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THE TRIBE LICININI (COLEOPTERA: CARABIDAE): A REVIEW OF THE GENUS-GROUPS AND OF THE SPECIES OF SELECTED GENERA

George E. Ball

Department of Entomology, University of Alberta,
Edmonton, Alberta T6G 2E3, CANADA

Abstract.—Evidence for monophyly of the Tribe Licinini is found in synapotypic character states of mouthparts (mandibles, primarily reduction of occlusal ridges and grooves) and the head capsule of larvae, with a distinct ventral apotome. Illustrations of mouthparts of adults of representative licinines show four basic types, which distinguish four subtribes: Dicaelina, Dicrochilina (new subtribe), Lestignathina (new subtribe) and Licinina (including the South American genus *Eutogeneius*). Structure of the mandibles and of the fore coxal cavities indicate relationships as follows: Dicaelina + ((Dicrochilina + Lestignathina) + Licinina). A review of the genus *Diplocheila* Brullé reveals for the subgenus *Diplocheila* new synonymy: *Pterostichus* (*Platysma*) *karikali* Jedlička, 1969 = *Diplocheila distinguenda* LaFerté, 1851. A review of the geographical history of subgenus *Isorembus* Jeannel indicates that the *striatopunctata* group was divided in two by opening of the Atlantic Basin, isolating one monophyletic segment in the Nearctic Region, and one in the Palaearctic Region, the latter withdrawing subsequently from Western Europe, and surviving in Western China. Review of recently collected material of the subgenus *Liodicaelus* (gen. *Dicaelus* Bonelli) reveals a new species—*D. franclemonti* (type locality—MEXICO, state of Nuevo Leon, Cerro Potosi, a mountain northwest of Galeana). Reexamination of the type material of *D. laevipennis dicaeloides* Ball suggests that this taxon is consubspecific with *D. l. laevipennis* LeConte. The names are synonymized accordingly. Reconstruction of the geographical history of *Liodicaelus* suggests that this lineage is of Late Miocene origin (ca. 12 million years before present), and that differentiation has been the result of vicariance and dispersal, with the oldest barrier between the Sierra Madre Oriental and the Sierra Madre Occidental. Study of the mouthparts of *Badister reflexus* LeConte reveals that, in the West Indies, the mandibles are dimorphic, with either the right or left mandible deeply notched dorsally. This feature of asymmetry was used to diagnose subgenera: left mandible notched, *Baudia* Ragusa; right mandible notched, *Badister* (*sensu stricto*) Clairville. Because it seems clear, now, that the genetic basis for mandibular difference is simple, the groups based on this feature alone should be reassessed.

DEDICATION

Jack Franclemont was a superb mentor, guiding one along the way by example rather than by precept. It was my good fortune to have been his first graduate student, though it was rumored that on more than one occasion he declared that never again would he have another coleopterist as a student—one of the few promises that he did not keep.

Our association at Cornell was not confined to laboratory and office. I learned under his tutelage that field trips could be civilized and even civilizing experiences, rather than akin to military assault operations. And, on many Sundays, my wife Kay, our two sons and I were invited to his home for dinner—a culinary experience that we valued. But we valued even more Jack's thoughtfulness in extending the invitations.

Kay and I continue to enjoy Jack's company when staying with him in his Snyder Heights home, during our pilgrimages to Ithaca and Cornell. It has occurred to me from time to time that one could spend profitably a sabbatical leave, sitting in his living room, listening to music from his tapes and records, dining at his table, and reading the rich supply of literature that comes to hand so readily.

Nearly 38 years ago, I completed a thesis about classification of licinine carabid beetles. I think that Jack eventually became mildly interested in these fine creatures, though initially he viewed with amused disdain my extolling of their virtues.

On this grand and joyous occasion, as we celebrate Jack's 80 years of life, I am pleased to have the opportunity to dedicate this review to him, with the hope that it will bring back old and hopefully pleasant memories, and that he will find therein some justification for the time and effort that he devoted to making my first review of the licinines a presentable scientific document.

INTRODUCTION

Having completed a major treatment of a taxon, systematists tend to seek other taxa, rather than to review again the group that has already been treated extensively—even though a good taxonomic work poses nearly as many questions as it answers. In part, I suppose, after an intensive study of a particular group, one loses a certain amount of interest in it, and in part, at the time of doing the study, one becomes aware of the possibilities at hand in other taxa that are readily accessible to analysis.

After publishing a revision of the North American Licinini (Ball, 1959), I proceeded to investigate other taxa, though two short studies clarified some points that were of special interest to me (El Moursy and Ball, 1959; Ball, 1966b). The idea for the present publication came with the need to offer something suitable for the Franclemont *Festschrift.* It began with some observations of the West Indian species of the licinine genus *Badister.* With interest in licinines rekindled, I thought about other matters related to *Badister.* Then, because of my interest in Middle American Carabidae, the Mexican species of *Dicaelus* (*Liodicaelus*) came to mind. Certain interesting observations about licinines that I had made during the past 30 years seemed worth including. Previous statements that I had published that proved incorrect required correction. And the mouthparts, especially the mandibles, that seemed of great potential importance in licinine classification and that had not been studied in detail, commended themselves for examination. Collectively, these items constitute a highly eclectic review of licinine Carabidae, their relationships, and geographical distribution.

MATERIAL AND METHODS

Material

This study is based on detailed examination of about 200 adult licinines, including representatives of the four subtribes recognized and the genera known from North America. Most of the material studied is in the Strickland Museum, Department of Entomology, University of Alberta (UASM). Other collections from which material was borrowed are listed below, along with names of the curators, and a four-letter coden used in the text for identification of the lending institution.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, U.S.A. 10024 (L. H. Herman);
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D. H. Kavanaugh);
CMNC	Department of Zoology, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada (R. S. Anderson);
CNCI	Canadian National Collection of Insects, Biological Resources Division, Centre for Land and Biological Resources Research, K. W. Neatby Building, CEF, Ottawa, Ontario K1A 0C6, Canada (Y. Bousquet);
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, U.S.A. 32601 (R. E. Woodruff);
LSUC	Louisiana State University Insect Collection, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana, U.S.A. 70803 (V. L. Moseley);
MCZC	Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. 02138 (D. G. Furth);
SEMC	Snow Entomological Museum, The University of Kansas, Lawrence, Kansas, U.S.A. 66045-2119 (R. Brooks);
UCBC	Division of Entomology and Parasitology, University of California, Berkeley, California, U.S.A. 94720 (J. Chemsak);
UCDC	The Bohart Museum of Entomology, University of California, Davis, California, U.S.A. 95616 (R. O. Schuster);
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560 (T. L. Erwin);
ZMUC	Department of Entomology, Zoological Museum, University of Copenhagen, Universitetsparken, DK-2100, Kobenhavn O. (O. Martin); and
ZSMM	Zoologische Staatssammlung; Münchhausenstrasse 21, D-8000, München 60, Federal Republic of Germany (G. Scherer).

Methods

Comparative morphology, phylogenetic relationships and classification.—Studies reported are at three hierarchical levels: subtribal, involving groups of genera; subgeneric, and intrasubgeneric; and intraspecific. At the subtribal level, because my principal goals were to assay and describe structural features used previously in classification and to achieve thereby an improved understanding of licinine relationships, I used an exemplar method, i.e., one or a few taxa that were readily available to me, to analyze the characters of a grouping recognized previously. To this study, I added as well published studies of other character systems, including chromosome number, defensive secretions, and characteristics of larvae.

Being interested in phylogenetic relationships as a basis for classification, I attempted to establish transformation series, and to position the licinine taxa accordingly. To polarize the transformation series, I used as outgroup the pterostichine genus *Loxandrus* LeConte, because it seemed to be in most respects less derived than the licinines, and yet to exhibit some features of the licinine ground plan, such as form of the male fore tarsomeres and having a pair of pits in the ventral surface of the mentum.

For the subgenus *Isorembus* Jeannel, I reviewed a flawed previous effort to establish the phylogenetic relationships of the species groups by using the outgroup method, with the other two subgenera of the genus *Diplocheila* Brullé as outgroups.

For the subgenus *Liodicaelus* Casey, I had the opportunity to undertake a more detailed study, having at hand representatives of all known taxa. However, the data available were not sufficient to permit a very convincing evolutionary treatment, and so I confined my activities to improving means of identifying the taxa and to documenting more fully their geographical ranges. Using essentially the commonality principle in the absence of a clearly specified outgroup, I recognized one species as the probable primitive adelphotaxon of the other four, and postulated that the latter group comprised a monophyletic assemblage.

For the genus *Badister,* I postulated infraspecific dimorphism in mandibular asymmetry of *B. reflexus* LeConte, a character that was regarded by most previous authors as of generic or subgeneric value. To make such a postulate required a further postulate about conspecificity. Recognition of the two mandibular morphs as members of the same species was based on their overall detailed similarity in features (principally male genitalia) whose variation signals specific differences throughout the genus *Badister.*

Biogeographical analysis.—For the subgenus *Isorembus* Jeannel and *Liodicaelus* Casey, I commented about their distribution patterns in an evolutionary context. I compared the distribution patterns of these taxa to similar patterns of other taxa that had been analyzed more rigorously, and reasoned by analogy that such similarities reflected similar histories of dispersal and vicariance.

Measurements.—These were used to indicate size and proportions for specimens of *Liodicaelus.* The following measurements were made, using an ocular micrometer in a Wild S5 Stereobinocular Microscope, at a magnification of 25×:

length of head—linear distance from base of the left mandible to the posterior margin of the left eye;
width of head—maximum linear transverse distance across eyes, from outer margin to outer margin;
length of pronotum—linear distance from anterior (apical) to posterior (basal) margin, measured along the mid-line;
width of pronotum at apex—linear transverse distance between antero-lateral angles, measured at right angle to the long axis;
maximum width of pronotum—maximum linear transverse distance across pronotum, measured at right angle to long axis;
length of elytra—linear distance from basal ridge to elytral apex;
width of elytra—maximum transverse distance across elytra, measured at right angle to long axis.

These measurements were added or combined in ratios, and designated as follows:

SBL—Standardized Body Length—sum of length of head, pronotum, and elytra;
EW—width of elytra, and also maximum body width;

PW/HW—width of pronotum/width of head;
PL/PWA—pronotum: length/width at apex;
EL/EW—elytra: length/width

For SBL, PW/HW, PL/PWA and EL/EW, means were calculated and results presented in Tables 3–6. Also, a scattergram was prepared (Fig. 15), based on PL/PWA and EL/EW for discrimination among the species of *Liodicaelus.*

Dissections.—These were made using standard techniques. Genitalia were preserved in glycerine, in microvials, pinned beneath the specimens from which these sclerites had been removed. Larger parts, or those that had been gold-coated for study with the Scanning Electron Microscope, were glued to cards, and pinned beneath the specimens from which they had been removed.

Illustrations.—A Cambridge S-250 Scanning Electron Microscope was used to examine and photograph gold-coated sclerites. Line drawings were prepared by using a *camera lucida* attached to a Wild S5 Stereobinocular Microscope.

Terms for structural features

Most of the words used to designate details of structures are found in entomology textbooks or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use. I provide information about such words here.

Body parts.—The term "segment" is restricted to those body parts that reflect embryonic somites. Thus, somite-like portions of the abdomen are referred to as segments. Abdominal segments are designated by a Roman numeral that corresponds to the respective somites. The first complete sternum is III, and the last one that is completely sclerotized and normally exposed is VII.

Portions of limbs are designated by the suffix "-mere," the prefix depending upon the limb in question—antenno, palpo, tarso, etc.

Labium.—The word "ligula" is used for glossae + paraglossae. In turn, the fused, sclerotized glossae characteristic of carabids are termed the glossal sclerite.

Elytra.—Longitudinal grooves on the dorsal surface, or remnants thereof ("striae" of most authors) are designated as interneurs (Erwin, 1974:3–5).

Ovipositor.—The terminal parts are referred to as stylomeres. The thick marginal setae on stylomere 2 are ensiform setae.

Terms for phylogenetic aspects

These are standard, except for "adelphotaxon." This word was introduced by Ax (1987:36) as a substitute for sister taxon. The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages and thus does not require translation.

RELATIONSHIPS OF THE LICININI

Jeannel (1941) included in the Callistomorphi the families Callistidae (including the oodines), Licinidae, and Panagaeidae. Kryzhanovskij (1983:88–89), using a more traditional system of ranking, included the tribes Licinini, Callistini, and Oodini in the supertribe Callistitae, placing the Panagaeini in the supertribe Panagaeitae, along with the Peleciini. Erwin (1985:468) separated also the panagaeines from the Callistitae, including in the Panagaeitae as well the Afrotropical Bascanini and the Peleciini (*sensu latiore*). Considering the shared derived features of callistites (*sensu* Kryzhanovskij and Erwin) and at least panagaeines, exhibited by adults (including paramedian mental pits, and defensive secretions [see below]) and by larvae, it seems best to include the two complexes in a single supertribe. Straneo and Ball (1989:85) placed the peleciines as *incertae sedis,* near the base of the subfamily Harpalinae (*sensu* Erwin, 1985:468).

Within the callistite assemblage, the tribe Licinini probably occupies a basal position—at least such is suggested by the distinctive pattern of volatile organic compounds comprising the defensive secretions of the pygidial glands. A basal position for the Licinini is indicated also by features of the fore coxal cavities—probably plesiotypically uniperforate, whereas oodines, callistines and panagaeines exhibit the probably apotypic feature of biperforate coxal cavities. I postulate the following system of relationships: Licinini + (Oodini + (Callistini + Panagaeini)). See below for details.

GENERIC CLASSIFICATION

Important recent references to Licinini are: Darlington (1968:14–19), treating the genera and species of New Guinea; Lindroth (1968:939–944 and 1969:945–967 and 1121), treating the Canadian and Alaskan taxa; Kryzhanovskij (1983:274–276), treating the fauna of the USSR; Freude (1976:254–260), treating the fauna of Middle Europe; and Moore et al. (1987:263–269), cataloguing the Australian taxa.

Freude (1976), evidently following Jeannel (1942), placed *Licinus* and *Badister* in the subfamilies Licinitae and Badisteritae, respectively, thus separating these two genera as widely as either is separated from other carabid subfamilies, such as Pterostichitae and Harpalitae. Such ranking does not coincide with the affinities of these genera, as explained by Ball (1959), and amplified below.

Ball (1959:7) arranged the licinine genera in four groups which he regarded as the equivalent of subtribes. Two were named: Dicaelina (Group 1) and Licinina (Group 2), leaving Groups 3 and 4 unnamed. They are named here: Lestignathina (name based on that of the first described genus included in this group—*Lestignathus* Erichson [1842:132]), new subtribe (Group 3); and Dicrochilina, new subtribe (Group 4).

Two genera, the northeastern Australian *Mecynognathus* MacLeay and Chilean *Eutogeneius* Solier (1849:253), were excluded from the classification because Ball had not seen specimens. Jeannel (1942:991) placed the enigmatic *Mecynognathus* in the Licinini because of the strikingly modified mouthparts of the adults. Darlington (1961:18) included *Mecynognathus* in the Tribe Pterostichini, as did Moore (1965:22), based on overall similarity and chorological affinity to the clearly pterostichine genus *Paranurus* Tschitschérine.

Although I have not studied material of *Eutogeneius fuscus* Solier (1849:255) in great detail, I have seen the holotype in the Oberthür-Chaudoir Collection (Mus. Nat. Hist. Nat., Paris), and two additional specimens in the Canadian National Collection of Insects, Ottawa. A male exhibits adhesive vestiture of articulo-setae on the front tarsus (Stork, 1980:287), and the mandibles are short and broad, with broad apices. On the basis of these observations, *Eutogeneius* is assigned to the subtribe Licinina.

Ball (1959:6–8) used features of the adult mandibles as the primary basis for classifying the licinine genera, but he provided only a superficial account of these structures. A more detailed description of the licinine mandibles is presented below, based on Acorn and Ball (1991). Study of the mouthparts was extended to include the labrum, maxillae, and labium. The adhesive vestiture of the anterior tarsi of males was examined in some detail. Also, a few specimens were examined for the condition of the fore coxal cavities. As noted in the Methods section above, the pterostichine genus *Loxandrus* was used as an out-group.

Based on published information, additional characters for classification were sought in the defensive secretions of adults, in structural features of the larvae, and in chromosome number.

Mandibles

As explained by Acorn and Ball (1991) carabid mandibles are trigonal in form, each tapered from a broad base to a narrow, more or less pointed apex (Fig. 1A–B). Laterally broad and with a triangular depression in the outer face (the scrobe), the mandible is sloped toward the occlusal surface (Fig. 1C–D), or the edge that opposes the other mandible, and is involved in biting or gripping the food items. In dorsal aspect, two imprecisely defined areas are recognized: a terebra, extending from the apical incisor tooth (Fig. 1A, i) to a transverse plane, extended through the terebral tooth (tt). Posterad the terebra is the broader basal area. A series of ridges and teeth are on the occlusal margin, as follows, anteriorly to posteriorly, and dorsally to ventrally (Fig. 1A–E): incisor tooth; terebral ridge (tr), or if two, superior terebral (str) and inferior terebral (itr); terebral tooth; retinaculum (r), in most groups with teeth (anterior, art, and posterior, prt), and a ridge (rr). The end of the retinaculum is marked in most taxa by a deep groove, the anterior occlusal groove (aog) posterior to which is the molar area, divided or not by a posterior occlusal groove into a more anterior premolar ridge and/or tooth, and a posterior molar ridge and tooth. These distinctions are not required here, and the molar area is designated simply m. Ventrally, a groove extends diagonally or more or less parallel to the occlusal margin—the ventral groove (Figs. 1E–F, vg). Arising from the ventral groove is a brush of microtrichia (vmt).

Mandibles of *Loxandrus* LeConte (Fig. 1A–F).—The terebra occupies about ⅔ of the mandible, as is true of most carabid mandibles (Acorn and Ball, 1991). On the left mandible (Fig. 1A, C, E), the superior (str) and inferior (itr) terebral ridges meet at the terebral tooth (tt). The tooth and ridges comprise the occlusal portion of the terebra. Posterad the terebral tooth, the occlusal surface is occupied by the retinaculum, or retinacular ridge (rr) which extends ventrad the terebral ridge. The anterior occlusal groove (aog) at the posterior margin of the retinaculum, is marked distinctly. Posterad the groove is the molar area (m), which in *Loxandrus* is ridged (Fig. 1C), and extends anteriorly as a ridge (Fig. 1F) beneath the retinaculum. The ventral groove (Fig. 1E, vg) is moderately long and its brush is comprised of rather short microtrichia (vmt). The right mandible (Fig. 1B, D, F) is similar to the left except that the retinacular ridge (rr) is more prominent and terminates anteriorly in a pronounced anterior retinacular tooth (art), referred to by Bell (1960:100) as the canine tooth.

Mandibles of representative species of *Chlaenius* are described and illustrated by Bell (1960:163, figs. 122–131). Spence (1982:571, fig. 5A) illustrated mandibles of an oodine. Both groups are characterized by long terebrae, a complete set of teeth and ridges, and occlusal grooves.

By contrast and in general, mandibles of licinine adults exhibit more extensive ventral grooves (Fig. 1K–L, 2E–F, K–L, and 3E–F, K–L), and less complex occlusal margins that lack an occlusal groove separating the molar area from the retinaculum (Figs. 1G–L, 2A–L, 3A–L). The occlusal margin posterad the terebral tooth is named here basal ridge (br), because it is unclear (except in *D. daldorfi,* Fig. 1G–L) how much of this margin is retinacular and how much is molar.

Mandibles of subtribe Dicaelina.—These are illustrated by specimens of *D. daldorfi* Crotch (Fig. 1G–L) and *D. polita* Dejean. See also the mandibles of *Dicaelus* (*Liodicaelus*) (Figs. 13A–L, 14A–F).

The terebral ridge is nearly straight, with the incisor quite broad (Figs. 1G–H, 2A–B). In occlusal aspect (Figs. 1I–J, 2C–D), the terebral surfaces are quite broad and sloped diagonally ventro-laterally. In contrast to *Loxandrus,* dicaeline mandibles are more slender basally. The ventral groove of *Diplocheila* mandibles bears brushes of very long microtrichia (Figs. 1K–L, 2E–F), but the microtrichia are shorter in *Dicaelus* (Figs. 13E–F, K–L, and 14E–F). The dicaeline terebra is about half the length of the mandible.

The terebrae of *D. daldorfi* (Fig. 1G–H) are about as broad as those of *D. polita* (Fig. 2A–B), and the occlusal surface on the right mandible is smooth (Fig. 1J) rather than diagonally ridged, as in *D. polita* (Fig. 2D). The left mandible of *D. daldorfi* exhibits a small supraterebral tooth (Fig. 1G, stt), a unique feature of this species. (Unfortunately, the dorsal surface of the specimen illustrated is worn somewhat, and irregular.) The retinaculum is small (Fig. 1G, I). The right mandible of *D. daldorfi* (Fig. 1H, J) lacks a clearly marked retinaculum.

The left terebral tooth of *D. polita* (Fig. 2A, E) is more prominent, and the left mandible has a small retinacular tooth (Fig. 2A, art) and a rather indistinct retinacular ridge (Fig. 2E).

The left terebral tooth of *D. polita* (Fig. 2A, E) is more prominent; the retinacular tooth is small (Fig. 2A, prt), and the retinacular ridge is rather indistinct. The right mandible (Fig. 2B, D) is without a clearly marked retinaculum.

Mandibles of subtribe Dicrochilina (Fig. 2G–L).—Terebrae are short, not more than one-third the length of the mandibles (Fig. 2G–H), and the basal part is relatively slender (Fig. 2I–J). The terebral teeth (tt) are small, the right one isolated from the superior terebral ridge (str) by a notch. The left mandible exhibits two terebral ridges (Fig. 2G, str and itr). The retinacula are absent. The ventral grooves bear long and densely packed microtrichia (Fig. 2K–L).

Mandibles of subtribe Lestignathina (Fig. 3A–E).—Markedly flattened dorso-ventrally, especially the terebrae (Fig. 3C–D), dorsally these mandibles exhibit broad terebrae, very slender and sharp incisors, and very prominent and sharp terebral teeth (Fig. 3A–B, i and tt). The terebral area is less than half the length of the mandible. Ventral retinacular or molar ridges are not indicated. The microtrichia of the ventral grooves are short (Fig. 3E–F, vmt).

Mandibles of subtribe Licinina (Fig. 3G–L).—These sclerites are very broad, especially basally (Fig. 3G–H, K–L), and thick (Fig. 3I–J). The terebrae are narrow in the horizontal plane, comparatively short, with occlusal margins nearly straight, and terebral teeth thick and prominent, and incisors blunt (Fig. 3I–J). The basal areas of both mandibles are markedly thickened, especially that of the right mandible, which has also a dorsal boss (Fig. 3I–J, b). The thickened terebral and basal areas of the right mandible are separated from one another by a low area, referred to as a notch (Fig. 3J, n). The left mandible does not exhibit such a notch. Such asymmetry between mandibles is a common feature of the Licinina, some taxa with the right mandible notched, others with the left, and still others with either mandible notched (see below, under *Badister reflexus* LeConte). The ventral grooves have short microtrichia (Fig. 3K–L, vmt).

The mandibles of the Licinina are without retinacular and molar ridges.

Mandibles of *Badister* are illustrated in Figures 19A–H and 20A–F. The terebral ridges of both mandibles are short, and are deflected ventrally, causing the mandibular apices to appear very broad in the anterior aspect (Fig. 20A–B).

Labrum (Figs. 4A-I, and 5A-D)

Licinines exhibit variously modified labra, most with a more or less pronounced medial notch. For comparison, illustrations of a more generalized labrum are provided (*Loxandrus pactinullus* Allen, Fig. 4A–B).

Labrum of *Loxandrus* (Fig. 4A–B).—This sclerite is about rectangular, with the anterior margin slightly concave (Fig. 4A), or straight. Dorsally, six long setae form a transverse row near the anterior margin. Ventrally, the labrum bears an epipharynx comprised in carabids of trichoid sensilla (Fig. 4B, ets) flanked each side by a group of microtrichia (Fig. 4F–G, emt). Liebherr (1991a:10–11, and Figs. 2, 8, 14, 20) showed a similar pattern for platynines, and that number of sensilla is correlated positively with body size.

Labrum of subtribe Dicaelina (Fig. 4C–G).—The anterior margin is more or less deeply notched, and in outline the labrum varies from transverse (Fig. 4E) to about quadrate (Fig. 4C). Dorsal setae vary in number from four (Fig. 4C, E) to six. Ventrally, the trichoid sensilla of the epipharynx are long and submarginal, the central part of the labrum being absent. The patches of microtrichia are more (Fig. 4F) or less (Fig. 4D) extensive.

The labra of subgenus *Isorembus* and of genus *Dicaelus* are much less modified, with the anterior margin less deeply and broadly notched, and trichoid sensilla of the epipharynx shorter.

Labrum of subtribe Dicrochilina (Fig. 5A–B).—In outline, the labrum is longer than wide, with anterior margin broadly concave. Dorsally are six marginal setae. Ventrally, the epipharyngeal trichoid sensilla are of average length and number. The microtrichia are numerous, and form a central "Y" figure, with the stem prominent (Fig. 5B, etr).

Labrum of subtribe Lestignathina (Fig. 4H–I).—For the Licinini, the labrum is markedly transverse and short. The central portion is present, and in fact is projected as a small tooth. The dorsal marginal setae number four. Ventrally (Fig. 4I), the trichoid sensilla are few, and the microtrichia are grouped in two small basal patches, one each side of the mid-line.

Although typical of *Siagonyx,* a labrum of this type is atypical for the Lestignathina as a whole, with adults of the other genera exhibiting a normal licinine labrum, quadrate in outline, with the central area absent.

Labrum of subtribe Licinina (Fig. 5C–D).—The form varies appreciably from asymmetric with an irregular anterior margin to symmetric, with a deep central notch (Fig. 20A–B). Dorsally, six setae comprise the marginal row (Fig. 5C). Ventrally, the epipharyngeal trichoid sensilla are few, and microtrichial patches are absent (Fig. 5D).

Maxillae (Fig. 6A-H)

In form and sclerites present, licinine maxillae are about average for adult carabids. Palpomeres vary in proportions. Vestiture of the lacinia and development of the lacinial tooth seem to offer the most useful features for classification.

Maxillae of subtribe Dicaelina (Fig. 6A–B).—The lacinial tooth (lt) is curved slightly. In dorsal aspect, the occlusal margin of the lacinia has a dense array of slender setae which extends on to the dorsal surface near the apex (Fig. 6A). Ventrally, the occlusal margin has several rows of stout setae which extend on to the ventral surface basally (Fig. 6B). Palpomere 3 (Fig. 6A, mp-3) is subequal in length to palpomere 2 and is distinctly longer than palpomere 4.

Maxillae of subtribe Dicrochilina (Fig. 6C–D).—These are similar to the maxillae of the Dicaelina (see above), except that the lacinial tooth is curved more sharply in relation to the long axis of the lacinia.

Maxillae of subtribe Lestignathina (Fig. 6E–F).—The lacinia exhibits a sinuate lateral margin, is widened apically, and the apical tooth is sharply bent, in fact slightly recurved at apex (Fig. 6E, lt). In dorsal aspect, the slender setae are relatively few and quite short. Ventrally, the stout setae are rather few also (Fig. 6F). (Sparse setation of the lacinia is exhibited also by oodines of the genera *Anatrichis* LeConte and *Oodinus* Motschulsky ([Spence, 1982:572, fig. 7A, B]). Palpomere 3 (Fig. 6E, mp-3) is much shorter than either 2 or 4.

Maxillae of subtribe Licinina (Fig. 6G–H).—The lacinial tooth (Fig. 6G, lt) is very prominent and is bent at a right angle to the long axis of the lacinia. Slender setae are in several not particularly dense rows, and some of them are curved apically. A few setae extend on to the dorsal surface preapically. Ventrally, the stout setae are prominent and in several rows along the occlusal margin. The basal area has few setae (Fig. 6H).

Labium (Figs. 7A-E and 8A-D)

The licinine labium is characterized by absence of a mental tooth, and by a bisetose glossal sclerite. Other features vary from subtribe to subtribe, as noted below. The bisetose submentum is taxonomically featureless.

Labium of subtribe Dicaelina (Fig. 7A–C).—Separated from the submentum by a complete suture, the mentum is transverse, with broad lateral lobes (11), and epilobes (el) with apices terminated at the apices of the lateral lobes. Ventrally, the mentum has a moderately deep median sinus, and bears a pair of paramedial setae, and near the base a pair of pits (Fig. 7A, mp) with small pores in the surface (Fig. 7C). Allen and Ball (1980:507, fig. 25B) illustrated similar structures for taxa of *Loxandrus.* Mental pits are common in *Chlaenius* (Bell, 1960:100, and 163, figs. 132–135), in

Panagaeini and in the Oodini (Spence, 1982:572, fig. 8A). Bell (1960:100) stated that licinines were without these pits. Their function is unknown, but it seems more likely that they are sense organs rather than "... simply the outward manifestations of inwardly-directed apodemes" (Allen and Ball, 1980:488). The paraglossae (pg) of the prementum are narrow lobes extended beyond the apex of the glossal sclerite (gl). Dorsally, the paraglossae are covered with an extensive vestiture of microtrichia (Fig. 7B), as is true also for the oodine genus *Anatrichis* (Spence, 1982:572, fig. 9A). Palpomere 2 is bisetose.

Labium of subtribe Dicrochilina (Fig. 7D–E).—In general, this complex of sclerites is much like that of the Dicaelina, differing as follows. Lateral lobes (Fig. 7D, ll) are longer, and the apices of the epilobes (el) extend clearly beyond the apices of the lateral lobes. Palpomere 2 is quadrisetose.

Labium of subtribe Lestignathina (Fig. 8A–B).—The mentum is asetose and lacks pits (Fig. 8A). The medial sinus is shallow, so that the medial part is quite broad. The apices of the epilobes (el) are coextensive with the apices of the lateral lobes (ll). The paraglossae (pg) are small, and are not extended beyond the apex of the glossal sclerite (gl), which is convex and is projected anteriorly. Dorsally, the surface of the ligula (paraglossae + glossae) is covered with isodiametric microsculpture, the sculpticells with surfaces convex (Fig. 8B). Each paraglossa has a row of small microtrichia. Palpomere 2 is bisetose.

Mentum and submentum are fused, i.e., the mental suture is absent or incomplete. Horn (1881:143) noted that the mental suture is absent from the specimen of *Lestignathus* that he examined. Sloane (1898:488) pointed out that this suture is absent also from the labia of *Lacordairia, Siagonyx, Hormacrus, Platylytron,* and *Microferonia.* Further, he countered Horn's argument that *Lestignathus* is a platynine rather than a licinine.

Labium of subtribe Licinina (Fig. 8C–D).—The mentum is bisetose (punctures evident near posterior margin of the deep medial sinus, but setae broken), and the ventral surface is without pits (Fig. 8C). Lateral lobes (ll) are average, with apices of epilobes (el) coextensive with apices of lateral lobes. The anterior margin of the glossal sclerite (gl) is slightly convex and slightly projected. For *Licinus,* the paraglossae (pg) are short and broad and not extended beyond the apex of the glossal sclerite. Dorsally, each paraglossa has a covering of long setae apically (Fig. 8D, pts) and a vestiture of microtrichia basally. In contrast, for *Badister,* the paraglossae are substantially longer than the glossal sclerite, and the dorsal surfaces of the paraglossae have a covering of apically broad, flat microtrichia, and marginally, hair-like microtrichia. For both of these genera, palpomere 2 is bisetose.

Fore coxal cavities

According to Jeannel (1941:78–82), one of the features diagnostic of the callistomorph assemblage is biperforate fore coxal cavities. This is correct for the Callistini, Oodini, and Panagaeini. However, condition of the fore coxal cavities varies within the Licinini: Dicaelina and Licinina have uniperforate cavities (i.e., a sclerotized bridge dividing each cavity is lacking), but Dicrochilina and Lestignathina have biperforate cavities.

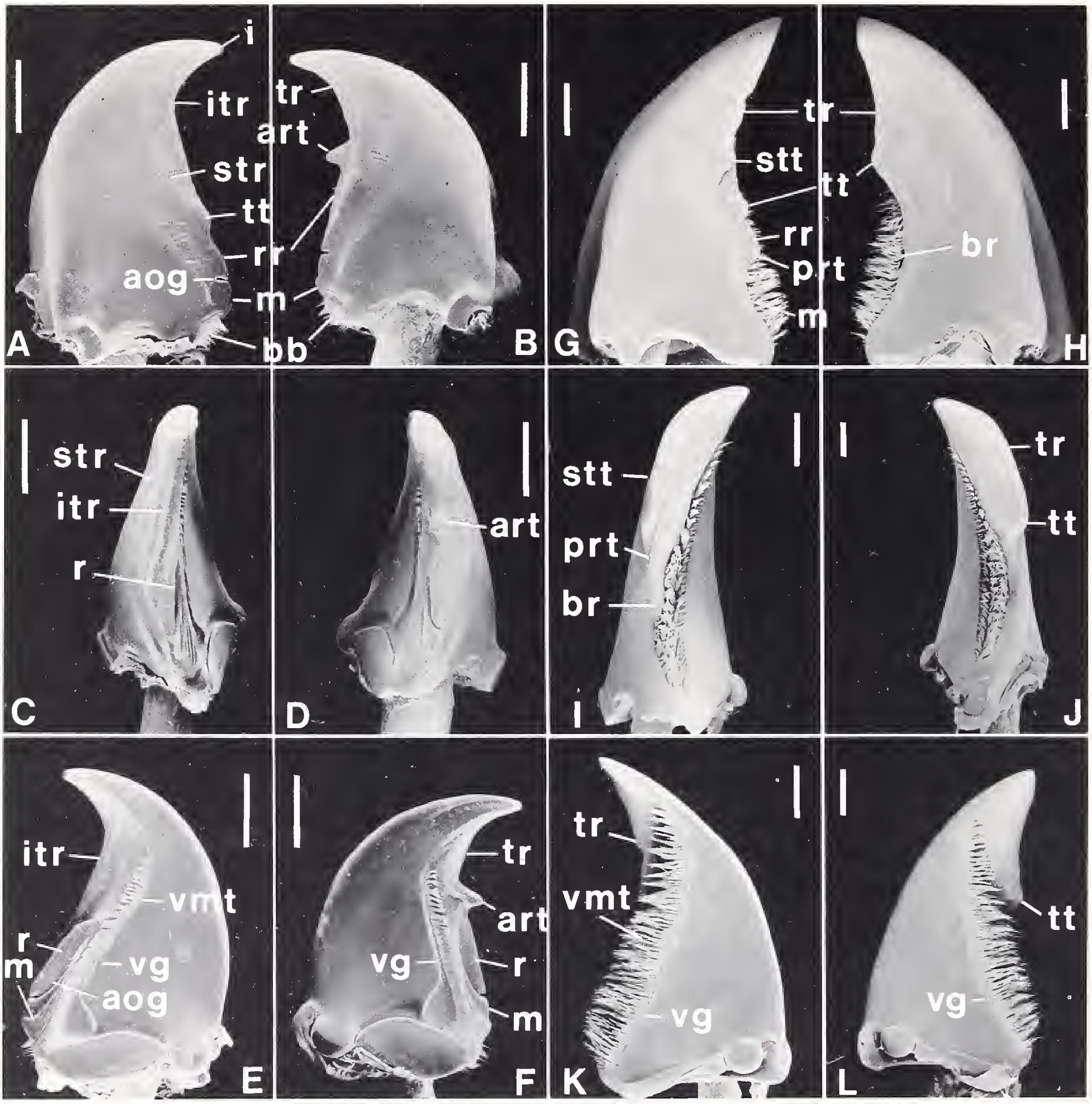


Fig. 1A–L. SEM photographs of mandibles of *Loxandrus pactinullus* Allen and *Diplocheila daldorfi* Crotch. A–F, *L. pactinullus*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D, and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *D. daldorfi* Crotch: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: aog, anterior occlusal groove; art, anterior retinacular tooth; bb, basal brush; br, basal ridge; i, incisor; itr, inferior terebral ridge; m, molar tooth; prt, posterior retinacular tooth; r, retinaculum; rr, retinacular ridge; str, supraterebral ridge; stt, superior terebral tooth; tt, terebral tooth; vg, ventral groove; vmt, ventral microtrichia. Scale bars: A–F = 200 μm; G–I = 400 μm.

Male fore tarsi and adhesive vestiture (Fig. 9A–I)

A diagnostic feature of the supertribe to which the Licinini belong (Callistomorphi Jeannel, 1941; Kryzhanovskij, 1983; or Patellimanes of 19th Century authors) is size of male fore tarsomeres and their adhesive vestiture. The group is characterized by

Table 1. Defensive compounds secreted by the pygidial glands of adult Licinini, and released by spraying (data from Moore, 1979:195, table 1).

Subtribe	Compounds		
	Formic acid	Hydrocarbons	Aliphatic ketones
Dicaelina[1]	X		
Dicrochilina	X	X	X
Lestignathina[2]	X	X	
Licinina[3]	X	X	

[1] *Dicaelus,* only.

[2] *Siagonyx,* only.

[3] *Licinus* and *Badister,* only.

having at least some of the tarsomeres widened asymmetrically, and with a dense vestiture of adhesive setae, designated articulo-setae by Stork (1980:287). Within the Licinini, size of male fore tarsomeres and extent of vestiture vary appreciably.

Male fore tarsomeres of subtribe Dicaelina (Fig. 9A–C).—Tarsomeres 1–3 slightly expanded on medial side, with typical callistomorph adhesive vestiture ventrally (Fig. 9B–C).

Male fore tarsomeres of subtribe Dicrochilina (Fig. 9D–F).—Tarsomeres 1–3 expanded diagonally medially (Fig. 9D), rather like loxandrine tarsomeres (Allen and Ball, 1980:511, fig. 43A–B). Ventral adhesive vestiture of articulo-setae (Fig. 9E–F), arranged in four diagonal parallel rows on tarsomeres 1 and 2, only two rows on tarsomere 3.

Male fore tarsomeres of subtribe Lestignathina.—In form and vestiture, these are like the tarsomeres of the Dicaelina.

Male fore tarsomeres of subtribe Licinina (Fig. 9G–I).—Tarsomeres 1 and 2 (Fig. 9G) expanded markedly, ventral adhesive vestiture of articulo-setae (Fig. 9H–I) on tarsomeres 1 and 2 (or on 1–3), densely packed.

Defensive secretions of the Licinini

Moore (1979) compared the defensive secretions of the pygidial glands of a broad taxonomic representation of carabid genera. He reported that callistomorphs produce a wide range of volatile organic compounds: hydrocarbons, aliphatic ketones, saturated esters, formic acid, phenols, aromatic aldehydes, and quinones. From an evolutionary perspective, production of a mixture of hydrocarbons and formic acid probably is plesiotypic for callistomorphs, this feature being widespread in the subfamily Harpalinae, which includes the Callistitae. Within the latter group, however, only the licinines exhibit this feature: oodines secrete unsaturated acids, only; callistines, hydrocarbons, phenols, and quinone; and panagaeines, hydrocarbons, aliphatic ketones and phenols. Presumably, absence from the defensive repertoire of hydrocarbons and/or formic acid is the result of loss, and the production of other volatile organic compounds is a gain, both being apotypic. Thus, licinines are relatively primitive compared to the other tribes with respect to production of defensive secretions.

The pattern within the Licinini is shown in Table 1. Members of all subtribes

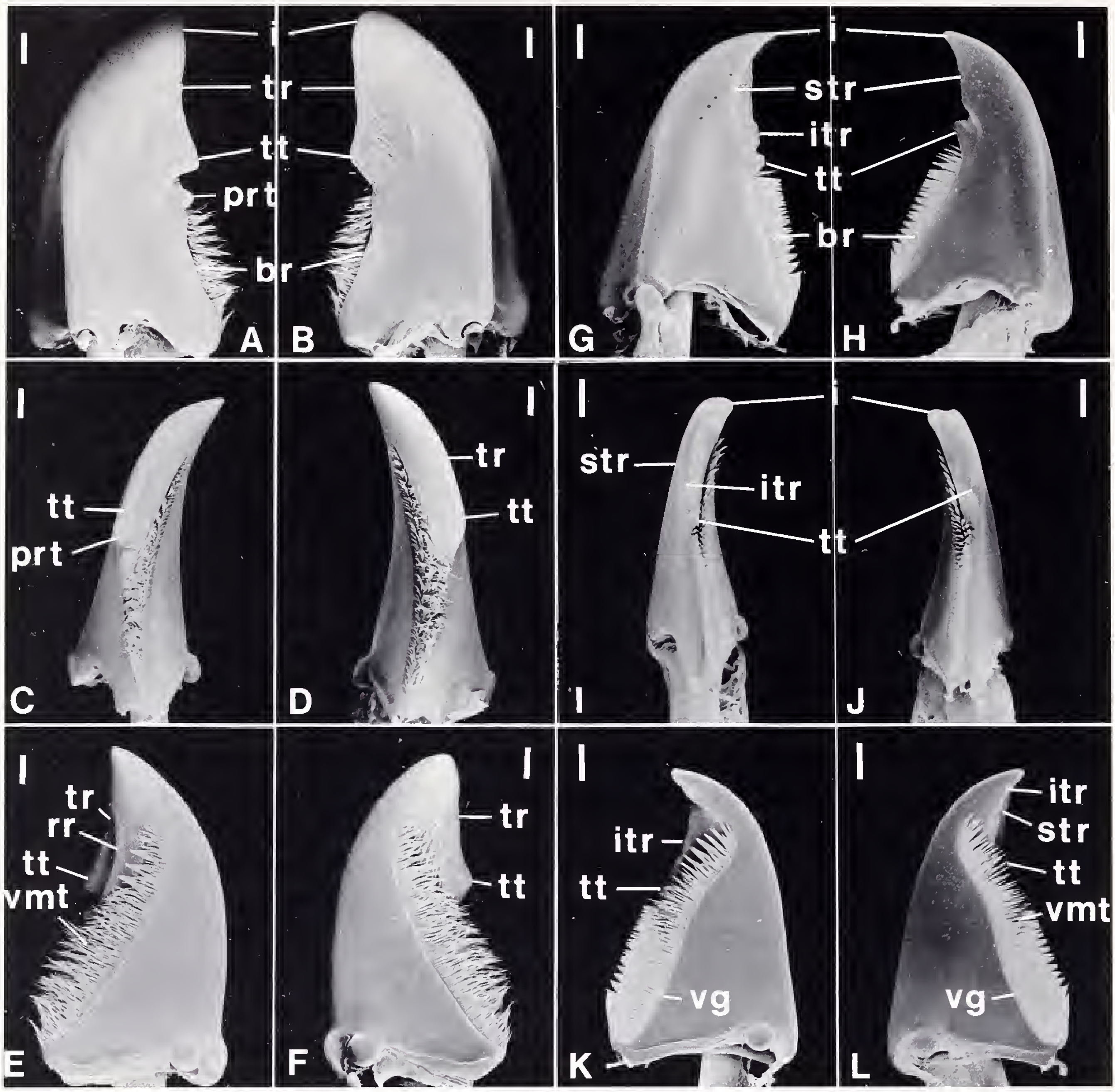


Fig. 2A–L. SEM photographs of mandibles of *Diplocheila polita* Dejean and *Dicrochile goryi* Boisduval. A–F, *Diplocheila polita*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *Dicrochile goryi*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; i, incisor; itr, inferior terebral ridge; prt, posterior retinacular tooth; rr, retinacular ridge; str, superior terebral ridge; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 200 μm.

produce formic acid, and all but the Dicaelina produce hydrocarbons. Only the Dicrochilina produce aliphatic ketones. Absence of hydrocarbons and production of aliphatic ketones are regarded as apotypic features.

Characteristics of larvae

Within the Carabidae, licinine larvae are distinguishable by three features: head dorsally with frontal sutures extended posteriorly to the occipital suture; cervical

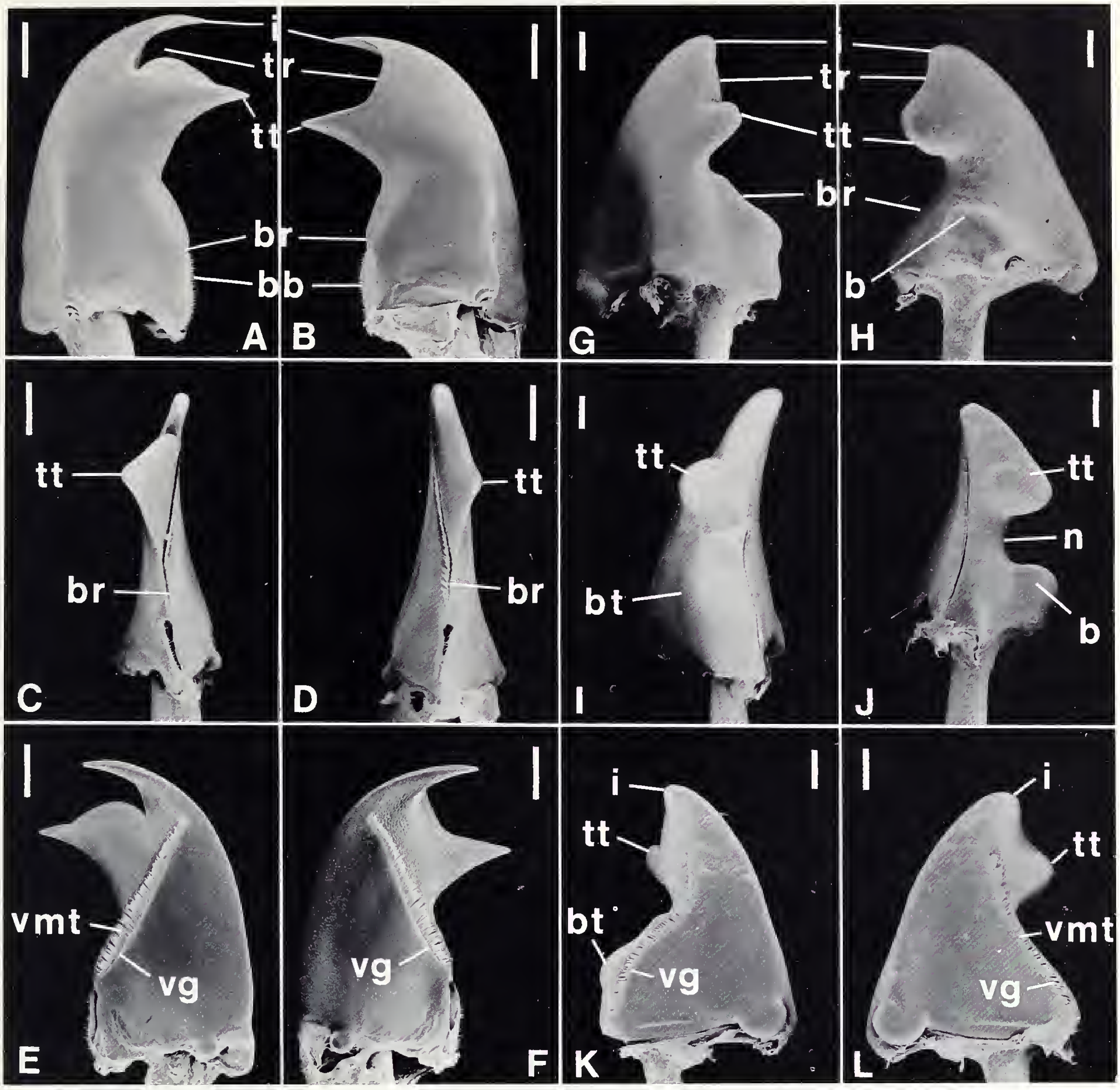


Fig. 3A–L. SEM photographs of mandibles of *Siagonyx* species? and *Licinus punctatulus* Fabricius. A–F, *Siagonyx* sp?: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *Licinus punctatulus*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: b, dorsal boss; bb, basal brush; br, basal ridge; bt, basal tooth; i, incisor; n, notch in dorsal surface; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; vmt, ventral microtrichia. Scale bars = 200 μm.

suture forked, ventral apotome gula-like (Jeannel, 1942:989; Moore, 1966:160); antennae elongate, at least 1.5× as long as mandibles (van Emden, 1942:44–45). Most known taxa have the occlusal margin of the terebra and posterior margin of the retinaculum denticulate or serrate (van Emden, 1942:44–45).

Although the tribe is diagnosed clearly by structural features of larvae, and although the few genera for which larval features are known (*Dicaelus*; *Diplocheila*; *Dicrochile*; *Siagonyx*; *Dilonchus*; *Licinus*; and *Badister*) are readily distinguished from one an-

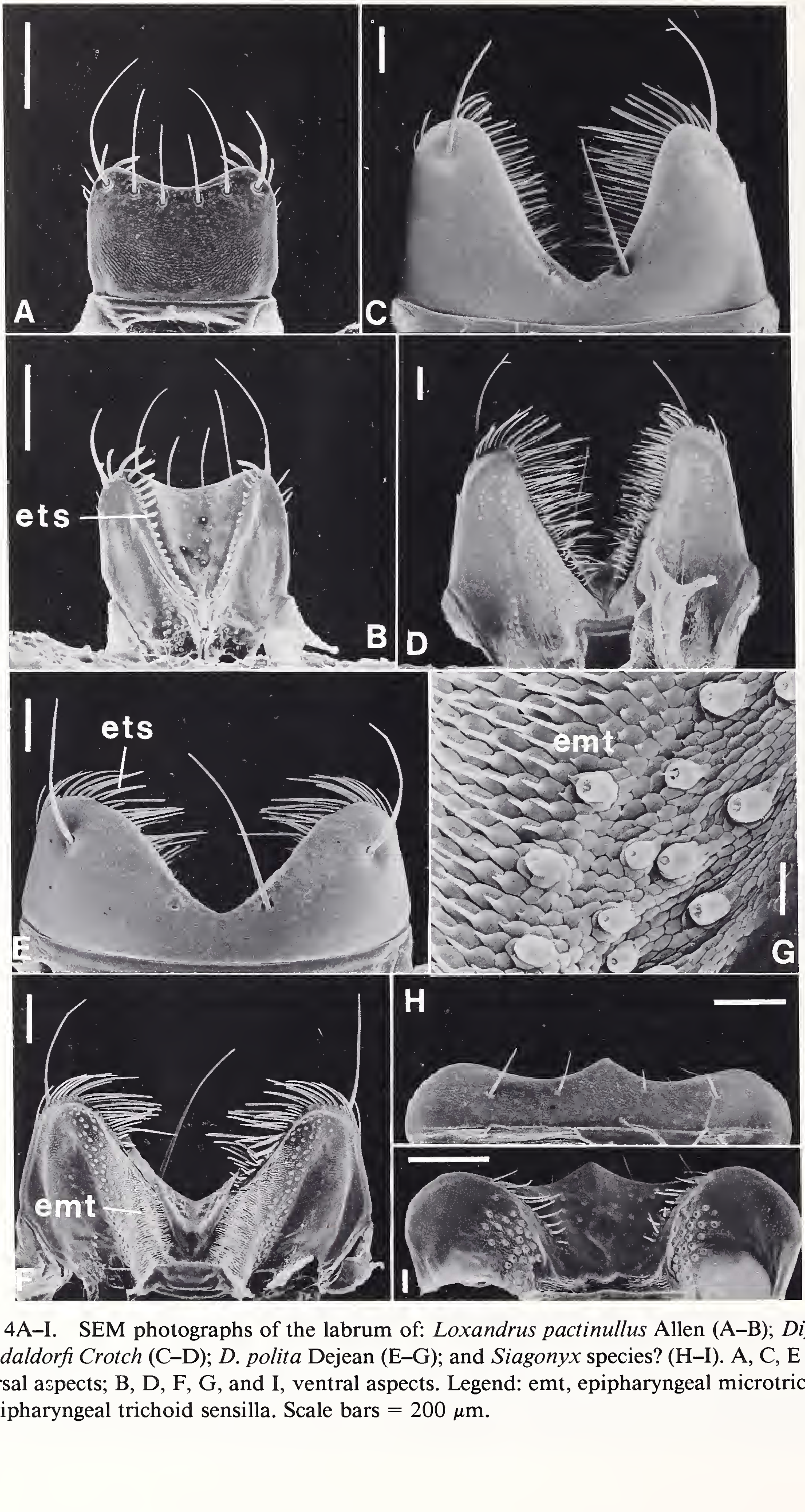


Fig. 4A–I. SEM photographs of the labrum of: *Loxandrus pactinullus* Allen (A–B); *Diplocheila daldorfi Crotch* (C–D); *D. polita* Dejean (E–G); and *Siagonyx* species? (H–I). A, C, E and H, dorsal aspects; B, D, F, G, and I, ventral aspects. Legend: emt, epipharyngeal microtrichia; ets, epipharyngeal trichoid sensilla. Scale bars = 200 μm.

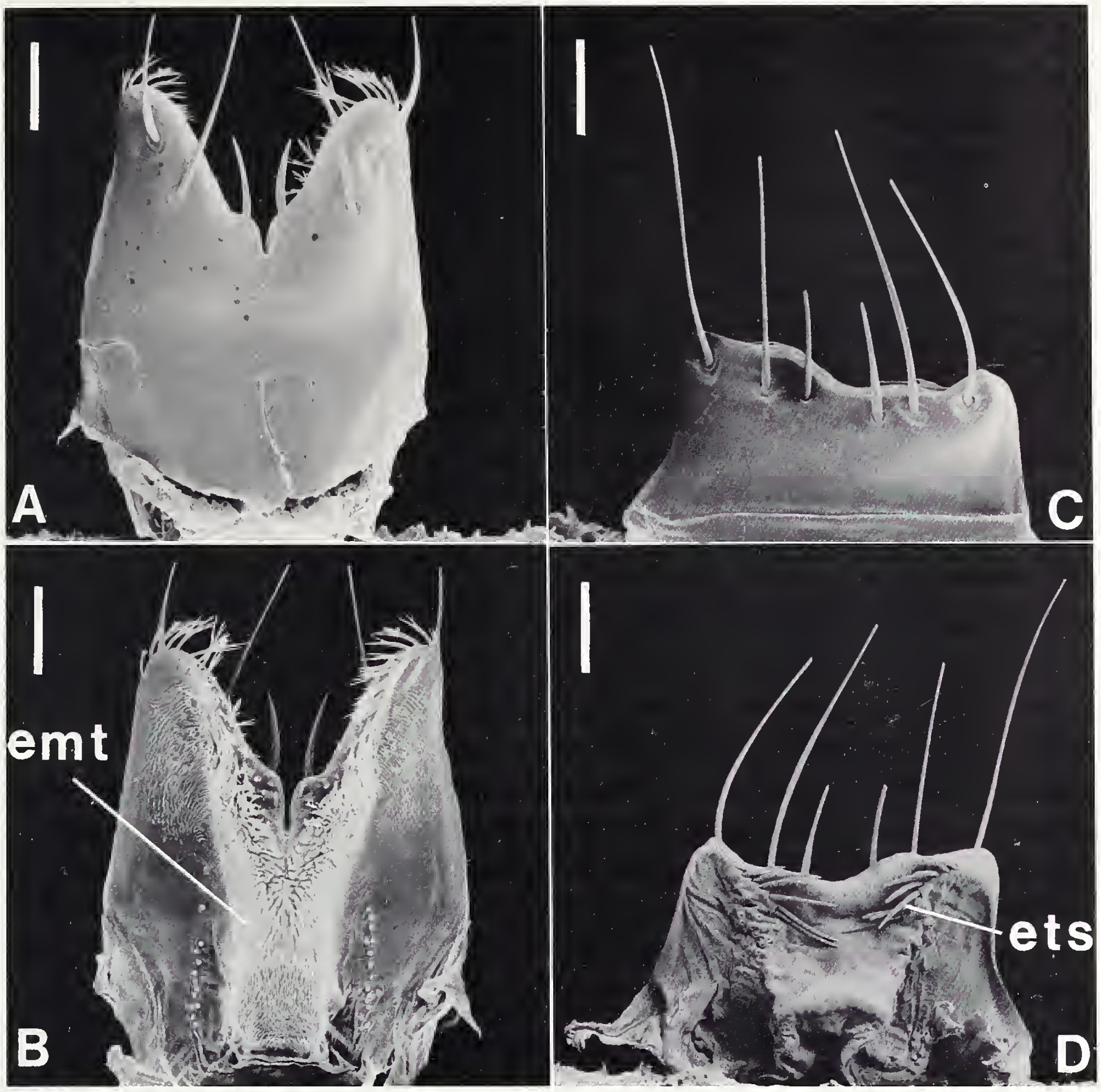


Fig. 5A–D. SEM photographs of the labrum of: *Dicrochile goryi* Boisduval (A–B); and *Licinus punctatulus* Fabricius (C–D). A and C, dorsal aspects; B and D, ventral aspects. Legend: emt, epipharyngeal microtrichia; ets, epipharyngeal trichoid sensilla. Scale bars = 200 μm.

other, some groupings provided by these character states do not coincide with the subtribal limits based on adult features. For example, Jeannel (1942:990) grouped *Licinus* with *Dicaelus* in the Licinitae, and placed *Badister* by itself, in the Badisteritae. The smooth mandibles characteristic of *Diplocheila* larvae isolate this genus from all of the others, the latter exhibiting mandibles with serrate-edged terebrae and retinacula. In contrast, Moore (1966:160) noted that the larvae of *Lestignathus* and *Dicrochile* differed markedly from one another, and that such difference was in agreement with placing them in different groups of genera.

Chromosome numbers of Licinini

Serrano (1986:224) postulated 37 as a basic diploid chromosome number for Licinini and for "modern" groups of Carabidae generally (i.e., Harpalinae *sensu* Erwin, 1985). Numbers are as follows: for subtribe Dicaelina, represented by *Diplocheila* (three species), 37–42; and for subtribe Licinina, represented by *Badister anomalus* Perris, 45, and by *Licinus* (two species), 26 and 38 (Serrano and Yadav,

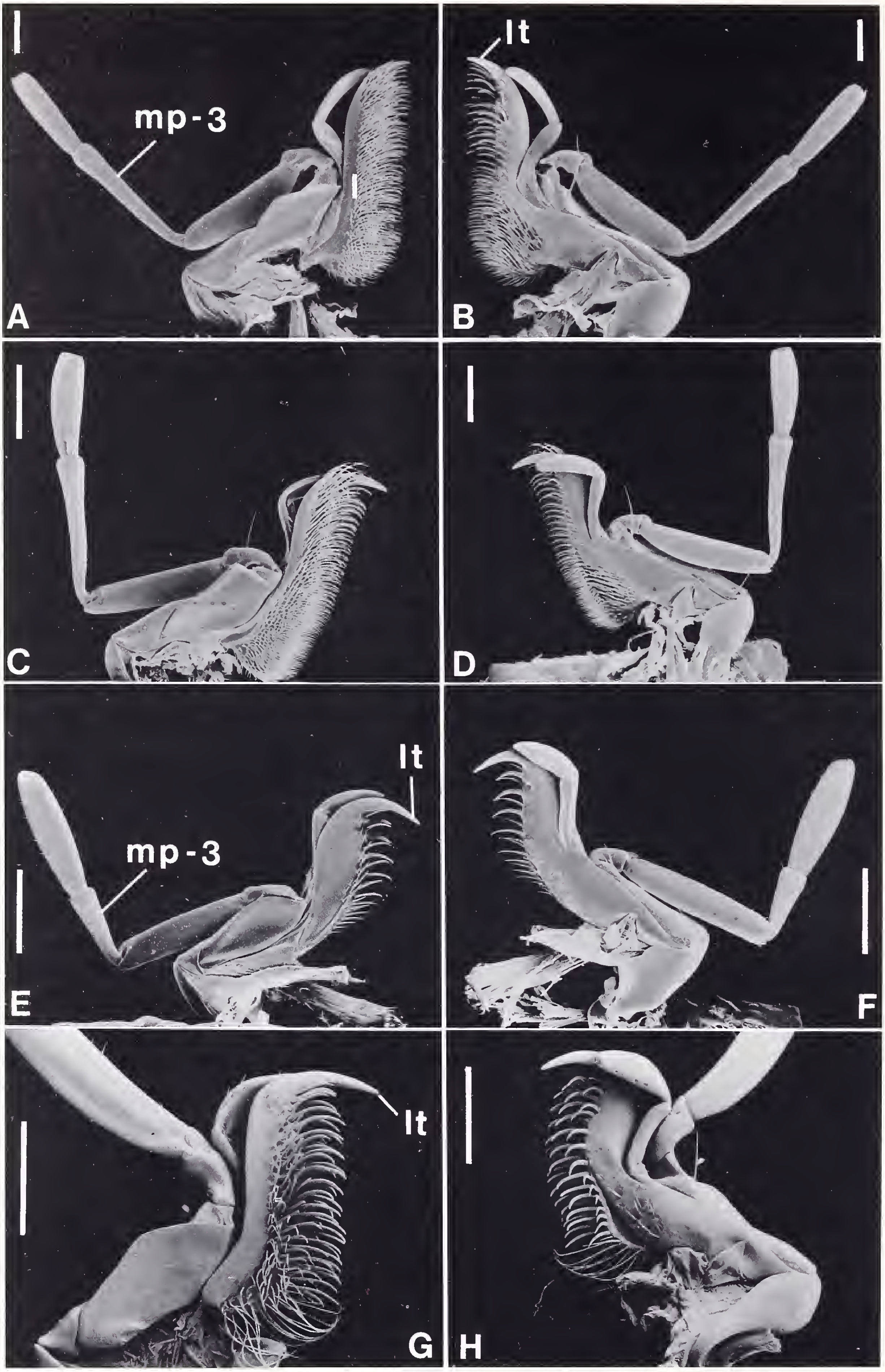


Fig. 6A–H. SEM photographs of the left maxilla of: *Diplocheila daldorfi* Crotch (A–B); *Dicrochile goryi* Boisduval (C–D); *Siagonyx* species (E–F); and *Licinus punctatulus* Fabricius (G–H). A, C, E and G, dorsal aspects; B, D, F and H, ventral aspects. Legend: l, lacinia; lt, lacinial tooth; and mp-3, maxillary palpomere 3. Scale bars = 400 μm.

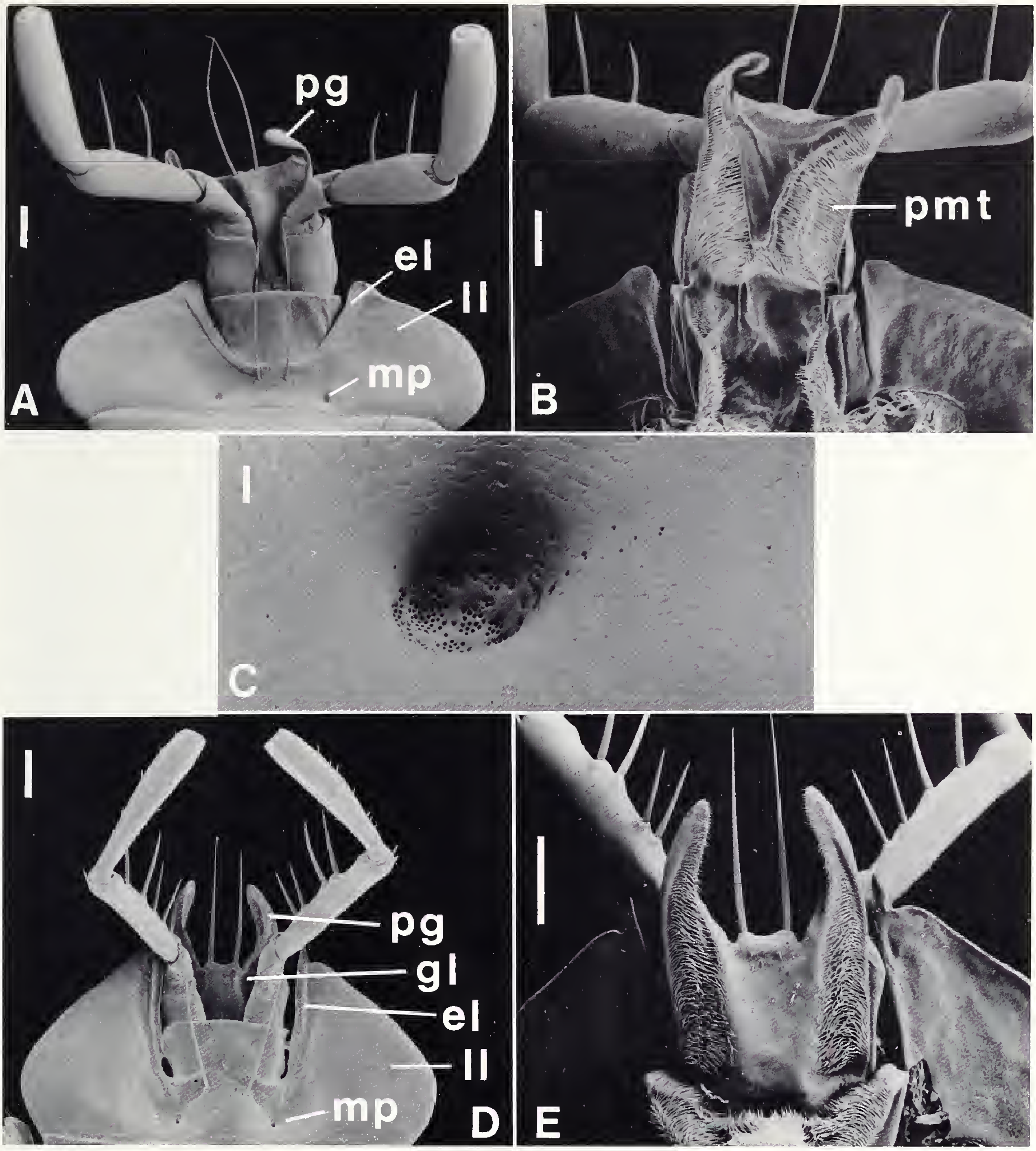


Fig. 7A–E. SEM photographs of the labium (mentum and prementum) of: *Diplocheila polita* Dejean (A–C); and *Dicrochile goryi* Boisduval (D–E). A, C and D, ventral aspects; B and E, dorsal aspects; C, enlargement of mental pit, showing pores. Legend: el, epilobe; gl, glossal sclerite; ll, lateral lobe; mp, mental pit; pg, paraglossa; and pmt, paraglossal microtrichia. Scale bars: A–B, D–E = 200 μm; C = 10 μm.

1984:351, table 1; Serrano et al., 1986:134). These numbers indicate marked overlap at the subtribal and generic levels, and thus, they are of little use in suprageneric classification, except to confirm further the harpaloid affinities of the Licinini. Within genera, at the species level, chromosome number likely is useful. Serrano (1986:325) notes that, although similar in form and other structural features of adults, *Licinus aequatus* Serville (2N = 26) and *L. punctatulus* Fabricius (2N = 38) differ markedly

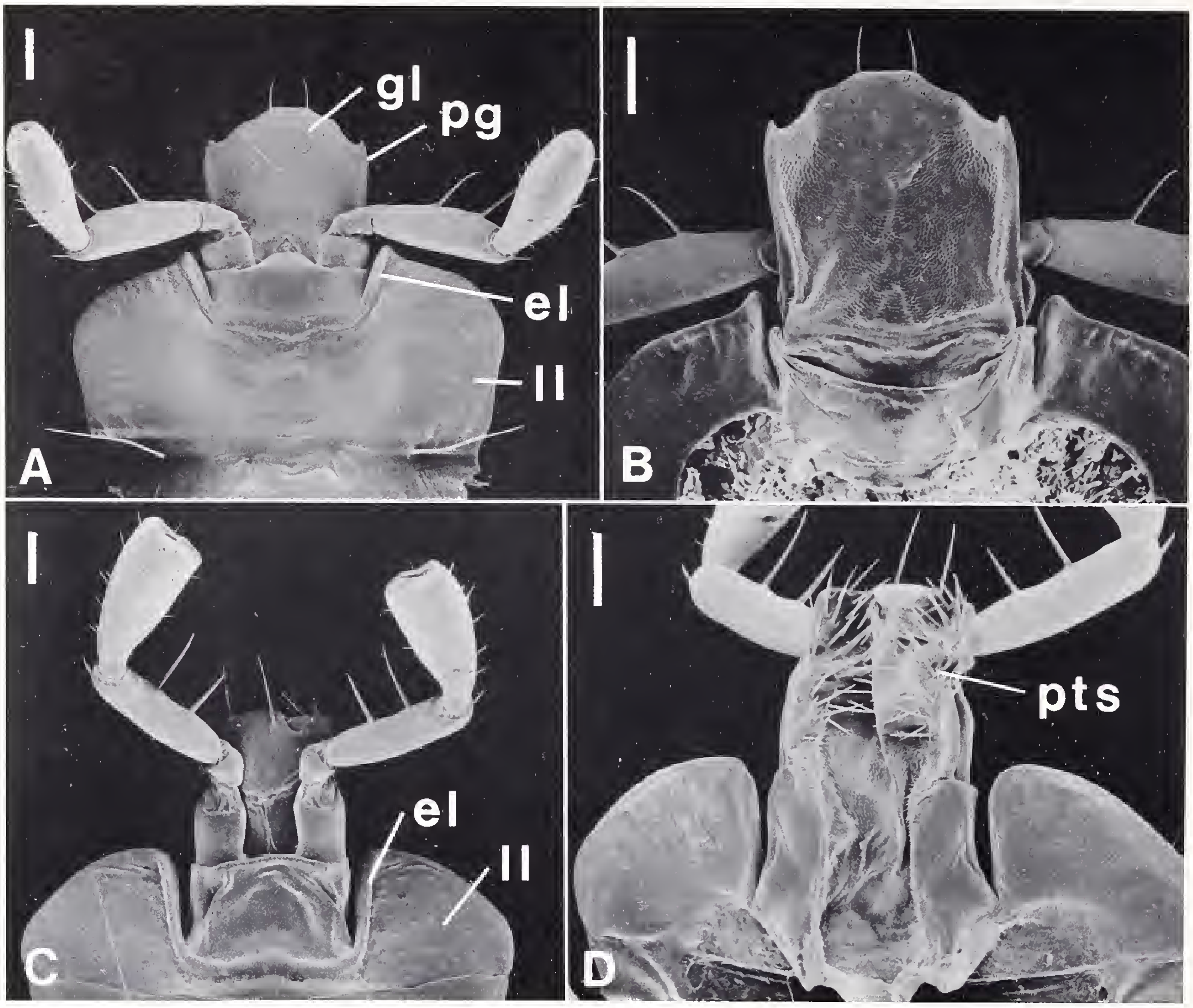


Fig. 8A–D. SEM photographs of the labium (mentum and prementum) of: *Siagonyx* species? (A–B); and *Licinus punctatulus* Fabricius (C–D). A and C, ventral aspects; B and D, dorsal aspects. Legend: el, epilobe; gl, glossal sclerite; ll, lateral lobe; pg, paraglossa; and pts, paraglossal trichoid sensilla. Scale bars = 200 μm.

in chromosome number, indicating that karyotypic change has been more rapid than morphological change.

Food of Licinini

Lindroth (1986:403) reported that the larvae and probably also the adults of *Licinus depressus* Paykull ate snails. Harde (1984:106) reported that members of *Licinus hoffmannseggi* Panzer and unspecified species of *Badister* were molluscivores. Ball (1959:53) and Lindroth (1969:948) cited records of *Dicaelus purpuratus* Bonelli eating snails. I observed specimens of *Diplocheila oregona* Hatch in captivity eating snails. To obtain the soft tissue, the beetles bit through the mollusc shells.

Mandibles of the lestignathines, with their long, slender incisors and terebral teeth, appear rather like those of cychrines (cf. Ball, 1966a:723, fig. 2A–B), which are known to prey on snails. However, rather than biting through the shell, a cychrine attacks the soft tissue by inserting its narrow head into the operculum. Perhaps lestignathines behave in the same manner.

Based on these few observations, I postulate that molluscivory is a general feature of licinines, and that such behavior is ancestral in this lineage.

Monophyly of the tribe Licinini

Efforts have not been made previously to establish that the tribe Licinini is monophyletic. Ball (1959), for example, accepted implicitly the judgment of previous workers that the Licinini is a natural group, based primarily on modifications of the mouthparts, and principally the labrum and clypeus, with anterior margins of each more or less markedly excavated. As noted above, these features vary markedly within the Licinini. Other features of adults are likely not apotypic at the tribal level (number of supraorbital setae; adhesive vestiture of the fore tarsi; form of male genitalia) or are shared with other callistites (condition of the fore coxal cavities; mental pits). Larval features, such as long cerci (or urogomphi) and long antennae are shared variously with other callistites.

A few features of adults, reasonably interpreted as apotypic, characterize the Licinini and help to establish monophyly of the group: reduction of the length of the mandibular terebra relative to the basal area, absence of occlusal grooves, and an extensive ventral groove; and the labial mentum without a tooth and with the median sinus more extensive than usual (except in some lestignathines). Larval features that seem likely to be apotypic for the Licinini are: dorsal surface of the head with frontal sutures extended posteriorly to the occipital suture; and ventrally, with the cervical suture branched, isolating a median apotome. Additionally, I infer that molluscivory is a ground-plan feature, and is probably the driving selective force involved in modifications of the mandibles.

Relationships of subtribes of Licinini

Within the Licinini, details of the mouthparts, especially the mandibles, seem to establish the monophyly of the Dicrochilina, Lestignathina, and Licinina. Additionally, within the Licinini, only the Dicrochilina have aliphatic ketones in their defensive secretions.

Evidence for monophyly of the Dicaelina, however, is less convincing. The larva of *Diplocheila,* for example, has a smooth, rather than serrate, terebral margin. This latter feature is characteristic of *Dicaelus* and the other groups of Licinini. The Dicaelina exhibit the most primitive mandibles (terebra relatively long, and various taxa with indications of remains of the retinaculum). Adults of *Dicaelus* lack hydrocarbons from their defensive secretions, producing formic acid only. Defensive secretions of *Diplocheila* have not been studied. If it is found that members of this genus also lack hydrocarbons, then this feature will serve as diagnostic for the Dicaelina.

At present then, the monophyly of the subtribe Dicaelina has not been established: either *Diplocheila* or *Dicaelus* may be more closely related to the derived subtribes than to one another. For example, the terebral margin and retinaculum of the mandibles of larvae of *Dicaelus* are serrate or denticulate, like those of known members of the other subtribes. In contrast, the larval mandibles of *Diplocheila* are smooth. If, as seems likely, the serrate mandibles are derived, then this feature could indicate that *Dicaelus* is related more closely to the other subtribes than to *Diplocheila.*

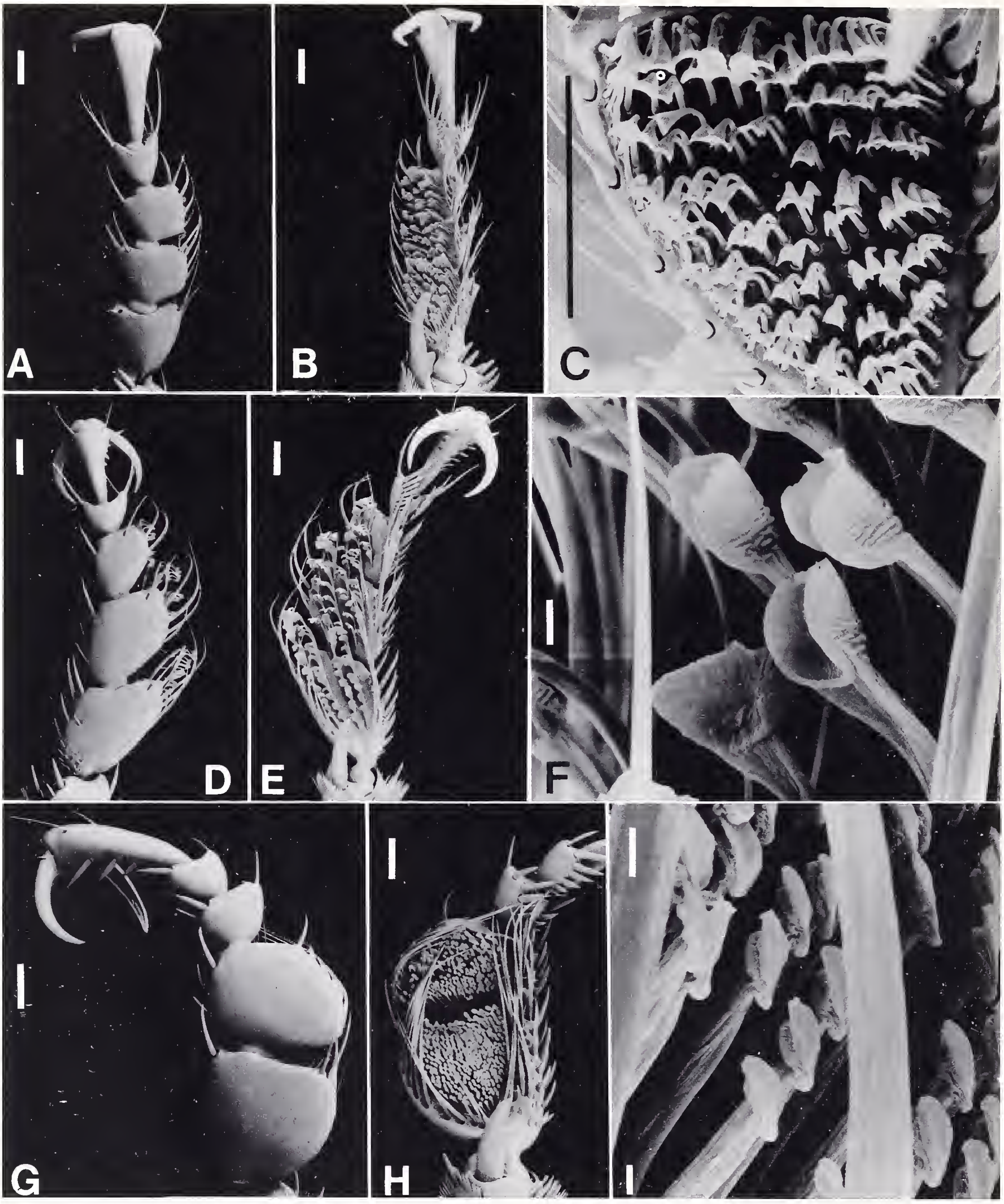


Fig. 9A–I. SEM photographs of left fore tarsus of males of: *Diplocheila polita* Dejean (A–C); *Dicrochile goryi* Boisduval (D–F); and *Licinus punctatulus* Fabricius (G–I). A, D and G, dorsal aspects; B, C, E, F, H and I, ventral aspects. Scale bars: A–E, G, H = 200 μm; F, I = 10 μm.

However, until such relationship can be established firmly, it seems best to include these two genera in a single dibasic subtribe rather than recognizing two monobasic groups.

The markedly shortened terebra characteristic of the Dicrochilina, Lestignathina and Licinina is accepted as evidence for the monophyly of these three groups, which collectively, I refer to as the derived assemblage. Within this assemblage, monophyly of the Dicrochilina and Lestignathina is postulated, on the basis of the biperforate coxal cavities exhibited by the members of this complex.

I believe, then, that the Dicaelina, if monophyletic, is the adelphotaxon of the derived assemblage of subtribes. Within the latter, the Dicrochilina and Lestignathina comprise a lineage that is the adelphotaxon of the Licinina. In summary, the subtribes of Licinini are related as follows: Dicaelina + ((Dicrochilina + Lestignathina) + Licinina).

KEY TO SUBTRIBES, BASED ON FEATURES OF THE MOUTHPARTS OF ADULTS

1. Mandibular terebra longer, about ½ length of mandible (Fig. 2A); terebral tooth small (Fig. 2A–B) or absent. Maxilla with lacinial tooth less prominent (Fig. 6A), occlusal margin densely setose; palpomere 3 longer than palpomere 4 (Fig. 6A–B, mp-3). Labium (Fig. 7A) with complete suture between submentum and mentum; mentum ventrally bisetose, paramedian pits (mp) near base of mentum, and palpomere 2 bisetose or quadrisetose .... Subtribe Dicaelina

1′. Mandibular terebra smaller, about ⅓ length of mandible (Figs. 2G, 3A, G); terebral tooth various. Maxilla with lacinial tooth and proportions of maxillary palpomere 3 various. Labium with suture between mentum and submentum complete or not; mentum bisetose or asetose, with or without paramedian pits, and labial palpomere 2 bisetose or quadrisetose 2

2.(1′) Mandible with terebral tooth small (Fig. 2G–H, tt). Maxilla (Fig. 6C) with lacinial tooth (lt) moderately prominent, occlusal margin densely setose; maxillary palpomere 3 (mp-3) longer than palpomere 4. Labium (Fig. 7D) with complete suture between submentum and mentum; mentum bisetose, and with paramedian pits basally (mp); labial palpomere 2 quadrisetose ....Subtribe Dicrochilina

2′. Mandible with terebral tooth prominent, either sharply pointed (Fig. 3A–B), or broad and blunt (Fig. 3G–H). Maxilla with lacinial tooth prominent, occlusal margin less densely setose (Fig. 6E–H), and maxillary palpomere 3 various. Labium suture between submentum and mentum complete or reduced; mentum bisetose or asetose, paramedian pits absent, and labial palpomere 2 bisetose 3

3.(2′) Mandibles about symmetrical, with incisor and terebral tooth long, slender, and pointed sharply (Fig. 3A–B). Maxilla with occlusal margin of lacinia sparsely setose (Fig. 6E–F); and maxillary palpomere 3 (mp-3) much shorter than 4. Labium with suture between submentum and mentum reduced or absent; mentum asetose, and medial sinus shallow (Fig. 8A) .... Subtribe Lestignathina

3′. Mandibles markedly asymmetrical, either right or left with large basal boss (b) and deep notch (n) dorsally (Figs. 3G–H, 17B–C, 18D–E); terebral tooth broad and blunt (tt). Maxilla with occlusal margin of lacinia moderately setose (Fig. 6G–H); and maxillary palpomere 3 (mp-3) subequal in length to 4. Labium with suture between mentum and submentum complete; mentum bisetose, and medial sinus deep (Fig. 8C) .... Subtribe Licinina

Genus *Diplocheila* Brullé

Ball (1959:11) arranged the species of *Diplocheila* in three subgenera: one monobasic, the Oriental *Neorembus* Ball; and two polybasic—the Oriental-eastern Palaearctic *Diplocheila* (*sensu stricto*) and the widespread *Isorembus* Jeannel. Comments about the latter subgenera are as follows.

Subgenus *Diplocheila* (*sensu stricto*)

The species of this subgenus are difficult to distinguish from one another, especially using only external features of adults. More generally, these beetles resemble specimens of *Pterostichus* Bonelli. Probably such resemblance accounts for the following synonymy.

Pterostichus (*Platysma*) *karikali* Jedlička

Type material of *P. karikali* Jedlička, 1969 includes a holotype and 62 paratypes, in the ZSMM. The holotype is labelled: "S. Indien 1964/ Pondicherry State/ Karikal XI/ P. S. Nathan leg"; "Holotypus" [pink paper]; "Pterostichus/ karikali/ sp. n [handwritten]/ det. Ing. Jedlička" [pink paper]. Paratypes are from Karikal, also, and labels are similar to those associated with the holotype. All specimens in the type series are typical of *Diplocheila* (*sensu stricto*) *distinguenda* in the diagnostic features of that species (Ball, 1959:31, and fig. 59). Accordingly, I propose the **new synonymy**: *Pterostichus karikali* Jedlička, 1969 = *Diplocheila distinguenda* Laferté, 1851.

Subgenus *Isorembus* Jeannel

Ball (1959:48–49) organized the species of *Isorembus* in three groups: *zeelandica* group, with four species confined to the Oriental Region and eastern part of the Palaearctic Region; the *aegyptiaca* group, with three species that range collectively throughout the African continent and Madagascar, and on the southern edge of the Palaearctic Region eastward to Pakistan; and the *striatopunctata* group, confined to the Nearctic Region. Subsequently (Ball, 1966b:25), the southern Chinese species *Diplocheila minima* Jedlička (1931:103) was added to this species group. A formal reconstructed phylogeny is offered for the species groups, incorporating *D. minima* into the system that was proposed previously (Ball, 1959:91–94, and diagram 1). Comments about geographical history of the *striatopunctata* group are offered, below.

Reconstructed phylogeny.—See Figures 10 and 11. The basis for designation of character states as plesiotypic or apotypic is outgroup comparison, using as outgroups the genus *Dicaelus* and the hypothesized common ancestor of the subgenera *Diplocheila* (*sensu stricto*) and *Neorembus*. Ball (1959:91, lineage 14) lists ancestral states for *Isorembus* (Fig. 11, lineage V, here).

Figure 10 shows that few characters were available for reconstructing the phylogeny. It shows also that most of the changes were losses or reductions.

Evidence for group membership of *D. minima* was based originally on overall similarity (Ball, 1966b), although in fact two synapotypic features support this assignment, as is shown in Figure 10. In the 1966 paper, I stated mistakenly that the *aegyptiaca* group was characterized in part by a beaded (or margined) intercoxal process of the prosternum, a feature of the *striatopunctata* group and of *D. minima*. As indicated in Figure 10, the intercoxal process of members of the *aegyptiaca* group is unmargined. Absence of ensiform setae from the ovipositor stylomeres of females of the Nearctic species indicates that this geographically circumscribed assemblage is monophyletic.

Geographical distribution and history

Ball (1959:96–98 and 1966b:22–25) discussed the geographical history of *Isorembus* against a geological background of continental stability, with the only possible terrestrial connection between Eurasia and North America being Beringia, in the north. More recently, it has become clear (and generally accepted by geologists) that continents have shifted in relation to one another, and that the disappearance of major epicontinental seaways has changed radically the configuration of land, and of sea basins (Noonan, 1988:40–43, and references cited therein).

Allen (1983), Noonan (1988) and Liebherr (1991a:137) have discussed the distribution patterns of various insect taxa (carabids and others) in the light of this geodynamic theory. It seems appropriate to extend such analysis to *Isorembus,* through correlation of the reconstructed phylogeny with past geological events (Liebherr, 1986:161).

The distribution pattern of *Isorembus* was illustrated by Ball (1966b:23, fig. 7), and it is tabulated in Figure 11. In more detail, the *aegyptiaca* group is marginal in the Oriental Region, being represented there by a single species in northern India, and *D. minima,* of the *striatopunctata* group is known only from Szechuan, in southern China—well to the west of the known range of the *zeelandica* group, which extends from the tropics of the Oriental Region to the cool temperate parts of the eastern Palaearctic Region. The ranges of the *zeelandica* and *aegyptiaca* groups are each more or less continuous.

In contrast, the range of the *striatopunctata* group is broadly interrupted, with a monophyletic assemblage of eight species in the Nearctic Region and a single species known only from Szechuan. Climatic tolerance of the Nearctic assemblage of the *striatopunctata* group extends from boreal conditions (two species) to the tropics (one species), with six species in the general area of cool to warm temperate conditions. To explain this pattern of geographical and ecological distribution, the following sequence of events is postulated.

1. Origin of *Isorembus* in Laurasia, probably in early Tertiary time, this stock becoming widespread, and occupying Euramerica, to the west of Turgai Straits, and southern Asiamerica in the east (Fig. 11, lineage V; see also Noonan, 1988: 42, fig. 3).
2. The eastern fragment of ancestral *Isorembus* differentiated into the ancestral stock of the *zeelandica* group (Fig. 11, lineage W), while the western fragment produced the ancestral stock of the *aegyptiaca-striatopunctata* groups (lineage X).
3. Separation of lineage X by an unknown vicariance event into a more southern stock (lineage Y), the ancestor of the *aegyptiaca* group, that eventually dispersed into the Afrotropical Region, and a more northern stock (lineage Z), the ancestor of the *striatopunctata* group.
4. Separation of the North American tectonic plate from Laurasia, with the consequent formation of the Atlantic Ocean basin, leading to division of lineage Z into the ancestor of the *D. minima* clade, and the ancestor of the extant Nearctic species of the *striatopunctata* group.
5. The Nearctic clade of the *striatopunctata* group, differentiated, and extending its overall climatic tolerance, entered the boreal forest, as the climate cooled in

later Tertiary time. Also, by overseas dispersal, one species extended its range to Cuba, in the West Indies.

6. The Palaearctic clade, meanwhile, extended its range across much of the temperate parts of the Palaearctic Region, but eventually became extinct over most of this area.

The large gap in the range of the *striatopunctata* group deserves additional comment. Although *Diplocheila minima* is isolated from the Nearctic clade of the *striatopunctata* group by thousands of kilometres, the extent of the terrestrial component of this separation may be comparatively recent. Based on fossil evidence, Coope (1979:264) noted that:

> "In response to climatic oscillations of the Quaternary, species of Coleoptera have altered their geographic ranges on an enormous scale so that where a species is today may give us little evidence of its geographical history."

Two examples are offered in support of this statement, as follows. Coope (1973) reported that the aphodiine scarabaeid species *Aphodius holdereri* Reitter, known now from Tibet, only, was represented in Britain as recently as 26,000 years before present. Hammond et al. (1979) reported that the staphylinid species *Anotylus gibbulus* (Eppelsheim) known today only from eastern China and the Caspian Sea region, was present in Britain and eastern Canada during the Pleistocene, fossils having been collected in deposits ranging in age from ca. 39,000 to 300,000 years before present. Both of these species have undergone comparatively recent and dramatic range changes. It would seem possible, therefore, that the *Diplocheila striatopunctata* group was represented in Europe until the climatic changes of the Pleistocene epoch, with extensive subsequent extinction. Only *D. minima* survives, whose range may have extended far to the west of its present location, in southwestern China.

The main point of this discussion is that the distribution pattern of the *striatopunctata* group can be fitted very readily to the vicariance models proposed by Allen (1983) and Noonan (1988). Tempting as it is to propose a Jurassic origin for the *striatopunctata* group (cf. Allen, 1983:626, fig. 65), with postulated vicariance events paralleling so closely the reconstructed phylogeny of the *striatopunctata* group, it seems better to think in terms of a more recent origin and differentiation, and thus to postulate use of the warm temperate land connections across the North Atlantic Ocean in early Tertiary time (cf. Matthews, 1979:37, fig. 23). A Beringian route, postulated by Ball (1959, 1966b), seems less likely, in view of the present distribution pattern of the Nearctic clade, with its species concentration in the east and in warm temperate areas.

New World species

Although Lindroth (1968:939) referred to Ball's (1959) revision of Licinini as having been done "with utmost accuracy," in fact I confused the names of two species of Nearctic *Diplocheila*: *D. modesta* Casey, 1920 is conspecific with *D. assimilis* LeConte, 1844, and the names therefore are synonymous; and *D. assimilis* Ball, 1959 (not LeConte) is conspecific with *D. impressicollis* Dejean, 1831. Lindroth (1968: 943–944) made the necessary corrections in the valid names for these species.

Table 2. Distribution pattern of the *Diplocheila striatopunctata* group in the Nearctic Region.

Species	Geographical zones				
	East coastal states	Mid-west to 100th meridian	West of 100th to Rockies	West of Rockies	No. geog. zones
obtusa LeC.	X	X	X	X	4
striatopunctata LeC.	X	X	X	X	4
assimilis LeC.	X	X			2
impressicollis Dej.	X	X			2
major LeC.	X	X			2
oregona Hatch			X	X	2
undulata Carr		X	X		2
nupera Casey	X				1
Total species	6	6	4	3	

Diplocheila nupera Casey

Locality record.—This rarely collected Floridian endemic, is known only from the southern half of that state (Ball, 1959:73). An additional record is:

> Monroe County, Big Pine Key, Long Beach, June 21, 1990; three males, six females, collected by R. S. Anderson, from *Sesuvium* litter (CMNC).

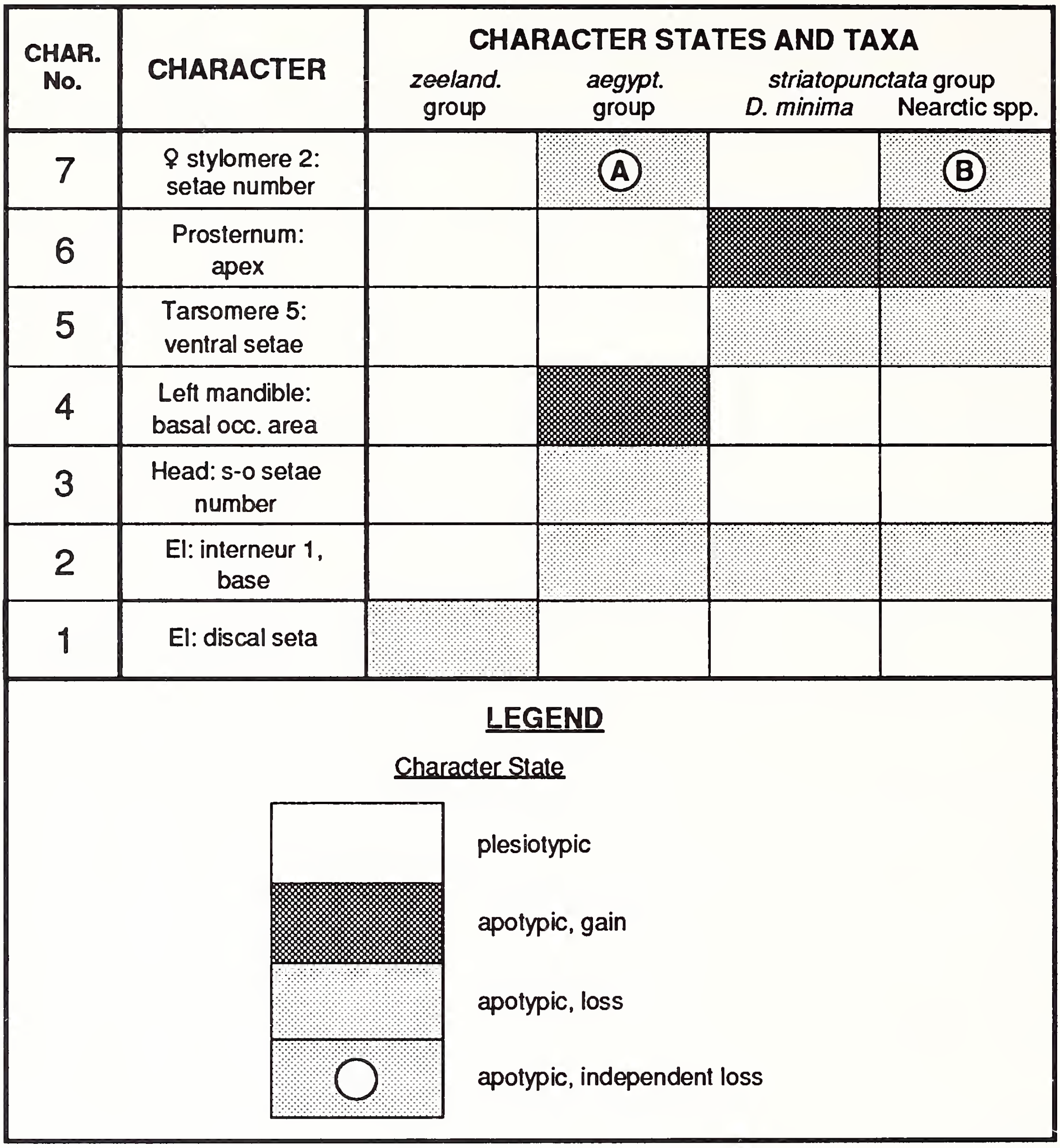
The specimens were collected just above high tide line, by sifting debris consisting of parts of dead *Sesuvium* plants and material washed on land by the sea. Like most other members of this genus, adults of *D. minima* probably are hygrophilous, and on Big Pine Key, probably they live near the fresh water marshes that occur there (R. S. Anderson, pers. comm.). Thus, I believe that the sea beach record is accidental for this species.

Diplocheila undulata Carr

Locality record.—This rarely collected species is known from a few localities in Illinois, Manitoba, and Alberta. The species was described in 1920 on the basis of specimens labelled "Edmonton, Alberta" (Ball, 1959:8). Lindroth (1969:946) noted "Ecology not recorded for this species." Because its putative adelphotaxon, *D. obtusa* LeConte is unusual for *Isorembus,* living in mesic to dry situations, I assumed that *D. undulata* lived in similar habitats.

However, five specimens were collected in May and June, 1985, in pitfall traps placed at the edge of a permanent marl pond, and in adjacent sedge marsh, at Wagner Bog, which is located ca. 13 km west of Edmonton's city limits.

Technically, Wagner Bog is a mixed mire, with calcareous mud pools, and supporting a rich flora, including brown mosses and some *Sphagnum* (Vitt, 1982:17–22). Thus, *Diplocheila undulata* is hygrophilous, occupying a distinctive habitat. One of 60 species of carabids taken at Wagner Bog, *D. undulata* shares this area with many northern groups of ground beetles, such as *Blethisa, Elaphrus, Loricera, Patrobus, Agonum* (subgenus *Europhilus*), and *Chlaenius.*



CHAR. No.	CHARACTER	CHARACTER STATES AND TAXA			
		zeeland. group	*aegypt.* group	*striatopunctata* group	
				D. minima	Nearctic spp.
7	♀ stylomere 2: setae number		░ Ⓐ		░ Ⓑ
6	Prosternum: apex			▓	▓
5	Tarsomere 5: ventral setae			░	░
4	Left mandible: basal occ. area		▓		
3	Head: s-o setae number		░		
2	El: interneur 1, base		░	░	░
1	El: discal seta	░			

LEGEND

Character State

□ plesiotypic

▓ apotypic, gain

░ apotypic, loss

░ ○ apotypic, independent loss

Fig. 10. Characters and phylogenetic designation and distribution of character states among the species groups of subgenus *Isorembus* Jeannel.

Genus *Dicaelus* Bonelli

Ball (1959:102–103) arranged the 14 species of this genus recognized at that time into three subgenera: *Liodicaelus* Casey; *Paradicaelus* Ball; and *Dicaelus* (*sensu stricto*). Casual examination of additional material of *Paradicaelus* and subgenus *Dicaelus* that I have collected or received for identification has not revealed new taxa or any marked flaws in the classification that I proposed. Lindroth (1969:948) stated that he ". . . had nothing to add on the taxonomy of the genus," and confined his treatment to means of identification and characterization of the species of *Dicaelus* occurring in Canada.

Work in México during the past three decades produced new locality records and

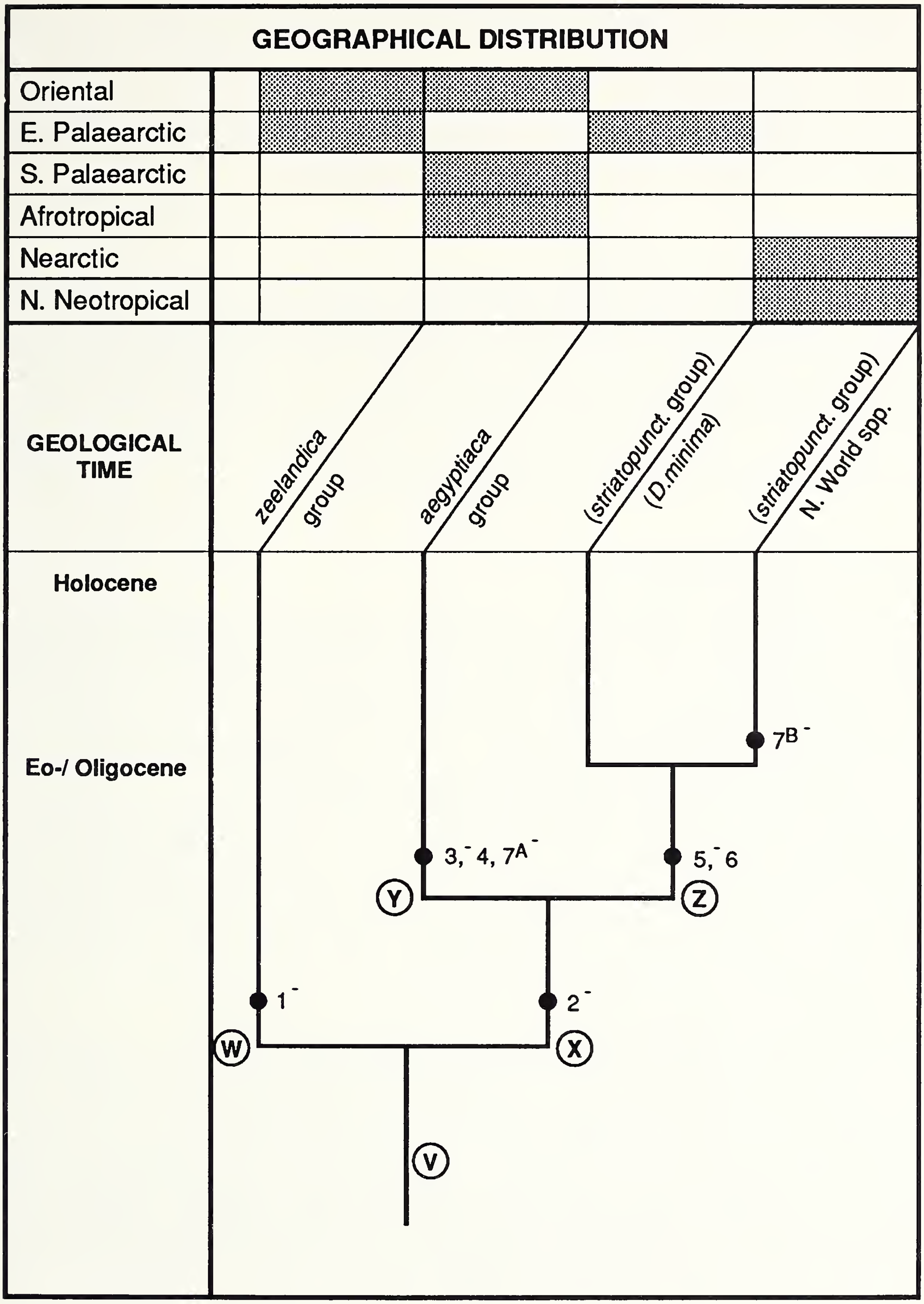


Fig. 11. Reconstructed phylogeny and geographical distribution of the species groups of subgenus *Isorembus* Jeannel.

a new species of *Liodicaelus,* as noted below. Also, the new material has led to modification of some previous decisions about ranking and recognition of taxa.

Because of the taxonomic importance of mandibles and diagnostic value of body proportions, these features are reviewed separately from the following descriptive treatment of taxa. A revised key to the species of *Liodicaelus* is provided, to accommodate the new species and taxonomic changes proposed.

Subgenus *Liodicaelus* Casey

Figure 12 illustrates the habitus of a specimen of *Liodicaelus.* The most important feature for recognition is the nearly smooth elytra, resulting from absence of interneurs (or their reduction to rows of punctures), and flattening of the intervals. The subgenus is circumscribed geographically, being represented: only in the Great Plains States (and southern Alberta) west of the 100th meridian; in the southwest in New Mexico and Arizona; and in the mountains of México southward to the Trans-Volcanic Sierra (Figs. 17 and 18). Habitats occupied are grassland and dry to mesic forest, ranging in altitude from near sea level to more than 2,000 m.

Structural features: mandibles

The mandibles of *Liodicaelus* are average for Dicaelina: retinacular and molar ridges, occlusal grooves, and basal brush absent; ventral grooves each with short microtrichia (Fig. 13F, vmt). The left mandible lacks a terebral tooth, or has a small one; the terebral tooth of the right mandible is prominent.

Mandibles of *D. abbreviatus* Bates (Fig. 13A–F).—Left mandible (Fig. 13A, C, E) with terebral tooth (Fig. 13A) blunt, hardly projected; basal ridge narrow, not widened. Right mandible (Fig. 13B, D, F) average for *Liodicaelus.*

Mandibles of *D. laevipennis* LeConte (Fig. 13G–L).—Left mandible (Fig. 13G, I, K) with terebral ridge (tr) and basal ridge (br) nearly continuous, terebral tooth (tt) very small, hardly projected; basal ridge (br) slightly convex, evenly curved, in ventral aspect hardly extended beyond tips of ventral microtrichia (Fig. 13K). Right mandible (Fig. 13H, J, L) with terebral tooth prominent.

Mandibles of *D. franclemonti,* new species (Fig. 14A–F).—Left mandible (Fig. 14A, C, E) with terebral ridge (tr) and basal ridge (br) in one continuous curve, terebral tooth not evident; basal ridge projected well beyond tips of ventral microtrichia (Fig. 14F, vmt), and thickened as blunt basal tooth (bt). Right mandible (Fig. 14B, D, F) average for *Liodicaelus*: terebral tooth (tt) blunt and somewhat worn.

Comparisons.—These mandibles form a transformation series, from *D. abbreviatus,* with the best developed terebra, including tooth, to *D. franclemonti,* with terebra reduced and basal area enlarged. However, this sequence cannot be the complete basis for a reconstructed phylogeny, as indicated below (see notes about phylogenetic relationships, for *D. franclemonti*).

Structural features: measurements and body proportions

Tables 3–6 provide quantitative data about variation in size (length) and in proportions. For *Liodicaelus,* most such differences are not useful for distinguishing all

Table 3. Variation in Standardized Body Length (mm) among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

Species and population sample	Males			Females		
	N	Range	Mean	N	Range	Mean
D. franclemonti, n. sp.						
Alazanas, Coahuila	1	14.9				
Cerro Potosi, N.L.	1	16.2		1	16.8	
D. suffusus Casey						
1959 data	6	13.4–14.8	14.3	6	12.1–15.5	14.4
Tres Rios (Son.), Chih.	5	11.1–12.2	11.7	3	12.0–12.4	12.3
vic. Col. Garcia, Chih.	7	12.3–13.2	12.8	6	13.1–13.3	13.2
vic. Madera, Chihuahua					12.7–13.6	13.1
vic. Tomochic, Chih.	7	12.9–14.3	13.5	5	12.8–13.9	13.3
D. abbreviatus Bates						
1959 data	1	15.2		3	15.3–15.6	15.4
W Huejuquillo el Alto Jal.	1	14.9				
W El Vergel, Durango	1	14.5				
D. l. laevipennis LeConte						
1959 data (*l. laev.*)	16	16.5–20.0	18.8	9	17.2–19.0	18.4
1959 data (*l. dicael.*)	3	17.0–17.6	17.3	11	17.1–19.1	18.0
Pinos Altos Mtns., N.M.	14	13.4–15.6	14.7	8	14.1–15.7	14.9
Col. Zaragosa, Chih.				1	17.2	
vic. Madera, Chihuahua	1	18.1				
D. l. flohri Bates						
1959 data	2	18.7–20.5	19.6	1	19.2	
Atlacomulco, México	3	16.2–16.8	16.5			
El Temascal, Durango	3	15.3–17.9	16.3	10	16.2–18.7	17.7
D. chermocki Ball						
1959 data				7	17.8–20.0	18.8
Huachuca Mtns., Arizona	2	17.2–18.3	17.8			

individuals of any one species from all other species, but they show trends, which may be employed in analysis of relationships.

Figure 15 is a scattergram on which are plotted values for the ratios PL/PWA and EL/EW. Because I do not have the original data summarized in the 1959 paper (tables 46, 47, 49), I have plotted only the mean values for these samples.

The position on the graph for each species is explained in simple terms, as follows. Points for *Dicaelus suffusus* occupy a central area, indicating pronota not especially narrowed apically, and elytra that are relatively narrow.

The points for both *D. chermocki* and *D. franclemonti* are low and more or less central on the graph, indicating broad pronota apically (to accommodate an enlarged head—cf. Fig. 12), and elytra of average proportions.

The points for *D. abbreviatus* occupy the left side of the graph, indicating short, broad elytra and pronotal apices that vary from broad to relatively narrow.

Table 4. Variation in values for the ratio PW/HW among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

	Males			Females		
Species and population sample	N	Range	Mean	N	Range	Mean
D. franclemonti, n. sp.						
Alazanas, Coahuila	1	1.67				
Cerro Potosi, N.L.	1	1.64		1	1.63	
D. suffusus Casey						
1959 data	6	1.75–2.00	1.87	6	1.73–1.84	1.78
Tres Rios (Son.), Chih.	5	1.72–1.90	1.79	3	1.66–1.77	1.70
vic. Col. Garcia, Chih.	7	1.70–1.87	1.77	6	1.80–1.88	1.84
vic. Madera, Chihuahua				3	1.84–1.88	1.85
vic. Tomochic, Chih.	7	1.78–1.91	1.84	5	1.86–1.88	1.87
D. abbreviatus Bates						
1959 data	1	2.10		3	1.97–2.06	2.01
W Huejuquillo el Alto Jal.	1	1.94				
W El Vergel, Durango	1	2.06				
D. l. laevipennis LeConte						
1959 data (*l. laev.*)	16	1.99–2.20	2.10	9	1.94–2.20	2.09
1959 data (*l. dicael.*)	3	2.00–2.09	2.04	11	1.92–2.10	2.02
Pinos Altos Mtns., N.M.	14	1.86–2.09	1.97	8	1.88–2.03	1.97
Col. Zaragosa, Chih.				1	1.90	
vic. Madera, Chihuahua	1	2.07				
D. l. flohri Bates						
1959 data	2	2.06		1	2.12	
Atlacomulco, México	3	1.95–2.00	1.98			
El Temascal, Durango	3	2.03–2.17	2.11	10	1.98–2.20	2.08
D. chermocki Ball						
1959 data				7	1.53–1.71	1.62
Huachuca Mtns., Arizona	2	1.56–1.68	1.62			

The points for *D. laevipennis* are relatively high on the graph, indicating average elytral proportions but narrowed pronotal apices.

Overall, something of a radial pattern is indicated, with the center represented by *D. suffusus,* and outliers in different directions being: *D. chermocki* and *D. franclemonti*; *D. abbreviatus*; and *D. laevipennis.* No doubt, this pattern will be of use in phylogenetic analysis, although I doubt that the similarity exhibited by *D. chermocki* and *D. franclemonti* indicate close relationship of these taxa.

KEY TO SPECIES AND SUBSPECIES OF SUBGENUS *LIODICAELUS* CASEY (MODIFIED FROM BALL, 1959:169)

1. Elytral interval 7 not carinate. Elytra relatively short and broad, EL/EW 1.30–1.36 .... *D. abbreviatus* Bates

Table 5. Variation in values for the ratio PL/PWA among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

	Males			Females		
Species and population sample	N	Range	Mean	N	Range	Mean
D. franclemonti, n. sp.						
Alazanas, Coahuila	1	1.00				
Cerro Potosi, N.L.	1	0.98		1	0.95	
D. suffusus Casey						
1959 data	6	1.19–1.23	1.20	6	1.10–1.21	1.16
Tres Rios (Son.), Chih.	5	1.12–1.20	1.16	3	1.09–1.15	1.13
vic. Col. Garcia, Chih.	7	1.08–1.18	1.14	6	1.11–1.17	1.14
vic. Madera, Chihuahua				3	1.08–1.14	1.11
vic. Tomochic, Chih.	7	1.10–1.18	1.15	5	1.08–1.14	1.11
D. abbreviatus Bates						
1959 data	1	1.20		3	1.11–1.22	1.17
W Huejuquillo el Alto Jal.	1	1.07				
W El Vergel, Durango	1	1.24				
D. l. laevipennis LeConte						
1959 data (*l. laev.*)	16	1.15–1.34	1.23	9	1.18–1.26	1.21
1959 data (*l. dicael.*)	3	1.25–1.28	1.26	11	1.15–1.22	1.18
Pinos Altos Mtns., N.M.	14	1.18–1.29	1.24	8	1.15–1.30	1.21
Col. Zaragosa, Chih.				1	1.15	
vic. Madera, Chihuahua	1	1.25				
D. l. flohri Bates						
1959 data	2	1.24–1.30	1.27	1	1.24	
Atlacomulco, México	3	1.16–1.28	1.23			
El Temascal, Durango	3	1.14–1.21	1.17	10	1.13–1.21	1.17
D. chermocki Ball						
1959 data				7	0.98–1.05	1.00
Huachuca Mtns., Arizona	2	1.02–1.08	1.05			

1′. Elytral interval 7 carinate near humerus (cf. Fig. 12). Elytra of most specimens longer and more slender, EL/EW 1.34–1.52 2

2(1′). Head relatively large, PW/HW 1.53–1.71, and apical margin of pronotum relatively broad, PL/PWA 0.95–1.08 (cf. Fig. 12) 3

2′. Head smaller, PW/HW 1.66–2.17 and apical margin of pronotum relatively narrow, PL/PWA 1.08–1.34 4

3(2). Elytral interneurs each a row of clearly impressed punctures. Range—mountains of southwestern Arizona .... *D. chermocki* Ball

3′. Elytral interneurs impunctate, each a very shallow indistinct stria, or elytra smooth, without indication of interneurs (Fig. 12). Range—mountains of Sierra Madre Oriental, México .... *D. franclemonti,* new species

4(2′). Size smaller, Standardized Body Length less than 15 mm (most specimens 12–14 mm). Pronotum anteriorly relatively broader (PL/PWA 1.23 or less) *D. suffusus* Casey

4′. Size larger, SBL 13 mm or more (most specimens 15–18 mm). Pronotum anteriorly relatively narrower (most specimens with PL/PWA more than 1.20; cf. Fig. 15) ... 5

Table 6. Variation in values for the ratio EL/EW among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

	Males			Females		
Species and population sample	N	Range	Mean	N	Range	Mean
D. franclemonti, n. sp.						
Alazanas, Coahuila	1	1.44				
Cerro Potosi, N.L.	1	1.46		1	1.47	
D. suffusus Casey						
1959 data	6	1.46–1.52	1.50	6	1.44–1.55	1.48
Tres Rios (Son.), Chih.	5	1.41–1.50	1.45	3	1.41	1.41
vic. Col. Garcia, Chih.	7	1.40–1.50	1.46	6	1.36–1.46	1.40
vic. Madera, Chihuahua				3	1.38–1.43	1.40
vic. Tomochic, Chih.	7	1.36–1.42		5	1.33–1.41	1.38
D. abbreviatus Bates						
1959 data	1	1.33		3	1.30–1.36	1.32
W Huejuquillo el Alto Jal.	1	1.29				
W El Vergel, Durango	1	1.34				
D. l. laevipennis LeConte						
1959 data (*l. laev.*)	16	1.42–1.55	1.48	9	1.40–1.50	1.44
1959 data (*l. dicael.*)	3	1.45–1.48	1.46	11	1.40–1.54	1.44
Pinos Altos Mtns., N.M.	14	1.34–1.46	1.39	8	1.34–1.44	1.39
Col. Zaragosa, Chih.				1	1.39	
vic. Madera, Chihuahua	1	1.42				
D. l. flohri Bates						
1959 data	2	1.50–1.52	1.51	1	1.46	
Atlacomulco, México	3	1.40–1.43	1.42			
El Temascal, Durango	3	1.35–1.37	1.36	10	1.31–1.40	1.35
D. chermocki Ball						
1959 data				7	1.45–1.52	1.48
Huachuca Mtns., Arizona	2	1.34–1.41	1.38			

5(4′). Elytra with each interneur indicated by row of distinct punctures. Range—Chihuahua and Sonora, north to southern Alberta .... *D. l. laevipennis* LeConte

5′. Elytra with interneurs 1–3 each indicated by row of distinct punctures; interneurs 4–8 either not evident, or punctures of interneurs 4–6 small, indistinct. Range—southern Durango, in the Sierra Madre Occidental, south to the state of México, in the Trans-Volcanic Sierra .... *D. laevipennis flohri* Bates

THE SPECIES OF *LIODICAELUS*: NOTES, DESCRIPTIONS, AND DISTRIBUTION RECORDS

Dicaelus (Liodicaelus) franclemonti, new species

Type material.—HOLOTYPE male, labelled: "MEX. Nuevo Leon/ Cerro de Potosi/ 12.4 mi. n.w./ Galeana, 7200′/ e. slope/ X.17.65"; "George E. Ball/ D. R. Whitehead/ collectors" (USNM). ALLOTYPE female, labelled same as holotype

Fig. 12. Photograph of allotype of *Dicaelus* (*Liodicaelus*) *franclemonti,* new species, illustrating habitus. SBL = 16.8 mm.

(USNM). One additional PARATYPE, labelled: "MEX. Coahuila/ 21 km. e. San/ Antonio de las Alazanas 2550 m/ oak-madroño/ fir forest/ July 25, 1975"; "MEX EXP. 1975/ G. E. Ball &/ H. E. Frania/ collectors" (UASM).

Type locality.—México, state of Nuevo Leon, the mountain Cerro Potosi, northwest of Galeana.

Derivation of specific epithet.—Based on the surname of John G. Franclemont; this species is named in his honor, to commemorate on his 80th birthday his dedication to entomology and to the education of systematic entomologists.

Recognition.—Adults of this species share the following unique combination of character states: integument black, elytra virtually smooth, with traces only of smooth, impunctate interneurs (Fig. 12); head and apical margin of pronotum relatively broad. Males have a dorso-preapical projection on the median lobe, and the internal sac has four spines, only.

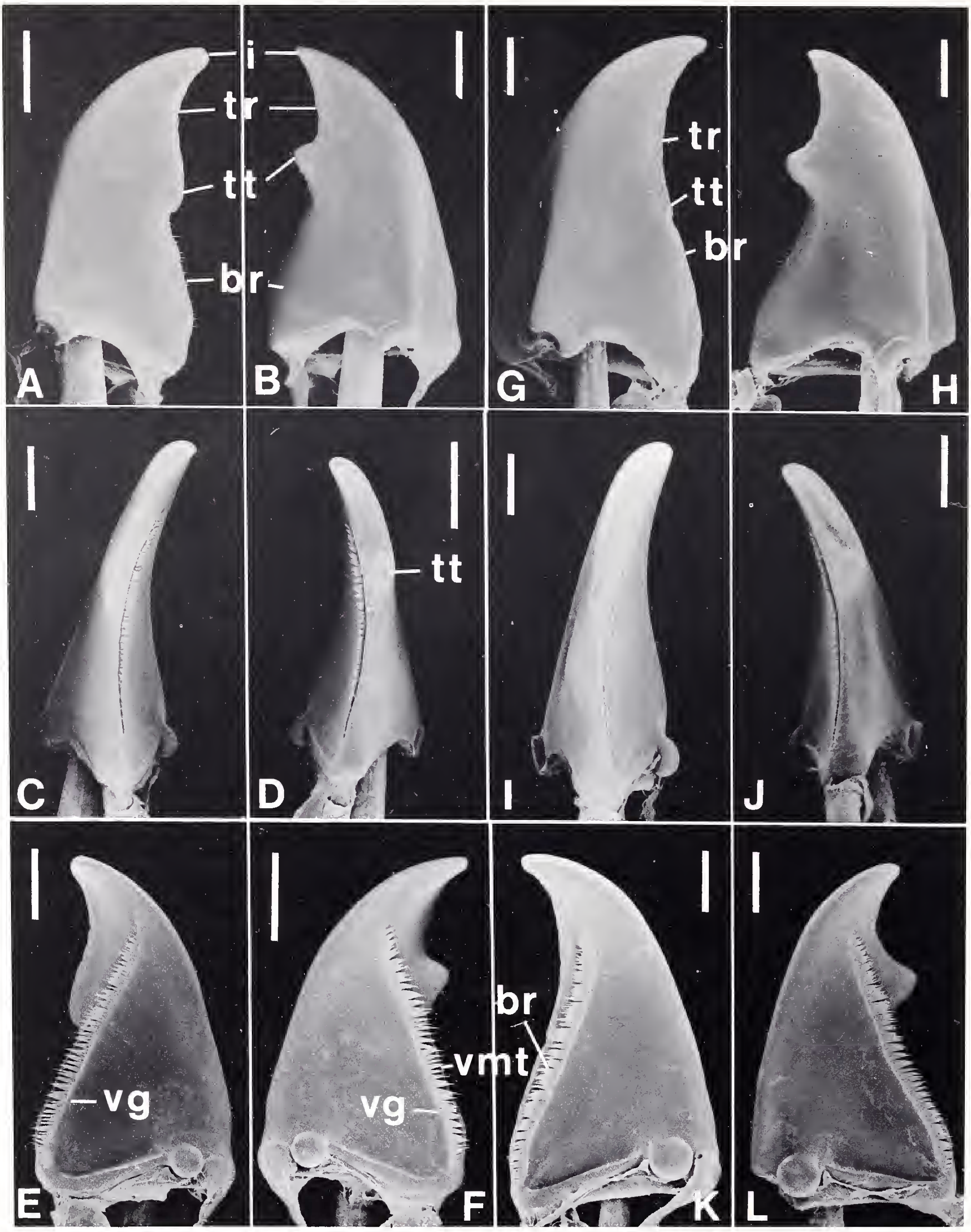


Fig. 13A–L. SEM photographs of the mandibles of *Dicaelus abbreviatus* Bates and of *D. laevipennis* LeConte. A–F, *D. abbreviatus*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *D. laevipennis*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; i, incisor; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 400 μm.

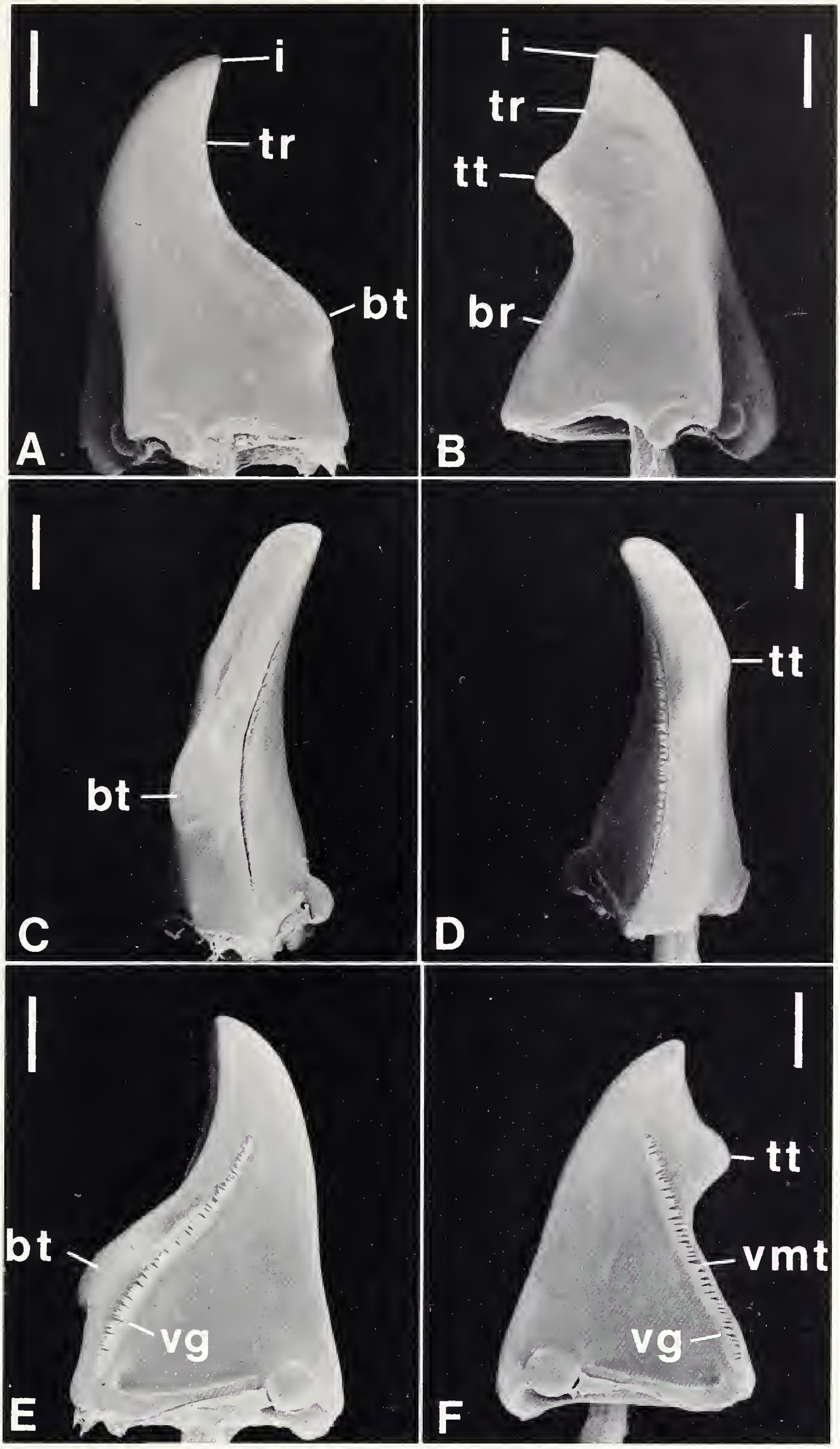


Fig. 14A–F. SEM photographs of the mandibles of *Dicaelus franclemonti,* new species: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; bt, basal tooth; i, incisor; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 400 μm.

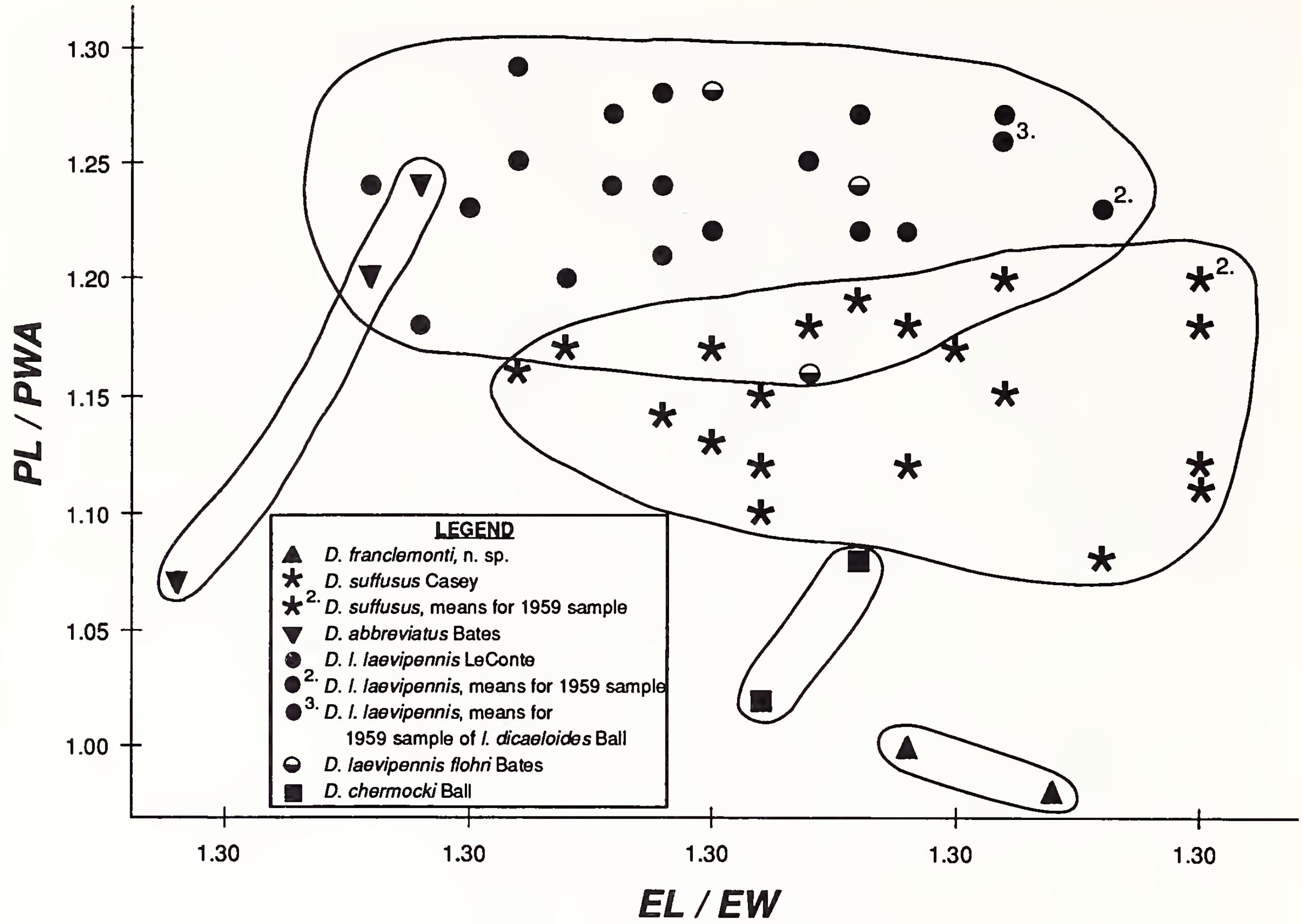


Fig. 15. Scattergram for ratios PL/PWA and EL/EW for the species of subgenus *Liodicaelus* Casey.

In body proportions, adults of *D. franclemonti* are most like those of *D. chermocki.* Smooth elytra, with hardly distinguishable impunctate elytral interneurs, distinguish *D. franclemonti.* Reduced elytral interneurs are characteristic of *D. laevipennis flohri* and *D. abbreviatus,* but adults of these species have smaller heads and prothoraces with narrower anterior margins.

Description.—With the character states of subgenus *Liodicaelus.* Habitus as in Figure 12. Data about Standardized Body Length, elytral width, and ratios PW/HW, PL/PWA, and EL/EW are presented in Tables 3–6. Integument black generally, with palpomeres dark rufo-piceous. Microsculpture of body generally isodiametric, sculpticells small and on dorsal surface slightly convex. Dorsal surface with soft silky luster. Head and pronotum with surface features as for other species of *Liodicaelus* (cf. Ball, 1959:176). Mandibles as in Fig. 14A–F. Elytra each with interval 7 toward humerus carinate, each carina ca. 0.25 length of elytron, and broader basally than in the other carinate species of *Liodicaelus*; otherwise, dorsal surface virtually smooth, interneurs indicated by indistinct lines. Sternum VII with apical setae 4–5 in males, and 2–4 in females.

Male genitalia. As in Figure 16A, B. Median lobe in left lateral aspect with basal part bent obliquely quite markedly; shaft with ventral surface straight, apex acute (Fig. 16A); in ventral aspect (Fig. 16B), apical portion straight, not curved to right; apex obtusely and evenly rounded, not notched shallowly. Internal sac with four large spines, only. Parameres average (cf. Ball, 1959, fig. 112c, d).

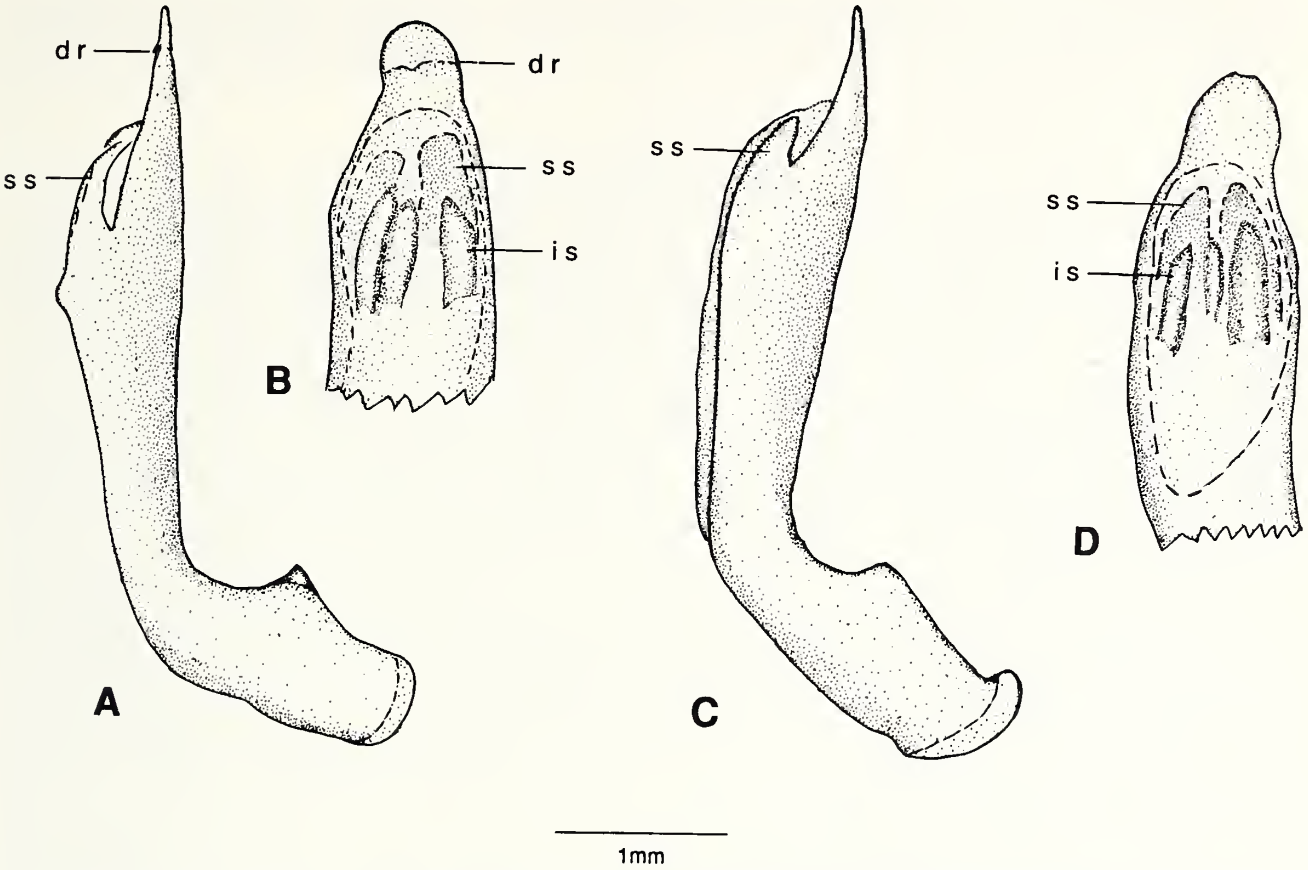


Fig. 16A–D. Line drawings of male genitalia of species of *Liodicaelus* Casey. A–B, median lobe of *D. franclemonti,* new species: A, median lobe, left lateral aspects; B, median lobe, apical portion, ventral aspect, showing armature of internal sac. C–D, median lobe of *D. chermocki* Ball: C, median lobe, left lateral aspect; and D, median lobe, apical portion, ventral aspect, showing armature of internal sac. Legend: dr, dorsal ridge; is, spine of internal sac; and ss, sclerotized strip.

Habitat.—On Cerro Potosi, the holotype and allotype of *D. franclemonti* were collected at an altitude of 2,200 m, in a damp stream bed, under stones, with a covering of oak and pine litter. The paratype male, collected near San Antonio de las Alazanas at 2,550 m, was under a log, in a dry conifer-oak forest. Therefore, I infer that *D. franclemonti* is an inhabitant of the mesic to dry montane forests that are characteristic of the upper slopes of the northern sierras, in México.

Geographical distribution (Fig. 17).—This species is known from the northern part of the Mexican Sierra Madre Oriental, only.

Chorological affinities.—*D. franclemonti* is isolated geographically from all other known species of *Dicaelus.* The other species of *Liodicaelus* occur to the north, in Texas (Fig. 18), or westward, in the Sierra Madre Occidental, or southward, in the Trans-Volcanic Sierra.

Phylogenetic relationships.—Based on features of the male genitalia, *D. franclemonti* is postulated to be the most primitive extant member of *Liodicaelus,* and to be the adelphotaxon of the other species of this subgenus. In turn, these species comprise a monophyletic assemblage, based on absence of the dorsal preapical ridge of the male median lobe, which is postulated to be a loss. This latter species assemblage is not analyzed further now, though the sequence of species used in the text and summarized here indicates how I believe they are related, based on details of mandibular structure and body form: *D. suffusus-abbreviatus-laevipennis-chermocki.*

Dicaelus suffusus Casey

This species was known previously from "the Sierra Madre Mountains of Chihuahua, Mexico" (type area) and from the Chiricahua Mountains of Arizona (Ball, 1959:177–178). Additional material documents more fully the range of *D. suffusus.*

Type locality.—Here restricted to the vicinity of Madera, Chihuahua, México.

Material examined.—Forty four specimens, from the following localities (Fig. 17).

U.S.A. ARIZONA. **Cochise County**. Female, Chiricahua Mts.: X.4.1937 Bryant Lot 65 (CASC). Male, Pinery Canyon, VII.9.1956; H. & A. Howden (CNCI). 2 females, Rustlers Park, 2,500 m, VII.14.1952, H. B. Leech, J. W. Green (CASC). 3 females, Rustlers Park, 2,560 m, VII.26–27.1979; A. Smetana (CNCI).

MÉXICO. CHIHUAHUA. 4 males, 4.8 km S Colonia Garcia, pine-oak-madroño forest, 2,130 m, VIII.4&28.1980; G. E. Ball, D. Shpeley, & W. Fraga (UASM). Male, 4 females, Colonia Garcia, meadow & adj. pine-oak forest, 2,130 m, VIII.5&28.1980; Ball, Shpeley & Fraga (UASM). 24 km E Creel, meadow, 2,200 m, VIII.24.1980; Ball, Shpeley & Fraga (UASM). Male, 2 females, 1.3 km NE Ejido Zaragosa, pine-oak forest, 1,850 m, VII.22.1979; J. S. Ashe, Ball & Shpeley (UASM). Male, ca. 14.8 km. E Ejido Zaragosa, pine-oak-aspen forest, 2,120 m, VIII.3.1980; Ball, Shpeley & Fraga (UASM). 2 females, 8.8 km W Madera, 2,270 m, VIII.30.1974; Ball & H. E. Frania (UASM). One female, 10.5 km W Madera, 2,320 m, pine-oak forest, 2,320 m, VIII.29–30.1974 (UASM). 3 males, 28.3 km E Mesa de Tres Rios (Sonora), pine-oak forest, 2,160 m, VII.7.1983; Frania, R. Jaagumagi & Shpeley (UASM). 7 males, five females, 25.4 km N Tomochic, pine-oak forest, 2,250 m, VIII.25.1980; Ball, Shpeley & Fraga (UASM).

SONORA. Male, female, Sierra Huachinera, 32–34 km NE Nacori Chico, pine-oak forest, 1,950 m, VIII.6–7.1982; G. E. & K. E. Ball & S. McCleve (UASM). Female, Sierra Huachinera, 56 km NE Nacori Chico, pine-oak forest, 2,330 m, VIII.8.1982; Ball, Ball & McCleve (UASM). Male, female, 18.5 km E Mesa de Tres Rios, pine-oak forest, 2,440 m, VII.7.1983; Frania, Jaagumagi & Shpeley (UASM).

Dicaelus abbreviatus Bates

Described originally as a variety of *D. laevipennis* LeConte (Bates, 1891:239), from Refugio, Durango, this taxon is ranked as a distinct species on the basis of consistency of its diagnostic features (including mandibles, Fig. 13A–F) over its fairly extensive geographical range, and though it has not been collected in the exact same places as any other taxa of *Liodicaelus,* its range is partially overlapped by the range of *D. laevipennis flohri* Bates (Fig. 17). Thus, *D. abbreviatus* maintains its distinctiveness in parapatry, if not sympatry.

Material examined.—Four specimens from the following localities (Fig. 17).

MÉXICO. DURANGO. Female, 68 km W Durango, 2,438 m, VI.18.1971 (CNCI). Male, 4.8 km E El Salto, VI.21.1964 (CNCI). Male, 72.9 km W Huajuquillo el Alto (Jalisco), rd. to Jesus Maria (Nayarit), 2,540 m, VII.28.1985, H. E. Frania, D. Shpeley (UASM).

SINALOA. Male, 199.4 km W El Vergel (Chihuahua), 2,400 m, pine-oak-madroño litter, VII.16.1983 (UASM).

Dicaelus laevipennis LeConte

Ball (1959:169–175) recognized four geographical races of this species: *D. l. laevipennis*; *D. l. dicaeloides* Ball; *D. l. abbreviatus,* and *D. l. flohri* Bates. See above for taxonomic treatment of *D. abbreviatus.* The subspecies *D. l. dicaeloides* (type locality Cloudcroft, Otero Co., New Mexico [Ball, 1959:172]) was based on primarily the mandibular features of the type material. Re-examination of part of the type series satisfies me that the differences between the mandibles of this named form and nominotypical *D. laevipennis* is the result of wear, and thus without taxonomic significance. Accordingly, these two forms are regarded as consubspecific, and the name *D. l. dicaeloides* is a junior subjective synonym of *D. l. laevipennis* (**new synonymy**).

The gap in geographical range between *D. l. laevipennis* and *D. l. flohri* (Figs. 17 and 18) is substantial, but I think it represents a collecting artifact, only.

Material examined.—Forty five specimens of *D. l. laevipennis* and 13 specimens of *D. l. flohri,* from the following localities.

D. l. laevipennis LeConte (Fig. 18)

U.S.A. ARIZONA. **Apache County.** Male, St. Michael's, VI.8.1971; D. Brzoska (SEMC). **Cochise Co**. Male, Hwy. 666, 2.6 km SE Interstate Hwy 10, VII.29.1985; D. Brzoska (SEMC). **Coconino Co**. Female, Hwy. 64, S Grand Canyon Nat. Park, VIII.31.1967; P. S. Bartholemew (CASC). **Mojave Co**. Male, Peach Springs, VIII.22.1967; S. McCleve (SMCC). **Navajo Co**. Male, Show Low, IX.5.1967, Bartholemew (CASC). **County not determined.** Female, White Mts; D. K. Duncan (CASC).

COLORADO. **Fremont Co**. Female, Phantom Canyon. IX.13.1964; B. H. Banta (CASC). **Kiowa Co**. Female, Arlington, VIII.16.1947; H. G. Rodeck (CASC). **Routt Co**. Male, Steamboat Springs, 2,073 m, VI.15.1945; Bryant Lot (CASC). **Teller Co**. Male, Manitou, VIII.21.1958; A. C. Cole (CNCI).

MONTANA. **Gallatin Co**. Male, Bozeman, V.18.1926 (CNCI).

NEW MEXICO. **Bernalillo Co**. Female, Albuquerque, IX.19.1965; P. S. Bartholemew (CASC). **Grant Co**. Male, Hwy. 61, 51.8 km E Beaverhead, 2,469 m, IX.13.1967; Ball, T. L. Erwin & R. E. Leech (UASM). 5 males, 4 females, 16.1 km NE Pinos Altos, IX.12.1967; Ball, Erwin, & Leech (UASM). Male, 2 females, Hwy. 25, 46.8 km NE Pinos Altos, 1,920 m, IX.13.1967; Ball, Erwin & Leech (UASM). **Hidalgo Co**. Female, 3.2 km NE Rodeo, VII.30.1963; A. Rathke (CNCI). **Otero Co**. Female, Lincoln Nat. Forest, 3.2 km NE Cloudcroft, 2,530 m, VII.13.1969; A. Smetana (CNCI). **Rio Arriba Co**. Male, Capulin Mountain, IV.21.1951; Bryant Lot 5 (CASC). **Socorro Co**. Male, Magdalena Mountains, 32.2 km S Magdalena, 2,316 m, VIII.19.1969; G. E. & K. E. Ball (UASM).

SOUTH DAKOTA. **Fall River Co**. Female, Hot Springs, IX.19.1906; E. Van Sant (CASC).

MÉXICO. CHIHUAHUA. Female, 4.5–6.5 km N Ejido Zaragosa, dry pine-oak forest, under logs, 2,000 m, VII.23.1979; J. S. Ashe, G. E. Ball & D. Shpeley (UASM).

Male, Hwy. 16, 21 km SE Madera, 2,100 m, grassland, IX.1.1974; Frania & Ball (UASM).

D. l. flohri Bates (Fig. 17)

MÉXICO. DURANGO. 2 males, 11 females, Reserva de la Biosfera La Michilia, El Temascal meadow, Potrillo La Laguna, 5 km S Trampa Las Casas, VIII.19.1980; Ball, Shpeley & Fraga (UASM).

MÉXICO (state of). 3 males, 6.4 km N Atlacomulco, 2,652 m, VIII.15.1974; C. W. & L. O'Brien & B. Marshall (UASM).

ZACATECAS. Male, 1.9 km SW Villa de los . . .[?], 2,350 m, VIII.1966; D. Thompson (UASM).

Dicaelus chermocki Ball

The original description of this species was based on seven females, males being unknown at that time (Ball, 1959:177). Subsequently, males were collected, and the genitalia (Fig. 16C–D) were found to be identical to those of *D. laevipennis* and the other taxa recognized in 1959.

Dicaelus chermocki is known only from the Huachuca and Chiricahua Mountains of southeastern Arizona (Fig. 17). The few additional specimens collected since 1959 confirm the distinctness of the species, and extend its altitudinal range downward from 2,286 m in the Huachuca Mountains to 1,402 m, at Sierra Vista, which is located at the base of that mountain range.

Material examined.—Three specimens from the following localities (Fig. 17).

U.S.A. ARIZONA. **Cochise County**. Huachuca Mts.: male, Carr Cn., fir-pine forest, 2,150 m, VII.23.1976; Ball, J. M. Campbell & P. M. Hammond (UASM); male, Ramsey Cn., III.22.1956, F. G. Werner, G. D. Butler (UASM). Female, Sierra Vista, VII.29.1963, R. F. Sternitsky (CNCI).

Notes about geographical history of *Liodicaelus*

Ball (1959:185) noted the general association of *Liodicaelus* with the Madro-Tertiary flora, but did not attempt a biogeographic analysis because the species were known from few localities, and thus their ranges were understood inadequately. The additional locality data presented above improves knowledge of the species ranges, and the new species provides a new perspective. Furthermore, Liebherr (1991a:137–150, 1991b) provided a valuable general vicariance-based model and geological time-frame for interpretation of distribution patterns of montane taxa in México and southwestern United States.

Briefly stated, Liebherr's analysis explains the geographical history of vicariously distributed taxa in terms of a sequence of range barriers operating in sequence:

1. isolation of the Trans-Volcanic Sierra (M) from the northern Sierra Madre Oriental (A′) + northern Sierra Madre Occidental (A + B) + southeastern Arizona (A″) + the rest of North America (N.A.);
2. isolation of A′ from (A + B) + A″ + N.A.;
3. isolation of (A + B) from A″ + N.A.;
4. isolation of A″ from N.A.

Table 7. Distribution pattern of the taxa of subgenus *Liodicaelus* Casey, in terms of vicariance areas of Liebherr (1991b).

Taxon	Areas[1]				
	M	A′	A + B	A″	N.A.
franclemonti, n. sp.		X̲[2]			
suffusus Casey			X[3]	X	
abbreviatus Bates			X̲		
l. laevipennis LeC.			X[3]	X	X
l. flohri Bates	X		X[4]		
chermocki Ball				X̲	

[1] Areas: M, Trans-Volcanic Sierra; A′, northern Sierra Madre Oriental; A + B, northern Sierra Madre Occidental; A″, southwestern U.S.A. (see text for details); and N.A., North America, north, west and east of A″.

[2] X̲, a species known from a single area, only.

[3] In the northern part of A + B, only.

[4] In the southernmost part, only.

The time span inferred for this sequence of events is ca. 12 million years, beginning in Late Miocene.

The species of *Liodicaelus* are placed, in Table 7, in the context of Liebherr's analysis. Four points emerge: first, each area has a taxon that is endemic or nearly endemic to it; second, although *D. abbreviatus* and *D. suffusus* are in the Sierra Madre Occidental, their ranges seem not to overlap; third, the northern Sierra Madre Oriental has in it a taxon that is postulated to be the most primitive member of the subgenus, and to be the adelphotaxon of the remaining taxa; and fourth, ignoring the gap that separates *D. l. laevipennis* from *D. l. flohri,* the total range of *D. laevipennis* bridges all of the vicariance areas, except for the Sierra Madre Oriental. Points one and two, regarding endemism, indicate that differentiation in *Liodicaelus* has been influenced by the same sets of barriers and conditions that have influenced differentiation of many other taxa in northern México. To this extent, the data for *Liodicaelus* fit the general geographical pattern described by Liebherr. However, concerning the phylogenetic pattern, the fit of the taxa of *Liodicaelus* is inexact (point three). One would expect the most primitive adelphotaxon, postulated to be *D. franclemonti,* to be in the Trans-Volcanic Sierra and perhaps the southern part of the Sierra Madre Occidental—i.e., in the area occupied by *D. l. flohri.* This element of discordance suggests that the sequence of vicariance events for *Liodicaelus* was different from the sequence indicated by Liebherr's interpretation of the data that he used.

Because of the extensive range overlap of *D. laevipennis* with the ranges of the other species, the distribution data suggest also that the barriers in the west, between the Trans-Volcanic Sierra, the northern Sierra Madre Occidental and the Rocky Mountain outliers in Arizona are more readily penetrated than the barrier between the Sierra Madre Oriental and the Sierra Madre Occidental. Indeed, in spite of the postulated Pleistocene connections between the eastern and western montane biotas, there is evidence to the contrary—for example the *Carabus forreri* (S. M. Occidental-

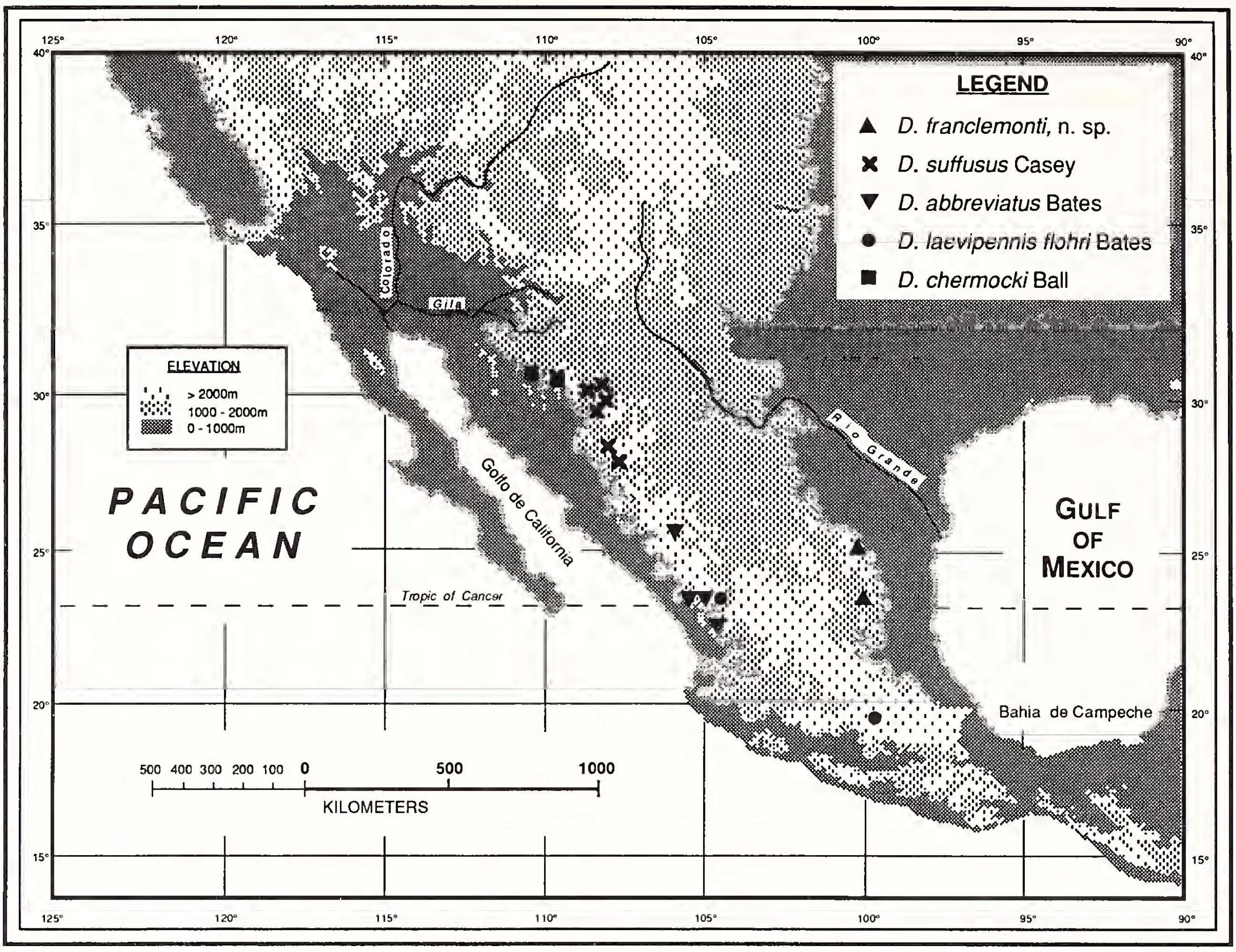


Fig. 17. Geographical distribution of the taxa of subgenus *Liodicaelus* Casey (except *D. l. laevipennis*) in México and southwestern United States.

southern Arizona)—*C. hendrichsi* (S. M. Oriental) species pair, absence of *Scaphinotus* from the Sierra Madre Oriental, and primitive species of subgenus *Progaleritina* Jeannel and of *Pasimachus* Bonelli isolated in the eastern Mexican forests from their western counterparts.

Nonetheless, I am disinclined to believe that a single general sequential pattern of taxon/area relationships exists, just as I am inclined to believe that barriers between adjacent mountain systems are permeable to semi-permeable as frequently as they are impermeable to taxa on either side of them. Probably different taxa, even with flightless adults and though they occupy similar habitats, differ in their tolerances to environmental conditions. Thus, what is an impermeable barrier to one taxon is crossed with difficulty by some others, and with ease by still others. Given a geographical situation such as one encounters in northern México and southwestern United States, one can expect to find a general concordance of taxon/area patterns, but not one that is precise.

Nonetheless, I am intrigued by and appreciate the elegance of Liebherr's analysis that is based on principles of cladistic biogeography. As well, I concede that a cladistic analysis of the taxa of *Liodicaelus* may, after all, support the pattern that he has postulated.

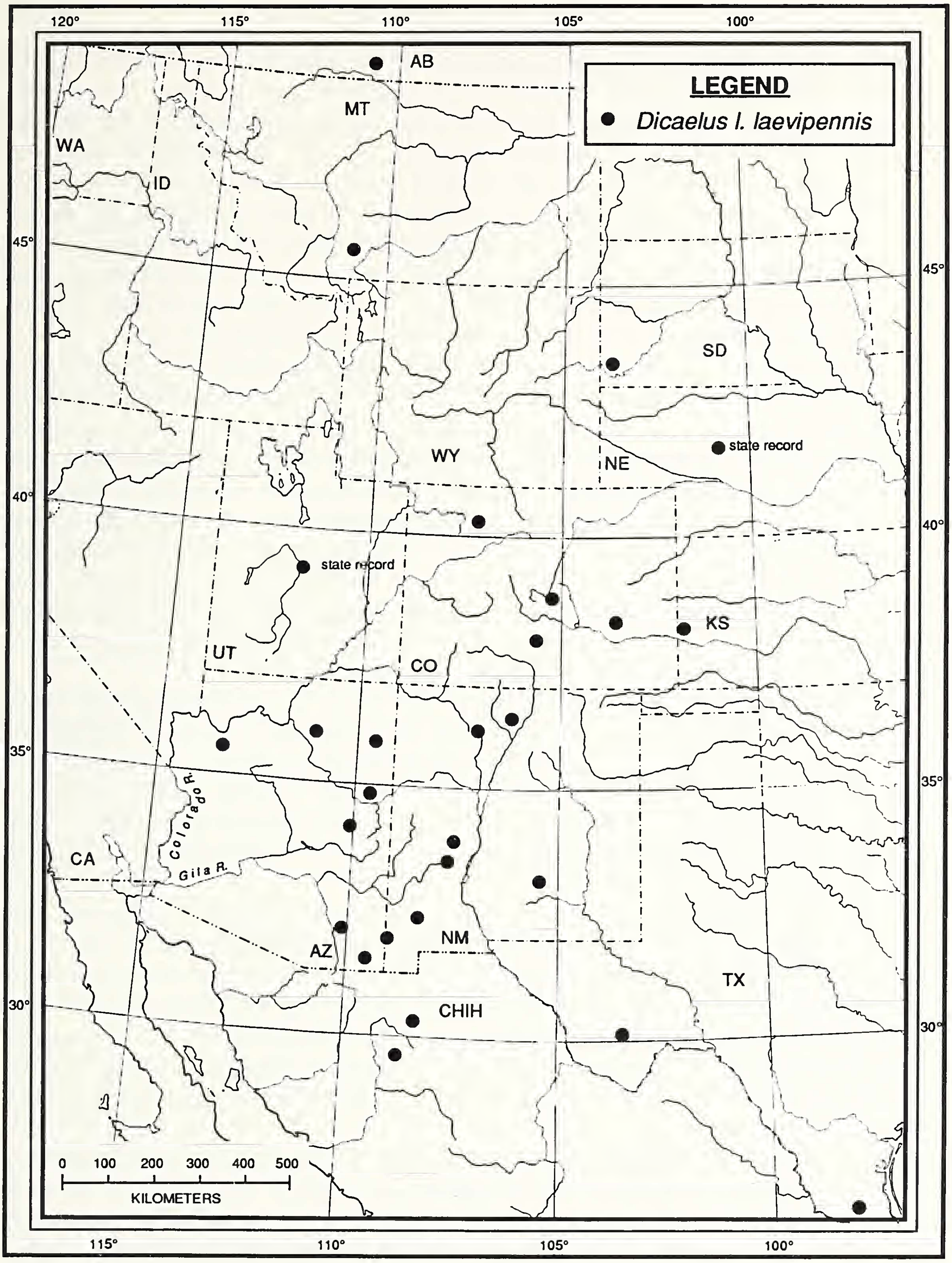


Fig. 18. Geographical distribution of *Dicaelus l. laevipennis* LeConte.

Genus *Badister* Clairville

Specimens of *Badister* are rare in collections, primarily because they are small, rather inconspicuous, and most of them live in habitats so wet that they are avoided by most collectors. Nonetheless, I have seen many specimens during the past years, and identifying them has given sufficient opportunity to test the delimitation of taxa recognized in my treatment of the genus (Ball, 1959:191–241). Further, Lindroth (1969:955–967) confirmed implicitly my species-level treatment, though he differed with some of my interpretations of supraspecific relationships and classification. Such differences require comment, and some new information has become available that seems worthy of reporting, as detailed below. Also, I take this opportunity to offer a more detailed treatment of microsculpture for several species.

In classifying the North American species of *Badister* (Ball, 1959:190–191), I recognized three subgenera: *Badister* (*sensu stricto*), *Trimorphus* Stephens and *Baudia* Ragusa. These taxa were characterized primarily by details of mandibular structure and tarsal setation: right mandible with dorsal surface notched, and tarsomere 5 with a row of setae on each ventro-lateral margin (*Badister*); right mandible with dorsal surface notched, tarsomere 5 with ventro-lateral margins asetose (*Trimorphus*); and left mandible notched, tarsomere 5 with ventro-lateral margins asetose (*Baudia*). For classification of the species of subgenus *Badister,* I used the ranks of complex and group, as follows: *bipustulatus* complex—*bipustulatus* group (5 species), and *neopulchellus* group (5 species); *pulchellus* complex—*pulchellus* group (including *B. pulchellus* LeConte, only), and *elegans* group (5 species).

Lindroth (1969:955–967), who preferred not to use a formal subgeneric rank, recognized four species groups: *notatus* group, including only *B. notatus* Haldeman, that I included in subgenus *Badister*; the *pulchellus* group, for the other species of subgenus *Badister*; the *transversus* group, for the single Nearctic species (*B. transversus*) that I included in subgenus *Trimorphus*; and the *reflexus* group for most of the species of *Baudia.* He did not recognize formally any ranks between group and subgenus.

Lindroth's assignment of *B. notatus* to a group equal in rank to a subgenus, was based on the several striking features that are unique in the genus, such as reduction of microsculpture, reduction of wings and loss of ability to fly, and development of convex elytral intervals. However, *B. notatus* exhibits the derived feature of large spines in the internal sac, which is characteristic of the *elegans* group. Thus, Lindroth classified *B. notatus* on the basis of phenetic distinctness, whereas I classified it on the basis of what is interpreted to be a shared derived feature; in other words, I used phylogenetic principles.

Lindroth (1969:962) accepted my judgement that *B. transversus* was isolated from the other subgenera of *Badister,* but he did not agree that it was related to the type species of *Trimorphus* (*B. sodalis* Duftschmid), although both species are similar in mandibular notching, and both have tarsomere 5 asetose. Noting the similarity between members of *Baudia* and of *B. transversus* in reduced tarsal setation and transverse pronotal microsculpture, Lindroth (1969:956) implied that the latter species was a *Baudia* derivative, whose mandibles exhibited reverse asymmetry (i.e., the right mandible notched, rather than the left). He concluded the argument by suggesting that the difference in which one of the mandibles of a pair was notched was the result

Table 8. Notching of mandibles among West Indian population samples of *Badister reflexus* LeConte.

Island(s)	Notched mandible		Total
	Left	Right	
Bahamas	4	0	4
Cuba	4	2	6
Jamaica	2	0	2
Cayman Islands	1	10	11
Hispaniola			
Haiti	1	4	5
Dom. Republic	3	3	6
Total	15	19	34

of a very simple genetic difference. If this is so, mandibular notching cannot be regarded as a reliable character for grouping the species of *Badister.* This matter is addressed below, following description of the clypeus, labrum and mandibles of *Badister.*

Labrum, clypeus and mandibles of *Badister* (Figs. 19A-H and 20A-F)

The mouthparts of *Badister* adults are modified strikingly, particularly the labrum, clypeus and mandibles. The clypeus (Fig. 20A–B, cl) is narrow, sharply bent in a dorso-ventral plane, with two prominent lateral setae. The labrum (l) is deeply, angularly notched, with six marginal dorsal setae.

Structure of the mandibles (Figs. 19A–H, 20C–F).—This pair of sclerites is typical of the Licinina in being short and broad, lacking molar teeth, retinaculum and occlusal grooves. Strikingly asymmetrical, one of the pair has a deep dorsal notch (Figs. 19A, B, E, and 20E–F), and ventrally (Fig. 19G–H) the ventral groove of the notched mandible is markedly curved.

For the subgenus *Baudia* Ragusa, notching of the left mandible is normal (Fig. 19A–B, E–G, n) the notch being located between an anterior much enlarged terebral tooth (tt) and posterior basal boss (b). The occlusal margin in dorso-lateral aspect (Fig. 19B–G) is markedly bent. The right mandible (Fig. 19C, D, F, H) is without the deep dorsal notch, and without the basal boss. For the subgenus *Badister* (*sensu stricto*), the right mandible is notched (as in Fig. 20E–F), with enlarged terebral tooth and basal boss, and the left mandible is without notch or projections.

Most known species of *Badister* are constant in which mandible is notched—either right or left, but not both. The West Indian populations of *Badister reflexus* LeConte are exceptional, in that either mandible of a pair is notched, as illustrated in Figures 19 and 20. This species has been placed in the subgenus *Baudia* Ragusa (Ball, 1959: 221), a group characterized by having the left mandible notched.

Implications for classification.—The data for *Badister reflexus* seem to support Lindroth's opinion that the notching pattern of the mandibles is determined by a simple genetic change. I doubt that such a character by itself is likely to distinguish monophyletic lineages. Thus, it seems best either to abandon the subgenera as they

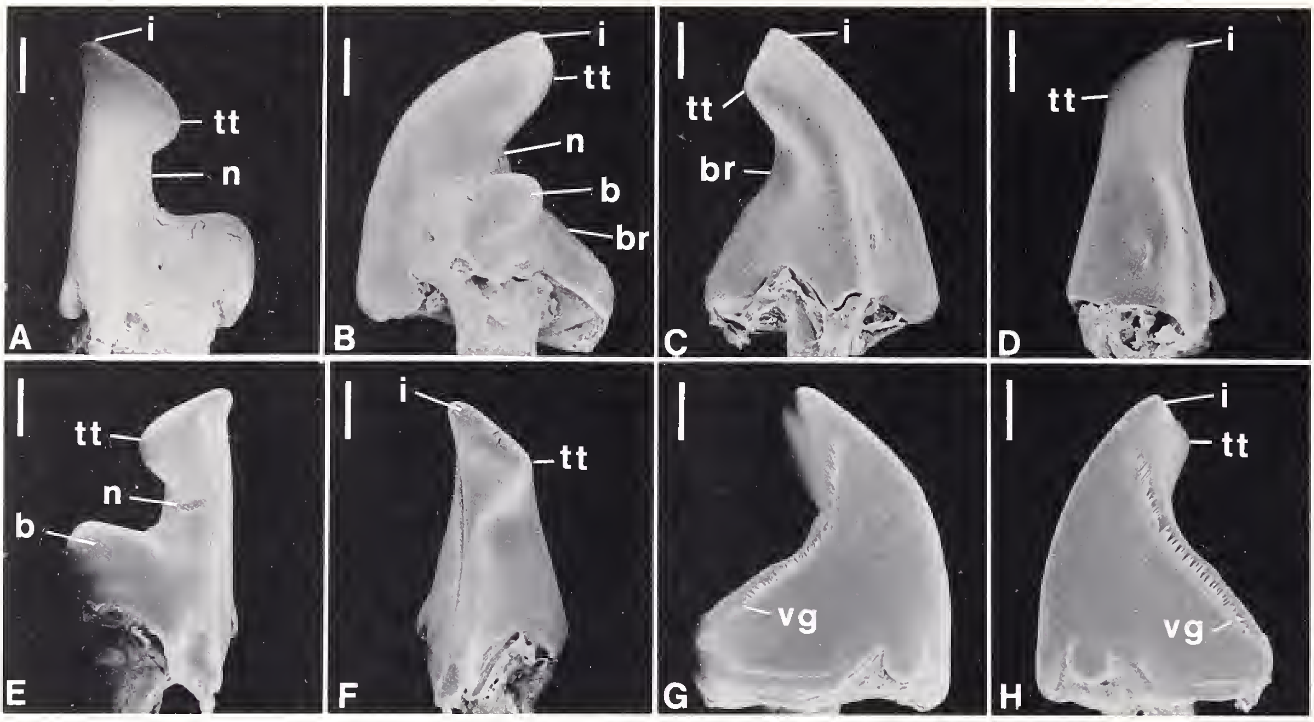


Fig. 19A–H. SEM photographs of the mandibles of *Badister reflexus* LeConte: A, B, E, and G, left mandible, lateral, dorsal, occlusal and ventral aspects, respectively; C, D, F and H, dorsal, lateral, occlusal, and ventral aspects, respectively. Legend: b, basal boss; br, basal ridge; i, incisor; n, notch in dorsal surface; tt, terebral tooth; and vg, ventral groove. Scale bars = 100 μm.

are diagnosed at present, or to acknowledge that each is likely to be a polyphyletic assemblage and to use it because of tradition or convenience.

Microsculpture of *Badister* (Fig. 21A-H)

Elytral microsculpture in the *bipustulatus* complex.—Most species of *Badister* with which I am familiar either lack elytral microsculpture (*B. notatus* Haldeman) or have markedly transverse and closely packed meshes (*B. neopulchellus* Lindroth, Fig. 21A–B), with very narrow sculpticells (s), and an iridescent luster—a condition designated as "grated" by Allen and Ball (1980:486). An exception is *Badister obtusus* LeConte (Figs. 21C–D), with the mesh pattern slightly transverse, sculpticells wider, and surface rather dull—lacking iridescence. There is an ecological correlate to this difference: *B. neopulchellus* is markedly hygrophilous, whereas *B. notatus* and *B. obtusus* occupy the forest floor in damp to dry areas, but not in association with standing water.

It is accepted generally that isodiametric microsculpture (Fig. 21E–F) is plesiotypic, and any other conditions are more or less apotypic, in a transformation series, with the markedly transverse grated condition marking the far end. I had assumed that the series was essentially irreversible. If this were so, then *B. obtusus* should occupy a relatively primitive position. However, with *Badister obtusus* being part of a derived clade in a lineage nearly all members of which exhibit grated microsculpture (Ball, 1959:233, Diagram 3), it seems unlikely that this species can be regarded as ancestral to the lineage as a whole. Accordingly, I conclude that the non-grated microsculpture exhibited by *B. obtusus* is derived from the grated condition, and that this derivation

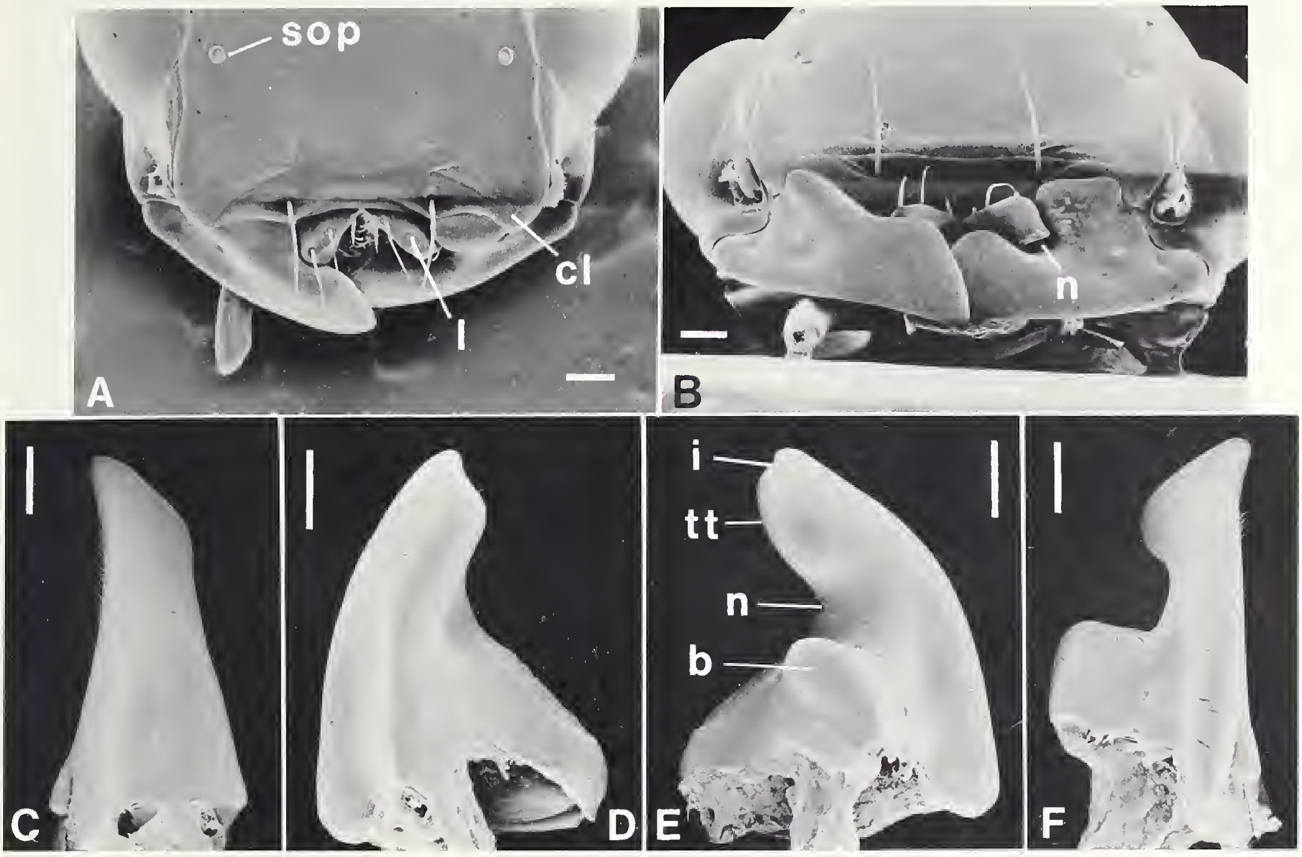


Fig. 20A–F. SEM photographs of anterior part of head and mandibles of *Badister grandiceps* Casey and *B. reflexus* LeConte. A–B, *B. grandiceps*: A, head, labrum and mandibles, dorsal aspect; B, same, frontal aspect. C–F, mandibles of *B. reflexus*: C–D, left mandible, lateral and dorsal aspects, respectively; and E–F, right mandible—dorsal and lateral aspects, respectively. Legend: b, basal boss; cl, clypeus; i, incisor; 1, labrum; n, notch; sop, supraorbital setigerous puncture; tt, terebral tooth. Scale bars = 100 μm.

represents an evolutionary reversal. In turn, this reversal is associated with life in an environment different from the environment occupied by most species of *Badister*.

Microsculpture of the head in the *reflexus* group.—Most species of *Badister* exhibit isodiametric sculpture on the dorsal surface of the head capsule. Adults of *B. ocularis* exhibit such sculpture (Fig. 21E–F; the left supraorbital setigerous puncture [sop] is shown, for orientation). A related species, *B. grandiceps* Casey, exhibits sculpture on the vertex that is slightly transverse (Fig. 21G–H). Although the difference is not much, and is not easily perceived even with relatively high power of a dissecting microscope, it is sufficient to cause structural color, so that the vertex of a typical *B. grandiceps* adult has a rather indistinct band of purple coloring on the vertex.

Geographical distribution of *Badister*

Ball (1959:190) reported *Badister* to be represented on every continent except South America. Recently, I saw a specimen with the character states of *Baudia* from Tucuman, Argentina, collected in January, 1979 by R. Goldbach (CNCI). Also, I participated in collecting a series of specimens with the characteristics of subgenus *Badister* in Amazonian Peru. These species will be studied and described, not necessarily by me, at some future date.

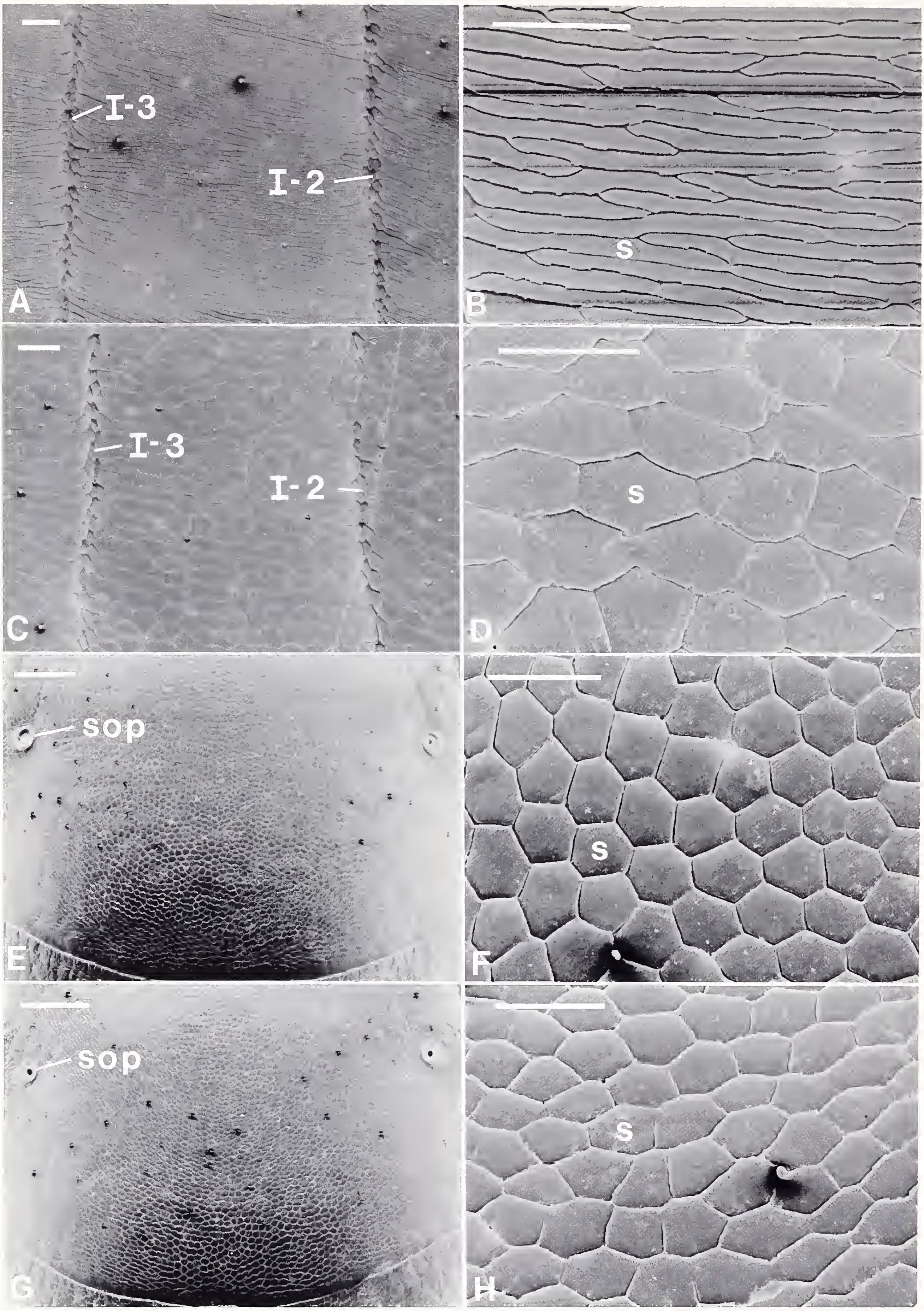


Fig. 21A–H. SEM photographs of microsculpture on various sclerites of members of *Badister* Clairville: A–B, interval 3, left elytron, of *B. neopulchellus* Lindroth; C–D, same of *B. obtusus* LeConte; E–F, vertex of head of *B. ocularis* Casey; G–H, same of *B. grandiceps* Casey. Legend: I-2, interneur 2; I-3, interneur 3; s, sculpticell; sop, supraorbital setigerous puncture. Scale bars: A–D, F, H = 20 μm; E, G = 100 μm.

Notes and new distribution records

Provided here for selected species are observations about variation, and about geographical distribution, including range extensions. The species sequence is the same as in Ball (1959:189–228).

Badister neopulchellus Lindroth

This is a wide-ranging species in North America, from the boreal forest in the north southward to Georgia in the east, and Texas, in the west. A record not previously published, extending the range of *B. neopulchellus* southward in the west, is based on a single female: U.S.A. CALIFORNIA **San Bernardino County**. Mountain Pass, IV.11.1942; O. Bryant (CASC).

Badister obtusus LeConte

Basically northern and wide-ranging in the boreal forest, *B. obtusus* is distributed southward only at higher altitudes in the Rocky Mountains and outlying ranges. New records are the following.

CANADA. NORTHWEST TERRITORIES. 2 females, Fort Wrigley, IX.27.1929; O. Bryant (CASC).

U.S.A. NEW MEXICO. **San Miguel County**. Sangre de Cristo Mountains, 3.2 km W Gascon, Rio de Gascon, 2,438 m, VIII.8.1963; G. E. & K. E. Ball (UASM).

TEXAS. **Culberson County**. Male, Guadalupe Mts., Nat. Park, Bocil, 2,407 m, IX.13.1988; R. S. Anderson (UASM).

Badister elegans LeConte

This species was known previously from the Great Plains states, southward to Brownsville, Texas. The following records establish its presence in northern México.

COAHUILA. Female, 31.2 km E San Pedro, V.31.1981; J. Doyen (UCBC).

TAMAULIPAS. Male, 3 females, 15.9 km W La Pesca, at U-V light, X.28.1965; G. E. Ball & D. R. Whitehead (UASM).

Badister vandykei Ball

The description of this species was based on a single male, collected in Baja California. The following record establishes occurrence of this species on the adjacent mainland of México.

SINALOA. Male, female, 41.8 km N Perico, VIII.13.1960; P. H. Arnaud, E. S. Ross & D. C. Rentz (CASC).

Badister flavipes mexicanus Van Dyke

The description of this subspecies was based on a single female collected at Oaxaca City, in southern México. Because the other subspecies were northern (Ball, 1959: 211–213), ranging as far south as Texas on the mainland and the Bahamas in the West Indies (Darlington, 1953), it was not unexpected that *B. f. mexicanus* would occur in much of the intervening area, and thus would be wide-ranging in México.

The following records confirm this expectation. Mainly eastern in distribution, the altitudinal range of *B. f. mexicanus* extends from near sea level to about 1,500 m. Specimens were collected in sites ranging from mesic to wet (i.e., palm savanna). During daylight hours, specimens were found under cover (principally leaf litter). Some were collected at U-V light at night, indicating nocturnal flight activity.

CHIAPAS. 4 females, Aguatenango, pasture-lake (under cow droppings, near water), VI.26.1972; G. E. Ball & P. E. Meyer (UASM). Male, Palenque ruins, U-V light, 91.4 m., V.22.1972; G. E. Ball, K E. Ball & P. E. Meyer (UASM).

MORELOS. 4 females, Santa Rosa, 5.1 km N Zacatepec, 975 m, II.31.1966; M. W. McFadden & D. R. Whitehead (UASM). 4 males, female, 8.7 km E Cuernavaca, pedregal, 1,420 m, U-V light, V.29–30.1966; Ball & Whitehead (UASM), Male, Tejalpa, VI.23.1963; Whitehead (UASM).

NUEVO LEON. Female, Santa Rosa Canyon, 23.8 km W Linares, 732 m, U-V light, VII.6–7.1966; Ball & Whitehead (UASM).

OAXACA. Female, Oaxaca (city), XI.1968; G. Pollard (UASM). Female, Pueblo Nuevo, VIII.1–12.1986; H. & A. Howden (UASM).

SAN LUIS POTOSI. 2 females, El Salto Falls, U-V light, VII.7.1966; R. E. Woodruff (FSCA).

PUEBLA. Male, Puente Ahuehueyo, ca. 10 km W jct. Hwys 115 & 190, 1,280 m, VIII.10.1965; Ball & Whitehead (UASM).

TABASCO. Male, female, S. Ciudad Pemex, 53 m, U-V light, V.22.1972; Ball, Ball & Meyer (UASM).

TAMAULIPAS. Male, 2 females, Sierra de Tamaulipas, Hwy. 180, 76.6 km N Aldama, ca. 150 m, palm savanna, XII.8.1978; Ball & Ball (UASM). 2 males, Gomez Farias, Naciemiento del Rio Frio, VI.29.1969; S. & J. Peck (UASM).

Badister reflexus LeConte

Geographical variation.—As noted above, either the left or right mandible of adults of this species is notched. On the mainland (Yucatan Peninsula to southern Ontario) and in the Bahamas archipelago in the West Indies, only the left mandible is notched. In the Greater Antilles and Cayman Islands, either the left or right mandible is notched, as indicated in Table 8. A notched right mandible is predominant in Hispaniola and the Cayman Islands, while a notched left mandible is predominant in Cuba and Jamaica. However, the sample sizes are too small to be confident that the suggested pattern reflects reality.

Geographical distribution and localities.—This species was known to be wide-ranging in eastern United States and adjacent parts of southern Canada, from Ontario to "Texas" (no specific locality), and eastward to the Bahamas and Greater Antilles. The following list documents occurrence of *B. reflexus* in Texas, the West Indies and México.

U.S.A. TEXAS. **Cameron County**. Female, Brownsville, X.42; E. S. Ross (CASC).

MEXICO. QUINTANA ROO. 4 males, 5 females, 5 km W Chetumal, Hwy. 186, mercury vapor & U-V light, V.20.1987; E. G & T. J. Riley (LSUC).

WEST INDIES. BAHAMAS. 2 males, Rum Cay, nr. Port Nelson, III.16.1953; Van Voast (AMNH). Male, female, Cat Island, Arthur's Town, VII.29.1935; W. J. Clench (MCZC).

CAYMAN ISLANDS. 5 males, 5 females, Grand Cayman, South Sound, light trap B, IV.17–VIII.26.1938; C. B. Lewis & G. H. Thompson (MCZC).

CUBA. Female, Baragua, XI.12.1925; G. F. Stahl (MCZC). 2 males, 2 females, Cienfuegos, Soledad, IV–X.1926, 1936; P. J. Darlington, Jr. (MCZC). Female, Imias Camaguey, 8-1966, F. de Zayas (MCZC).

HISPANIOLA. **Dominican Republic**. 3 males, 2 females, Sanchez, VIII.1938; P. J. Darlington, Jr. (MCZC). Male, 2 females, Puerto Plata, VIII.29–IX.2.1938; P. J. Darlington, Jr. (MCZC). **Haiti**. 3 females, swamps N. Dessalines, IX.11.1934; P. J. Darlington, Jr. (MCZC).

JAMAICA. Male, Clarendon Parish, Portland Ridge, nr. Jackson Bay Cave, 12 m, V.4.1973; D. & M. Davis (USNM). Female, Good Hope, VIII.11.1966; H. F. Howden (CNCI).

Badister parviceps Ball

The original description of this species (Ball, 1959:225–226) was based on material from the central and northeastern states, and from eastern Ontario. Lindroth (1969: 967) reported additional localities in Manitoba and eastern British Columbia, and suggested that *B. parviceps* probably is transcontinental in distribution. This species is less hygrophilous than the other members of the *reflexus* group, occurring in leaf litter in mesic, shaded sites that are not in direct contact with standing water. Below are noted localities from farther south, extending the known range of this species to eastern Texas.

U.S.A. TEXAS. **Brazos County**. Female, Koppe's Bridge, ca. 8 km SW college Station, berlese, III.10.1988; R. S. Anderson (UASM). Male, same as above, but with note: riparian ravine, leaf litter, berlese (UASM). **Houston County**. Male, female, Big Slough Wild Area, FR 517 & Four C's hiking trail, bottomland, hardwood, litter, berlese, V.9.1988; Anderson (UASM). **Tyler County**. Male, female, 4.5 km W, 3 km N, Spurger Beech Wood Trail, litter, berlese, IV.24.1988; Anderson (UASM). **Walker County**. Female, Huntsville State Park, pine-hardwood forest, litter, berlese, IV.14.1988; Anderson (UASM).

Badister submarinus Motschulsky

I doubted that this species, known only from two females ostensively collected at Sacramento, California, was a North American resident, imagining instead that the specimens had been collected elsewhere and had been mislabelled. Lacking a male for study, I included this species in subgenus *Baudia, incertae sedis,* because the classification of the species of this group is based on male characters (Ball, 1959: 228). About eight years ago, I found in material for identification sent from the Zoological Museum at Copenhagen (ZMUC), a third specimen (also a female) of *B. submarinus,* labelled: "Oregon, U.S.A."; "Upper Klamath Lake at Algoma, Klamath Co. Oregon"; "4100 ft. 11.X.1949 E. Suenson." This record confirms that *B. submarinus* is a western North American resident. However, it must remain *incertae sedis* until a male is located and its genitalia studied.

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A major part of this paper is the set of plates of photographs taken with the Scanning Electron Microscope. They, and the structures illustrated, were prepared in a cooperative operation by G. D. Braybrook, D. Shpeley, and J. S. Scott, who are technologists in my Department. Mr. Scott prepared also the habitus photograph of *Dicaelus franclemonti,* and final versions of the maps and other figures.

G. Scherer, of the Zoologische Staatssammlung, München, made me welcome during a visit to his institution, and arranged for the loan of the type series of *Pterostichus karikali.* Y. Bousquet, of what is now the Division of Biological Resources, and was formerly the Biosystematics Research Centre, Ottawa, made it possible for me to examine the licinines in his care during several visits to his institution. N. E. Stork, of The Natural History Museum, London, responded with alacrity to my frantic request for last-minute assistance. David H. Kavanaugh, of the California Academy of Sciences, San Francisco, arranged for the loan of an extensive array of licinines that I had not seen previously. I appreciate very much the special assistance of these colleagues, and as well, the cooperation of the other curators and collections managers whose names appear in the list of institutions from the collections of which study material was received.

As I learned so well from my association with Jack Franclemont, much of the pleasure of systematic entomology is obtained through life in the field, where one hunts out and assembles the specimens and knowledge that make possible all of the subsequent descriptions and analyses. The pleasure that I enjoyed in finding the *Liodicaelus* material in the mountains of northern México and southwestern United States was enhanced by association with the late D. R. Whitehead, and D. Shpeley, H. E. Frania, S. McCleve and W. Fraga. Not only did I enjoy their company, but I appreciated as well the specimens that they found. My wife's name appears on many of the specimen labels, and I am pleased to acknowledge her contributions, also.

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