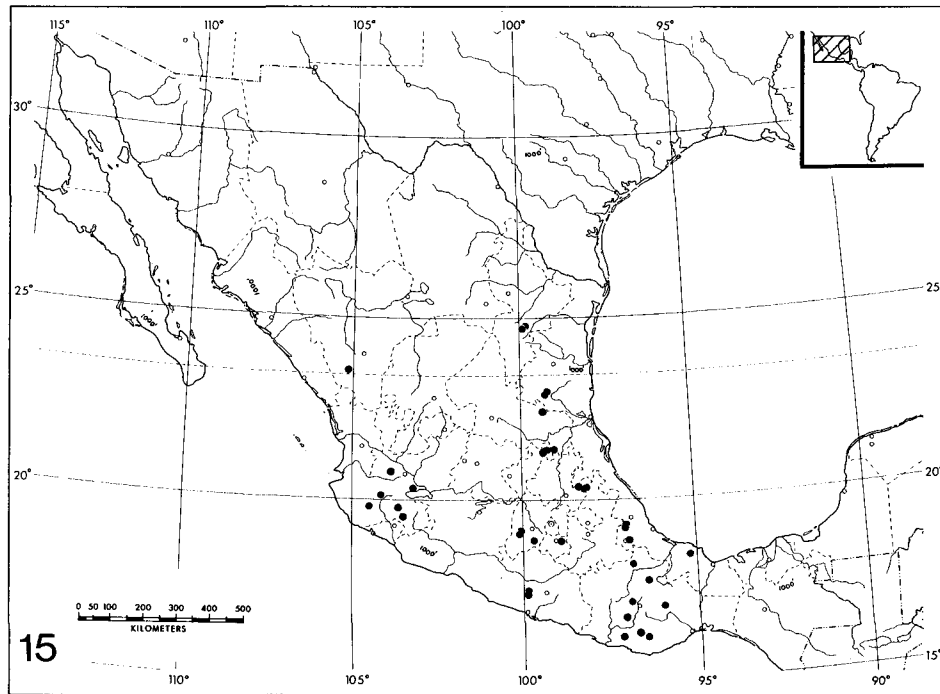
Map 15. Distribution of *Nicrophorus olidus* in Mexico.

INDEX TO NAMES OF TAXA
(Synonyms in italics)