THE SPECIES OF THE NEOTROPICAL GENUS *TRICHOPSELAPHUS* CHAUDOIR (COLEOPTERA: CARABIDAE: HARPALINI): CLASSIFICATION, PHYLOGENY AND ZOOGEOGRAPHY

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Six species of this genus (type species – Trichopselaphus subiridescens *Chaudoir, 1843) are arrayed in two groups:* magnificus *group –* T. gloriosus *new species (type locality – BRAZIL, S. Antonio de Barra, Pr. de Bahia), and* T. magnificus *new species (type locality – PERU, Satipo);* subiridescens *group –* T. erwinorum *new species (type locality – COSTA RICA, Puntarenas, 2.0 km n Monteverde, sw slope Cerro Amigos, 1680 m),* T. meyeri *new species (type locality – MEXICO, Chiapas, Sierra de Colmena, San Cristobal trail 700–762 m);* T. minor *Bates, 1882; and* T. subiridescens *Chaudoir. The genus, species groups and species are described and characterized by illustrations of habitus and character states of adults. The following hypotheses about evolution of the genus are presented. Probable monophyly of* Trichopselaphus *is established on the basis of this combination of apotypic character states: form pterostichoid, body sub-terete in cross section; pronotum cordate or subcordate; front tibia thickened, apical margin sinuate; middle tarsi of males without ventral adhesive vestiture; elytra subiridescent, microsculpture meshes transverse; dorsum with metallic reflection. The sister group is not specified but is probably either an extant species group of* Selenophorus *or a genus closely related to* Selenophorus. *A reconstructed phylogeny is provided, based on analysis of transformation series of 23 characters, with major structural changes involving mouthparts (mandibles, and form and proportion of maxillary palpomeres), form of the apex of the male median lobe, structure of the ovipositor and associated abdominal sclerites (sternum 8, sternum 10, valvifer, and stylomere 2), and form of the hind legs of males. Sexual dimorphism is striking in* T. minor *and* T. subiridescens, *involving intraspecific differences in body size, head size, form of pronotum, and form of hind legs. Relatively larger size of males suggests that sexual behaviour may involve male/male combat; form of the hind legs of males suggests a distinctive way of holding females during copulation. Various features suggest that adults are specialized for life on the floor of tropical forests, burrowing either in compact litter, or in soil: transverse microsculpture, subcylindrical body, expanded fore tibiae, absence of adhesive vestiture from the middle tarsi of males, and relatively large prothorax. Limited diversity and divergence, pattern of geographical distribution, and pattern of holomorphological similarities of adults including inferred relationships to selenophorine Harpalini, suggest that* Trichopselaphus *arose in South American tropical lowland forest in the pre-Pliocene time. A vicariance pattern developed when one lineage dispersed to Middle America, probably crossing salt water barriers, with the South American stock giving rise to the* magnificus *group, and that of Middle American giving rise to the* subiridescens *group. The South American stock produced two known species. The Middle American stock developed a second vicariance pattern, with the lower Middle American stock producing* T. erwinorum, *and that of Nuclear Middle American giving rise to ancestral* T. meyeri-minor-subiridescens. *Development of an unknown barrier probably divided the range of the latter stock, producing two groups, one of which gave rise to* T. meyeri, *and the other to ancestral* T. minor-subiridescens. *Subsequently, dispersal of the latter stock produced the last vicariance pattern, with ancestral* T. minor *in Nuclear Middle America, and ancestral* T. subiridescens *isolated in islands in Lower Middle*

America. In late Pleistocene-Holocene time, T. subiridescens *extended its range northward to Guatemala in Middle America, and southward to nearly the southern edge of the tropics, in South America.*

Seis especies de este género (tipo Trichopselaphus subiridescens *Chaudoir, 1843), están distribuidas en dos grupos – el grupo* magnificus – T. gloriosus *nueva especie (tipo localizado en BRASIL, S. Antonio de Barra, Pr. de Bahía), y* T. magnificus *nueva especie (tipo localizado en PERU, Satipo). El grupo* subiridescens – T. erwinorum, *nueva especie (tipo localizado en COSTA RICA, Puntarenas, a 2.0 km norte de Monteverde, falda suroeste de Cerro Amigos, a 1860 metros), el* T. meyeri *nueva especie (tipo localizado en MEXICO, Chiapas, Sierra de la Colmena, a 700–762 metros del camino de San Cristóbal), et* T. minor *Bates, 1882, y el* T. subiridescens *Chaudoir. El género, los grupos de especies y las especies estdn representadas y caracterizadas por medio de ilustraciones de sus costumbres y de las características del ambiete de los adultos. A continuactíon se presenta una hipótesis sobre la evolución de los géneros. La posibilidad de que exista la monofília entre los* Trichopselaphus, *está establecida sobre la base de una combinación apótica del ambiente incluída en el genérico diagnóstico. Su grupo más allegado no se especifíca, pero debe ser ó un grupo de especie existente de* Selenophorus *ó un género muy parecido a éstos. Una filogenía reconstruída es presentada, basada en los análisis de las series de transformaciones de 23 características, con cambios estructurales importantes implicando a las partes de la boca (las mandíbulas y la forma **y** proporción de los palpómeres maxilares), a la forma del ápice del lóbulo mediano del macho, a la escructura del ovipositor y sus placas abdominales adyacentes, (el esternón octavo, el esternón décimo, el valvificador y el stylomere 2), y a la forma de las patas traseras de los machos. El dimorfismo sexual es muy notable en* T. minor *y* subiridescens, *implicando las diferencias intraespecficas en el tamaño del cuerpo, la cabeza, la forma del pronotum y la de las patas traseras. El hecho de que el tamaño de los machos sea relativamente mas grande, tiende a indicar que la conducta sexual involucraría luchas entre los machos; la forma de las patas traseras de ellos indican una manera determinada de sujetar la hembra durante el coito. Varios aspectos fisionómicos señalan el hecho de que los adultos están dotados para poder vivir en el suelo de los bosques tropicales, y para amadrigarse ya bien sea en los deshechos húmedos y compactos o en la tierra; éstos son la micro-escultura transversal, la forma del cuerpo sub-cilíndrico, las tibiae delanteras extendidas, el carecimiento de las vestiduras adhesivas desde los tarsi centrales de los machos y el tamaño relativament grande del pro-torax.*

La diversidad y la divergencia limitadas, la norma en que se encuentra la distribución geográfica y la semajanza holomorfológicas de los adultos, incluyendo las relaciones inferidas en los selenophorine Harpalini, insinúan que los Trichopselaphus *surgieron de los suelos llanos de los bosques tropicales de la America del Sur durante la era Cenozoica. Un modelo parecido se desarrollócuando un linaje se dispersó hasta la America Meridional, probablemente durante una travesía en aguas saladas, con una clase parecida al de la América del Sur, dando orígen al grupo* magnificus *y el modelo de la América Meridional dando origen al grupo* subiridescens. *La estirpe de la America del Sur produjo dos especies conocidas. La de la American Meridonal ceró un segundo modelo con el mas bajo de la America Meridional produciendo* T. erwinorum, *y el model Nuclear de la America Meridional dió orígen al ancestral* T. meyeri-minor-subiridescens.

El desarrollo de una barrera desconocida probablemente dividió la serie de esta última estirpe, produciendo dos grupos. uno de ellos dió orígen a T. meyeri *y el otro al ancestral* T. minor-subiridescens *Por consiguiente, la dispersión de la último modelo con ancestral* T. minor *en el Núcleo de la América Meridional y con ancestral* T. subiridescens *en islas en la part baja de la América Meriodional. A fines de la época Pleistocene-Holocene,* T. subiridescens *extendió su tango hacia el norte de Guatemala 6 hacia el sur hasta casi el borde de los trópicos en la América del Sur pro done está unida.*

INTRODUCTION

Systematists are drawn to study groups of organisms whose members are either pleasing to the eye and thus a delight to examine, or whose included taxa, though the members are plain, are numerous and difficult to distinguish, and thus present a challenge to both one's discriminatory ability and to one's perseverance. Most harpaline genera are in the latter category. However, there are exceptions, and *Trichopselaphus* is one; the adults are pleasingly proportioned and some are brilliantly colored.

Preliminary study showed that adults of two species (*T. minor* Bates and *T. subiridescens* Chaudoir) exhibited sexual dimorphism in form of the pronotum, which, as far as I know, is unique in Carabidae. Further, adults of these species also exhibited sexual dimorphism in the hind femora, a feature unique in the Tribe Harpalini. These characters rendered the group of more than usual interest. Additionally, at first glance, the group offered characters that seemed to form clear-cut phenoclines, so it seemed especially suitable for phylogenetic analysis.

Zoogeographically, the range of *Trichopselaphus* spans both South and Middle America, so I thought its species might provide a model for discussion of dispersal and vicariance in relation to these land masses.

Labium. (Fig. 12 and 15). Mentum with anterior margin concave, edenate. Prementum with ligula expanded apically (markedly so in *T. gloriosus*, Fig. 12), bisetose ventrally, and series of hairs dorsally at apex. Paraglossae glabrous, shorter than (Fig. 12), or longer than (Fig. 15), ligula. Palpus with articles broad, terminal palpomere hairy, penultimate article plurisetose, palpomere 1 with one seta or several setae at apex (Fig. 12 and 15).

Thorax. Pronotum as in Fig. 1 to 8. More or less cordate in form, disc broad, sloped rather steeply antero-laterally; anterior and posterior margins shallowly concave; lateral margins beaded, more or less sinuate posteriorly; anterior angles slightly obtuse, postero-lateral angles sub-rectangular. Median longitudinal impression shallow or deep (*T. magnificus*); postero-lateral impression deep, narrow, isolated from lateral margin, or broad, shallow, and extended to lateral margin. Prosternum sparsely setose, apex of intercoxal process with several long setae.

Pterothorax with metasternum sparsely setose.

Legs. In proportion generally average for Harpalina. Front tibia thickened. Apical margin sinuate, outer apical angle produced or not (Fig. 16A and 18A) terminated by one spine, apical spur broader than pre-apical spur. Middle tibia normal, or thickened, slightly bowed, and more setose than usual (*T. gloriosus*). Hind femur and tibia normal (Fig. 16B) or in males of *T. minor* and *T. subiridescens*, femur expanded with ventral projection (Fig. 17 and 18B) and tibia bowed slightly or markedly. Front tarsomeres expanded in members of both sexes; male with adhesive vestiture on front tarsomeres only, middle tarsomeres slender like hind tarsomeres. Basitarsus of hind tarsus average, not approximating combined lengths of tarsomeres 2 and 3.

Elytra. Oblong; sides straight medially, preapically subsinuate; apically and laterally sloped gradually or abruptly. Humeri prominent and toothed (Fig. 1) or rounded (Fig. 2 to 8). Striae various: of average depth with intervals slightly convex; or deeper, with intervals markedly convex; scutellar stria of average length, or markedly reduced. Stria 2 with five or more setigerous punctures; stria 5 with few setigerous punctures, in most specimens with one or two near base and one or two near apex, or stria 5 impunctate; stria 7 with five or more punctures (*T. gloriosus*), or impunctate.

Hind Wings. Reduced (*T. gloriosus*), or of normal length and with venation normal for Harpalina. Oblongum cell large, wedge cell narrow.

Abdomen. Sterna average for Harpalina; surfaces sparsely setose.

Male genitalia. Median lobe with dorsal membranous area extensive. Ostium of internal sac dorsal. Apical area simple (Fig. 19A), with small dorsal projection (Fig. 20A) or hypertrophied (Fig. 21 and 22A). Internal sac with armature various (Fig. 20C and D, and Fig. 22A).

Ovipositor and associated sclerites. Tergum 8 as in Fig. 26A average for Harpalina. Sternum 8 with apodemes short, base of each hemisternite normally sclerotized (Fig. 23A), or short, and basal areas of hemisternites reduced (Fig. 27A), or apodemes long (Fig. 24A). Tergum 10 with central area extensively and continuously membranous (Fig. 23B), or with membranous area divided by narrow sclerotized strip (Fig. 27B). Sternum 10 extensive, more or less trigonoid, with row of setae posteriorly (Fig. 24B) or narrow, sclerotized strip, with setae postero-laterally (Fig. 26D), or irregularly sclerotized, or unsclerotized. Valvifer average for Harpalina, that is, moderately elongate, narrowed posteriorly and anteriorly (Fig. 23C), or shorter and broad apically and basally (Fig. 25D).Stylus average for Harpalina (Fig. 23C and 24D), or stylomere 2 reduced but blade-like (Fig. 25D and 26F), or palpiform (Fig. 27C).

Larvae. – Van Emden (1942: 40, 72) characterized in a key to carabid larvae some Brasilian specimens that he assigned with doubt (indicated by a question mark following the name) to *T. subiridescens.* These specimens did not exhibit character states that van Emden regarded as diagnostic of larval Selenophori.

Geographical distribution. – The range of *Trichopselaphus* extends from Uruguay northward to the edge of the tropics, in eastern Mexico (Fig. 28).

KEY TO ADULTS OF THE SPECIES OF *TRICHOPSELAPHUS* CHAUDOIR

1 (0) Metepisternum with lateral margin longer than anterior margin; humerus of elytron not toothed . . . . 2.

1′ Metepisternum with lateral and anterior margins subequal; humerus of elytron with prominent tooth; hind wings short stubs . . . . *T. gloriosus,* new species, p. 454.

2 (1) Dorsum uniformly colored; mandible with dorsal surface shallowly strigulose, apex of left mandible tapered, not notched (Fig. 10E): pronotum smooth. . . . . 3.

2′ Dorsum of head and pronotum bright coppery green, elytra darker, dull greenish; mandible with dorsal surface strigulose, apex of left mandible broadened (Fig. 9D), shallowly notched; pronotum with shallow, coarse punctures, near middle of anterior and posterior margins . . . . *T. magnificus,* new species, p. 455.

Methods. – Taxonomic principles, criteria for ranking of species-group taxa, and general working methods employed were the same as explained previously (Ball 1970, 1972, and 1975; and Ball and Nègre, 1972), and are not repeated here.

Measurements were used to indicate variation in size and in proportions. The following measurements were made, using an ocular micrometer, in a Wild Stereobinocular microscope, at a magnification of 25X:

length of head – linear distance from base of left mandible to posterior margin of left compound eye;
width of head – maximum linear distance across head, including compound eyes;
maxillary palpus, length of article 3 – maximum linear distance from base to apex;
maxillary palpus, length of article 4 – maximum linear distance from base to apex;
length of pronotum – linear distance from anterior to posterior margin, measured along the mid-line;
distance of lateral seta of pronotum from anterior margin – linear distance from the anterior margin of the setal socket on the left side of the pronotum to the anterior margin;
width of pronotum at apex – maximum linear distance between anterior angles, measured at right angles to the mid-line;
pronotum, maximum width – greatest linear transverse distance, measured at right angles to the mid line;
width of pronotum at base – maximum linear distance between posterior angles, measured at right angles to the mid-line;
length of elytra – linear distance from basal ridge to apex of left elytron (or right, if the latter was longer);
length of hind femur – maximum linear distance from base to apex, measured on the anterior surface (this is the surface that is ventrally directed, with the leg flattened against the body);
width of hind femur – maximum linear distance measured at right angles to long axis of femur, from dorsal to ventral margin, on the anterior surface (with the anterior surface facing ventrally, the dorsal and ventral margins are directed anteriorly and posteriorly, respectively).

These measurements were combined in ratios or added as follows:

SBL – standardized body length: sum of length of head, pronotum and elytra;
MP: 1-3 / 1-4 – maxillary palpus, length of article 3 / length of article 4;
hF: w/l – hind femur, width/length;
Hw/Pw – width of head/width of pronotum;
P: l/w – pronotum: length/width;
P: Sd/l – pronotum: distance of lateral seta from anterior margin/length;
P: wA/wB – pronotum: width at apex/width at base;
Pl/El – length of pronotum/length of elytra.

Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine, in microvials, pinned beneath the specimen from which the parts had been removed. Larger parts were glued to cards, and pinned beneath the specimens from which they had been removed.

CLASSIFICATION

Trichopselaphus Chaudoir

Trichopselaphus Chaudoir, 1843: 399. – Lacordaire, 1854: 283–286. – Horn, 1881: 180.

Bates, 1882: 64. – Tschitscherine, 1900: 343, 351. – Csiki, 1932: 1080. – van Emden, 1942: 40, 72. – 1953: 515, 518. – Noonan, 1976: 42. – Reichardt, 1977: 429. – Shpeley and Ball, 1978 (in press).

TYPE SPECIES (by monotypy). – *Trichopselaphus subiridescens* Chaudoir, 1843.

This genus was established for *T. subiridescens* Chaudoir, 1843, and the species was based, evidently, on a female (Chaudoir did not mention the highly characteristic male hind femora, and described the hind tibia as slender, only), without maxillary palpi. The description featured mouthparts, but Chaudoir noted that the species was related to *Acinopus, Paramecus,* and others, a conclusion that could have been reached only if he relied on similarity in body form exhibited by members of these genera.

In fact, as Tschitscherine (1900: 343) pointed out, the members of *Trichopselaphus* are pterostichoid in body form. On the basis of this, plus the modified hind legs of males of *T. subiridescens* and extended front tarsi of females of these species, Tschitscherine placed the genus in its own subtribe, namedby him Trichopselaphini. Csiki (1932: 1080) followed this assignment. Van Emden (1953: 515) however, setting aside the markedly distinctive sex-associated features of the species known to him, recognized the correct relationships of the genus, and assigned it to the selenophorine assemblage. Noonan (1976: 42) and Reichardt (1977: 429) accepted this assignment.

The following key is modified from the key to the Harpalina in Reichardt (1977: 427–428), emphasizing the distinguishing features of *Trichopselaphus.*

1 (0) Elytral striae without setigerous punctures . . . . Genus-group Harpali and *Aztecarpalus* Ball.

1′ Elytron with at least stria 2 with small setigerous punctures . . . . 2.

2 (1′) Clypeus with anterior margin concave, basal membrane of labrum more or less exposed . . . . *Barysomus* Dejean, *Amblygnathus* Dejean.

2′ Clypeus with anterior margin straight or slightly concave, basal membrane of labrum not exposed . . . . 3.

3 (2′) Prothorax elongate in front of coxae, distance from anterior margin of pronotum to anterior coxal rim twice distance from latter point to apex of intercoxal process . . . . *Stenomorphus* Dejean.

3′ Prothorax of normal proportions, not prolonged anteriorly. . . . . 4.

4 (3′) Basitarsus of hind leg elongate, longer than tarsomeres 2 + 3; elytral striae 2, 5, and 7 with setigerous punctures . . . . *Selenophorus* Dejean, *Gynandropus* Dejean, *Athrostictus* Bates, *Discoderus* LeConte.

4′ Hind basitarsus shorter than tarsomeres 2 + 3; elytral stria 2, or striae 2 and 5, or striae 2, 5, and 7 with setigerous punctures . . . . 5.

5 (4′) Front tibia with outer apical angle prolonged as broad lobe with several spines; outer margin crenate; dorsal surfaces of tarsomeres glabrous; basitarsus of hind leg not much longer than tarsomere 2; ventral surface of body with sparse covering of short setae; body markedly convex, cylindridal in cross section . . . . *Anisocnemus* Chaudoir.

5′ Front tibia with outer apical angle not prolonged, or prolonged in form of sharp narrow projection (Fig. 16A), flanked but not terminated by spines; outer margin not markedly crenate; dorsal surfaces of tarsomeres setulose; basitarsus of hind leg longer than tarsomere 2, almost as long as 2 + 3 (Fig. 16B); ventral surface of body sparsely setulose; body moderately convex, ovoid in cross section . . . . *Trichopselaphus* Chaudoir.

scape, latter unisetose, pedicel with preapical ring of setae, only.

Mouthparts. Mandibles as in Fig. 9A-D. Maxillary stipes unisetose at base. Labium with ligula moderately expanded apically, as in Fig. 12.

Prothorax. Pronotum as in Fig. 2. Cordate, disc almost flat, sloped gradually laterally. Anterior and posterior margins almost straight, lateral margins markedly sinuate posteriorly; anterior angles obtuse, posterior angles almost rectangular. Lateral margin with bead widened markedly posteriorly. Median longitudinal impression deep, postero-lateral impressions oblong, broad, and deep; marginal grooves deep.

Legs. Average for genus. Front tibia latero-apically with four stout setae. Front femur with ventral surface flat, or slightly convex. Middle and hind tibiae each sub-cylindrical, not explanate.

Elytra. Sides parallel medially, laterally gradually sloped, sinuate pre-apically, apical declivity not suddenly and steeply sloped. Basal groove straight, humeral angles rounded, not toothed, nor prominent. Striae deep, scutellar stria short. Intervals convex, interval 7 not more prominent than others. Setigerous punctures in striae 2 and 5, only.

Ovipositor and associated sclerites. Sternum 8 with lateral apodemes elongate basal areas of hemisternites normally sclerotized (Fig. 24A); tergum 10 average; sternum 10 trigonoid with more densely sclerotized patches near base, setose apically (Fig. 24B) valvifer average for Harpalina (Fig. 24C); stylus as in Fig. 24D, stylomere 2 large, markedly falcate.

Type material. – Holotype female, labelled: Satipo, Peru Feb. 1944 Paprzyski [MCZ].

Derivation of specific epithet. – Like the specimens of *T. gloriosus,* this harpaline also requires a superlative to designate its magnificent form and color. – hence, *magnificus.*

Geographical affinities. – The type locality is far west of the known localities for *T. gloriosus,* and is west also of known South American localities for *T. subiridescens* (Fig. 28).

Relationships. – As indicated above, this species is probably related to *T. gloriosus,* but probably not very closely.

The *subiridescens* Group

Included are *T. erwinorum,* new species, *T. meyeri,* new species, *T. minor* Bates, and *T. subiridescens* Chaudoir. Characteristics are: dorsal surface concolorous, shining; left mandible with apex tapered in anterior aspect (Fig. 10E) paraglossae expanded beyond apex of ligula, latter narrowed apically (Fig. 15); terminal maxillary palpomere much longer than penultimate palpomere (Fig. 14); postero-lateral impressions of pronotum sub-circular, not linear, and laterally in contact with lateral grooves; elytral intervals flat, striae not especially deep; ovipositor with valvifer reduced, apically broadly rounded; stylomere 2 falcate, but small (Fig. 25D and 26E) or palpus-like and setose (Fig. 27D). In addition to these features, the group is also characterized by phenoclines involving development of the hind femora, reduction of sclerites of the ovipositor, reduction of the penultimate maxillary palpomere, and development of complexity in form of the median lobe. Details are provided under "Evolutionary Considerations", below.

The *subiridescens* group seems to be centered in Middle America, for the four known species are represented there. Only *T. subiridescens* is known from South America (Fig. 28).

Trichopselaphus erwinorum, new species
(Fig. 3, 19A-B, 25A-D, 28-32)

In addition to the key characters, the two known specimens of this species differ from specimens of *T. meyeri,* new species, by larger body size, longer maxillary palpomere 3 and 4, and larger head. Also, the apex of the median lobe of the male specimen is simple and slender, without a small dorsal projection.

Description. – Data on SBL and in values for the ratios MP: 1-3/1-4, hF: w/l, Hw/Pw, P: Sd/l, P: l/w, P: wA/wB, and Pl/El are presented in Tables 1 to 8.

Form. As in Fig. 3.

Color. Dorsal and ventral surfaces black. Appendages rufous.

Microsculpture. Lines generally fine, meshes on head wider than on pronotum or elytra. Head (both sexes), dorsum, with meshes slightly transverse anteriorly, isodiametric posteriorly; pronotum of male with meshes transverse except isodiametric antero-medially; female, lines finer, meshes transverse throughout; elytra, with meshes transverse, narrow.

Luster. Dorsum generally shining, not silky, subiridescent.

What most sharply focussed my attention on the group, however, was the discovery of the first specimen that I had ever seen of *T. meyeri*, new species. This individual was collected by my friend and former graduate student, Peter A. Meyer, on a wet, steep mountainside in Chiapas, Mexico, and was one of eight specimens that he, our guide and I were able to find in a long, sodden day of walking on steep, slippery limestone trails in magnificent montane tropical forest, and searching through leaf litter and fallen logs for carabids. When I saw the specimen, I knew it represented an undescribed species. It seemed so distinctive, in fact, that I arrived at the generic identification in the field only by a process of elimination. Thus, both the day and the beetle were memorable. All of these factors induced me to devote considerable time and effort to study of the species of *Trichopselaphus.*

Included in this paper are the following: diagnoses and descriptions of, and keys to, the taxa (the genus, two species groups, and four new, and two previously described species), photographs illustrating habitus, line drawings illustrating selected diagnostic features, geographical ranges, and phylogenetic relationships, and development of phylogenetic and zoogeographic hypotheses to establish relationships of the species. The classification is based on this phylogenetic analysis.

This paper is part of a series that will treat all of the selenophorines of Middle America. To date, two papers have been published on *Aztecarpalus* Ball, (Ball, 1970, and 1976), and one by Shpeley and Ball is in press, dealing with the species and relationships of *Anisocnemus* Chaudoir.

MATERIALS AND METHODS

Material. -- The physical basis of this paper is 490 adults of *Trichopselaphus,* most of which represent *T. minor* Bates and *T. subiridescens* Chaudoir. I also examined type material of these two species.

Sources of the material are collections of the following institutions and individuals, indicated in the text by the associated abbreviations.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024;
BMNH	Department of Entomology, British Museum (Natural History) London, England SW7 5BD;
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118;
CNC	Canadian National Collection of Insects, Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario K1A 0C6;
FSCA	Florida State Collection of Arthropods, Box 1269, Gainesville, Florida 32601;
JNV	Collection of J. Nègre, 9, Boulevard de Lesseps, 78–Versailles, France;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138
MNHP	Entomologie, Museum National d'Histoire Naturelle, Paris, France;
MZSP	Museu de Zoologia da Universidade de São Paulo, Caixa Postal 7172, 04263, São Paulo, Brasil;
UASM	Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3;
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Insitution, Washington, D.C. 20560.

Borrowed material was returned to the appropriate lending institutions. The holotype of *T. meyeri,* and one paratype of *T. gloriosus* were deposited in the United States National Museum of Natural History.

3 (2) Pronotum with lateral seta conspicuously anterior to transverse line of maximum width; anterior margin laterally sparsely setose or glabrous; anterior tibia without apico-lateral projection (Fig. 16A) . . . . 4.

3′ Pronotum with lateral seta slightly anterior to transverse line of maximum width; anterior margin glabrous; anterior tibia with apico-lateral projection (Fig. 18A) . . . . 5.

4 (3) Pronotum with anterior margin with row of fine setae laterally . . . . *T. meyeri*, new species, p. 457.

4′ Anterior margin of pronotum glabrous . . . . *T. erwinorum*, new species, p. 456.

5 (3′) Paragena parallel-sided; male hind trochanter pointed apically, hind femur abruptly widened before middle (Fig. 18) . . . . *T. subiridescens* Chaudoir, p. 459.

5′ Paragena markedly narrowed posteriorly; male hind trochanter rounded apically, hind femur widened gradually (Fig. 17) . . . . *T. minor* Bates, p. 458.

The six species are arranged in two groups, characterized below.

The *magnificus* Group

Included are *T. magnificus*, new species, and *T. gloriosus*, new species. Characteristics of adults are: dorsal surface bicolored, head and pronotum coppery-green, elytra either bright or dull green, left mandible with apex broadly truncate; maxillary palpus with terminal and penultimate palpomeres of average length, subequal; labium with paraglossae not extended to apex of ligula, latter widened apically; posterior-lateral impressions of pronotum elongate, isolated broadly from lateral grooves; elytral intervals convex, striae deep; ovipositor with valvifer large, tapered apically, pointed or narrowly rounded; stylomere 2 falcate, blade-like, not reduced.

Females only are known, and the two species differ strikingly in habitus and form of the middle tibiae. The habital differences are generally correlated with wing loss, involving as they do shortening of the metathorax and hence elytra, which cover the hind body. The more cylindrical body form and strengthened sub-carinate elytral humeri of *T. gloriosus* females suggest that this species might be sub-fossorial. Thus, *T. gloriosus* is either in an adaptive zone different from that occupied by *T. magnificus*, or is more modified for existence in it.

The strikingly modified middle tibiae of *T. gloriosus* females are unlike those of any other member of the genus, and this is the only species of *Trichopselaphus* whose members have setigerous punctures in stria 7. Perhaps this is evidence that *T. gloriosus* is more distantly related to the other species of the genus than is implied by locating it in the *magnificus* group. Because material is so scant and subsequent discovery of annectant forms seems likely, I think it best to be conservative taxonomically, and not to erect a monobasic higher taxon for *T. gloriosus*.

Trichopselaphus gloriosus, new species
(Fig. 1, 9A-D, 11, 12, 23A-C, 28, 29, 32)

Specimens of this species are easily recognized by characters in the key, and by form of the middle tibiae which are expanded, slightly flattened, and curved. (Possibly these features are characteristic of females, only).

Description. – Data on variation in SBL and in the ratios MP: 1-3/1-4, P: Sd/l, hF: w/l, Hw/Pw, P: l/w, P: wA/wB, and Pl/El are presented in Tables 1 to 8.

Form. More convex than average for harpalines, broad (Fig. 1).

Color. Dorsal surface bright metallic green, coppery postero-medially; pronotum wth disc coppery-green laterally, elytra bright metallic green dorsally, laterally intervals 8 and 9 purplish; ventral surface rufo-piceous to rufous. Appendages generally dark rufous, except palpi and basal antennomeres paler rufous.

Microsculpture. Lines fine, hardly visible at 50X. Clypeus, central part of frons, and lateral areas of pronotum and elytra with lines better developed, meshes slightly transverse; posterior part of frons and disc of pronotum and elytra with meshes narrow and transverse.

Luster. Shining, but not iridescent.

Head. Frontal impressions small, shallow, punctiform. Paragena much wider than antennal scape.

Mouthparts. Mandibles as in Fig. 9A-D. Maxillae average for genus, stipes with two setae near base (Fig. 11). Labium with ligula expanded apically, terminal palpomere less globose than average for genus (Fig. 12).

Prothorax. Pronotum as in Fig. 1, cordate, disc broad, sloped rather steeply antero-laterally; anterior and posterior margins shallowly concave; lateral margins beaded, markedly sinuate posteriorly; anterior angles slightly obtuse, posterior angles subrectangular. Median longitudinal impression shallow; postero-lateral impressions narrow, linear, shallow; marginal grooves rather broad.

Pterothorax. Metasternum sparsely setose, reduced; metepisternum with anterior and outer lateral margins subequal.

Legs. Anterior femur with ventral surface broadly concave, flanked anteriorly and posteriorly by rather narrow ridge. Anterior tibia apically with about eight broad spines on lateral surface. Middle tibia curved, slightly explanate and flattened laterally; anterior surface with four rows of finer setae, in addition to thicker marginal setae. Posterior tibia less explanate than middle tibia, less curved, but with rows of fine setae.

Elytra. Fused along suture, strongly and abruptly downcurved laterally, apical declivity steep; lateral margins bowed medially, clearly sinuate preapically. Basal groove almost straight, humeral angle prominent, toothed. Striae deep, scutellar stria short. Setae in striae 2, 3 (near apex), 5 and 7, setigerous punctures in striae 2 and 5 very fine, difficult to see.

Hind wings. Reduced, short stubs.

Ovipositor and associated sclerites. Sternum 8 with hemisternites short, extensively sclerotized medially (Fig. 23A); tergum 10 average (Fig. 23B); sternum 10 reduced, not evident; valvifer average for Harpalina (Fig. 23C); stylomere 2 not as large and less falcate than that of female *T. magnificus* (Fig. 23C; cf. Fig. 24D).

Type material. – Holotype, female, Brazil, labelled: "S. Antonio de Barra, Pr. de Bahia, 11.12.1888, Grouvelle".[MNHP]. Paratypes, two females, labelled: "S. Antonio R.G. Norte Brasil 11. 1952, M. Alvarenga" [JNV and USNM].

Derivation of specific epithet. – In my opinion, members of this species are the most elegant New World harpalines in form and color. They are resplendent, or glorious, and the Latin form of the latter word is *"gloriosus"* – hence the name.

Geographical affinities. – The localities are in eastern Brazil (Fig. 28), south of the Equator and south of the Amazon basin, remote from known localities of other *Trichopselaphus* species.

Relationships. – This species shares with *T. magnificus* the apotypic features of bicolored dorsum, convex elytral intervals, broadened mandibular apices, and broadened ligula. Hence, I think the two species are related. However, the several unique features of female *T. gloriosus* suggest that the relationship is rather remote. Also, the plesiotypic form of the ovipositor stylus, and setae in stria 7 suggest that *T. gloriosus* is the closest of the extant species to the ancestral stock of this genus.

Trichopselaphus magnificus, new species
(Fig. 2, 24A-D, 28, 29, 32)

The only known specimen of this species is bicolored dorsally, like specimens of *T. gloriosus*, but its middle and hind tibiae are unmodified, the antennal scape and pedicel are not generally setose, and the maxillary stipes has a single baso-lateral seta.

Description. – Data on SBL and on values for the ratios MP: 1-3/1-4, P: Sd/l, hF: w/l, Hw/Pw, p: l/w, p: wA/wB, and Pl/El are presented in Tables 1 to 8. Body form average, not sub-cylindrical.

Form. Habitus as in Fig. 2.

Color. Dorsal surface bicolored, head and pronotum bright green, elytra dull metallic green.

Microsculpture. Lines fine, though easily seen at 50X. Meshes of head isodiametric, on pronotum mostly isodiametric, though transverse but wide near mid-line. Meshes of elytra transverse, narrower than meshes of pronotum.

Luster. Shiny, but not iridescent.

Head. Frontal impressions deep, each linear at bottom, sub-circular toward surface. Paragena much wider than antennal

Relationships of *Trichopselaphus* to other selenophorine genera are best determined by use of apotypic character states that are shared by the taxa being considered. Obvious candidates, absence of setigerous punctures from stria 7, and lack of adhesive vestiture from the middle tarsi of males, would unite in a polythetic group *Stenomorphus, Anisocnemus,* and most of the species of *Trichopselaphus.* However, it seems likely that these character states were lost or reduced independently, and it is therefore doubtful that they can be used to show relationships among these genera.

A special comment is required about the relatively short hind basitarsi, which also characterize adults of these genera. This feature could be plesiotypic, and these genera thus descendants of a stock that was ancestral to the selenophorines with long hind basitarsi. Or it could be apotypic, having evolved by reduction from the latter stock. If so, shortening might have evolved once and would constitute an apotypic character state for *Anisocnemus, Stenomorphus,* and *Trichopselaphus.* Or it might be apotypic and have evolved independently in the ancestral stocks of each of these genera. I favour the third choice by analogy with the previously discussed features, but a firm decision will have to be based on detailed study of the characters of all of the selenophorine genera.

For the present, I can only state my belief that the ancestor of *Trichopselaphus* was derived from a *Selenophorus*-like stock, whose adults were generalized in habitus, and inhabited the forest floor in the lowland tropics of the New World.

The following combination of external character states is diagnostic for *Trichopselaphus* adults: setigerous punctures in striae 2 only (few individuals), in striae 2 and 5, or in striae 2, 5, and 7; pronotum cordate, or subcordate; front tibia thickened, apical margin sinuate (Figs. 16A and 18A), externally with or without a projection terminated by a single spine, apical spur broader than preapical spur; hind basitarsus of normal size, not approximating in length tarsomeres 2 and 3; front tarsomeres expanded (more so in males than in females), ventrally those of females without special vestiture, those of males with normal adhesive vestiture; middle tarsomeres of males without adhesive vestiture; dorsal surface of pronotum and elytra subiridescent, microsculpture meshes transverse, narrow.

Description. — Form pterostichoid: body sub-terete in cross section, elongate, pronotum cordate or sub-cordate. Standardized Body Length about 7.0 to 13.0 mm. (Table 1).

Color. Dorsum black, or bright metallic green, coppery, or purplish. Ventral surface infuscated to black. Appendages black to clear rufous.

Microsculpture. Labrum with lines distinct, meshes slightly transverse, almost isodiametric. Clypeus with lines fine, meshes isodiametric in females, transverse in males. Head with vertex with meshes fine, isodiametric (females) to slightly transverse (males). Ventral surface of head with meshes transverse, lines close together, very fine, evanescent in males, or meshes isodiametric (*T. magnificus*). Proepipleuron and proepisternum with meshes narrow, longitudinally oriented. Thoracic sterna and pterothoracic pleura with meshes narrow, transverse (except meshes of mesepisternum of *T. gloriosus* specimens longitudinally oriented). Elytra with lines fine, meshes narrow, transverse, generally finer in males than in females; epipleuron with meshes longitudinally oriented. Abdomen with meshes transversely oriented.

Luster. Dorsum generally shining, metallic, pronotum and elytra with traces of iridescence.

Head. Average for Selenophori. Frontal impressions punctiform to basin-like, but without narrow lateral extensions to vicinity of compound eyes. Clypeus average. Eyes various: large, with paragena narrower than antennal scape; or smaller, and paragena wider than antennal scape. Antenna with scape and pedicel with sparse vestiture of short setae, in addition to longer setae at apices of these articles, or with only longer apical setae (*T. magnificus*); antennomeres of normal proportions.

Labrum. Larger than average for selenophorines (Fig. 13), apical margin distinctly angularly notched, lobes rounded apically.

Mandibles. Average for Harpalini, moderately long, markedly curved apically, dorsal surfaces flat, dorsal surface of left mandible rugulose in apical 0.66; right mandible with dorsal surface strigulose or smooth. Left mandible (Fig. 9A and 10A) similar to that of *Aztecarpalus schaefferi* (Ball, 1970: Fig. 2a and 2b), but terebra longer and cutting edge less curved; terebral tooth prominent, isolated from retinacular ridge by deep groove; ventral groove shallow, broad. Right mandible (Fig. 9B and 10B) with terebral tooth small, retinacular ridge prominent, posterior retinacular tooth not clearly indicated; premolar tooth small; ventral surface with ventral groove shallow, setose.

Maxillae. Average for Harpalini, as in Fig. 11 and 14. Stipes unisetose or bisetose (*T. gloriosus*, Fig. 11). Apical tooth of lacinia prominent. Galea with articles slender, setose or not (Fig. 11), palpomere 3 longer (Fig. 11), or shorter (Fig. 14).

Head. Enlarged in male, average in female. Frontal impressions small, moderately deep, punctiform. Paragena distinctly wider than antennal scape, not narrowed posteriorly.

Mouthparts. Not studied in detail, generally as in *T. subiridescens.* Maxillary palpomere 3 moderately elongate, palpomere 4 normally slender, not swollen.

Thorax. Pronotum of similar form in male and female (Fig. 3). Cordate, disc broad, sloped gradually laterally. Anterior margin shallowly concave, posterior margin straight, beaded; lateral margins broadly beaded, sinuate posteriorly. Anterior angles slightly obtuse, posterior angles rectangular to slightly obtuse. Median longitudinal impression shallow. Postero-lateral impressions broad, shallow, extended to lateral groove on side, typical for *subiridescens* group.

Legs. Average for genus, no special modifications evident. Hind femur of male slender (as indicated by values for ratio HF: w/l).

Elytra. Generally average for Selenophori, but striae crenulate-punctate.

Male genitalia. Median lobe with apical portion as in Fig. 19A-B; slender, without dorsal hook. Armature of internal sac not studied in detail (sac was damaged in attempting to evert it. No large spines were observed in inverted position).

Ovipositor and associated sclerites. Sternum 8 with apodemes short, basal areas of hemisternites normally sclerotized (Fig. 25A); tergum 10 average for Selenophori (Fig. 25B); sternum 10 trigonoid, evenly sclerotized through out length, row of setae apically (Fig. 25C); valvifer short and broad (Fig. 25D); stylus short, stylomere 2 falcate (Fig. 25D).

Type material. -- HOLOTYPE male, labelled: COSTA RICA, Puntarenas, 2.0 km N Monteverde sw slope Cerro Amigos 10° 19′ N, 84° 48′ W, 1680 m, 10 June, 1973, beneath logs, branch T.L. & L.J. Erwin. Exped #44 in Notebook 2 Erwin & Hevel Central American Expedition ADP 15751.

ALLOTYPE female, labelled: PANAMA Chiriqui 8.0 km W Boquete Quebrada Emporio 08° 47′ N, 82° 30′W, 220 m 19 June, 1973; beneath logs, branch T.L. & L.J. Erwin. Erwin Exped No. 65 in Notebook 2. Erwin & Hevel Central American Expedition ADP 17539. These are the only known specimens of this species. Both are in the entomological collections of the United States National Museum of Natural History.

Derivation of specific epithet. – This is the Latinized genitive plural of the surname of my friends, Terry and LaVerne Erwin, who collected the specimens and permitted me to study and describe them.

Geographical distribution. – Known only from Costa Rica and Panama, in Lower Central America.

Geographical affinities. – The range of this species is overlapped by that of *T. subiridescens* and *T. minor.*

Relationships. – Although the specimens of *T. erwinorum* and *T. meyeri* resemble one another rather closely, I believe that most of the similarities are the result of retention of ancestral features, or of parallelism. The simple male genitalia, maxillary palpi relatively long for the *T. subiridescens* group, and well developed sternum 10 of the female suggests that *T. erwinorum* is the most ancestral of the species contained in the *subiridescens* group.

Trichopselaphus meyeri, new species
(Fig. 4, 16A-B, 20A-D, 26A-F, 28-32)

In body form, adults of this species are most like those of *T. erwinorum.* The markedly reduced maxillary palpomere 3 distinguishes members of *T. meyeri* from those of *T. erwinorum.* Males of the former species have the apex of the median lobe slightly modified (Fig. 20A, cf. Fig. 19A), and females have sternum 10 reduced (Fig. 26D, cf. Fig. 25C).

Description. — Data on variation in SBL, and in the ratios MP: 1-3/1-4, P: Sd/l, hF: w/l, Hw/Pw, P: l/w, P: wA/wB, and Pl/El are presented in Tables 1 to 8.

Form. As in Fig. 4.

Color. Dorsal and ventral surfaces black in holotype, piceous to rufous in paratypes. Appendages rufous.

Microsculpture. Male with lines not evident at 50X on head (except clypeus), pronotum and elytra; meshes on clypeus effaced laterally, isodiametric medially. Females, lines on head and pronotum more distinct than on elytra; dorsum of head (and clypeus) – meshes isodiametric; pronotum – meshes narrow, transverse; elytra – meshes transverse, narrower than on pronotum.

Luster. Dorsum of head shining; pronotum rather silky in females, shining in males; elytra iridescent.

Head. Frontal impressions small, moderately deep, punctiform. Paragena distinctly wider than scape, not narrowed posteriorly.

Mouthparts. Average for *subiridescens* group, except maxillary palpomere unusually short.

Prothorax. Pronotum as in Fig. 4, similar in both sexes. Cordate, disc broad, sloped gradually laterally; anterior margin shallowly concave, posterior margin straight, beaded; lateral margins broadly beaded, sinuate posteriorly. Anterior angles slightly obtuse, posterior angles rectangular to slightly acute. Median longitudinal impression shallow; postero-lateral impressions average for *T. subiridescens* group. Anterior margin at each side with group of four to six setae.

Legs. Average for genus, no special modifications evident. Hind femur of male slender (indicated by values for ratio hF: w/l.

Elytra. Average for *Trichopselaphus.*

Hind wings. Fully developed.

Male genitalia. Median lobe as in Fig. 20A-B: apex with small dorsal projection. Internal sac as in Fig. 20C-D; group of enlarged microtrichia apically and basally; smaller microtrichia medially.

Ovipositor. Tergum 8 as in Fig. 26A; sternum 8 with apodemes short, medially extensively sclerotized (Fig. 26B); tergum 10 average for genus (Fig. 26C); sternum 10 narrowly sclerotized, with few setae latero-apically (Fig. 26D); valvifer short and broad (Fig. 26E); stylomere 2 sub-falcate, small, broad, with single seta pre-apically (Fig. 26F).

Type material. – HOLOTYPE male, labelled: "MEXICO Chiapas; Sierra de Colmena San Cristobal trail 2300–2800′ [= 700–853 m], June 8, 1972; P.A. Meyer, G.E. Ball, and K.E. Ball, collectors". The allotype is labelled: "MEX. Chiapas, e slope Sierra de la Colmena nr. "La Caverna" 16° 24′ 18″ N., 91° 24′ 16″W., VI. 4–13. 1972". The holotype is in the United States National Museum of Natural History; the allotype is in the Strickland Museum, Department of Entomology, University of Alberta.

There are six additional paratypes, labelled: "Córdova VC Mex, Fred Knab collection" (two females, USNM); "Córdova Mex Ver, Dr. A. Fenyes, A. Fenyes Collection" (two males, one female, CAS); "Lagos de Colores, Chiapas, Mex., VI. 14.1969, D.E. Bright" (female, CNC).

Derivation of specific epithet. – This species is named in honor of the collector of the holotype, Peter A. Meyer, whose company and assistance I enjoyed in Mexico during the 1972 field season.

Note on habitat. – The holotype and allotype were collected in montane rain forest. The allotype flew to an ultra-violet light, at night. The holotype was found on a forested mountain slope, in a crack in very dry clay soil (even though the leaf litter covering was soaked), about 0.5 m below the surface of the ground.

Geographical affinities. – The range of *T. meyeri* is overlapped by that of *T. minor.* The two are probably sympatric. I suspect that *T. subiridescens* and *T. meyeri* are sympatric too, probably in northern Central America.

Relationships. – The maxillary palpomeres, with 3 reduced and 4 expanded, modified male genitalia, and reduced ovipositor sclerites, suggest that this species is related to and probably represents the sister lineage of the one that gave rise to *T. minor* and *T. subiridescens.*

Geographical distribution. – This species is known from the tropical Mexican states of Chiapas and Veracruz. Probably these locations are in the northern part of this species' range.

Tripchopselaphus minor Bates
(Fig. 5, 6, 10A-E, 13-17, 21, 28-32)

Trichopselaphus minor Bates, 1882: 64. – Csiki, 1932: 1080.

In addition to the key characters, males of this species are easily recognized by the form of the median lobe, with apical area hypertrophied, and with a ventrally-directed projection (Fig. 21). Females are like those of *T. subiridescens*, but the eyes are smaller, and the paragenae are proportionately wider.

Description. – Data on variation in SBL and in the ratios MP: 1-3/1-4, hF: w/l, Hw/Pw, P: l/w, P: Sd/l, P: wA/wB, and Pl/El are presented in Tables 1 to 8, for a population sample from La Lima, Honduras.

Form. As in Fig. 5 and 6; elongate, slender, moderately convex.

Color. Dorsal surface generally dark, but margins of pronotum piceous. Palpi, legs, and antennae piceous, though rufous in partially teneral individuals.

Microsculpture. Dorsum with meshes generally transverse, shorter and wider on head than on pronotum and elytra.

Luster. Shining, with greenish-bronze reflections, subiridescent.

Head. Frontal impressions various, generally sub-circular, punctiform at bottom. Eyes large, paragena at narrowest point about 0.5 width of antennal scape.

Mouthparts. Typical for *T. subiridescens* group: mandibles as in Fig. 10A-D; labrum as Fig. 13; maxilla as in Fig. 14; and labium as in Fig. 15. Terminal palpomeres subglobose, densely setose.

Prothorax. Pronotum as in Fig. 5 and 6. Cordate (female), subcordate (male), disc convex, sloped steeply laterally; anterior margin shallowly concave, basal margin about straight; lateral margins beaded, narrowed posteriorly, sinuate posteriorly, more so in female than in male. Anterior angles obtuse, rounded: posterior angles rectangular to slightly obtuse. Median longitudinal impression sharply delimited, but shallow; postero-lateral impressions broad, extended to lateral grooves; marginal grooves sharp, narrow.

Legs. Anterior femur with ventral surface broadly, shallowly concave, concavity flanked by broad, rounded, raised area, not by sharp carinae. Anterior tibia with apico-lateral projection (cf. Fig. 18A). Hind femur and tibia dimorphic: normal in female, but in male femur with prominent tooth-like projection, tibia slightly bowed, trochanter broadly pointed at apex (Fig. 17). Tarsomeres setose dorsally.

Elytra. In form, average for *T. subiridescens* group. Setae in striae 2 and 5 near base and in apical 0.33, or absent from stria 5.

Male genitalia. Median lobe as in Fig. 21, apical area enlarged, with ventrally-directed denticulate process. Internal sac without enlarged macrotrichia.

Ovipositor and associated sclerites. Sternum 8 with hemisternites shorter than in *T. meyeri* female (cf. Fig. 25A); tergum 10, average, as in Fig. 23B; sternum 10 irregularly sclerotized, or unsclerotized, without setae apically. Valvifer short and broad (cf. Fig. 27C): stylomere 2 palpiform, generally sparsely setose (cf. Fig. 27C).

Type material. – Holotype male, labelled: "Type H.T." [circular label, ringed with red]; "Veracruz"; "Mexico Sallé Coll"; "BCA Col. 1.1" "Trichopselaphus minor Bates"; "Trichopselaphus minor Bates" [handwritten] [BMNH].

Geographical affinities. – The range of this species overlaps that of *T. meyeri* and the northern part of the range of *T. subiridescens* in Middle America.

Relationships. – Based on synapotypic character states of large eye size, reduced maxillary palpomere 3, sexual dimorphism of the pronotum, hypertrophied male genitalia, sternum 10 of female reduced, and palpiform stylus of the ovipositor, this species and *T. subiridescens* are sister taxa.

Geographical distribution and material examined. – The known range of *T. minor* extends in Middle America from Honduras to about the limit of the tropics in lowland eastern Mexico (Fig. 28). Perhaps the species is confined to Nuclear Middle America, though it seems more likely that the range extends farther south to those areas that became coninuous land in late Tertiary time.

I examined 277 specimens, from the following localities. HONDURAS. Cortes, La Lima, June 3, 1964, at U-V light, 274 specimens (USNM; FSCA; UASM). MEXICO. Veracruz, Orizaba (holotype). San Luis Potosi, Ciudad Valles, Palma Motel, VII.8-23. 1969, two specimens (MCZ).

Trichopselaphus subiridescens Chaudoir
(Fig. 7, 8, 18A-B, 22A-B, 27A-C, 28-32)

Trichopselaphus subiridescens Chaudoir, 1843: 402. – Lacordaire, 1854: 286-287. – Horn, 1881: 180. – Bates, 1882: 64. – van Emden, 1942: 72. – Reichardt 1977: 429.

Diagnostic characteristics are indicated in the key and in discussion of recognition features of *T. minor,* above.

Description. – Data on variation in SBL and in the ratios MP: 1-3/1-4, hF: w/l, Hw/Pw, P: l/w, P: Sd/l, P: wA/wB, and Pl/El, are presented in Tables 1–8, for various population samples.

Color, microsculpture, luster, and structure of head generally as in *T. minor.* Eyes not as enlarged as in adults of *T. minor,* body size on average larger, legs of males with hind femora more hypertrophied, hind tibiae more bowed and crenulate, and trochanters pointed (Fig. 18B).

Male genitalia. Median lobe with apical area hypertrophied (Fig. 22), with dorso-apical swelling. Internal sac with patch of enlarged macrotrichia near base.

Ovipositor and associated sclerites. Sternum 8 short, basal areas of hemisternites with sclerotization reduced (Fig. 27A); tergum 10 with sclerotized strip posteriorly, membranous areas divided into two parts (Fig. 27B); sternum 10, valvifer, coxite and stylus as in *T. minor* (Fig. 27C).

Type material. – In the Oberthür Collection, Box 205, are 16 authentic Chaudoir specimens, in front of the following label that is pinned in the box: "coerulescens Chaud Bresil Piedes C. Fald". [MNHP]. The original description was based on a female, and probably the first specimen of that sex in this series should be chosen lectotype.

Geographical affinities. – The range of this species overlaps the known range of *T. erwinorum,* and the southern portion of the range of *T. minor,* in Central America.

Relationships. – See discussion of this topic for *T. minor.*

Geographical distribution. - The range of this species extends from Uruguay and Bolivia on the South American continent, to Guatemala, in Nuclear Middle America (Fig. 28). The large hiatus in the range of this species in northern South America is likely the result of inadequate collecting. The fact that differences have not been found between Middle and South American populations suggests that this species is continuously distributed in the intervening areas.

I have seen 185 specimens from the following localities.

URUGUAY. Montevideo. (MZSP).

BOLIVIA. Cochabamba, Carrasco Siberia (MZSP): Cochabamba, El Limbo (MZSP). Santa Cruz, Sara Nueva Moka (MZSP).

BRAZIL. State of Minas Gerias: Campinas (USNM): Lambray (USNM): Serro de Caraca (MZSP). State of Paraná: Banhados R.R. from Curitiba to Paranaguá (CNC); Curitiba (MZSP); Ponta Grossa (AMNH). State of Santa Catarina: Corupa (AMNH); Hansa Humboldt (BMNH, MZSP): Jaraque (AMNH); Nova Teutonia (BMNH, MZSP); Rio Natal (AMNH); Rio Vermelho (AMNH). State of São Paulo: Barueri (MZSP); Cajurie (MZSP); Caminha Mari (USNM); Campinas (USNM); Ilha dos Buzios (MZSP); Juquia (MZSP); Pae Mathias (USNM); Rio de Janeiro (MZSP); Salesopolis, Est. Biol. Boraceia (MZSP, USNM); Santana (USNM); St. Anna (USNM); São Paulo (MZSP); Ubatuba (USNM); Ypiranga (MZSP).

PANAMA. Canal Zone, Cocoli (USNM). Chiriqui Fortuna lite trap 8°43′ N, 082°16′ W, 21 Nov., 1976-15 Jan., 1977 (USNM).

BRITISH HONDURAS. Punta Gorda (AMNH).

GUATEMALA. Cuchumatanes Mts. 5.6 mi [=9 km] n. Santa Cruz Barillas (UASM).

In South America, specimens were collected in every month of the year, except August. The Panamanian specimens were collected in May, and from November to January. The Guatemalan specimens were collected in August, at ultraviolet light.

Lacordaire (1854: 287) noted that large numbers of adults of this species were discovered on sea beaches in southern Brazil. Evidently they had been washed up, having fallen into the water in the course of mass flights.

EVOLUTIONARY CONSIDERATIONS

A principal concern of evolutionary analysis of a taxon is to reconstruct its phylogeny, either as the basis for classification, or for other purposes. In fact, the classification of *Trichopselaphus,* presented above, is based on phylogenetic considerations, as reviewed in this section. The data base for this analysis is confined to structural features of adults, for these are the only semaphoronts available for all species. More specifically, females are the only semaphoronts available for all species. Nonetheless, it should be possible to make at least preliminary inferences about relationships, and thus provide a basis not only for classification but also for making predictions that can subsequently be tested in terms of additional holomorphological features and additional taxa that will be discovered by future workers.

Monophyly of *Trichopselaphus*

Evidence for inferring a monophyletic origin of *Trichopselaphus* is the unique combination of features that characterize this group and constitute its diagnosis. Each of these features has almost certainly arisen several times in the Harpalini, but not in combination with the other features of the diagnosis. The distribution pattern of this group is also consistent with a unitary origin. Some of the structural features are consistent with life in an adaptive zone that is distinct from that of its closest relatives (burrowing for *Trichopselaphus*; soil surface, or surface-leaf litter interface for the putative sister group). These features (holomorphological, chorological and ecological) consitute the ancestral character states of *Trichopselaphus*.

Methods of Phylogenetic Reconstruction

These were formulated by Hennig (1966), and have been reviewed by various workers, including me (Ball, 1975), and Whitehead and Ball (1975). Recent, particularly clear treatments of this topic have been provided by Ross (1974), Hecht and Edwards (1977) and Ekis (1977).

A reconstructed phylogeny of taxa depends upon analysis of morphoclines or transformation series (two-state and more), the goal of which is to identify plesiotypic and apotypic states of each character. Determination of phylogenetic relationships depends upon grouping taxa by synapotypy (shared, derived character states). However, derived character states can be evolved independently in more or less closely related lineages. Thus, a second aspect of phylogenetic reconstruction is to distinguish synapotypy from convergence and parallelism. Methods to do so are described below.

The most generally used criterion to classify character states is frequency of occurrence, either within the group of taxa being studied (in-group comparison) or within related taxa, and especially, within the sister group (ex-group comparison). In a given phenocline (morphocline, transformation series) that state which occurs outside the group is regarded as plesiotypic. regardless of extent of distribution of the character state within the group. If a given character is confined to the group under consideration, that state which is most widely distributed is regarded as plesiotypic.

A second criterion involves group trends (Ross, 1974). For example, flight wings tend to be lost in carabids that inhabit certain types of habitats. Thus, in a given group, macroptery would be classified as plesiotypic, and brachyptery as apotypic. Eye loss or reduction in cave forms is another character state of this kind: that is, the most parsimonious explanation of absence of eyes among a group of cave beetles heretofore unstudied, would be loss of visual organs as a result of selection pressures exerted by the cave environment. Other criteria are discussed by Ekis (1977).

To distinguish between synapotypy and similarity resulting from parallelism/convergence, Hecht and Edwards (1977) proposed a weighting system of five categories. The greater the weight, the more certain it seems that shared derived character states result from common ancestry. Because of differences between types of characters used and amount of knowledge available about them, I had to modify their weighting system for use with *Trichopselaphus*, producing the following:

I. Loss of a structure
II. Simplification or reduction of a complex character
III. Simple change, involving color, or positions of isolated setae.
  a. Two states
  b. Three states

IV. Parts of a functional complex
    a. Two states
    b. More than two states.

For analysis of the data, I needed to use only criteria of frequency of occurrence (ex-group and in-group comparisons), and group trends. The "ex-group" referred to is generalized, including New World selenophorines as a whole, rather than any specific groups. This is because the sister group of *Trichopselaphus* has not been identified. Most of the characters used are in weighting groups III and IV.

Table 9 lists characters and character states by number, and Fig. 29 summarizes for each character the method of phylogenetic classification of its character states, the weighting group to which it was assigned, and the classification and distribution of each of its states. Characters are listed in the sequence in which they would appear on a detailed cladogram. A simplified cladogram is printed in Fig. 32.

Analysis of Characters

Notes are provided below about some of the characters used in the phylogenetic analysis which were expressed quantitatively in the text, and about form of the male median lobe, and sternum 8 and ovipositor stylus of females. Interpretation of these sex-associated characters may seem equivocal or incorrect, so they require detailed consideration.

Eye size (character 4). – Both states ("smaller"; "larger") are widespread among selenophorines, though small eyes are more frequent. Among adults of *Trichopselaphus,* too, smaller eyes are more common. Eyes were classified as "smaller" if an adjacent paragena was wider than the antennal scape. They were classified as "larger" if an adjacent paragena was either as wide as or narrower than an antennal scape. Width of the paragena varies inversely as size of eyes.

Maxillary palpus (Characters 6, 7, and 8, Fig. 11 and 14). – Although this is a structural and presumably functional complex, I have recognized three elements which I believe have evolved more or less independently from one another, and so can be weighted separately for phylogenetic purposes. Character 8 involves form and vestiture of palpomere 4. Its swollen form and relatively dense vestiture, characteristic of *T. meyeri, T. minor* and *T. subiridescens,* are unique among New World selenophorines, and this character state is thus apotypic. Partial independent development of this character state in relation to characters 6 and 7 is indicated by the position of the *magnificus* group: in measurements, the female of *T. erwinorum* is closer to the other members of the *subiridescens* group than to the members of the *magnificus* group. However, in form of palpomere 4, *T. erwinorum* is closer to the *T. magnificus* group.

One of the most interesting aspects of this character complex involves the striking difference between members of *T. erwinorum* and those of *T. meyeri* (Fig. 30). Adults of the two species resemble one another in habitus, position of the lateral seta of the pronotum, form of the ovipositor stylus, and color of antennae and legs. The principal reason, in fact, for believing that *T. meyeri* is more closely related to *T. minor* and *T. subiridescens* is sharing of structural details of the maxillary palpomeres.

Although values for the ratio MP: 1-3/1-4 must be related for each species to the sum of these measurements, the relationship is not simple. I believe that two factors are involved: one is an overall reduction in length of palpomeres 3 and 4, and the other is disproportionate reduction of article 3. Adults of *T. erwinorum* illustrate overall reduction in length of the articles, whereas members of the *T. meyeri-minor-subiridescens* complex exhibit disproportionate reduction in palpomere 3.

These characters together represent a transformation series, involving in sequence reduction of length, followed by further reduction of length in palpomere 3 and increase in bulk and hairiness of palpomere 4. This seems to be the general pattern. In detail, however, matters are more complicated, because overall length of the palpomeres seems to be related to body size. Thus, the single female of *T. erwinorum* is within the range of variation of *T. subiridescens* for both length of palpomeres and for SBL. For both of these features, the *T. erwinorum* female is beyond the range of both *T. minor* and *T. meyeri.*

Position of the lateral pair of pronotal setae (character 12). – In adults of most species of selenophorines, these setae are near the middle. This is true also of four of the six species of *Trichopselaphus,* and is indicated by values for the ratio P: Sd/l (Table 6). However, for specimens of *T. erwinorum* and *T. meyeri,* values for this ratio are low, indicating that the setae are more anterior in position. This latter character state is judged to be apotypic both by ex-group and in-group comparisons.

Punctation of stria 7 (character 15). – Presence of punctures in stria 7 is interpreted as plesiotypic because this character state is widespread in selenophorines. In *Trichopselaphus,* only the generally highly derived adults of *T. gloriosus* exhibit this state, and accepting it as plesiotypic requires its loss twice in the genus (once for the ancestral stock of *T. magnificus,* and once for the ancestral stock of the *subiridescens* group). If it were assumed that absence of punctures from stria 7 were plesiotypic for *Trichopselaphus,* then presence of the punctures in stria 7 would be apotypic for *T. gloriosus.* And, in support of such a possibility, I note that stria 3 also bears setigerous punctures near the apex. These are clearly a new development for the genus, and appearance of punctures in stria 7 might be part of a general tendency to increase such structures.

Against this possibility, I note a tendency among selenophorines to lose punctures from stria 7, exhibited not only by adults of *Anisocnemus* and *Stenomorphus,* but also by various species of *Selenophorus.* So, I am inclined to believe that loss of these setigerous punctures is the rule. Nonetheless, the argument is tenuous and my interpretation is at best weakly supported.

Hind femur of males (character 17, Fig. 16-18). – The relation between values for the ratio hF: w/l and SBL for males of the *subiridescens* group is illustrated by Fig. 31. A trend is indicated, from the more plesiotypic *T. erwinorum* and *T. meyeri,* to the more apotypic *T. minor,* and most apotypic *T. subiridescens.* Although a general relationship between body size and degree of hypertrophy of the hind femora is indicated, the relationship is not precise, because small males of *T. subiridescens* that are within the size range of *T. minor* have a higher value for the ratio than have comparable-sized specimens of the latter species.

Male genitalia-form of apex of median lobe (character 18, Fig. 19-22). – I believe that differences among males of the *subiridescens* group can be interpreted as a transformation series in the sequence *T. erwinorum-meyeri-minor-subiridescens.* This is not self-evident, though it is clear that the simple apex of the male of *T. erwinorum* appears to be the least evolved. I assume that, in the ancestry of the *T. meyeri-minor-subiridescens* complex, a tendency developed for modification of the form of the apex. This was least expressed in *T. meyeri,* was more pronounced in the common ancestor of *T. minor-subiridescens,* and reached maximum expression in *T. subiridescens.*

I must emphasize however, the weakness of the argument. It is equally possible that the dorsal hook of the median lobe in *T. meyeri* evolved independently of the hypertrophied apices characteristic of the median lobes of *T. minor* and *T. subiridescens.*

Sternum 8 of females (characters 19 and 20, Fig. 23A-27A). – Variants of this structure are classified as two characters to make easier the phylogenetic analysis. In the female of *T. magnificus,* the apodemes are elongate (Fig. 24A), compared to other *Trichopselaphus* females and those of other selenophorines, and this state is interpreted as apotypic.

On the other hand, in females of the remaining species of *Trichopselaphus,* sternum 8 is of average development (interpreted as plesiotypic), or the basal portions of the hemisternites are reduced (Fig. 27A), and/or the apodemes are reduced (Fig. 27A). Like the elements of the male genitalia, those of sternum 8 seem to form a several-stage transformation series, but involving reduction of a sclerite rather than hypertrophy.

Stylomere 2 of the ovipositor (Character 19, Fig. 23C, 24D, 25D, 26F, 27C). – Variants of this structure seem to me to form a transformation series involving, first, reduction of intensity or change in whatever may be the function of this sclerite (probably the cutting blade used in digging and shaping a cell in the ground, into which the eggs are deposited), so that the stylus becomes smaller and weaker. From the latter evolutionary position, one line evolved (the ancestral stock of *T. minor-subiridescens*) in which the function of the stylus changed – presumably from simply excavating a hole to one of forming a more elaborate chamber for the eggs. Although little is actually known about function of the ovipositor of harpalines, it is known that females of many groups of lebiines and chalaeniines have both modified styli and an associated behaviour pattern involving construction of elaborate forms of egg chambers.

Admittedly, the argument is tenous. It would be simpler to recognize the derived styli as of two types (*erwinorum-meyeri*; and *minor-subiridescens*), and not to suggest that they are parts of a transformation series. However, I believe that the hypothesis of a direct relationship between these types provides a line of thought that can be tested, and this is likely to be more useful than the simpler approach.

The Reconstructed Phylogeny

On the basis of synapotypic features, Fig. 29 shows two major complexes: the *magnificus-gloriosus* complex, and the *erwinorum-meyeri-minor-subiridescens* complex. It seems reasonable to suggest that these are a pair of sister groups.

Within the more diverse complex, the data seem to support two ways of grouping: *T. erwinorum* apart from the others; or *T. erwinorum-meyeri* apart from *T. minor-subiridescens.* The first arrangement implies that the apotypic states of characters 2, 3, and 12 evolved independently in *T. erwinorum* and *T. meyeri.* These features, involving color and position of a pair of setae, are each weighted as IIIa. This arrangement also suggests that the apotypic states of characters 7, 8, and 18 evolved in a common ancestor that gave rise to *T. meyeri* and *T. minor-subiridescens.* The latter group of features are weighted as IVb, involving proportions and form of palpal articles and form of the median lobe of the male genitalia. These features are weighted, more heavily because they are parts of structural complexes, and of several step transformation series.

The second arrangement makes a sister group of *T. erwinorum* and *T. meyeri,* and implies the reverse of the first arrangement: that is, that characters 2, 3, and 12 evolved in a common ancestry shared exclusively by *T. erwinorum* and *T. meyeri,* and that subsequently, the *T. meyeri* stock evolved the apotypic conditions of characters 7, 8, and 18, which are also characteristic of the *T. minor-subiridescens* stock. This phylogeny is possible, but I believe that future evidence is more likely to support the first arrangment, represented by Fig. 32.

Pattern of character evolution. – Of the 23 character transformations included in the reconstructed phylogeny, only four require more than a single origin of an apotypic character state. These are: color of legs and antennae (characters 2 and 3), and position of the lateral setae of the pronotum (character 12), each of which was evolved independently by *T. erwinorum* and *T. meyeri;* and degree of developemnt of sternum 10 (character 21), each of whose two apotypic states was evolved in the *magnificus* group and in the *subiridescens* group.

Loss was involved in evolution of two transformation series: punctures of stria 7 (character 15), and flight wings (character 16). Reduction was involved in six series: overall length of maxillary palpi (character 6), length of palpomere 3 (character 7), development of sternum 8 of females (character 19), development of sternum 10 (character 21), development of valvifers (character 22), and development of stylomere 2 (character 23).

The remaining 16 transformation series involved either increase or simple change in form or position. One of these, form of pronotum of males (character 10) involves a partial reversal to a more plesiotypic state: the prothoracic sides of males of *T. minor* and *T. subiridescens* are most subsinuate, and in this respect, are more like selenophorines in general than like other members of *Trichopselaphus.*

The overall pattern, then, is mainly one of divergence from the structural plan of the ancestral stock of the genus involving principally increases or simple changes in form or position. Of less frequency have been changes involving convergence, reduction, loss, and reversal.

Additional considerations about evolution of character complexes; burrowing adaptation, sexual dimorphism, and mouthparts require explicit comment.

Evolution of adaptations for burrowing. – I do not know by direct observation that adults of this genus are burrowers in soil, but I believe that they are, based on sub-cylindrical body form, slightly explanate front tibiae with apico-lateral projections (Fig. 18A), and absence of adhesive vestiture from the middle tarsi of the males. If this surmise is correct, other indications of burrowing adaptations should be evident. I have so interpreted the values for two ratios.

Many burrowing harpalines are characterized by relatively high values for the ratio Pl/El, which indicate that the prothorax is relatively large. For example, values for this ratio for adults of the burrowing species *Anisocnemus amblygonus* Shpeley and Ball are: for males, 0.43–0.47; for females, 0.38–0.43. Values for this ratio for samples of *Trichopselaphus* are comparable. Within the genus, members of the *magnificus* group have the highest values, suggesting perhaps, that such adults are the most highly modified for a burrowing existence.

A trend toward a relatively longer prothorax is also seen in values for the ratio P: l/w, with higher values exhibited by members of the *T. magnificus* group, and *T. minor* and *T. subiridescens* in the *T. subiridescens* group. It seems then, that this development occurred independently in both species groups.

One might expect that the taxa showing the greater modifications for burrowing might also tend to be more subterranean, and hence have smaller eyes. Within the *T. subiridescens* group, the opposite seems to be true: large eyes are characteristic of those species whose members have relatively longer prothoraces. I interpret this as indicating that life above the surface of the soil and litter, and thus in a zone of light, is an important component of the adaptive zones of these species.

In brief, I believe that selection for life in an adaptive zone that involves burrowing has been an important force in production of present-day divergence if not diversity, in *Trichopselaphus.*

Evolution of sexual dimorphism. – This topic is considered for the *subiridescens* group, only, for I have seen only females of the *T. magnificus* group. Like most selenophorine species, males and females of *T. erwinorum* and *T. meyeri* are very much alike, though not in all proportions. The sexes of *T. minor* and *T. subiridescens,* however, differ from one another in a number of external characteristics.

For the ratio Pl/El (Table 8), values for males of each species of the *subiridescens* group are relatively higher than those for their respective females. Either the pronota of the males are longer, or the elytra are shorter. Significance of this difference is not evident, although it suggests that males might be better adapted for burrowing than are females, or conversely, that females are better adapted for flight and dispersal than are males. Another possibility is that females require longer abdomens for egg production, hence longer elytra, and thus they exhibit lower values for the ratio Pl/El.

Males and females of *T. minor* and *T. subiridescens* differ from one another in form and proportions, as is illustrated by differences in values for the ratios Hw/Pw (Table 4) and P: wA/wB (Table 7). For *T. minor,* differences between the sexes in the ratio Hw/Pw seem to result from decrease in head size of males. Differences in values for the ratio P: wA/wB seem to result from a more markedly constricted base of the pronotum for females. The pronotum of males is more apotypic than that of females, because the latero-basal sinuation is lost or reduced in males.

For *T. subiridescens,* differences between the sexes for values in the ratio Hw/Pw seem to be the result of a relative increase in head size for females. Differences in values for the ratio P: wA/wB seem to result from a wider apex in females – perhaps a direct reflection of the larger head size.

Hypertrophy of the hind femora and bowing of the hind tibiae, developed in *T. minor* males, but most pronounced in males of *T. subiridescens,* provides one of the most striking instances of sexual dimorphism known for at least New World harpalines. Form of the hind appendages suggests that they are used by a male during mating, for grasping the female, and suggests further some elaborate behaviour pattern that is characteristic of these two species of *Trichopselaphus.* Antecedents for such a pattern should be sought in the more plesiotypic members of the *subiridescens* group, *T. erwinorum* and *T. meyeri.*

Another interesting difference in measurements between males and females of *T. minor* and *T. subiridescens* concerns overall size, as measured by standardized body length. On average, males are larger than females, and this is the reverse of the normal intraspecific relationship in size. Such a reversal is to be expected when the behaviour pattern requires combat among males for females, with males of larger size being at an advantage.

Thus, knowledge of behaviour of adults is likely to provide the clues necessary to understand the selective forces involved in evolution of the sexually dimorphic features of the species of *Trichopselaphus.*

Evolution of mouthparts. – Among differences between adults of the *magnificus* and *subiridescens* groups, none are more striking than the complex of features involving the organs of ingestion. These include form of mandibles, proportions of maxillary palpomeres, form of the ligula, and relative size of the ligula to the paraglossae. I infer from these two structural complexes either two different modes of feeding, and/or two different types of food. Because members of the *magnificus* group are apotypic with respect to three of the four features (mandibles, ligula and paraglossae), it seems clear that the more apotypic mode of feeding, or food, should be characteristic of this group. However, I am not able to specify the nature of either food or feeding associated with either species group, though it is likely that adults of the *subiridescens* group eat angiospermous seeds – as do adults of various species of *Selenophorus* (Erwin, personal communication), and various other harpalines whose mouthparts are similar in structure to those of the *subiridescens* group. Perhaps adults of the *magnificus* group are seed eaters too, but specialize on seeds with peculiar properties. For the present, I can conclude only that food and feeding are likely to be important components of that complex of features with which is associated evolutionary divergence of *Trichopselaphus.*

Position of Trichopselaphus *in the evolutionary pattern of the Carabidae.* – Erwin (MS.) has proposed a generalized model relating in sequence the habitats occupied by Carabidae to their evolution. Basically, the hypothesis is that the major center of carabid evolution is the tropical wetlands, and this complex of habitats is occupied by evolutionary "generalists". Various sequences of habitats lead from the wetlands to various termini: mountain tops (both tropical and temperate); grasslands; desert; tree tops; and caves. These are populated by evolutionary "specialists".

Erwin describes carabid evolution in terms of "pulses", involving principally uni-directional shifts from the tropical wetlands to other types of habitats, with consequent taxonomic differentiation, specialization, super specialization, and ultimately, extinction in terminal habitats. In the process of evolution, adaptive radiation takes place in the various habitats, with consequent structural and behavioural modifications. Thus, it is possible to use this system as a basis for classification of taxa, and thereby to determine how far a group has departed from the most active zone of major evolutionary differentiation. It is also possible to use the system in a search for sister groups: a more plesiotypic sister group would be expected in the same habitat, or in a more generalized one; a more apotypic sister group would be expected in the same habitat or in a more specialized one.

Members of *Trichopselaphus* evidently occupy lowland (and low montane) tropical forest, and I suggest that they are burrowers in the forest floor, or else in the lowermost layers of damp leaf litter (transverse microsculpture that is characteristic of individuals of this genus is generally characteristic of inhabitants of wet, compact, highly organic substrate (Erwin MS)). I classify them as "forest floor specialists" in Erwin's system. Thus, *Trichopselaphus* is only one step removed from the tropical wetlands habitats. Further, I suggest that the sister group of *Trichopselaphus* was either a forest floor specialist, or a "waterside generalist", that occupied wetland habitats.

Zoogeography

This genus includes too few species and ranges are not well enough known to warrant an extended consideration of geographical distribution. Nonetheless, it is worth pointing out how the distribution pattern, as it is presently conceived, relates to current understanding of the general pattern of tropical American zoogeography. Whitehead's synthesis (1976: 191–198) provides a suitable background, as well as references to the more general literature related to this topic. Ball (1975) and Rosen (1975) provide a general background about geological and topographic events for Middle America during the later part of the Tertiary Period.

Whitehead's synthesis has some general components and some that are more especially related to events of the Quaternary. Four major points comprise the synthesis. First, the Middle American fauna includes three principal elements based on source areas: endemic ancestral complexes (groups known only from Middle America, and of uncertain relationships); old South American ancestral complexes (groups with endemic species in Middle America, and with relatives in South America); and recent arrivals from North and South America (widespread species, represented in Middle America, and either in North America or South America or both). Second, patterns of species differentiation are either islandic (ranges restricted, allopatry of close relatives the rule), or continental (ranges more extensive, sympatry the rule). Third, islandic patterns predominate among elements living at high elevations, and among ecological specialists living at lower elevations. Fourth, islandic patterns tend to reflect Pleistocene climatic cycles and/or results of altitudinal shifts induced by the taxon cycle (taxon pulses, Erwin, MS).

Elements of the distribution pattern of *Trichopselaphus* can be fitted to this synthesis. Briefly, this genus is represented in Middle America, by one wide-ranging species that occurs also in South America (interpreted as a recent arrival from the latter continent), and endemic Middle American taxa (interpreted as descendants from an ancestral stock that arrived in pre-Pleistocene time). Populations of the Middle American species live at lower elevations, but the pattern of range overlap in relation to phylogenetic relationships is such as to suggest islandic speciation. However, overlap is sufficiently extensive to suggest that most differentiation was in pre-Pleistocene time. Thus, most of the "islands" on which differentiation occurred are not Pleistocene biogeographic islands referred to by Whitehead. There is not evidence of vertical displacement upward, and the present-day overlap in ranges suggests that species are behaving as if they were of the "continental" type – that is, populations consist of vagile individuals adapted to exploit the sort of patchy environment characteristic of tropical forest at lower elevations. A more detailed account of geographical history of *Trichopselaphus* follows.

The pattern of distribution of the extant species of *Trichopselaphus* seems simple, but it is really rather complex. The *magnificus* group seems to be confined to South America, to the south of the east-west trending ridges of the Andes. On the other hand, the center of diversity of the *T. subiridescens* group is Middle America, with the structurally most highly derived species being the most widespread (*T. subiridescens*), its range extending from the Middle American state of Guatemala to southeastern South America (Fig. 28), and its sister species (*T. minor*) known only from Middle America. The hypothesized system of phylogenetic relationships seems to require dispersal of the ancestor of the *subiridescens* group out of South America to Middle America, and then a later return of the most highly derived species to the former land mass. Details are provided below.

It seems reasonable to suggest that the area of origin of *Trichopselaphus* is the lowland forests of South America, for this area is the center of diversity of selenophorine Harpalini in the New World, and one gets the impression that the general evolutionary-geographical pattern of selenophorines has been one of dispersals northward through Middle America terminating in temperate parts of North America. I assume that the limited diversity of the genus and its morphological compactness are indications that the group is not old (i.e., that it arose sometime during Tertiary, not Mesozoic, time), so that explanations for its diversification must be sought in events of Middle to Late Tertiary time. These considerations, then, serve as the basis for the following hypothesis, which is illustrated by Fig. 32.

Following origin of the genus in pre-Pliocene time in South America (Ancestor "X"), which might have involved a shift from wetlands to forest floor habitats, dispersal to what were then islands of "Lower" Central America took place. This resulted in a vicariance pattern with the stock that remained in South America (Ancestor "A") giving rise to the *magnificus* group. In turn, this differentiated, possibly as the result of range disruption, ultimately producing the extant species *T. magnificus* and *T. gloriosus.* (Eventually, it should be possible to fit the distribution pattern of the *magnificus* group to climatic and geologic events of Tertiary-Quaternary time in South America, as described by Meggers *et al.* (1973). To do so, however, will require better knowledge of this species group than is presently available.)

Meanwhile, the Middle American stock (Ancestor "B"), progenitor of the *subiridescens* group, dispersed northward over water barriers, reaching "Nuclear" Middle America. This produced another vicariance pattern, with the islandic stock giving rise to *T. erwinorum,* and the Nuclear Middle American stock (Ancestor "C") producing the ancestral *T. meyeri-minor-subiridescens* stock.

Subsequently, the latter group differentiated to produce *T. meyeri* and the ancestral stock ("D") of *T. minor-subiridescens.* I am unable to suggest confidently either the nature or position of the barrier that led to this differentiation. In turn, re-dispersal to some Middle American island could have produced the final vicariance pattern, with the Nuclear Middle American isolate giving rise to *T. minor,* and the islandic stock producing *T. subiridescens.* Finally, following closure of the sea barriers and other events in late Pliocene-early Pleistocene time dispersal took place, with *T. minor* reaching the northern limits of the Neotropical Region, in Mexico, and *T. subiridescens* spreading northward at least to Guatemala, and southward into South America almost to the southern edge of the tropics.

I think that the most interesting aspect of this distribution pattern is the relatively very extensive range of *T. subiridescens.* It seems most parsimonious to propose origin of this species in lower Middle America, but then one has to account for a southward dispersal that carried the species to the southern edge of the tropics without spreading to the much closer northern edge. Possibly, *T. subiridescens* did range farther north, but for some reason died out in Mexico.

Of course, another way to account for the pattern would be in terms of a South American origin for *T. subiridescens,* followed by a re-dispersal into Middle America. However, in the absence of good evidence for such a double movement, it seems preferable to rely on the geographically less complicated system of explanation.

Nonetheless, the general hypothesis for the geographical history of *Trichopselaphus* requires several crossings of sea barriers, and associated north-south and south-north movements, which are analogous to the back and forth dispersals hypothesized by Hershkovitz (1966) in his reconstruction of the geographical history of peromyscine rodents. Of course, this analogy does not prove the reality of either hypothetical system, but it does illustrate that such a complex pattern is not unique to either mice or beetles. Because we expect repetitions of patterns in nature (Whitehead, 1976: 198), it seems reasonable to argue that a reconstruction that requires a repetitive pattern is more likely to be correct then one that requires a unique pattern.

According to I.R. Ball (1975) and Whitehead (1976: 198) a zoogeographical hypothesis should be accompanied by predictions of the nature of discoveries yet to be made, even though the causal events occurred in the past. It is also desirable to indicate discoveries that should be made, if the hypothesis is correct. Such predictions provide tests of the validity of the hypothesis.

My zoogeographical hypothesis involves three principal elements: a South American origin for *Trichopselaphus*; dispersal northward from South America to Middle America and differentiation in the latter area of the dispersing stock as a result of isolation and further dispersal; and comparatively recent re-dispersal to South America. The following sorts of discoveries would invalidate the hypothesis. First, discovery of an old *Trichopselaphus* stock (brachypterous adults, related to *T. gloriosus*), or a sister group of the genus in North or Middle America (or elsewhere) would show that the ancestral group was more widespread than I postulate. Thus, the center of origin of the group would not have to be South America. Second, discovery of a basal species of the *subiridescens* group confined to South America would show that the origin of the group was not related to isolation of the ancestral stock in Middle America. Third, discovery of a still more highly evolved sister species of *T. subiridescens* in South America would indicate that the common ancestor of the two had returned to that continent previous to the time suggested by the hypothesis, and that *T. subiridescens* might be South American in origin. Therefore, my first prediction is that these discoveries will not be made. The remaining predictions concern discoveries that I think are likely to be made.

The second prediction is that the *T. magnificus* group contains more than just two species. This is based on four considerations: *a,* the group has been in existence in South America long enough to have generated more diversity than is presently known for it; *b,* the amount of divergence between adults of *T. gloriosus* and *T. magnificus* suggests that they are not very closely related, and hence that intermediate forms had to have existed, and might still be extant; *c,* taxa with brachypterous adults tend to be rich in species; and *d,* the seemingly disorderly distribution pattern of the *magnificus* group does not make sense – the extensive gap between known areas for the described species may be expected to house additional species. Points *b, c,* and *d* are not related to the zoogeographic hypothsis as such, for they are based on more general considerations.

Third, if the *magnificus* group is represented in Middle America, adults of such species will be macropterous, will be closely related to their South American counterparts, and will be confined to lower Middle America. This is based on the inference that the center of evolution of the *magnificus* group has been South America, and that if the group has entered Middle America it has done so comparatively recently, and by flight.

Fourth, the *subiridescens* group does not contain many more species than are presently known. This is based on the inference that the group has differentiated comparatively recently, and that the species are wide-ranging, not very variable, and are likely to be moderately to highly vagile.

Fifth, if additional presently known species of the *subiridescens* group are in South America, they are in the northern part of the continent, only – i.e., north of the Amazon basin. This is based on the primary inference that the center of origin of the *subiridescens* group has been Middle America, and on the secondary inference that species of this group, other than *T. subiridescens,* are only moderately vagile, so they have not been able to spread as far as that species.

CONCLUSIONS

To some, it may seem that this phylogenetic analysis of this genus is too bold, because it is based on data that seem too limited. Hence, the possibility for errors is too great. To some others, it might seem that this analysis is fruitless because there is no fossil evidence to indicate even approximate ages of the taxa. I am certainly aware of such shortcomings, but nonetheless I feel obliged to provide a framework within which to consider the primary data that have been gathered about the species of this group. I am not concerned that my hypotheses may be proven invalid. I am concerned that they might not even be tested. Hopefully, they will be, and I look forward to learning about the results.

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The field parties with which I was associated in Mexico managed to turn up very few specimens of *Trichopselaphus.* The beetles seem to be rare, and so I owe a special debt of gratitude to my field companions who either found or helped to find these insects: in 1972, K.E. Ball and P.A. Meyer; in 1974, D.R. Whitehead and H.E. Frania.

I owe a special debt of gratitude to my friends, the Littles (Henrique, Juana, and Rebecca), who, on two occasions, made my associates and me welcome in their home in the wonderful rain forest, the Lacandone Selva, on the slopes of the Sierra de la Colmena, in Chiapas, Mexico. It was here that we collected our specimens of *Trichopselaphus meyeri,* and I suspect that without the opportunity to obtain the material, this paper would not have been written. It is one of the minor tragedies of modern life that the Littles, who gave so much to their neighbors, and asked only to be left in peace were subsequently driven from their sylvan paradise to satisfy the greed of a selfish, minor but rich and politically influential *ranchero* whose claim to the land was legally doubtful, but whose might in the form of weapons and the will to use them was unquestionable.

I did not report here the results of preliminary analyses of the data about relationships of the species of *Trichopselaphus*, based on techniques of numerical taxonomy. These analyses were conducted by various participants in Paleontology 620, a senior seminar course at the University of Alberta, at a meeting of which I presented my data. The results obtained were at variance with my original notions about relationships, and so I reconsidered my views. However, investigation of additional character systems eventually satisfied me that my original interpretation was the most reasonable. The new data were not included in the numerical analysis, so it seemed pointless to deal in detail with the latter. Nonetheless, I express my appreciation to my colleagues, M.W. Carmichael, M.V.H. Wilson, A.L. Wells, and H.D. Seus, whose thoughtful evaluations of my data caused me to seek additional evidence.

Preliminary drafts of the manuscript on which the paper is based were read by J.S. Nelson (Department of Zoology, University of Alberta), J.S. Ashe of my Department, and D.R. Whitehead (Insect Identification, Agricultural Research Service). On the basis of advice received, I modified extensively my views about the geographical history of *Trichopselaphus*, and I must acknowledge especially the extensive and penetrating comments about this topic that D.R. Whitehead took the time and trouble to make.

Photographs of *Trichopselaphus* were taken by J.S. Scott, who also prepared the diagrams and plates. Locality and statistical data were compiled by D. Shpeley. M.J. Figueroa prepared the Spanish translation of the abstract, and she and P. Thornton typed the final draft of the manuscript.

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Table 1. Data on Variation in Standardized Body Length (mm.) Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	9.88				
T. meyeri	Sra. Colmena, Chis., MEX.	1	7.60				
T. meyeri	Cordoba, Veracruz, MEX.	2	7.52- 7.96	7.74			
T. minor	Orizaba, Veracruz, MEX.	1	9.48				
T. minor	La Lima, HONDURAS	15	8.68-10.20	9.35	±0.10	0.39	4.17
T. subiridescens	Chiriqui, PANAMA	4	9.96-11.28	10.65			
T. subiridescens	Nova Teutonia, BRAZIL	6	8.08-12.20	10.25			
T. subiridescens	Hansa Humbolt, BRAZIL	4	11.12-11.68	11.34			
T. subiridescens	Pac Mathias, BRAZIL	4	10.56-11.84	11.35			
T. subiridescens	Ipiranga, BRAZIL	9	11.20-12.64	11.72			
T. subiridescens	Salesopolis, BRAZIL	18	8.40-12.68	10.82	±0.27	1.14	10.52
FEMALES:							
T. magnificus	Satipo, PERU	1	11.76				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	9.88				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	11.92-12.92	12.42			
T. erwinorum	Chiriqui, PANAMA	1	9.20				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	7.68				
T. meyeri	Lagos Colores, Chis., MEX.	1	8.28				
T. meyeri	Cordoba, Veracruz, MEX.	3	8.08- 8.16	8.12			
T. minor	La Lima, HONDURAS	15	8.52- 9.84	9.10	±0.06	0.39	4.29
T. subiridescens	Chiriqui, PANAMA	7	8.88-10.56	9.77			
T. subiridescens	Nova Teutonia, BRAZIL	15	7.44-11.60	10.12	±0.21	1.19	11.06
T. subiridescens	Ipiranga, BRAZIL	8	9.80-11.44	10.49			
T. subiridescens	Salesopolis, BRAZIL	26	9.16-11.68	10.60	±0.13	0.66	6.18

Table 2. Data on Variation in Values for the Ratio MP: 1-3/1-4 Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.706				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.652				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.583				
T. minor	La Lima, HONDURAS	15	0.538-0.652	0.590	±0.01	0.03	5.70
T. subiridescens	Salesopolis, BRAZIL	18	0.592-0.692	0.626	±0.01	0.03	4.24
FEMALES:							
T. magnificus	Satipo, PERU	1	1.083				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.923				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.882-0.938	0.910			
T. erwinorum	Chiriqui, PANAMA	1	0.750				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.542				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.640	0.574			
T. meyeri	Cordoba, Veracruz, MEX.	3	0.500-0.640	0.574			
T. minor	La Lima, HONDURAS	15	0.586-0.667	0.624	±0.01	0.02	3.46
T. subiridescens	Salesopolis, BRAZIL	26	0.586-0.731	0.660	±0.01	0.04	6.04

Table 3. Data on Variation in Values for the Ratio hF: w/l Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.214				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.245				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.241-0.245	0.243			
T. minor	Orizaba, Veracruz, MEX.	1	0.257				
T. minor	La Lima, HONDURAS	15	0.258-0.294	0.278	±0.002	0.010	3.60
T. subiridescens	Chiriqui, PANAMA	4	0.297-0.391	0.343			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.300-0.392	0.352			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.319-0.356	0.334			
T. subiridescens	Pae Mathias, BRAZIL	4	0.398-0.417	0.406			
T. subiridescens	Ipiranga, BRAZIL	9	0.348-0.391	0.369			
T. subiridescens	Salesopolis, BRAZIL	18	0.305-0.400	0.354	±0.007	0.031	8.67
FEMALES:							
T. magnificus	Satipo, PERU	1	0.238				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.273				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.267-0.269	0.268			
T. erwinorum	Chiriqui, PANAMA	1	0.238				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.250				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.250				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.232-0.241	0.236			
T. minor	La Lima, HONDURAS	15	0.210-0.246	0.233	±0.002	0.008	3.51
T. subiridescens	Chiriqui, PANAMA	6	0.219-0.250	0.236			
T. subiridescens	Nova Teutonia, BRAZIL	15	0.214-0.246	0.228	±0.002	0.009	3.89
T. subiridescens	Ipiranga, BRAZIL	8	0.214-0.238	0.226			
T. subiridescens	Salesopolis, BRAZIL	26	0.210-0.247	0.231	±0.001	0.008	3.57

Table 4. Data on Variation in Values for the Ratio Hw/Pw Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.855				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.773				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.769-0.797	0.783			
T. minor	Orizaba, Veracruz, MEX.	1	0.679				
T. minor	La Lima, HONDURAS	15	0.671-0.737	0.703	±0.004	0.018	2.56
T. subiridescens	Chiriqui, PANAMA	4	0.666-0.750	0.699			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.707-0.800	0.745			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.717-0.744	0.730			
T. subiridescens	Pae Mathias, BRAZIL	4	0.680-0.735	0.716			
T. subiridescens	Ipiranga, BRAZIL	9	0.706-0.778	0.725			
T. subiridescens	Salesopolis, BRAZIL	18	0.678-0.750	0.719	±0.005	0.021	2.95

Table 4 (Continued)

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
FEMALES:							
T. magnificus	Satipo, PERU	1	0.820				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.769				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.754-0.787	0.770			
T. erwinorum	Chiriqui, PANAMA	1	0.812				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.785				
T. meyeri	Lagos, Colores, Chis., MEX.	1	0.760				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.786-0.823	0.802			
T. minor	La Lima, HONDURAS	15	0.741-0.782	0.760	±0.003	0.011	1.44
T. subiridescens	Chiriqui, PANAMA	7	0.802-0.842	0.823			
T. subiridescens	Nova Teutonia, BRAZIL	15	0.814-0.861	0.839	±0.003	0.014	1.66
T. subiridescens	Ipiranga, BRAZIL	8	0.810-0.907	0.855			
T. subiridescens	Salesopolis, BRAZIL	26	0.798-0.871	0.831	±0.004	0.020	2.41

Table 5. Data on Variation in Values for the Ratio P: l/w Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.747				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.727				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.708-0.725	0.716			
T. minor	Orizaba, Veracruz, MEX.	1	0.769				
T. minor	La Lima, HONDURAS	15	0.696-0.788	0.755	±0.005	0.021	2.78
T. subiridescens	Chiriqui, PANAMA	4	0.791-0.833	0.813			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.767-0.825	0.799			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.774-0.822	0.803			
T. subiridescens	Pae Mathias, BRAZIL	4	0.752-0.812	0.778			
T. subiridescens	Ipiranga, BRAZIL	9	0.783-0.867	0.817			
T. subiridescens	Salesopolis, BRAZIL	18	0.768-0.828	0.803	±0.004	0.017	2.15
FEMALES:							
T. magnificus	Satipo, PERU	1	0.770				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.780				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.746-0.787	0.766			
T. erwinorum	Chiriqui, PANAMA	1	0.688				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.682				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.685				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.681-0.720	0.705			
T. minor	La Lima, HONDURAS	15	0.700-0.763	0.730	±0.004	0.015	2.10
T. subiridescens	Chiriqui, PANAMA	7	0.750-0.829	0.791			
T. subiridescens	Nova Teutonia, BRAZIL	15	0.736-0.808	0.771	±0.005	0.020	2.59
T. subiridescens	Ipiranga, BRAZIL	8	0.744-0.800	0.778			
T. subiridescens	Salesopolis, BRAZIL	26	0.742-0.833	0.775	±0.004	0.022	2.89

Table 6. Data on Variation in Values for the Ratio P: Sd/l Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.226				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.271				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.200-0.261	0.230			
T. minor	Orizaba, Veracruz, MEX	1	0.367				
T. minor	La Lima, HONDURAS	15	0.317-0.403	0.335	±0.006	0.024	6.76
T. subiridescens	Chiriqui, PANAMA	4	0.395-0.459	0.424			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.375-0.435	0.401			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.416-0.467	0.439			
T. subiridescens	Pae Mathias, BRAZIL	4	0.398-0.417	0.406			
T. subiridescens	Ipiranga, BRAZIL	9	0.346-0.432	0.401			
T. subiridescens	Salesopolis, BRAZIL	18	0.352-0.433	0.396	±0.006	0.024	6.12
FEMALES:							
T. magnificus	Satipo, PERU	1	0.402				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.338				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.341-0.365	0.353			
T. erwinorum	Chiriqui, PANAMA	1	0.290				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.267				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.200				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.200-0.276	0.240			
T. minor	La Lima, HONDURAS	15	0.317-0.400	0.354	±0.005	0.020	5.64
T. subiridescens	Chiriqui, PANAMA	7	0.364-0.407	0.386			
T. subiridescens	Nova Teutonia, BRAZIL	15	0.350-0.414	0.379	±0.005	0.019	5.01
T. subiridescens	Ipiranga, BRAZIL	8	0.361-0.412	0.385			
T. subiridescens	Salesopolis, BRAZIL	26	0.338-0.418	0.368	±0.004	0.021	5.71

Table 7. Data on Variation in Values for the Ratio P: wA/wB Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.940				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.980				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.964-1.000	0.982			
T. minor	Orizaba, Veracruz, MEX.	1	1.017				
T. minor	La Lima, HONDURAS	15	0.931-1.000	0.962	±0.005	0.021	2.18
T. subiridescens	Chiriqui, PANAMA	4	0.966-1.000	0.988			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.944-1.031	0.987			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.971-1.030	1.014			
T. subiridescens	Pae Mathias, BRAZIL	4	0.986-1.048	1.008			
T. subiridescens	Ipiranga, BRAZIL	9	0.960-1.046	1.010			
T. subiridescens	Salesopolis, BRAZIL	18	0.946-1.064	1.010	±0.008	0.033	3.30

Table 7 (Continued)

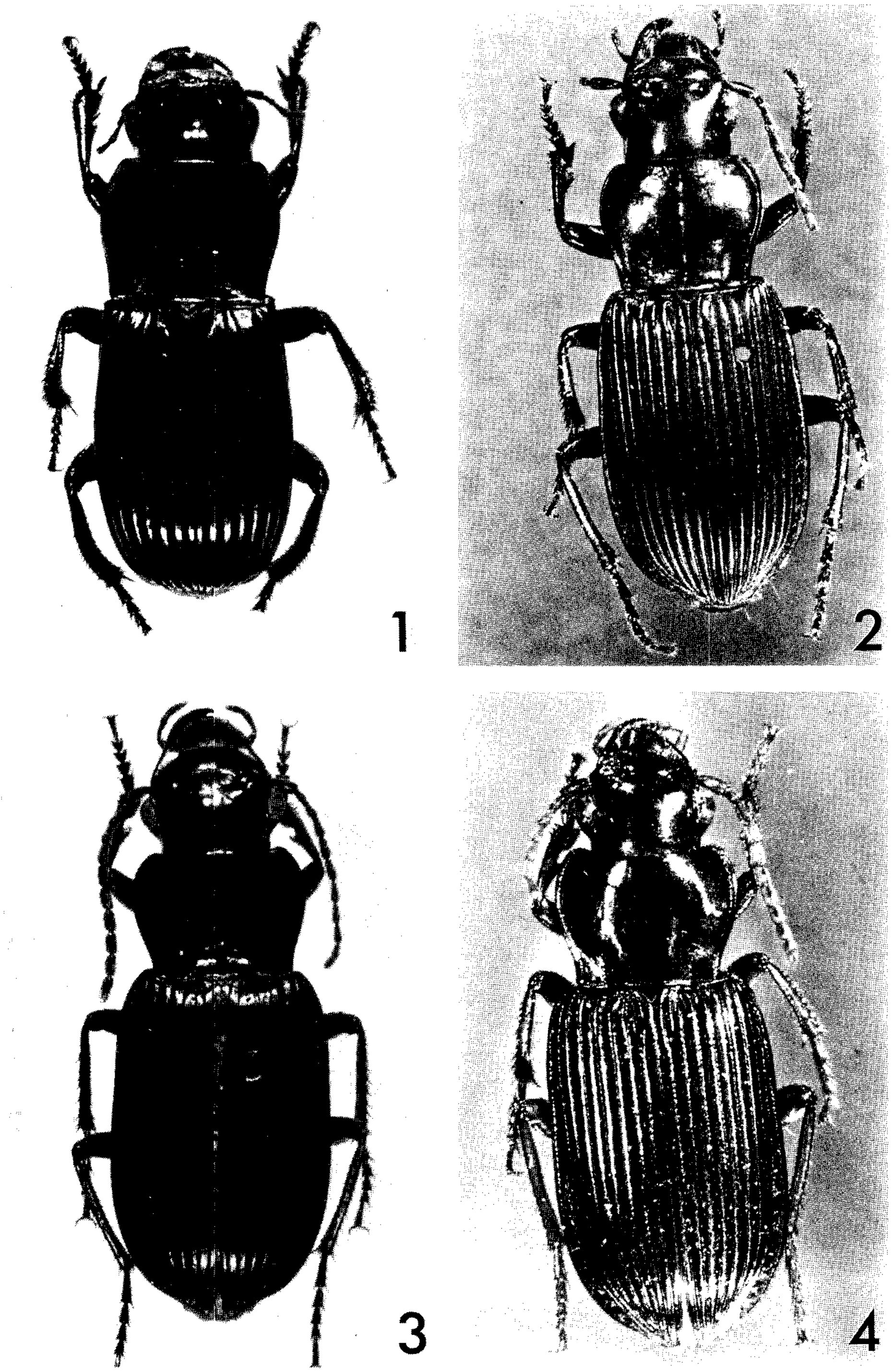
Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
FEMALES:							
T. magnificus	Satipo, PERU	1	1.026				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.855				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.900-0.917	0.908			
T. erwinorum	Chiriqui, PANAMA	1	0.846				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	1.000				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.980				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.981-1.038	1.006			
T. minor	La Lima, HONDURAS	15	0.982-1.075	1.037	±0.007	0.027	2.60
T. subiridescens	Chiriqui, PANAMA	7	1.071-1.204	1.148			
T. subiridescens	Nova Teutonia, BRAZIL	15	1.077-1.271	1.157	±0.014	0.054	4.66
T. subiridescens	Ipiranga, BRAZIL	8	1.103-1.179	1.165			
T. subiridescens	Salesopolis, BRAZIL	26	1.062-1.188	1.157	±0.008	0.042	3.61

Table 8. Data on Variation in Values for the Ratio Pl/El Among Population Samples of the Species of *Trichopselaphus* Chaudoir.

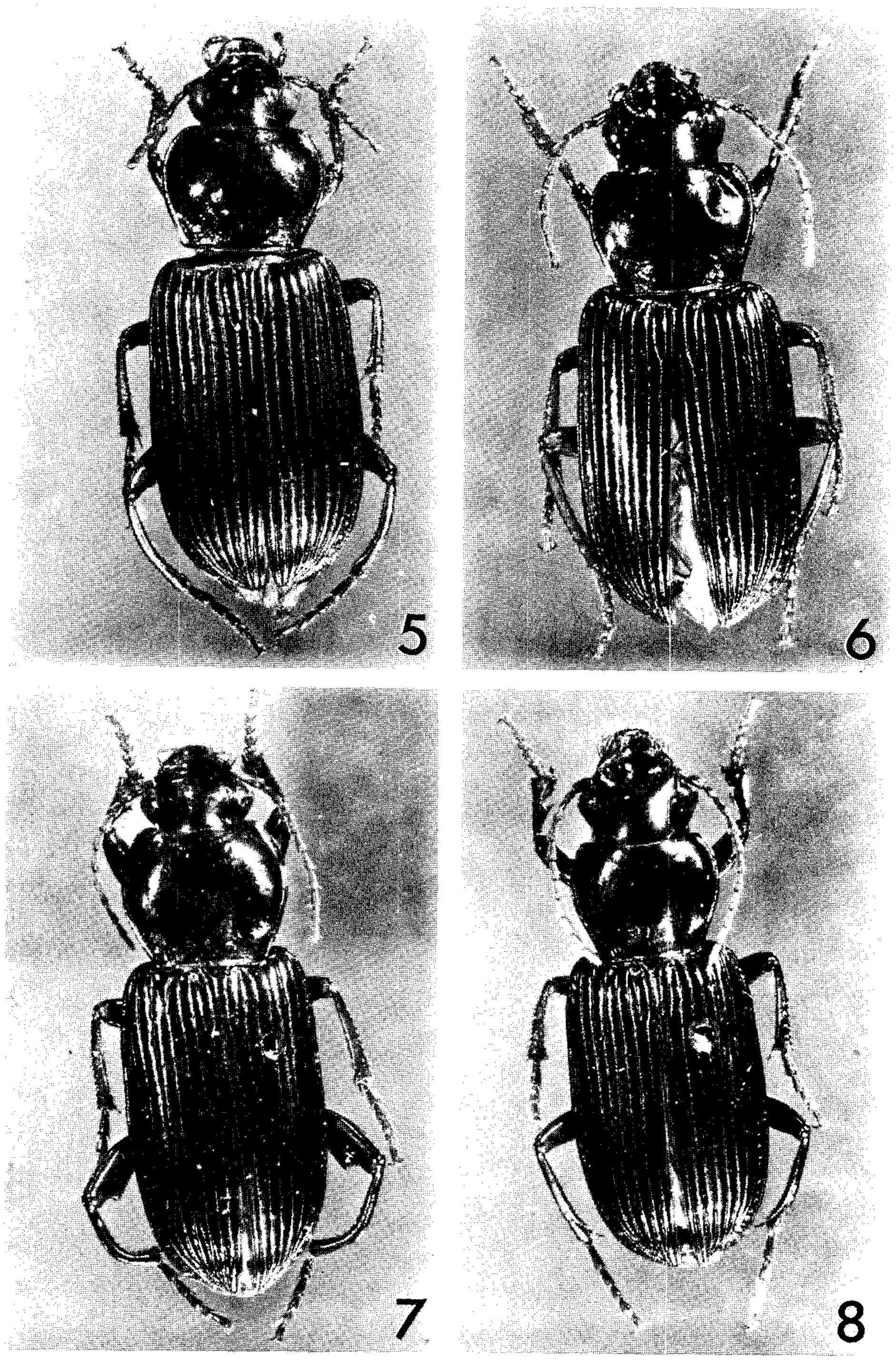
Species	Locality	N	Range	Mean	±S.E.	S.D.	C.V.
MALES:							
T. erwinorum	Puntarenas, COSTA RICA	1	0.380				
T. meyeri	Sra. Colmena, Chis., MEX.	1	0.384				
T. meyeri	Cordoba, Veracruz, MEX.	2	0.374-0.385	0.379			
T. minor	Orizaba, Veracruz, MEX.	1	0.390				
T. minor	La Lima, HONDURAS	15	0.364-0.406	0.383	±0.002	0.009	2.34
T. subiridescens	Chiriqui, PANAMA	4	0.375-0.418	0.395			
T. subiridescens	Nova Teutonia, BRAZIL	6	0.385-0.394	0.387			
T. subiridescens	Hansa Humboldt, BRAZIL	4	0.383-0.417	0.404			
T. subiridescens	Pae Mathias, BRAZIL	4	0.364-0.400	0.380			
T. subiridescens	Ipiranga, BRAZIL	9	0.383-0.406	0.395			
T. subiridescens	Salesopolis, BRAZIL	18	0.378-0.405	0.392	±0.002	0.008	1.98
FEMALES:							
T. magnificus	Satipo, PERU	1	0.412				
T. gloriosus	S. Antonio de Barra, BRAZIL	1	0.490				
T. gloriosus	S. Antonio R.G. Norte, BRAZIL	2	0.429-0.459	0.444			
T. erwinorum	Chiriqui, PANAMA	1	0.355				
T. meyeri	Arroyo Sta. Maria, Chis., MEX.	1	0.354				
T. meyeri	Lagos Colores, Chis., MEX.	1	0.366				
T. meyeri	Cordoba, Veracruz, MEX.	3	0.345-0.370	0.356			
T. minor	La Lima, HONDURAS	15	0.347-0.397	0.366	±0.003	0.011	3.00
T. subiridescens	Chiriqui, PANAMA	7	0.348-0.391	0.372			
T. subiridescens	Nova Teutonia, BRAZIL	15	0.349-0.371	0.359	±0.002	0.008	2.22
T. subiridescens	Ipiranga, BRAZIL	8	0.343-0.380	0.362			
T. subiridescens	Salesopolis, BRAZIL	26	0.355-0.382	0.366	±0.001	0.008	2.32

Table 9. Characters and Evolutionary Classification of Character States of Adult *Trichopselaphus.*

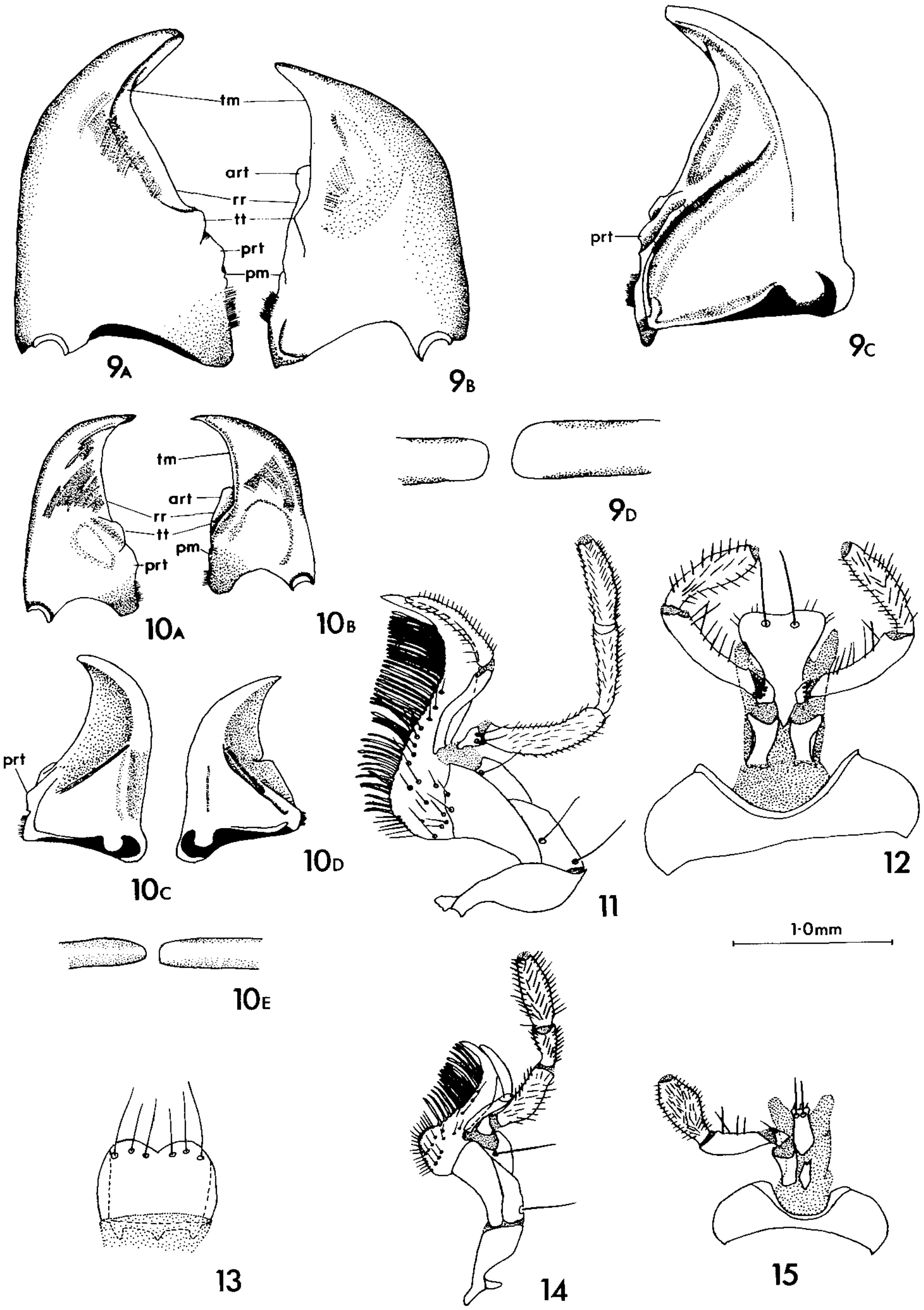
Character Number	Character	CHARACTER STATE Plesiotypic	Apotypic
1	Color – dorsum	black	coppery or green
2	Color – legs	black	rufous
3	Color – antennae	black	rufous
4	Eye – size	small	large
5	Mandibles – apex	narrower	truncate, broad
6	Maxillary palpus – Articles 3 + 4, length	longer	shorter
7	Maxillary palpus – Article 3	longer	shorter
8	Maxillary palpus – Article 4	not swollen	swollen
9	Pronotum – postero-lateral impressions	continuous with marginal grooves, shallow	separate from marginal grooves, deep
10	Pronotum – form	monomorphic	dimorphic
11	Pronotum – anterior marginal setae	absent	present
12	Pronotum – lateral setae	near middle	more anterad
13	Elytra – humeri	not dentate	dentate
14	Elytra – intervals	flat	moderately convex, markedly convex – 14'
15	Elytra – stria 7	punctate	impunctate
16	Wings	full, functional	reduced, non-functional
17	Hind femur – male	not dentate	small tooth large tooth – 17'
18	Male median lobe – form of apex	simple	small dorsal hook ventral hook – 18' apical knob – 18"
19	Female sternum 8 – reduction, medially or basally	normal	reduced medially reduced basally – 19' reduced basally and medially 19"
20	Female sternum 8 – lengthening	normal	elongate
21	Female sternum 10	sclerotization extensive, with apical setae	sclerotization reduced, with apical setae amorphous, no setae – 21'
22	Ovipositor, valvifer	well developed, narrowly rounded apically	shortened, broadly rounded apically
23	Ovipositor, stylomere 2	large, falciform	small, falciform palpiform – 23'



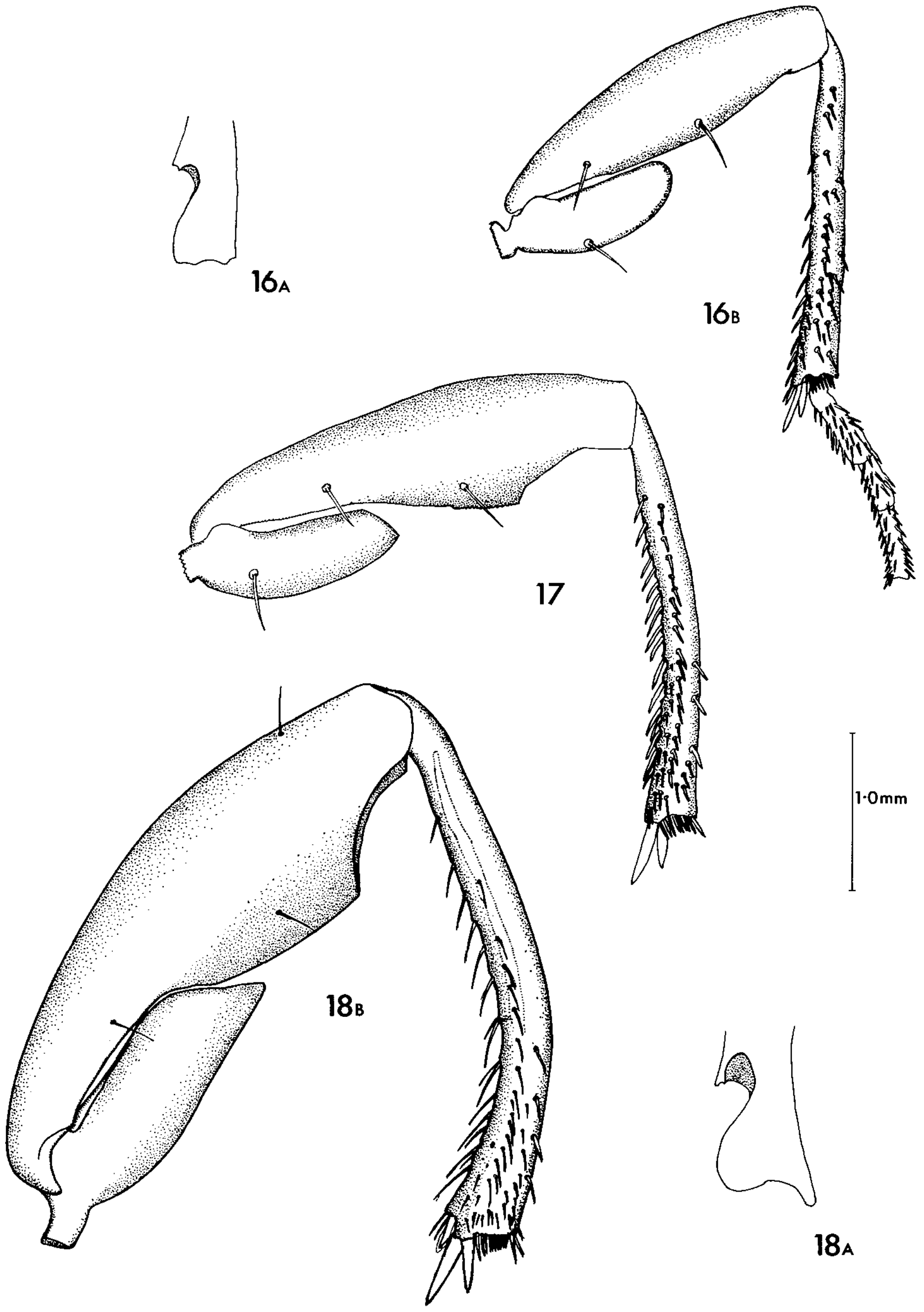
Figures 1 – 4. Photographs, illustrating habitus. Fig. 1, *T. gloriosus*, new species, female (SBL 11.92 mm). Fig. 2, *T. magnificus*, new species, female (SBL 11.76 mm). Fig. 3, *T. erwinorum*, new species, male (SBL 9.88 mm). Fig. 4, *T. meyeri*, new species, male (SBL 7.60 mm).



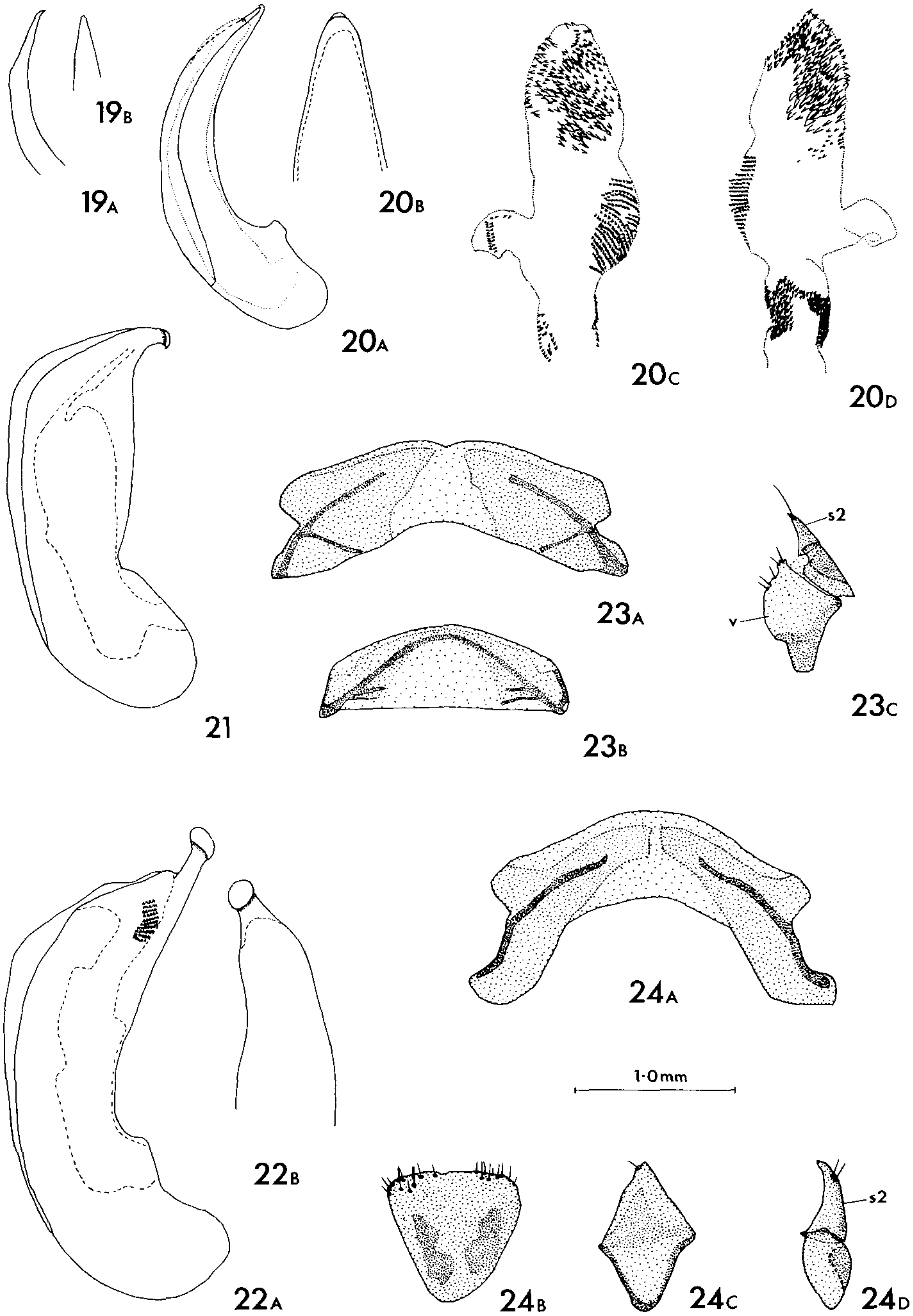
Figures 5 – 8. Photographs, illustrating habitus. Fig. 5, *T. minor* Bates, male (SBL 10.79 mm). Fig. 6, *T. minor* Bates, female (SBL 10.06 mm). Fig. 7, *T. subiridescens* Chaudoir, male (SBL, 10.87 mm). Fig. 8, *T. subiridescens* Chaudoir, female (SBL 10.87 mm).



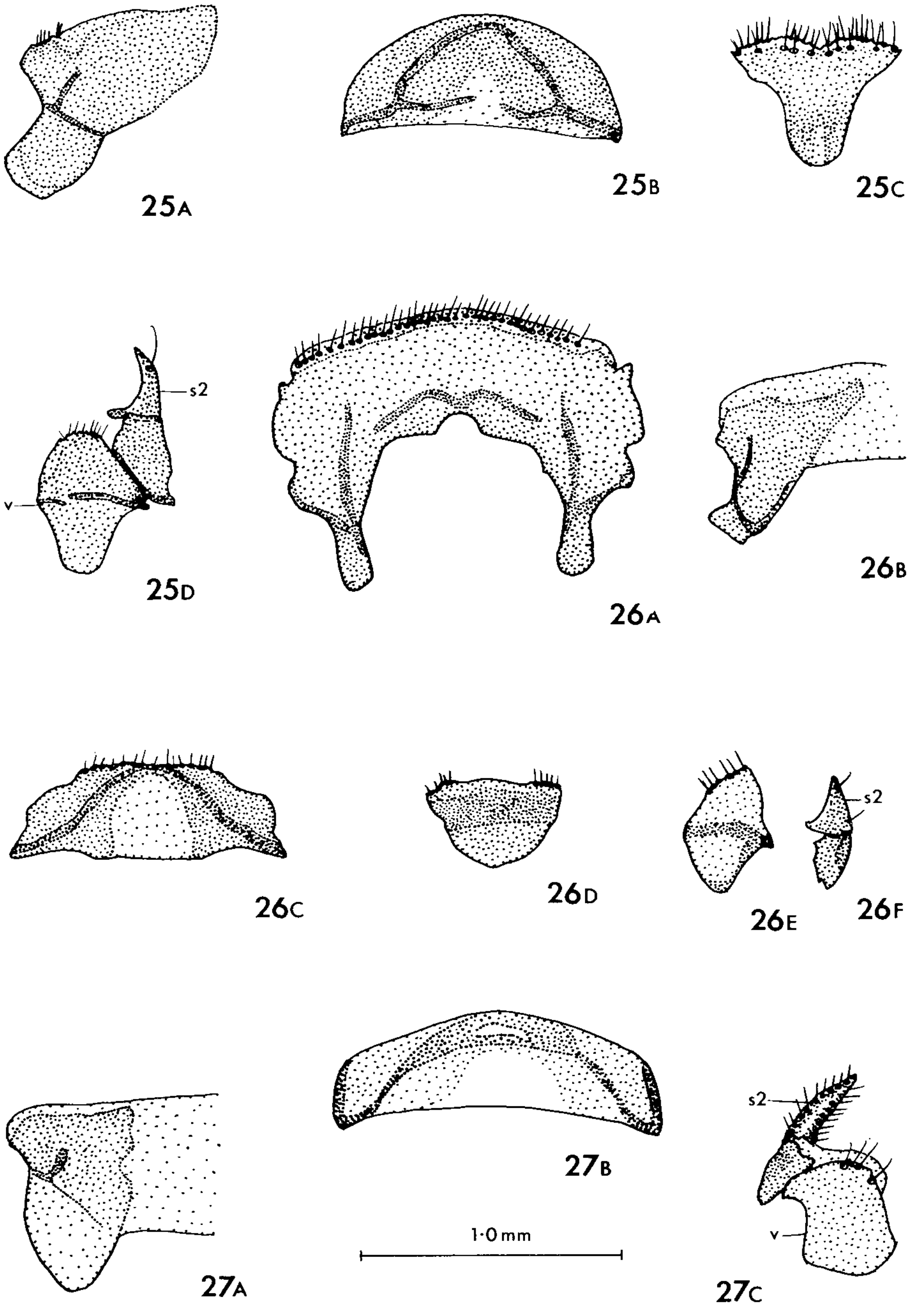
Figures 9 – 15. Fig. 9 and 10. Mandibles. Fig. 9, *T. gloriosus*, new species: A, left mandible, dorsal aspect; B, right mandible, dorsal aspect; C, left mandible, ventral aspect; D, apices of left and right mandibles, frontal aspect. Fig. 10, *T. minor* Bates: A, left mandible, dorsal aspect; B, right mandible, dorsal aspect; C, left mandible ventral aspect; D, right mandible, ventral aspect; E, left and right mandibles, frontal aspect of apices. Abbreviations: art-anterior retinacular tooth; pm - premolar tooth; prt - posterior retinacular tooth; rr - retinacular ridge; tm - terebral margin; tt - terebral tooth. Fig. 11, left maxilla of *T. gloriosus*, new species, ventral aspect. Fig. 12, Labium of *T. gloriosus* , new species, ventral aspect. Fig. 13, labrum of *T. minor* Bates, dorsal aspect. Fig. 14, left maxilla of *T. minor* Bates, ventral aspect. Fig. 15, labium of *T. minor* Bates, ventral aspect.



Figures 16 – 18. Fig. 16, legs of *T. meyeri,* new species: A, outline of apical portion of front tibia, anterior aspect; B, left hind trochanter, femur, tibia, and tarsomeres 1, 2, and 3. Fig. 17, left hind trochanter, femur and tibia of *T. minor* Bates. Fig. 18, legs of *T. subiridescens* Chaudoir: A, outline of apical portion of front tibia, anterior aspect; B, left hind trochanter, femur, and tibia.



Figures 19 – 24. Fig. 19, male genitalia, *T. erwinorum*, new species: A, median lobe, left lateral aspect; B, median lobe, apical portion, ventral aspect. Fig. 20, male genitalia, *T. meyeri*, new species: median lobe, A, left lateral aspect, B, apical portion, ventral aspect; internal sac, C, left lateral aspect, D, right lateral aspect. Fig. 21, male genitalia, *T. minor* Bates: median lobe, left aspect. Fig. 22, male genitalia, *T. subiridescens* Chaudoir: median lobe, A, left lateral aspect, B, apical portion, ventral aspect. Fig. 23, ovipositor and associated abdominal sclerites, *T. gloriosus*, new species: A, sternum 8, ventral aspect; B, tergum 10, dorsal aspect; C, valvifer (v), stylomeres 1 and 2 (s 2), ventral aspect. Fig. 24, ovipositor and associated abdominal sclerites, *T. magnificus*, new species: A, sternum 8, ventral aspect; B, sternum 10, ventral aspect; C, valvifer, ventral aspect; D, stylomeres 1 and 2.



Figures 25 – 27. Fig. 25, ovipositor and associated abdominal sclerites, *T. erwinorum*, new species: A, sternum 8, left hemisternite, ventral aspect; B, tergum 10, dorsal aspect; C, sternum 10, ventral aspect; D, valvifer (v), stylomeres 1 and 2 (s 2), ventral aspect. Fig. 26, ovipositor and associated abdominal sclerites, *T. meyeri*, new species: A, tergum 8, dorsal aspect; B, sternum 8, left hemisternite, ventral aspect; C, tergum 10, dorsal aspect; D, sternum 10, ventral aspect; E, valvifer; F, stylomeres 1 and 2, ventral aspect. Fig. 27, ovipositor and associated abdominal sclerites, *T. subiridescens* Chaudoir: A, sternum 8, left hemisternite, ventral aspect; B, tergum 10, dorsal aspect; C, valvifer (v), stylomeres 1 and 2 (s 2), ventral aspect.

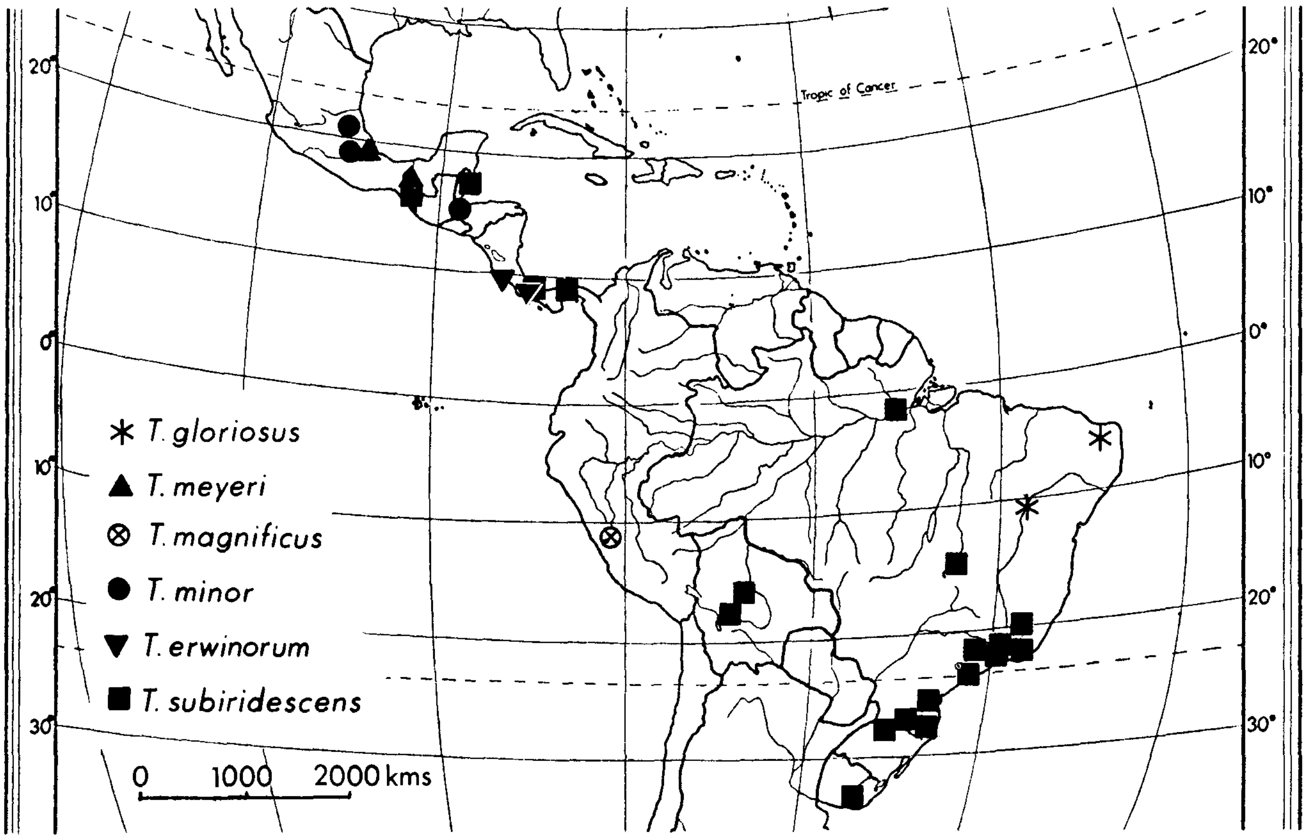


Figure 28. Map of Middle and South America, showing the geographical distribution of the species of *Trichopselaphus*.

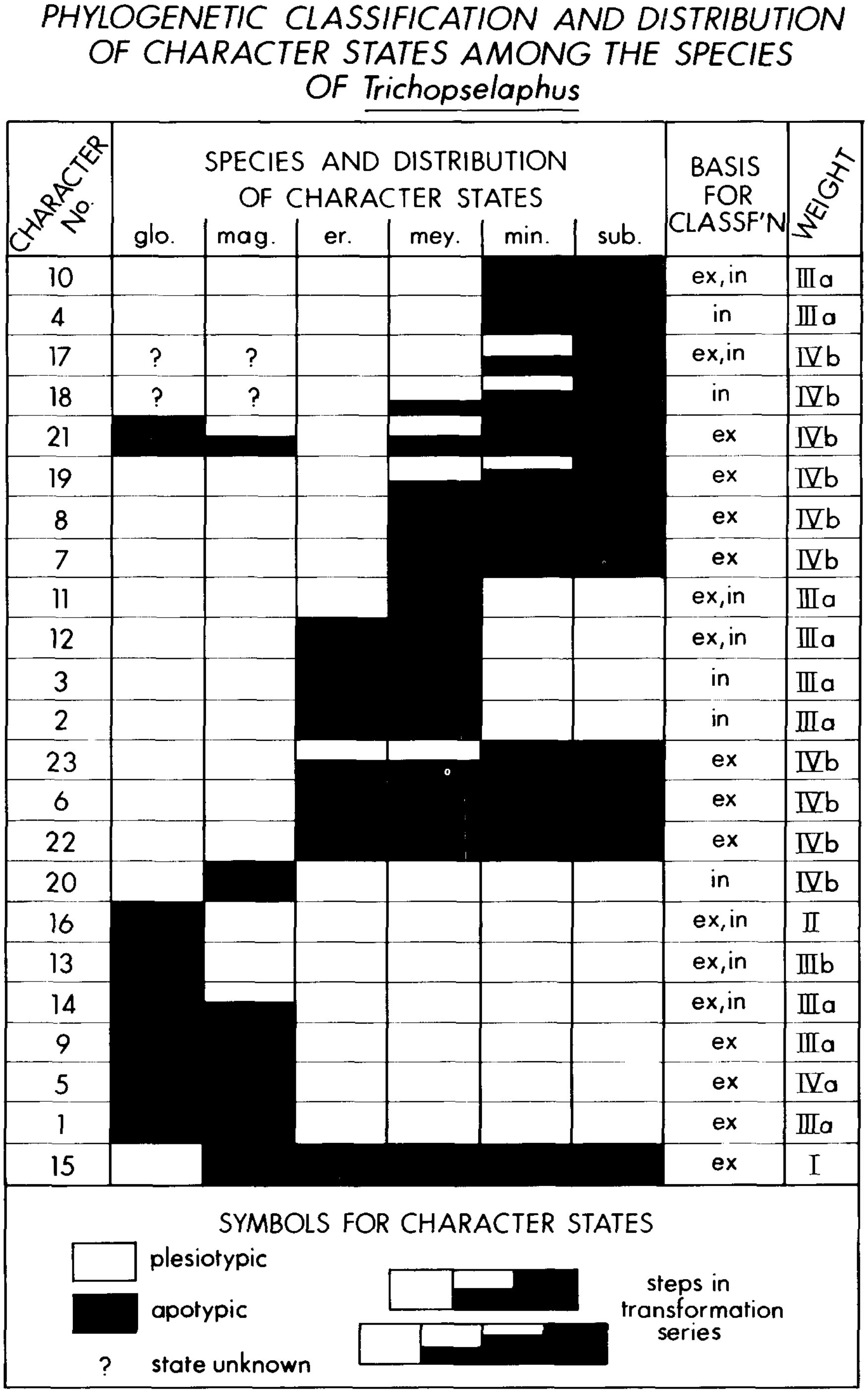


Figure 29. Diagram showing phylogenetic classification and distribution of character states among the species of *Trichopselaphus*.

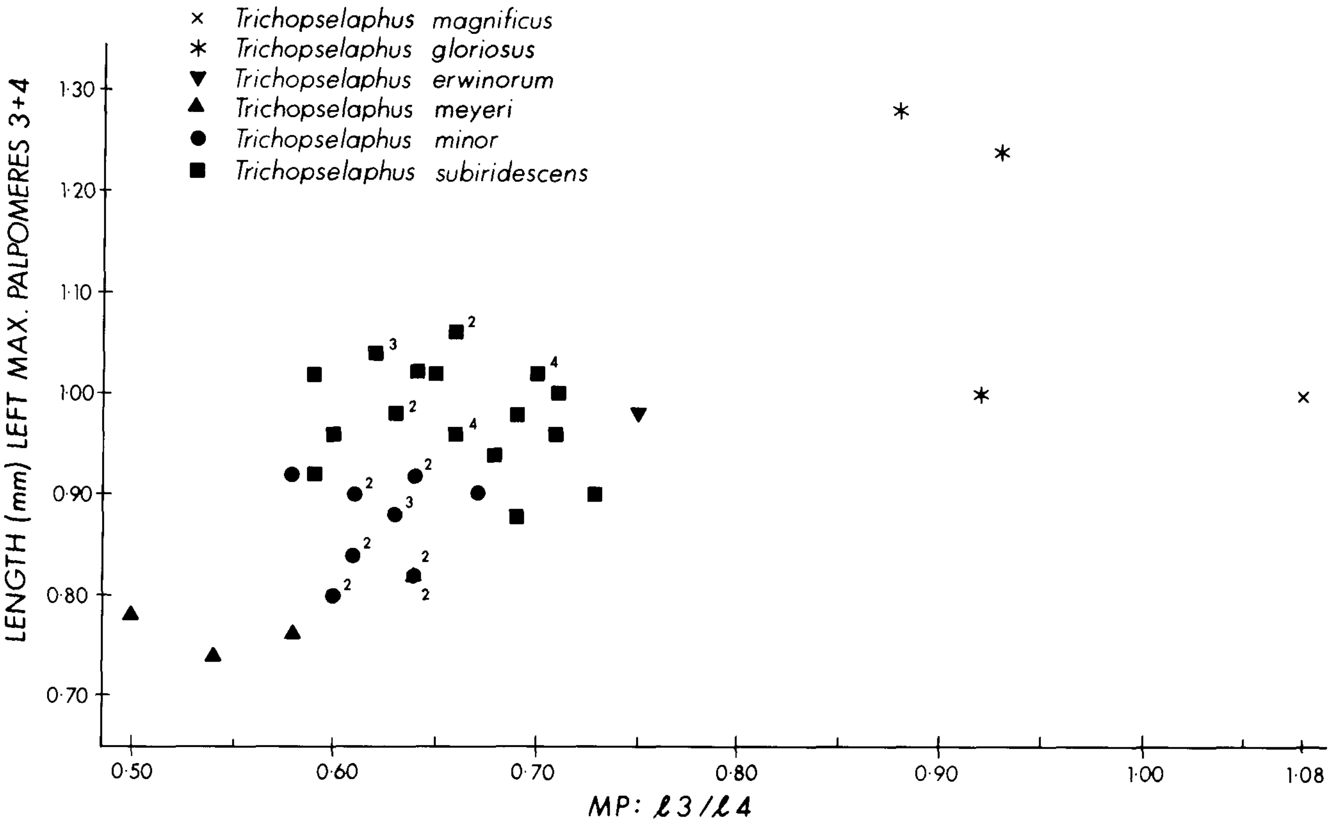


Figure 30. Diagram showing relationship between variation in length (mm) of maxillary palpomeres 3 + 4 and values for the ratio MP: l-3/l-4, among females of the species of *Trichopselaphus*.

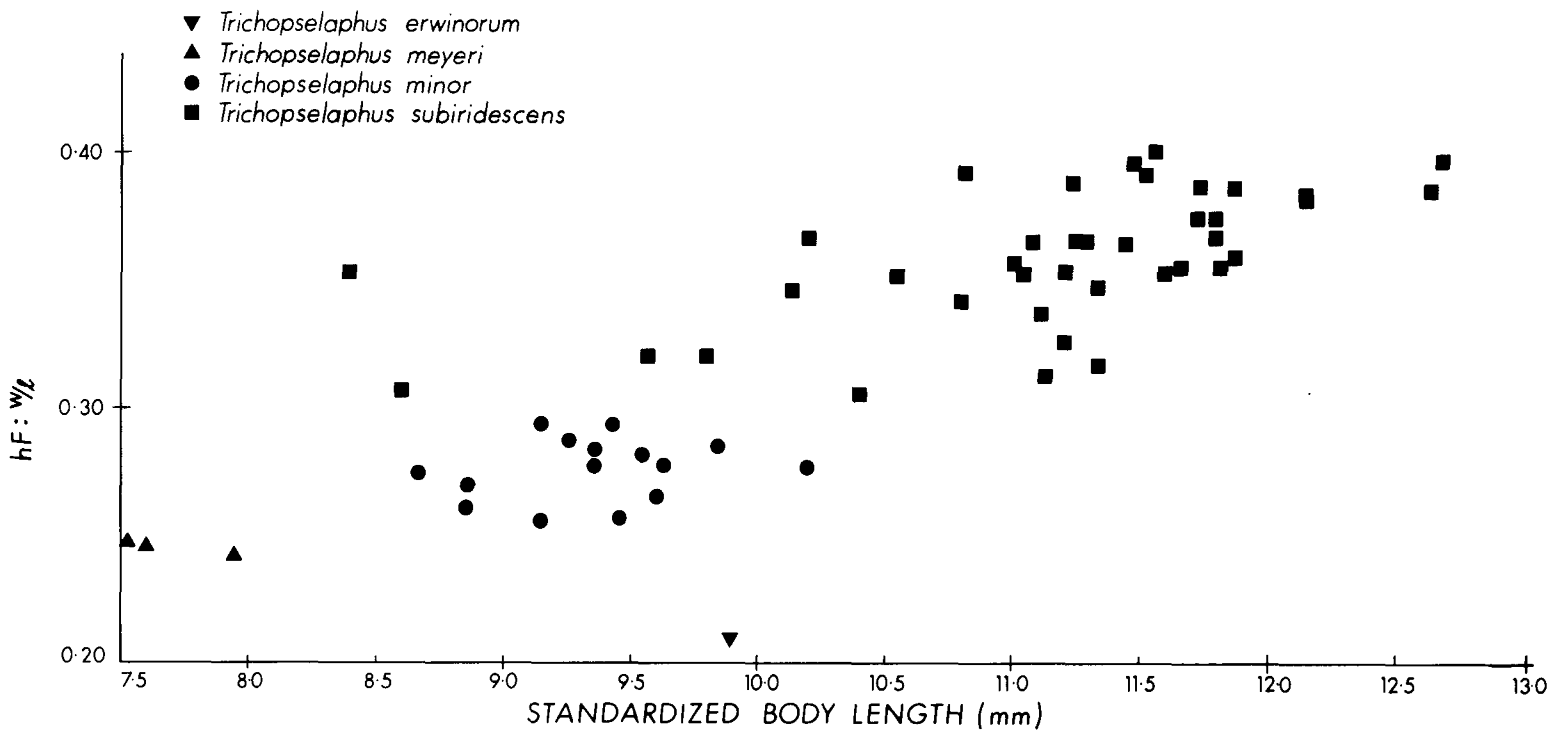


Figure 31. Diagram showing the relationship between standardized body length and the ratio hF: w/l, among males of the *subiridescens* group of *Trichopselaphus*.

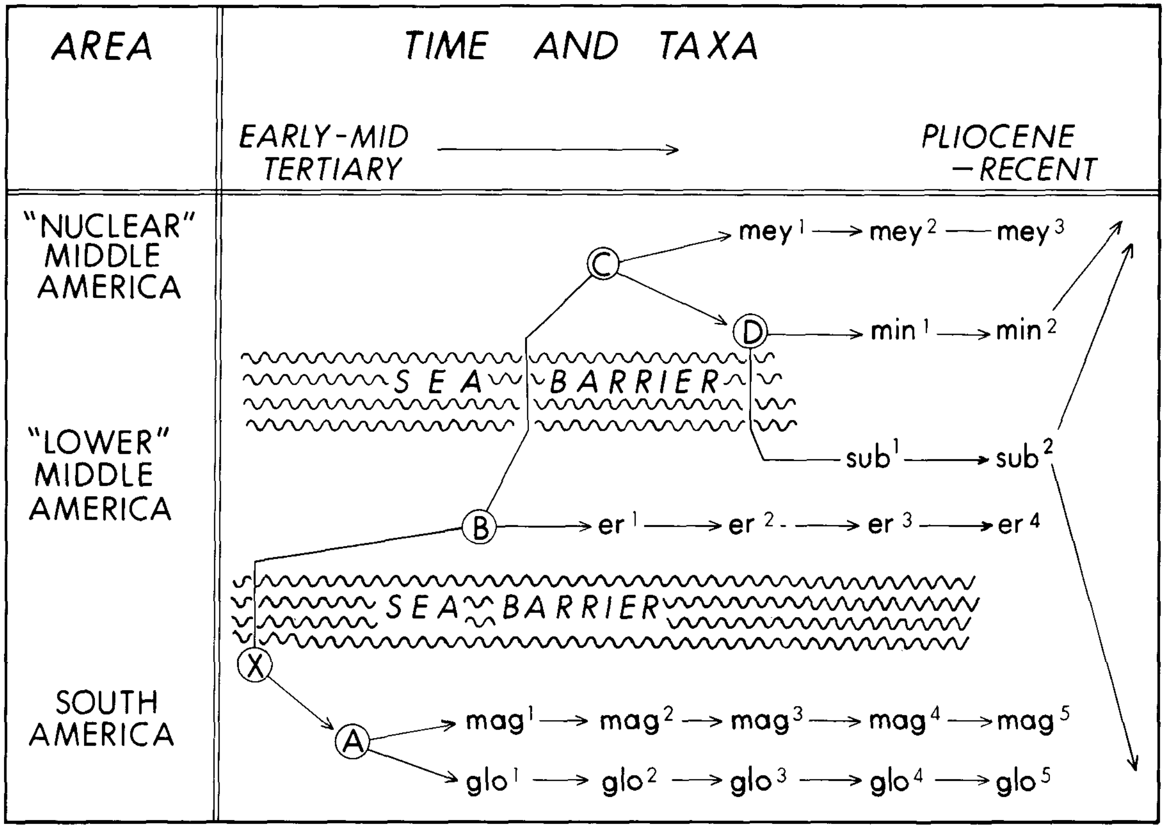


Figure. 32. Diagram showing the relationship between the reconstructed phylogeny of *Trichopselaphus* and changes in the distribution and land and sea in Middle America during the later Tertiary and Quaternary Periods. Encircled capital letters (X, A-D) represent hypothetical ancestors. Lines and arrows represent time and genetic connections among populations of *Trichopselaphus*. Abbreviations represent names of taxa, as follows: er – *T. erwinorum;* glo – *T. gloriosus;* mag – *T. magnificus;* mey – *meyeri;* min – *T. minor;* sub – *T. subiridescens.* Superscript numbers (1–5) represent relative ages of species populations, and they also are meant to imply change within lineages: the higher the number at the right of the diagram, the older the species.