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A TAXONOMIC, PHYLOGENETIC, AND ZOOGEOGRAPHIC  
ANALYSIS OF *LACCORNIS* GOZIS (COLEOPTERA: DYTISCIDAE)  
WITH THE DESCRIPTION OF LACCORNINI, A NEW TRIBE OF  
HYDROPORINAE

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ABSTRACT

All members of the genus *Laccornis* Gozis 1914 are keyed, described and illustrated; the genus *Laccornis* is redefined and the new, monobasic tribe *Laccornini* is erected for *Laccornis*. Phylogenetic and zoogeographic analyses demonstrate that members of *Laccornini* are restricted to the Northern Hemisphere and form the most plesiotypic tribe of *Hydroporinae*. Ten species are assigned to *Laccornis*. *Laccornis nemorosus*, new species, is described from Reelfoot Lake, Tennessee, USA and a lectotype male is designated for *L. deltoides* (Fall 1923) from Beaver Creek, Illinois. The species are assigned to three species-groups. Species-group I is monobasic and contains only the southern European species, *L. kocai* (Ganglbauer). It represents the sister clade to the remainder of *Laccornis* and was probably isolated in the early to mid-Cretaceous. Species-group II has three species; the most plesiotypic is the Holarctic species, *L. oblongus* (Stephens), and the more derived, Nearctic species pair of *L. conoideus* (LeConte) and *L. pacificus* Leech. This species-complex was isolated in Asiamerica by the late Cretaceous - early Cenozoic intercontinental seaway. The ancestral stock of *L. oblongus* was isolated in the Oligocene by the origin of the Bering Sea. Its modern occurrence in northwestern North America is probably the result of secondary and late Pleistocene events. Uplift of the Rocky Mountain chain in the late Miocene divided the common ancestor of *L. conoideus* (east of Rockies) and *L. pacificus* (west of Rockies).

Species-group III is the sister group to species-group II and contains *L. deltoides* (Fall), *L. nemorosus* n.sp., *L. latens* (Fall), *L. difformis* (LeConte), *L. schusteri* Wolfe and Spangler and *L. etnieri* Wolfe and Spangler. The ancestor of

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*this species-group was isolated in Euramerica in the late Cretaceous; its members are now distributed in eastern North America and are most diverse in the southeastern United States. No distinct, vicariant events are invoked to explain their present distribution.*

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#### INTRODUCTION

This project originated over ten years ago with what at the time seemed a relatively uncomplicated problem; *Laccornis difformis* (LeConte) of Fall (1923) was actually a complex of three species. However, what began as a restricted taxonomic investigation of the *L. difformis*-complex grew into a larger systematic investigation of not only this species-complex, but also of the genus *Laccornis* and eventually to a survey of basal lineages of Hydroporinae.

The scope of the problem was extended because a casual attempt to define the genus and later an intensive search for generic synapotypies failed to provide insight into what was and what was not "*Laccornis*". The problem became all the more difficult when we realized that *Laccornis* was a very primitive hydroporine, perhaps representing the sister group to all other hydroporines; this complicated the choice of an outgroup and attempts to polarize characters.

Recent studies have shed considerable light on most of the original problems (Wewalka 1969, 1981, Wolfe and Spangler 1985, Wolfe 1985, 1989, Roughley and Wolfe 1987). However, this publication advances previous analyses by: i) describing another new species, ii) taxonomically revising all known species and providing keys for their identification, iii) documenting distributions and habitats, iv) redescribing the genus, v) describing a new tribe to include *Laccornis*, vi) reconstructing a phylogeny, and vii) developing a zoogeographic hypothesis for the species included within *Laccornis*.

#### MATERIALS AND METHODS

##### Materials

*Source of specimens.*— Specimens used in this study were borrowed from the collections or institutions listed below, indicated in the text by the associated two-, three-, or four-letter codens.

- ANSP Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103, USA (D. Azuma).  
 AMNH American Museum of Natural history, Central Park West at 79th Street, New York, New York, USA 10024 (L.H. Herman).

AU	Auburn University, Department of Zoology-Entomology, Funchess Hall, Auburn, Alabama 36849 (G. Folkerts).
BMNH	British Museum (Natural history), Department of Entomology, Cromwell Road, London, SW7 5BD, England (N. Stork, M.E. Bacchus).
CARR	J.L. and B.F. Carr, 24 Dalrymple Green NW, Calgary, Alberta, Canada T3A 1Y2.
CAS	California Academy of Science, Department of Entomology, Golden Gate Park, San Francisco, California, 94118 USA (D.H. Kavanaugh).
CNC	Canadian National Collections, Biosystematic Research Centre, Research Branch, Ottawa, Ontario, Canada, K1A 0C6 (A. Smetana).
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14853 USA (Q. Wheeler).
FM	Field Museum of Natural history, Chicago, Illinois, 60605 USA (J. Ashe, L. Watrous).
INHS	Illinois Natural history Survey, Natural Resources Building, Urbana, Illinois, 61801 USA (W.U. Brigham).
IU	Indiana University, Department of Biology, Jordan Hall 138, Bloomington, Indiana, 47405 USA (F.N. Young).
JBWM	J.B. Wallis Museum, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2 (R.E. Roughley).
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02148 USA (A. Newton).
NMNH	Smithsonian Institution, National Museum of Natural history, Department of Entomology, Washington, D.C., 20560 USA (P.J. Spangler).
NMW	Naturhistorisches Museum Wien, Zoologische Abteilung (Insekten), Postfach 417, Burging 7, A-1014 Wien, Austria (F. Janczyk).
ODU	Old Dominion University, Department of Biology, Norfolk, Virginia, 23508 USA (J.F. Matta).
OSU	Oregon State University, OSU Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon, 97331 USA (G.L. Peters).
PM	Peabody Museum of Natural history, Yale University, 170 Whitney Avenue, P.O. Box 6666, New Haven, Connecticut, 06511 USA (C.L. Remington, D.G. Furth).
RU	Rutgers University, Department of Entomology and Economic Zoology, Cook College, P.O. Box 231, New Brunswick, New Jersey, 08903 USA (M. May).
SMK	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA (P. Ashlock).
SCSU	St. Cloud State University, Department of Biological Sciences, St. Cloud, Minnesota, 56301 USA (R. Gundersen).
SBSK	State Biological Survey of Kansas, the University of Kansas, 66044 USA (B. Coler).
UASM	Strickland Museum, University of Alberta, Department of Entomology, Edmonton, Alberta, Canada T6G 2E3 (G.E. Ball, D. Shpeley).
UC	University of Connecticut, Department of Biology, Storrs, Connecticut, 06268 USA (P.W. Severance).
UMMZ	University of Michigan, Museum of Zoology, Division of Insects, Ann Arbor, Michigan, 48109 USA (B. O'Connor).
UW	University of Wisconsin, Department of Entomology, Madison, Wisconsin, 53706 USA (W. Hilsenhoff).

- ZIH Zoologiska Institutionen Helsingfors Universitetet, N. Jänvägsgatan 13, F-00100 Helsingfors 10, Finland (O. Biström).  
ZM Zoology Museum, Department of Zoology, Helgonavägen 3, S-223 62 Lund, Sweden (R. Danielsson).  
ZSM Zoologische Staatssammlung München, Münchhausenstraße 21, D-8000 München 60, West Germany (G. Scherer).

### Methods

*Dissection, measurements and illustrations.*— Standardized techniques were used and these are described in Wolfe (1984, 1985) and Roughley and Pengelly (1982). Representatives of all specimens, except the rare *L. deltoides* (Fall), were completely disarticulated prior to detailed systematic study (see Wolfe 1985:133).

*Species concept.*— We use the evolutionary species concept as explained in Wiley (1981). We favor this concept because it is broadly applicable; it does not require evidence regarding reproductive isolation and all species are part of a phylogeny. All species concepts (biological, evolutionary or phenetic) initially require discernment of character discontinuities (Rosen 1978). In the process of partitioning specimens initially we used Erwin's (1970) criteria for species recognition: an array of specimens displaying a multidimensional continuum of characters which is separable from other sets of specimens by a distinct gap. For us, a sufficient gap could be a single character, provided there was substantial evidence for absence of intergradation.

The method of analysis and progressive grouping of specimens in this revision generally follows Roughley and Pengelly (1982). Specimens of *Laccornis* were segregated first on differences in aedeagal and/or anterior protarsal claw structure of males. Subsequently a search was made for correlation of these characters with other characters (antennal form, punctuation, elongate femoral setae, etc.). Thus the taxa were distinguished by means of phenetic methods. Subsequently these taxa were assessed using phylogenetic criteria. The evolutionary species concept could be considered as equivalent to the phenetic species concept since phenetic methods are used to delimit species. However, an important distinction is that, with the evolutionary species concept, a species almost always is distinguished by a synapotypy. Therefore species and all higher taxa are justified ultimately by synapotypic similarity.

Even though reproductive isolation is not a required element for the evolutionary species concept, evidence for intergradation versus isolation is useful and should be used if available. In revisionary research, absence of intergradation in areas of sympatry or parapatry almost always is the test for isolation. For allopatric populations, species status is considered justified if the gap among populations in question is equivalent to the disparity among species which occur sympatrically and in the absence of clinal trends of important characters. For sympatric populations, this test is maximally significant only if it involves sister species or at least closely related taxa. Within *Laccornis*, we did not find any sister species to be broadly sympatric. Therefore while we used the criterion of sympatry to invalidate certain characters (e.g., color characters), the taxa which we established cannot be evaluated by the sympatry criterion.

In consequence, the validity of the taxa that we propose rests on documentation of the distinctness or separateness of the lineages. For us, this is not just a matter of designating a gap, but, when possible, recognizing uniquely derived character states (autapomorphies) that suggest that distinct lineages have evolved. Conceivably, species could be found that lack autapomorphies (e.g., if

an ancestral species does not become extinct at the time of speciation event). In this latter situation, synapomorphies before and after (on the cladogram, above and below) the dichotomization in question are used to justify the species as a lineage.

In summary, evaluation of species status, even under the premises of the evolutionary species concept, requires a holistic approach and their recognition and evaluation requires phenetic, phylogenetic and chorological data. However, our species concept and analysis of relationships emphasizes a phylogenetic approach and we believe that this is less arbitrary than a study based completely on phenetics and/or presumed reproductive isolation.

*Descriptions.*— Distinction among tribal, genus, and species level characters is somewhat arbitrary. However, we divide characteristics among the three levels of classification based on the phylogenetic level at which character diversification first occurred, traditional use of characters in keying out tribes, genera, and species, and our own experience with the usefulness of the characters. Tribal and generic descriptions are presented traditionally. However, our species descriptions are in the form of a character matrix. This technique is modified from that of Erwin (1982). This character matrix format is not better in every way from traditional descriptions. For example, it is more difficult to describe subtle differences among characters when assigning them to a matrix. We compensate for this by providing figures of the alternative as well as the subtly differing character states. We prefer this method because, in addition to the advantages listed by Erwin (1982), it forces consistent treatment of virtually every character for each species under consideration; it makes comparison of characters conspicuous and it allows for easy addition of new characters. We use ten character systems with 55 characters with a total of 160 character states to describe the ten known species of *Laccornis*.

*Locality information.*— The known distribution of each species is shown in Figs. 21A-D. Exact locality data for specimens examined is on file at JBWM.

*Phylogenetic methods.*— The phylogenetic procedures used in this study are essentially Hennigian. The best general references for this approach are Wiley (1981) and Nelson and Platnick (1981); other useful references are Kavanaugh (1972, 1978), Whitehead (1972), and Ross (1974) and references cited therein.

Character states were polarized from a generalized, outgroup concept based on our studies of other groups of Dytiscidae. A general treatment of many of these is presented in Wolfe (1985, 1989) for members of Hydroporinae. In particular we examined the character states known from members of the tribe Methlini (especially *Celina hubbelli* Young) because methlines are a relatively plesiotypic group of hydroporines closely related to *Laccornis* (Wolfe 1985, 1989). When characterizing the plesiotypic state from methlines we also considered the state found in members of *Laccornellus* Roughley and Wolfe which is also a plesiotypic member of Hydroporini (Roughley and Wolfe 1987).

When characters existed in only two states (binary characters) polarization was a rather straight forward, unambiguous procedure for the characters examined in members of *Laccornis*. In most examples this was because the outgroup did not have the inferred apotypic state found within *Laccornis*. These binary characters therefore contribute to an initial framework of the cladogram. Multistate characters can be more difficult to resolve. This is because what may appear as a linear array of character states may be a number of more or less separate series of character transformations. In assessing such multistate characters we have found useful the computer program PAUP (Swofford 1985).

Multistate characters, when used in the process of tree construction with PAUP, can be considered as ordered or unordered and the ramifications of this designation are important. If a specific transformation series is stipulated for a character (*i.e.*, that character is ordered) then, when the tree is constructed using PAUP, this sequence may bring about homoplasy in a few to many other characters. For example, if a character sequence is specified initially as transforming from character state 0 to state 1 to state 2 then additional homoplasy will result in other characters if the sequence should have been 0 to 2 to 1. By analyzing the contribution of each character separately it was possible to discover which characters were contributing to homoplasy. Therefore our first task on discovering such characters was to very carefully re-analyze these characters to make sure that the evolution of the character states was as we had coded it. This was particularly helpful, for instance, in assessing the features of the male antennomeres of *Laccornis* which was much more complex than we had thought initially.

After reanalyzing each character which was contributing to homoplasy certain multistate characters remained difficult to polarize and to arrange into a sequence. The only way to choose among the array of possibilities available was by means of parsimony. Using this method the character states are unordered and the sequence of transformation which requires the fewest number of changes is accepted as correct.

While total reliance on ordered characters can artificially increase the amount of homoplasy within a cladogram similarly total reliance on unordered characters can overly minimize the amount of homoplasy that actually exists. Therefore we tried to balance our phylogenetic analysis by using both ordered and unordered formats to check the robustness of our phylogenetic hypotheses, to understand the contributions that each character was making to the cladogram and to test the validity of suspected evolutionary changes (see Phylogeny for details).

The value of synapomorphies that supported hypotheses of monophyly were evaluated with a consistency index (CI). This index is a measure of the amount of homoplasy within a character series and is calculated by dividing the range of a character (*i.e.*, the minimum number of character state changes possible) by the actual length that the character contributes to the cladogram. CI values close to zero indicate high degrees of homoplasy and a CI value of one indicate a perfectly consistent character with no homoplasy. For example, a binary character has a range or minimum possible length of one and if a binary character changes from 0 to 1 only once on a cladogram the CI value would be one. However, if a binary character undergoes one reversal (0 to 1 to 0) the actual length contributed would be two and the CI value (1 divided by 2) would be 0.5. The CI value for each character is given in Table 3.

#### STRUCTURAL FEATURES

##### Notes about taxonomic and phylogenetic characters

The characters below are discussed from anterior to posterior as they occur on the body of the insect and they are arranged sequentially in Table 1. Most character states will be easily understood from use of Table 1 and the figures. In the treatment below some character states found in the descriptions of species are discussed as well as our reasoning for the phylogenetic value of those characters used in the reconstructed phylogeny (Fig. 19).

*Antennal structure.*— Divergence in antennomere shape is remarkable among males of *Laccornis* (Figs. 3A-H). Males of all species except *L. kocai*

have some or all of antennomeres 3-7 modified. We at first suspected that the various antennal forms were part of a single morphocline. However, detailed studies of structural differences indicates that the spectrum of differences should be partitioned into two independent morphotypes - I and II.

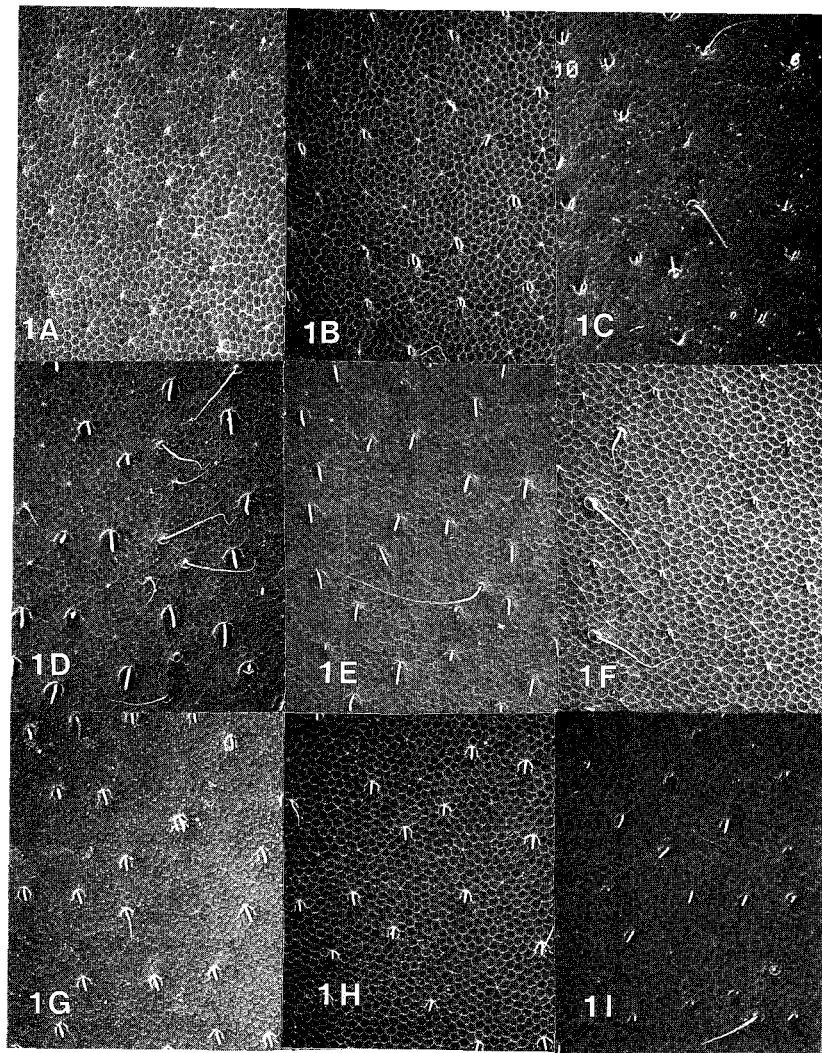
In morphotype I, antennomeres 3-5 are characterized as a unit and in morphotype II antennomeres 3-7 are characterized as a separate unit. In morphotype I, the least derived antenna is that of males of *L. latens* (Fig. 3A), and involves only antennomere 4; progressively greater change involves primarily modification of antennomere 4 (compare that of males of *L. latens*, Fig. 3A, to that of *L. difformis*, Fig. 3F, and to *L. nemorosus*, Fig. 3C, D, F) and to a lesser extent antennomeres 3 and 5. In morphotype II, the least modified antenna is that of males of *L. oblongus*. In male specimens of that species antennomeres 3-7 are modified, but barely so and predominantly on the ventral surface; successive modifications in other taxa (e.g., *L. conoideus*, Figs. 3E, H) involve only those antennomeres. Therefore, in both morphotypes, modification simultaneously affects either antennomeres 3-5 or 3-7, and antennomeres appear to change as a unit, in morphotypes I and II respectively.

Although there is increased size of antennomeres in morphotypes I and II, we are confident that morphotype I and II represent two independent character systems because numerous other comparisons of structure reveal substantial differences. For example, within morphotype I, the ventral surface of antennomere 4 becomes progressively more concave, the reticulation more effaced, and the posterior and/or anterior edge setose (compare Figs. 3F, G). Changes in morphotype II involve none of those modifications; the ventral surface becomes convex/sinuate on some antennomeres, reticulation becomes rugose and no setal development is evident (Fig. 3H). Antennomere shape within morphotypes I and II also is fundamentally different. In morphotype I, antennomere 4 appears to become progressively enlarged (compare Figs. 3A-C) but there is relatively little distortion of shape, even in the most derived state which is found on males of *L. deltoides* and *L. nemorosus*. In morphotype II, the posteroapical corner of antennomeres 3 and 4 is produced giving a distinctly asymmetric shape (Figs. 3E, H). Within each morphotype, changes appear correlated and we coded several associated changes as one integrated complex; coding of each morphotype for phylogenetic analysis is summarized in Table 3.

The completely unmodified antenna of males of *L. kocai* occurs also in the outgroup and that state is considered plesiotypic (Tables 3-5). For morphotype I, the second state of development (state 1) involves the barely perceptible enlargement of antennomere 4 (Fig. 3A); in state 2, antennomere 3 is slightly enlarged and antennomere 4 even more so, the ventral surface of antennomere 4 is a little more concave basally and setae occur along the posterior edge (Figs. 3B, F); in state 3, the fourth antennomere reaches maximum size, the ventral surface is distinctly concave, and setae are present on the anterior and posterior edge (Fig. 3C, G, 4I). For morphotype II, state 1 involves no antennomere enlargement, however, the ventral surface of antennomeres 3-7 are a little flattened with reticulate sculpticels elongated longitudinally and scarcely rugose. In state 2, antennomeres 3, 4, and 5 are distinctly enlarged asymmetrical, and the ventral surfaces are a little more convex/sinuate and distinctly rugose (Figs. 3E, H).

*Mouthparts and proventriculus.*— Mouthpart structure among Hydradephaga in general and Dytiscidae in particular is reviewed by Wolfe (1984, 1985). Mouthpart and proventricular structure are described in the tribal description and





Figures 1A-I. Elytral microsculpture (200X). A) *Laccornis kocai*, B) *L. oblongus*, C) *L. conoideus*, D) *L. pacificus*, E) *L. latens*, F) *L. nemorosus*, G) *L. difformis*, H) *L. schusteri*, I) *L. etnieri*.

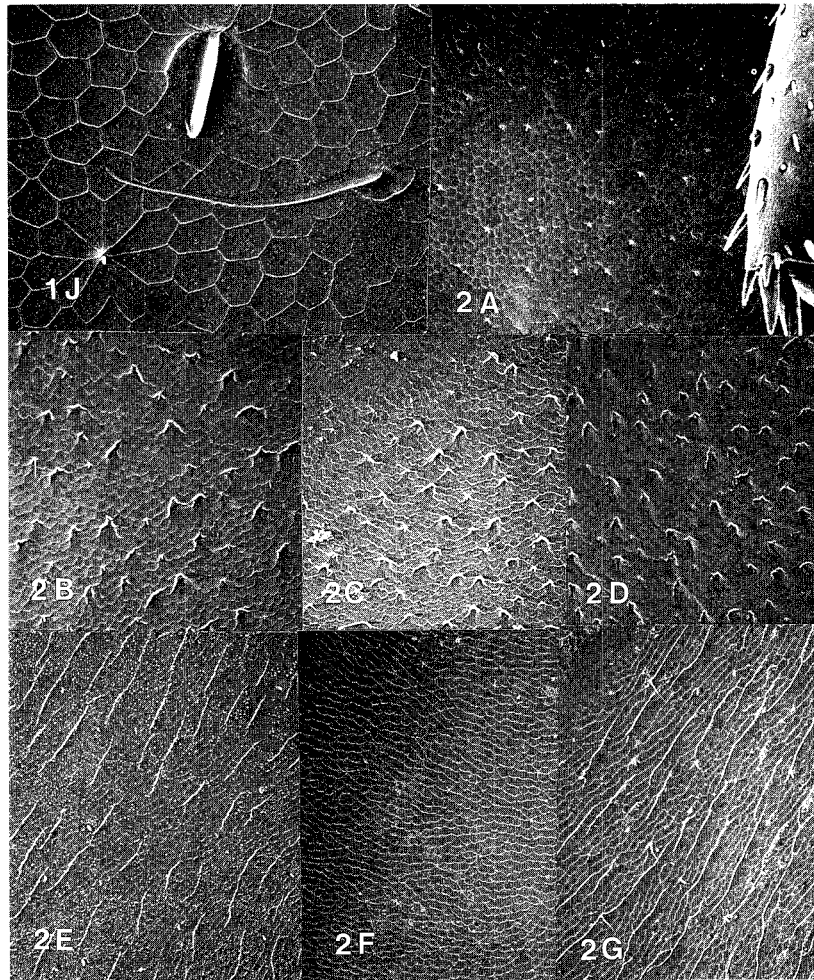
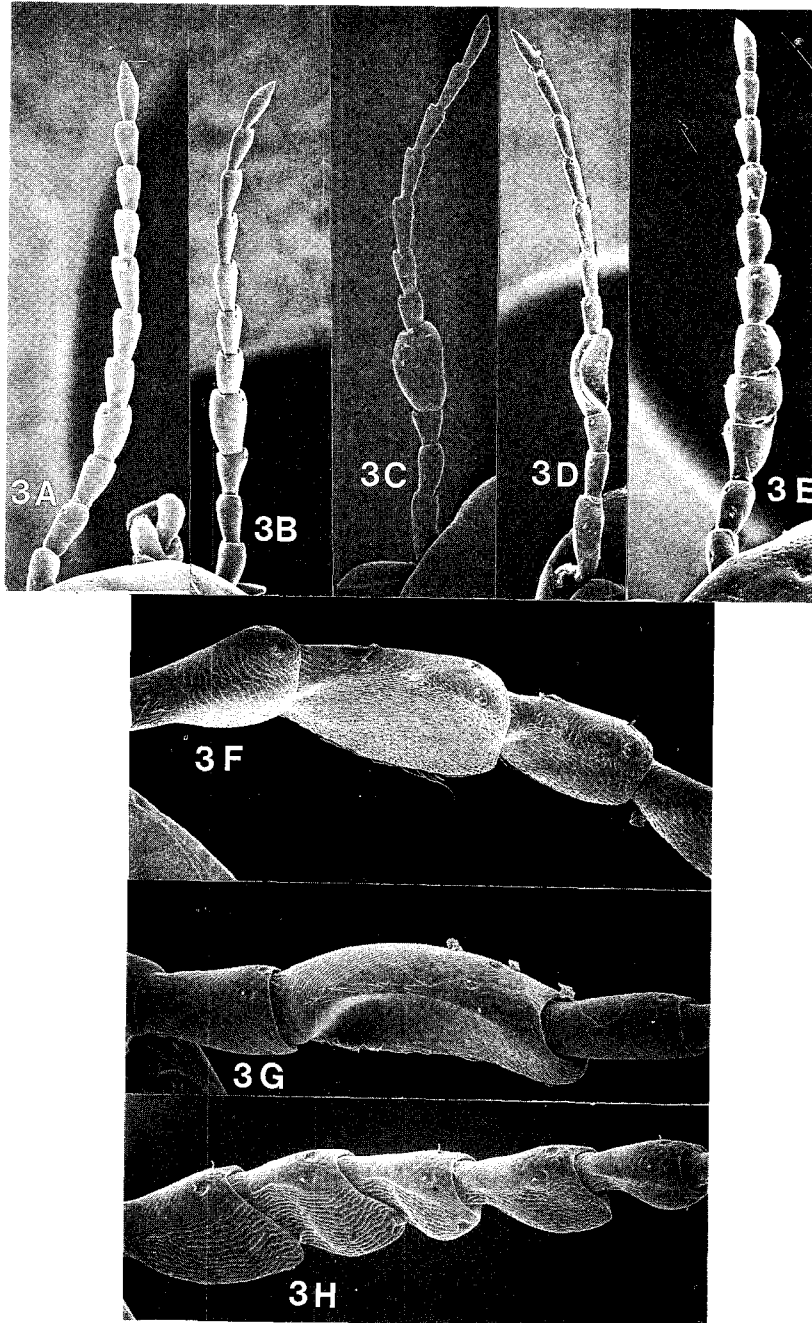


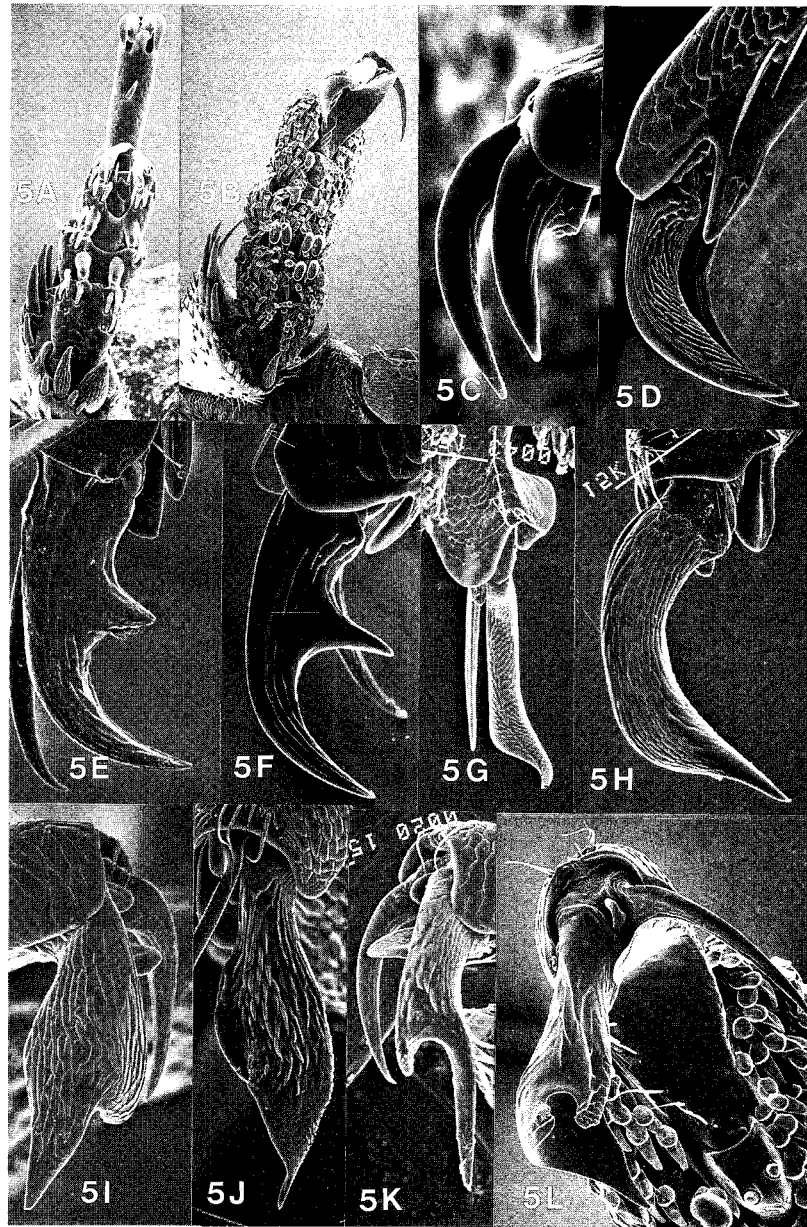
Figure 1J and 2A-G. Fig. 1J. Elytral microsculpture, *Laccornis pacificus* (1000x) showing reticulate pattern and from left to right, simple puncture, compound eccentric puncture and compound concentric puncture (with thickened sides). Figs. 2A-G. Metacoxal microsculpture. A) *Laccornis kocai* (200x), B) *L. oblongus* (200x), C) *L. conoideus* (200x), D) *L. pacificus* (200x), E) *L. latens* (150x), F) *L. nemorosus* (150x), G) *L. schusteri* (150x).



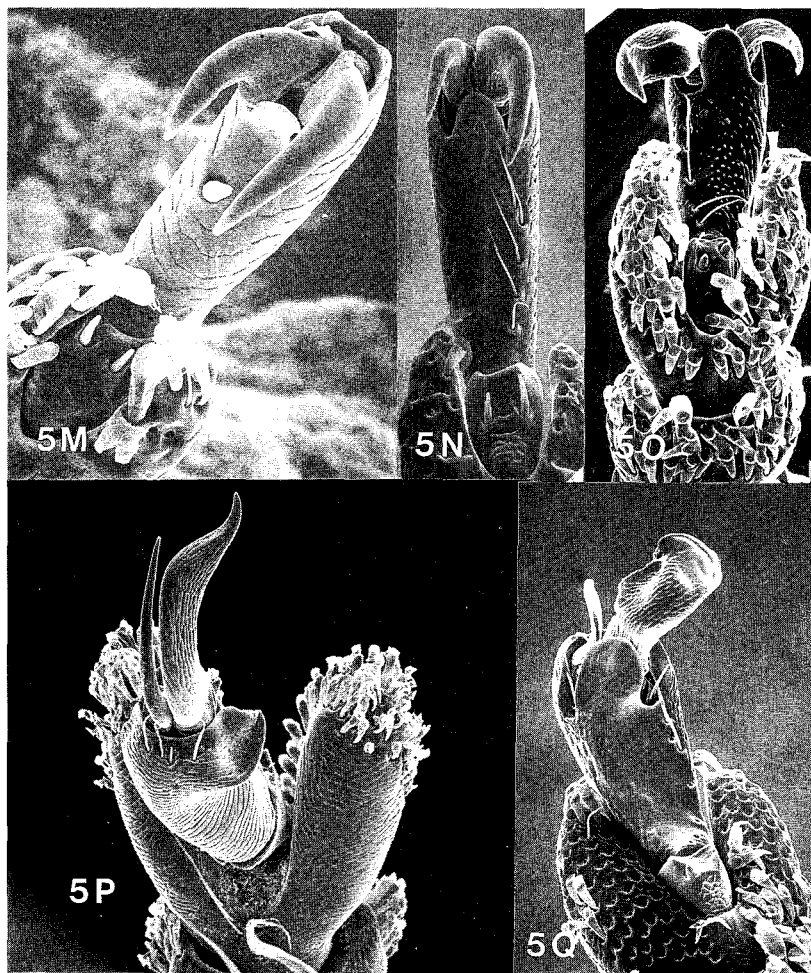
Figures 3A-H. Antennal structure. A) *Laccornis latens*, dorsal view, antennomeres 1-11 (50x), B) *L. schusteri*, dorsal view, antennomeres 1-11 (40x), C) *L. nemorosus*, dorsal view, antennomeres 1-11 (40x), D) *L. nemorosus*, anteroventral view, antennomeres 1-11 (40x), E) *L. conoideus*, dorsal view, antennomeres 1-11 (60x), F) *L. difformis*, anteroventral view, antennomeres 3-6 (150x), G) *L. nemorosus*, anteroventral view, antennomeres 3-5 (150x), H) *L. conoideus*, anteroventral, antennomeres 3-7, (150x).



Figures 4A-I. Prosternal structure. Figs. A-G. Prosternal process, ventral view unless otherwise indicated, A) *Laccornellus lugubris* (150x), B) *Laccornis kocai* (150x), C) *L. oblongus* (150x), D) *L. nemorosus* (80x), E) *L. nemorosus*, ventrolateral view showing depressed medial area (80x), F) *L. latens* (100x), G) *L. schusteri* (100x). Figs. 4H-I. Ventral anterolateral corner of prosternum, H) *L. oblongus*, cleft present (250x), I) *L. nemorosus*, pore present (200x).

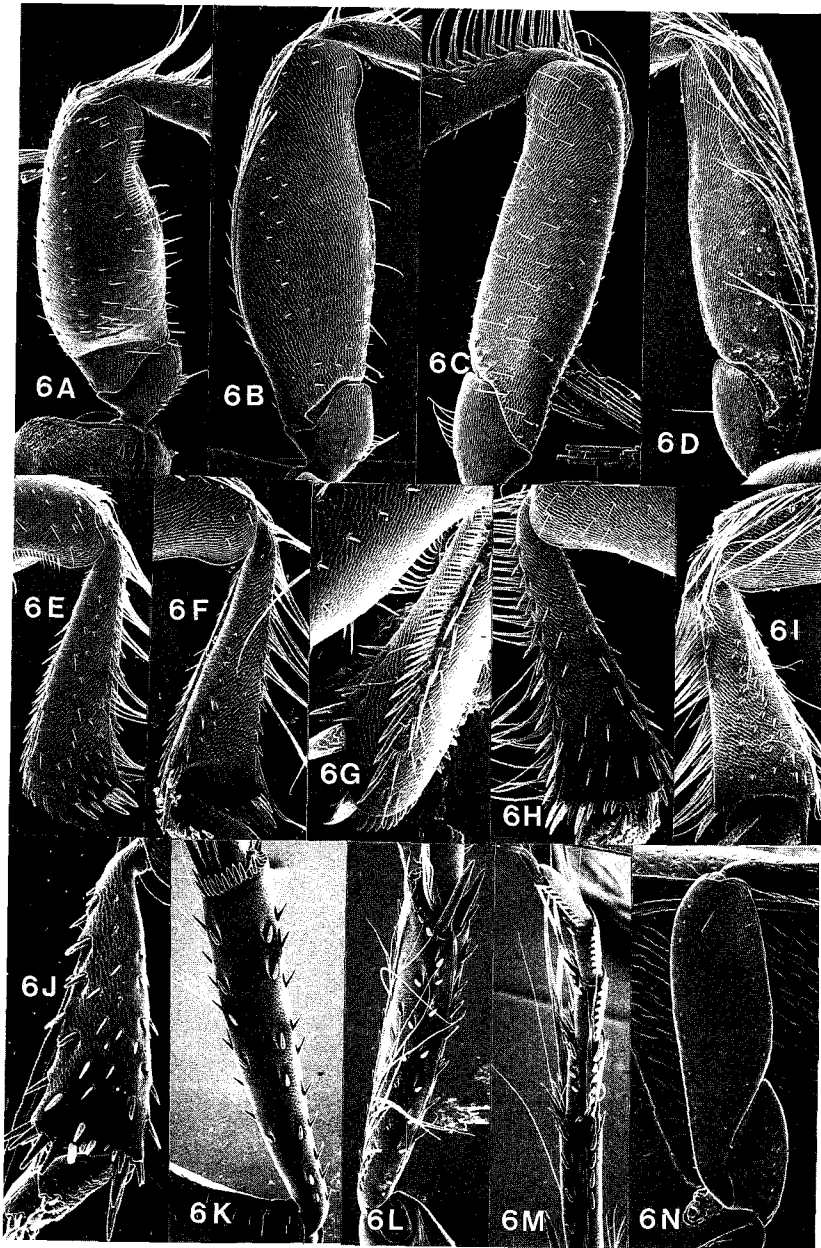


Figures 5A-L. Figs. 5A-B. Protarsus, ventral view. A) *Laccornis kocai*, two modified palettes on tarsomeres 1-3, B) *L. etnieri*, four modified palettes on tarsomeres 1-2. Figs. 5C-L. Protarsal claw structure. C) *L. kocai* (800x), D) *L. oblongus* (600x), E) *L. conoideus* (600x), F) *L. pacificus* (600x), G) *L. nemorosus*, note distinct asymmetry of protarsomere 5, ventral view (200x), H) *L. nemorosus*, lateral view (300x), I) *L. latens* (400x), J) *L. difformis* (300x), K) *L. schusteri* (300x), L) *L. etnieri*, note somewhat asymmetrical shape of fifth protarsomere, (300x).

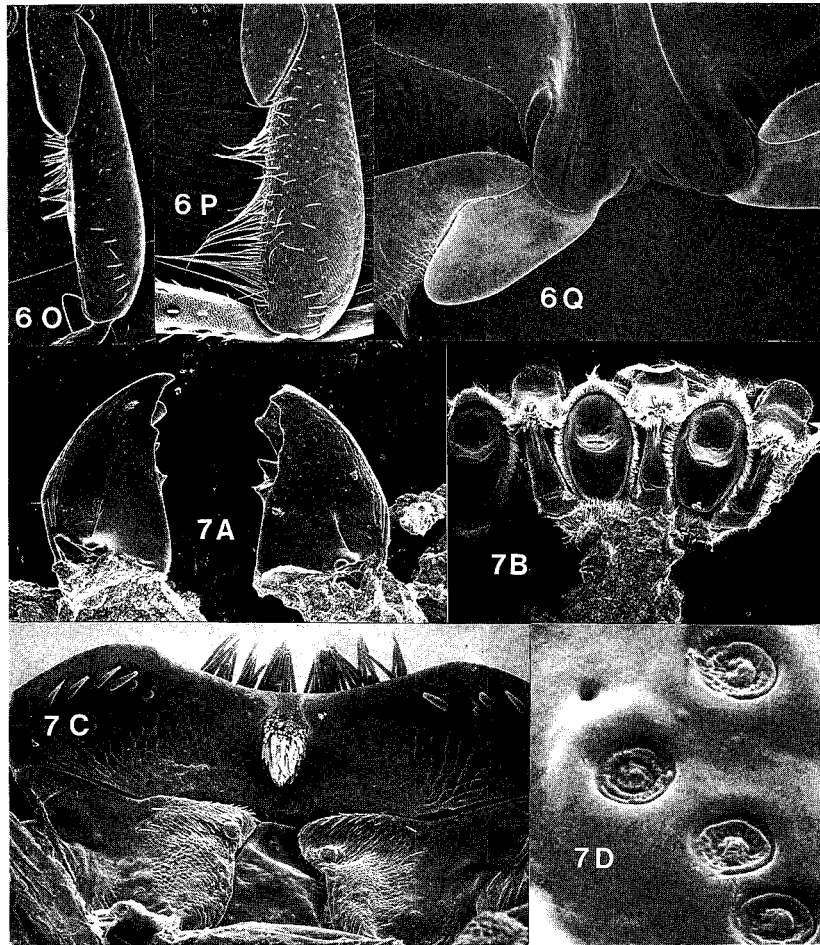


Figures 5M-Q. Protarsomeres 4 and 5. M) *Laccornis kocai*, ventral view (300X), N) *L. oblongus*, ventral view (300X), O) *L. latens*, ventral view (200X), P) *L. nemorosus*, dorsoapical view (200X), Q) *L. difformis*, ventral view (200X).



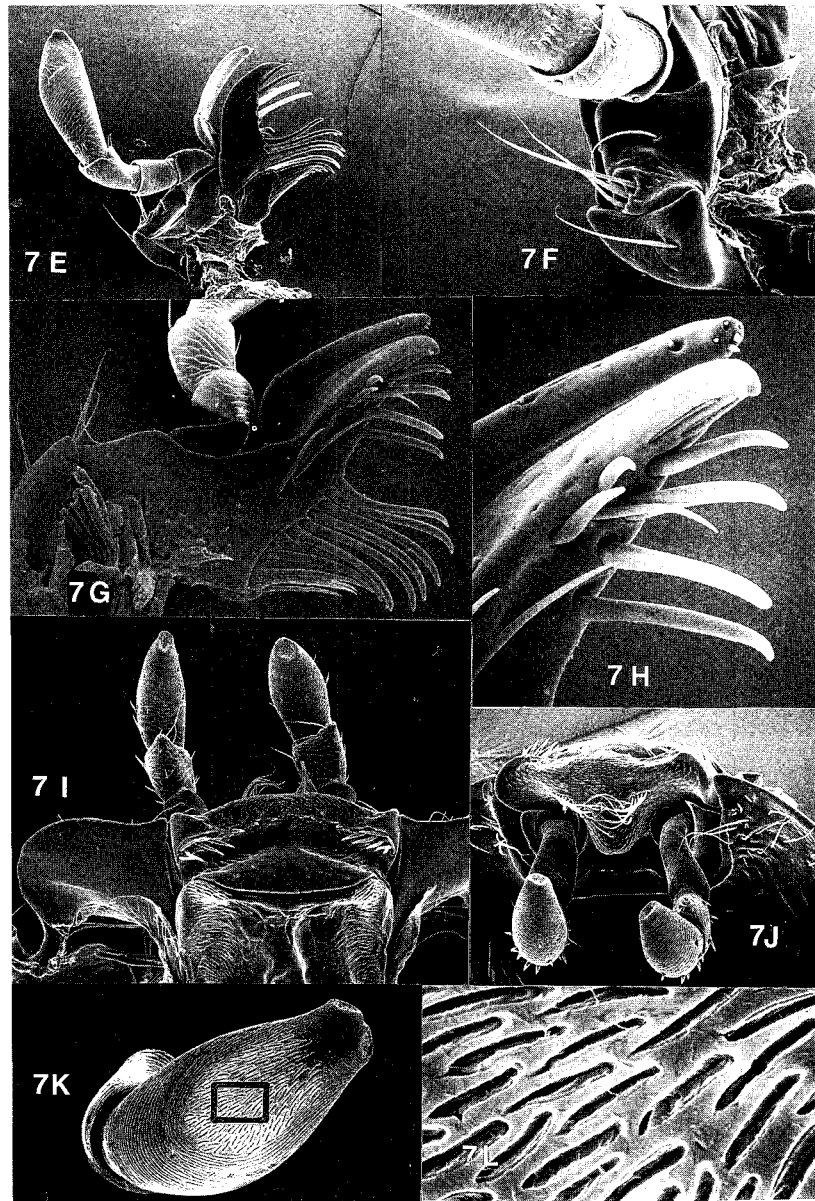


Figures 6A-N. Leg chaetotaxy. Figs. 6A-I, *Laccornis difformis*, J, *L. latens*, K-M, *L. kocai*, N, *L. latens*. A) Profemur, anterior view (80x), B) Profemur, posterior view (80x), C) Mesofemur, anterior view (80x), D) Mesofemur, posterior view (80x), E) Protibia, anterior view (80x), F) Protibia, posterior view (80x), G) Protibia, ventral edge (150x), H) Mesotibia, anterior view (80x), I) Mesotibia, posterior view (80x), J) Mesotibia, anterior view (100x), K) Metatibia, anterior view (80x), L) Metatibia, posterior view (80x), M) Metatarsus, ventral view (80x), N) Metafemur, anterior view (80x).



Figures 6 O-Q and 7A-D. Figs. 6O-P. Metafemur, ventral view. O) *Laccornis pacificus* (60x), P) *L. etnieri* (60x), Q) Metacoxal processes, base of each femur contacting process, (40x). Figs. 7A-D. Mouthpart and proventricular structure. A) Mandibles, *L. latens*, ventral view (80x), B) Proventriculus, *L. difformis*, (80x), C) Labrum and epipharynx, *L. difformis* (200X), D) Peculiarly modified epipharyngeal sensilla (6000x).





Figures 7E-L. Mouthparts. Figs. 7E-H, *Laccornis difformis*, I-L, *L. latens*. E) Maxilla, ventral view, arrow indicates basal sclerite, F) Cardo and stipes, showing setal pattern (300x), G) Maxilla, dorsal view (200x), apex further magnified in 7H, H) Lacinial tip, medial view, showing digitiform sensilla (500x), I) Labium, dorsal view (150x), J) Labium, ventral view, (150x), K) Apical labial palpomere, anterolateral view, box indicates area enlarged in 7L, L) Apical labial palpomere, enlargement of area indicated in 7K.

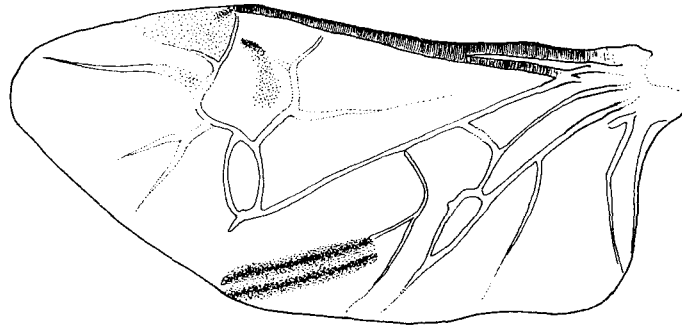
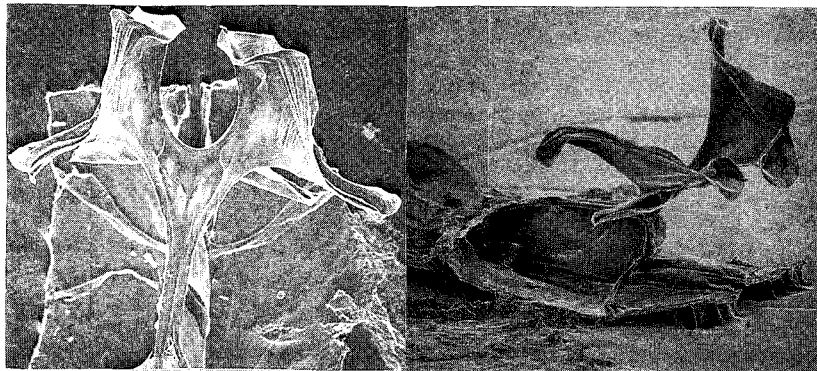
**7M****7N****7O**

Figure 7M-O. Thoracic structure. *Laccornis difformis*. M) Flight wing, N) Metafurca, dorsal view (30X), O) Metafurca, anterolateral view (30X).

they are illustrated in Figs. 7A-L but no characters were found that are useful in taxonomic or phylogenetic analyses within the genus.

*Prosternal process.*— Two important characters are associated with the prosternal process: general shape and longitudinal, medial convexity. The shape of the prosternal process varies gradually among members of *Laccornis*, however, the process is relatively broad in all species. The shape is narrow and elongate in specimens of the methline outgroup taxon, *C. hubbelli*. To polarize these character states an additional outgroup was necessary and *Laccornellus lugubris* (Aubé) was used for this (see Roughley and Wolfe 1987); the process in specimens of the latter species is long and slender (Fig. 4A) and that state is considered plesiotypic. Therefore, the broadened shape of members of *Laccornis* is a generic synapotypy.

The prosternal process is longitudinally and medially convex in most species. In specimens of *L. deltoides* (Fall) and *L. nemorosus*, n. sp., the convexity is scarcely developed and the middle of the prosternal process appears almost concave (Fig. 4D, E). Since the medial portion of the prosternal process of specimens of *C. hubbelli* is more distinctly elevated and convex that state is considered plesiotypic.

*Prosternal pore.*— The explanation of this state and the basis for its polarity is given in Wolfe (1985). The plesiotypic state is that of a V-shaped notch located at the anterolateral corner of the prosternum (Fig. 4H). The derived state (Fig. 4I) is a pore-like opening in the same position. In clean specimens the different states can be discerned at about 50x magnification.

*General leg chaetotaxy.*— We describe and illustrate by scanning electron microscope (SEM), in the tribal description, major setal and spine characteristics of legs. Leg chaetotaxy is very inadequately known and this review serves primarily as a starting point for future comparisons [but see information in Balfour-Browne (1940) and Wolfe (1985)]. In our overall survey we found five chaetotaxal characteristics (see below) useful for phylogenetic and/or taxonomic purposes.

*Femoral setae.*— On males of various species of *Laccornis*, elongate, femoral setae are present on the distal margin. These setae are distinct from the standard series of natatory setae (e.g., Fig. 6D). The elongate, femoral setae are present on mesofemora (only) of members of *L. conoideus* and *L. pacificus*, on metafemora (only) of members of *L. difformis*, *L. schusteri*, and *L. etnieri* (Fig. 6P), and on both meso- and metafemora (Fig. 6O) of members of *L. pacificus* and *L. conoideus*. Elongate femoral setae are absent from specimens in the outgroup (e.g., Fig. 6N) and therefore occurrence among some members of *Laccornis* is apotypic. We hypothesize that derivation of these setae on mesofemora occurred independently of development on metafemora. These elongate setae of the mesofemora and metafemora are easy to see at low magnifications and are useful for identification of male specimens.

*Mesotibial spines.*— Wolfe (1985) discusses the form of the mesotibial row of spines (compare Figs. 30-34 of Wolfe 1985). Among members of *Laccornis* there is a sublateral row of spines on the anterior surface of each mesotibia and proximity (denseness/sparseness) of spines in this sublateral row varies. Variation is somewhat gradual but we have partitioned variation in number of spines into two groups: eight or fewer (Fig. 6J), and nine or more spines (Fig. 6H). The continuous nature of variation in this character diminishes its reliability in phylogenetic reconstruction; however, members of *L. kocai* are clearly at the low end of spine number and that is the condition found in members of *C. hubbelli*. Therefore, while we think this character is evidence for the

primitiveness of *L. kocai*, it is not used directly in further phylogenetic resolution of the species, except by character correlation.

*Protarsal palettes*.— In male specimens of *L. kocai*, there are two enlarged palettes on each of protarsomeres 1-3 (Fig. 5A); there are four palettes on at least each of the first two protarsomeres of males of all other species (Fig. 5B). Two palettes per tarsomere occur in most groups of hydroporines and on specimens of *C. hubbelli*; therefore the higher number of modified palettes is considered apotypic.

*Spines of protarsomere 4*.— Protarsomere 4 of all hydroporines is very short and it is usually concealed between lobes of protarsomere 3. Two spines are located on protarsomere 4. In members of some species of *Laccornis*, these spines are longer and more slender (Fig. 5A, M, N); in members of other species, the spines are short and cone-shaped (Fig. 5O). Spines on the protarsomere 4 of *C. hubbelli* are long and slender and this state is considered plesiotypic.

*Sensilla of protarsomere 5*.— Protarsomere 5 of most hydroporines is elongate and extends well beyond the lobes of protarsomere 3. In specimens of *L. kocai*, sensilla on the ventral surface of protarsomere 5 are short and spine-like (Figs. 5A, M); in all other members of *Laccornis* seta-like sensilla are present (Figs. 5N, O, Q). The spine-like condition is evident in member of *C. hubbelli* and is considered plesiotypic.

*Ridge of protarsomere 5*.— Male specimens of *L. deltoides* and *L. nemorosus* have a ridge evident on the anteroapical edge of protarsomere 5 (Fig. 5P). The ridge is absent in members of all other species and the outgroup; therefore, presence of the ridge is considered apotypic.

*Lobe of protarsomere 5*.— The ventroapical lobe of protarsomere 5 tilts anteriorly so that its overall shape is asymmetrical in males of *L. difformis* (Fig. 5Q) and *L. etnieri*. This condition is not as pronounced in any other members of *Laccornis* (Figs. 5N, O) or the outgroup and thus asymmetry is considered apotypic.

*Claw structure*.— Anterior, protarsal claw characters of males are important in reconstructing the phylogeny as well as for identification of males of *Laccornis*. Modifications within the genus are remarkably divergent. Males of *L. oblongus* have the least modified claw wherein the anterior claw is slightly thickened (Fig. 5D). Males of *L. kocai* have a small basal lobe on the anterior, protarsal claw (Fig. 5C). Males of *L. pacificus* (Fig. 5F) and *L. conoideus* (Fig. 5E) possess a distinct medial tooth on the anterior, protarsal claw. Claw structure in males of *L. deltoides*, *L. nemorosus*, *L. latens*, *L. difformis*, *L. etnieri*, and *L. schusteri* is extremely complicated. The anterior, protarsal claw of male specimens of *L. deltoides* and *L. nemorosus* (Figs. 5G, H) is contorted and slightly expanded while in those of *L. latens* and *L. difformis* it is distinctly contorted and foliate (Figs. 5I, J). Males of *L. schusteri* and *L. etnieri* also have foliate, contorted claws, however, the end of the claw is truncate and the apex is displaced laterally (Figs. 5K, L). An indistinct lateral notch occurs in males of *L. difformis*, whereas a distinct lateral notch is evident in those of *L. etnieri*.

The anterior, protarsal claw of members of the outgroup is scarcely modified. Based on this, we interpret three independent changes in claw structure among lineages within *Laccornis*: 1) development of the basal lobe, 2) development of medial tooth, and 3) tendency towards the progressively more foliate/contorted condition described above. The lateral notch is considered separately and presence of the notch is apotypic.

*Elytral punctation*.— For terms for surface punctures/sensilla see Balfour-Browne (1940a) and Wolfe and Zimmerman (1984). On *Laccornis* specimens,

there are three kinds of punctures: 1) simple, 2) compound concentric with thickened walls, and 3) compound eccentric (see Fig. 1J). Simple punctures are present uniformly on elytral surfaces in all members of *Laccornis* but are extremely difficult to see except with the high magnification of SEM. Compound concentric, thick-walled punctures form the sparsely punctured, elytral striae (Fig. 1F). Compound, eccentric punctures are the most taxonomically important kind of puncture; eccentric punctation varies from almost invisible in members of *L. deltoides* and *L. nemorosus* (Fig. 1F) to relatively coarse and double-sized in members of *L. pacificus* (Fig. 1D).

*Metacoxal sculpture*.— As with elytral punctation, metacoxal punctation varies from almost effaced (Fig. 2F) to distinctly evident (Figs. 2B-D). However, the metacoxae of some specimens have short, impressed lines or strigae. This characteristic is dichotomous (present or absent), relatively easily visible and it is not sexually dimorphic. Therefore we have used it as a good taxonomic as well as a useful phylogenetic character. These strigae are present only in members of *L. latens*, *L. difformis*, *L. etnieri* and *L. schusteri* (Figs. 2E, G). Other species of *Laccornis* (Figs. 2A-D, F) lack metacoxal strigae as do members of the outgroup. Therefore its presence in the four species of *Laccornis* listed above is considered synapotypic.

*Apex of aedeagus*.— The apex of the aedeagus of males of most species is bent downward and/or reflexed to varying degrees. In members of *L. kocai* (Fig. 9), the distal portion is sinuate and bent upward at the tip. In male specimens of *L. etnieri* (Fig. 16), the tip of the aedeagus is deflected ventrally only slightly. Males of *L. difformis* (Fig. 17) and *L. schusteri* (Fig. 18) have the tip of the aedeagus more distinctly bent downward. In male specimens of *L. latens*, *L. deltoides*, and *L. nemorosus* (Figs. 13-15), the tip of the aedeagus is reflexed 180° such that the tip is oriented toward the base of the aedeagus. Males of *L. oblongus*, *L. pacificus*, and *L. conoideus* (Fig. 8, 11, 12) also have aedeagal apices that are reflexed 180° and in addition the reflexed portion is ligulate. Since the aedeagal apex of the outgroup is not ventrally bent or reflexed, the latter condition is considered plesiotypic. Progressively more bent/reflexed and ligulate apices are considered increasingly apotypic (see Table 3).

*Base of aedeagus*.— The base of the aedeagus is enlarged and expanded in members of *L. difformis*, *L. schusteri*, and *L. etnieri* (Figs. 16-18). That condition is absent in other members of *Laccornis* and the outgroup and the enlarged base is considered apotypic.

*Setae of aedeagus*.— In males of *L. oblongus* (Fig. 8), *L. conoideus* (Fig. 12) and *L. pacificus* (Fig. 11) long setae are present along each dorsolateral edge of the aedeagus; this condition is least developed in members of *L. conoideus*. Such setae are not present in any other members of *Laccornis* or the outgroup; presence is apotypic.

*Shape of aedeagus*.— In males of *L. difformis* (Fig. 17), *L. etnieri* (Fig. 16) and *L. schusteri* (Fig. 18) the aedeagus is expanded medially into a plate-like structure; this condition is unique to these three species and it is considered apotypic.

*Lateral projections of aedeagus*.— Males of *L. pacificus* and *L. conoideus* (Figs. 11, 12) have subapical anterolateral projections of the aedeagus (more distinctive in males of *L. conoideus*). Projections are absent in all other members of *Laccornis* and the outgroup and are considered to be apotypic.

*Shape and orientation of hinge of paramere*.— The hinge by which the paramere articulates with the aedeagus is enlarged and oriented horizontally in males of *L. oblongus*, *L. pacificus* and *L. conoideus* (Figs. 8, 11, 12). Associated

with this is a change in overall paramere shape such that the apical two thirds of the paramere is abruptly tapered. Among other species of *Laccornis* the hinge of the paramere is longitudinal (Figs. 9, 16) and the paramere is tapered gradually. These modifications (hinge enlargement, vertical orientation and shape change) are absent in other members of *Laccornis* and in the outgroup and therefore are considered apotypic.

*Setation of parameres.*— In males of *L. oblongus*, *L. conoideus*, and *L. pacificus* (Figs. 8, 11, 12), setae on parameres are arranged in two series: a vertically oriented, basal series and a dorsal, medial series. In all other species of *Laccornis* (Figs. 9, 13-18) and the outgroup there is only a single series on the ventral edge; this latter state is plesiotypic.

*Membrane of parameres.*— In males of *L. etnieri*, *L. difformis*, and *L. schusteri* a large membranous lobe is evident (Figs. 16-18) on the inner, subapical portion of the paramere. Since the lobe is not present in other taxa (Figs. 8, 9, 11-15), including the outgroup, its presence is judged apotypic.

*Coloration.*— Coloration is not very useful taxonomically. The dark (piceous) colour of the pronotum in contrast to lighter colour of the head and elytra of specimens of *L. latens* has been cited as diagnostic of that species. However, this condition also is closely approached in specimens of *L. difformis*, *L. etnieri*, and *L. schusteri*.

Specimens of many species (*L. pacificus*, *L. conoideus*, *L. latens*, *L. difformis*, *L. etnieri*, and *L. schusteri*) occasionally have a distinctly lighter, transverse band across the base of the elytra. As striking as that characteristic can be in some specimens it is virtually absent in others. We have not used colour as a phylogenetic character. However, when sorting specimens, it is useful to know that specimens of *L. deltoides* and *L. nemorosus* are more uniformly, lightly coloured than are those of any other species of *Laccornis*.

*Total length.*— Total length (and greatest width) was measured as described in Roughley and Pengelly (1982). These measurements are given for each taxon in Table 2. Because most of our samples are composed only of few specimens from separate localities and dates, we have not calculated a mean for any of these taxa but instead have concentrated on the range of this statistic. As such it falls into four non-overlapping categories which are useful taxonomically. These categories are 3.30 to 3.50 mm (*L. kocai* only), 4.32 to 4.92 mm (*L. oblongus*, *L. pacificus* and *L. conoideus*), 5.23 to 6.60 mm (most species of *Laccornis*) and 7.00 to 7.23 mm (*L. nemorosus*). By setting limits between the observed measurements we have used these measurements in the key below. These groupings of total length correlate fairly well with the phylogenetic groupings proposed on other characters but we have not used them in the phylogenetic reconstruction.

*Body shape.*— Among members of *Laccornis*, the outline of the body in dorsal view varies from rather oval to parallel-sided to posteriorly tapered. A rough measure of body shape can be achieved by total length/greatest width (Table 2). Differences among specimens of different species are subtle and therefore this character is of limited taxonomic value. However for some few species, body shape is somewhat distinctive: *L. kocai* is more oval than any of its congeners, *L. oblongus* is more parallel-sided, and *L. deltoides* and *L. nemorosus* are distinctly tapered posteriorly.

Table 1.

Matrix of structural characters used for description of species of *Laccornis*; see text for description of character states. kc- *Laccornis kocai*, ob-*L. oblongus*, pc-*L. pacificus*, cn-*L. conoideus*, lt-*L. latens*, dl-*L. deltoides*, nm-*L. nemorosus*, df-*L. difformis*, et-*L. etnieri*, sc-*L. schusteri*; 1=yes or character state present, 0=no or character state absent, S=sometimes, character state present or not. For consistency and clarity, antennal character states which form part of a morphocline and are recorded on successive antennomeres are characterized uniformly for all species.

	kc	ob	pc	cn	lt	dl	nm	df	et	sc
<b>1) ANTENNA</b>										
1.1) <i>Antennomere 7</i>										
1.1.1) <i>Enlargement</i>										
1.1.1.1) normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.1.1.2) slightly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.1.1.3) distinctly enlarged	0	0	0	0	0	0	0	0	0	0
1.1.1.4) greatly enlarged	0	0	0	0	0	0	0	0	0	0
1.1.2) <i>Ventral sculpture</i>										
1.1.2.1) reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.1.2.2) scarcely rugose	0	0	1	1	0	0	0	0	0	0
1.1.2.2) rugose (3 H)	0	0	0	0	0	0	0	0	0	0
1.1.3) <i>Ventral shape</i>										
1.1.3.1) normal	1	1	0	0	1	1	1	1	1	1
1.1.3.2) slightly flattened	0	0	0	0	0	0	0	1	1	1
1.1.3.3) slightly concave	0	0	0	0	0	0	0	0	0	0
1.1.3.4) distinctly concave	0	0	0	0	0	0	0	0	0	0
1.1.3.5) sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.2) <i>Antennomere 6</i>										
1.2.1) <i>Enlargement</i>										
1.2.1.1) normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.2.1.2) slightly enlarged	0	0	0	0	0	0	0	0	0	0
1.2.1.3) distinctly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.2.1.4) greatly enlarged	0	0	0	0	0	0	0	0	0	0

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Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.2.2)	Ventral sculpture										
1.2.2.1)	reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.2.2.2)	scarcely rugose	0	0	0	0	0	0	0	0	0	0
1.2.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.2.3)	Ventral shape										
1.2.3.1)	normal	1	1	0	0	1	1	1	0	0	0
1.2.3.2)	slightly flattened (3 F)	0	0	0	0	0	0	0	1	1	1
1.2.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.2.3.4)	distinctly concave	0	0	0	0	0	0	0	0	0	0
1.2.3.5)	sinuate/convex 3 E, H)	0	0	1	1	0	0	0	0	0	0
1.3	<i>Antennomere 5</i>										
1.3.1)	Enlargement										
1.3.1.1)	normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.3.1.2)	slightly enlarged	0	0	0	0	0	0	0	0	0	0
1.3.1.3)	distinctly enlarged	0	0	0	0	0	0	0	0	0	0
1.3.1.4)	greatly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.3.2)	Ventral sculpture										
1.3.2.1)	reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.3.2.2)	scarcely rugose	0	0	0	0	0	0	0	0	0	0
1.3.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.3.3)	Ventral shape										
1.3.3.1)	normal (3 A, D)	1	1	0	0	1	1	1	1	1	1
1.3.3.2)	slightly flattened	0	1	0	0	0	0	0	0	0	0
1.3.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.3.3.4)	distinctly concave	0	0	0	0	0	0	0	0	0	0
1.3.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.3.4)	Symmetry (dorsal outline)										
1.3.4.1)	rather symmetrical (3 A-D)			1	0	0	1	1	1	1	1
1.3.4.2)	distinctly asymmetrical (3 E, H)	0	0	1	1	0	0	0	0	0	0

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Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.4	<i>Antennomere 4</i>										
1.4.1)	Enlargement										
1.4.1.1)	normal size	1	0	0	0	0	0	0	0	0	0
1.4.1.2)	slightly enlarged (3 A)	0	1	0	0	1	0	0	0	0	0
1.4.1.3)	distinctly enlarged (3 B, F)	0	0	0	0	0	0	0	1	1	1
1.4.1.4)	greatly enlarged (3 C-E, G, H, 4I)	0	0	1	1	0	1	1	0	0	0
1.4.2)	Ventral sculpture										
1.4.2.1)	reticulate (3 F)	1	0	0	0	1	1	1	1	1	1
1.4.2.2)	scarcely rugose	0	1	0	0	0	0	0	0	0	0
1.4.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.4.3)	Ventral shape										
1.4.3.1)	normal	1	0	0	0	0	0	0	0	0	0
1.4.3.2)	slightly flattened	0	1	0	0	1	0	0	0	0	0
1.4.3.3)	slightly concave (3 F)	0	0	0	0	0	0	0	1	1	1
1.4.3.4)	distinctly concave (3 G)	0	0	0	0	0	1	1	0	0	0
1.4.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.4.4)	Symmetry (dorsal outline)										
1.4.4.1)	rather symmetrical (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.4.4.2)	distinctly asymmetrical (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.5	<i>Antennomere 3</i>										
1.5.1)	Enlargement										
1.5.1.1)	normal size (3 A)	1	1	0	0	1	0	0	0	0	0
1.5.1.2)	slightly enlarged (3 C, D)	0	0	0	0	0	1	1	1	1	1
1.5.1.3)	distinct enlarged	0	0	0	0	0	0	0	0	0	0
1.5.1.4)	greatly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0

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Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.5.2)	Ventral sculpture										
1.5.2.1)	reticulate	1	0	0	0	0	0	0	0	0	0
1.5.2.2)	scarcely rugose	0	1	0	0	0	0	0	0	0	0
1.5.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.5.3)	Ventral shape										
1.5.3.1)	normal	1	1	0	0	1	0	0	0	0	0
1.5.3.2)	slightly flattened (3 F)	0	0	0	0	0	1	1	1	1	1
1.5.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.5.3.4)	distinctly concave	0	0	0	0	0	0	0	0	0	0
1.5.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.5.4)	Symmetry (dorsal outline)										
1.5.4.1)	rather symmetrical (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.5.4.2)	distinctly asymmetrical (3 E)	0	0	1	1	0	0	0	0	0	0
<b>2) PROSTERNUM</b>											
2.1)	<i>Prosternal process</i>										
2.1.1)	Width										
2.1.1.1)	moderately broad (4 F)	0	0	0	0	1	0	0	0	0	0
2.1.1.2)	distinctly broad 4 B-E, G)	1	1	1	1	0	1	1	1	1	1
2.1.2)	Longitudinal convexity										
2.1.2.1)	moderately distinct (4 B, C, F, G)	1	1	1	1	1	0	0	1	1	1
2.1.2.2)	less evident	0	0	0	0	0	1	0	1	1	1
2.1.2.3)	scarcely evident (4 D, E)	0	0	0	0	0	0	1	0	0	0
2.2)	<i>Prosternal pore</i>										
2.2.1)	absent (slit present) (4 H)	1	1	1	1	0	0	0	0	0	0
2.2.2)	present (4 I)	0	0	0	0	1	1	1	1	1	1

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Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
<b>3) LEGS</b>											
3.1)	<i>Sublateral mesotibial spines</i>										
3.1.1)	6 or fewer (6 J)	1	0	0	0	0	0	0	0	0	0
3.1.2)	7 or more (6 H)	0	1	1	1	1	1	1	1	1	1
3.2)	<i>Mesofemoral elongate setae</i>										
3.2.1)	absent	1	1	0	0	1	1	1	1	1	1
3.2.2)	present	0	0	1	1	0	0	0	0	0	0
3.3)	<i>Metafemoral elongate setae</i>										
3.3.1)	absent (6 N)	1	1	0	0	1	1	1	0	0	0
3.3.2)	moderately evident (6 O)	0	0	1	1	0	0	0	0	0	0
3.3.3)	distinctly evident (6 P)	0	0	0	0	0	0	0	1	1	1
3.4)	<i>Protarsal enlarged palettes</i>										
3.4.1)	maximum of 2/row (5 A)	1	0	0	0	0	0	0	0	0	0
3.4.2)	maximum of 4/row (5 B)	0	1	1	1	1	1	1	1	1	1
3.5)	<i>Ridge of protarsomere 5</i>										
3.5.1)	absent (5 M,N)	1	1	1	1	1	0	0	1	1	1
3.5.2)	present (5 P)	0	0	0	0	0	1	1	0	0	0
3.6)	<i>Shape of protarsomere 5</i>										
3.6.1)	symmetrical (5 N,O)	1	1	1	1	1	1	1	0	0	1
3.6.2)	asymmetrical (5 Q)	0	0	0	0	0	0	0	1	1	0
3.7)	<i>Ventral sensilla of protarsomere 4</i>										
3.7.1)	spine-like (5 M)	1	0	0	0	0	0	0	0	0	0
3.7.2)	hairlike (5 N, O, Q)	0	1	1	1	1	1	1	1	1	1
3.8)	<i>Ventral spines of protarsomere 5</i>										
3.8.1)	elongate (5 N)	1	1	1	1	0	1	1	0	0	0
3.8.2)	cone shaped (5 O)	0	0	0	0	1	0	0	1	1	1

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
3.9)	<i>Anterior protarsal claw</i>										
3.9.1)	scarcely modified										
	(5 D)	0	1	0	0	0	0	0	0	0	0
3.9.2)	with basal lobe (5 C)	1	0	0	0	0	0	0	0	0	0
3.9.3)	with larger medial tooth										
	(5 F)	0	0	1	0	0	0	0	0	0	0
3.9.4)	with smaller medial tooth										
	(5 E)	0	0	0	1	0	0	0	0	0	0
3.9.5)	slightly contorted										
	(5 G, H)	0	0	0	0	0	1	1	0	0	0
3.9.6)	distinctly contorted										
	(5 I-L)	0	0	0	0	1	0	0	1	1	1
3.9.7)	apex laterally displaced										
	(5 K, L)	0	0	0	0	0	0	0	0	1	1
3.9.8)	apex rather medial										
	(5 I, J)	0	0	0	0	1	0	0	1	0	0
3.9.9)	with slight notch (5 J)	0	0	0	0	0	0	0	1	0	0
3.9.10)	with distinct notch										
	(5 L)	0	0	0	0	0	0	0	0	1	0
4)	<b>ELYTRA</b>										
4.1)	<i>Punctuation</i>										
4.1.1)	coarse (1 D)	0	0	1	0	0	0	0	0	0	0
4.1.2)	moderately coarse										
	(1 C)	0	0	0	1	0	0	0	0	0	0
4.1.3)	less coarse										
	(1 A, B, E, G-I)	1	1	0	0	1	0	0	1	1	1
4.1.4)	fine (1 F)	0	0	0	0	0	1	1	0	0	0
4.2)	<i>Internal ridge</i>										
4.2.1)	absent	1	0	0	0	0	0	0	0	0	0
4.2.2)	scarcely evident	0	1	1	1	0	0	0	0	0	0
4.2.3)	indistinct	0	0	0	0	0	0	0	1	1	1
4.2.4)	evident	0	0	0	0	1	1	1	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
<b>5) METACOA</b>											
5.1)	<i>Sculpture</i>										
5.1.1)	punctuation fine (2 A, F)	1	0	0	0	1	1	1	1	1	1
5.1.2)	punctuation coarse (2 B-D)	0	1	1	1	0	0	0	0	0	0
5.1.3)	strigae present (2 E, G)	0	0	0	0	1	0	0	1	1	1
<b>6) AEDEAGUS</b>											
6.1)	<i>Shape of base</i>										
6.1.1)	base enlarged (16-18)	0	0	0	0	0	0	0	1	1	1
6.2)	<i>Aedeagal setae</i>										
6.2.1)	not evident	1	0	0	0	1	1	1	1	1	1
6.2.2)	somewhat evident (8)	0	1	0	0	0	0	0	0	0	0
6.2.3)	distinctly evident (11, 12)	0	0	1	1	0	0	0	0	0	0
6.3)	<i>Anterolateral projections</i>										
6.3.1)	less distinct (11)	0	0	1	0	0	0	0	0	0	0
6.3.2)	less distinct (12)	0	0	0	1	0	0	0	0	0	0
6.4)	<i>Ventrally reflexed apex</i>										
6.4.1)	not ventrally reflexed (9)	1	0	0	0	0	0	0	0	0	0
6.4.2)	slightly vent. bent (17)	0	0	0	0	0	0	0	1	0	0
6.4.3)	distinctly vent. bent (16, 18)	0	0	0	0	0	0	0	0	1	1
6.4.4)	reflexed (8, 11, 12)	0	0	0	0	1	1	1	0	0	0
6.4.5)	reflexed and ligulate	0	1	1	1	0	0	0	0	0	0
6.5)	<i>Shape (dorsal view)</i>										
6.5.1)	not expanded apically or medially	1	1	1	1	1	0	0	0	0	0
6.5.1)	apex slightly expanded (14)	0	0	0	0	0	1	0	0	0	0
6.5.2)	apex distinctly expanded (15)	0	0	0	0	0	0	1	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
6.5.3)	aedeagus expanded medially (16-18)	0	0	0	0	0	0	0	1	1	1
<b>7) PARAMERES</b>											
7.1)	<i>Setal series</i>										
7.1.1)	ventrally only (9, 13-18)	1	0	0	0	1	1	1	1	1	1
7.1.2)	ventrally and dorsally (8, 11, 12)	0	1	1	1	0	0	0	0	0	0
7.2)	<i>Apex</i>										
7.2.1)	not expanded	1	1	0	0	1	1	1	1	1	1
7.2.2)	expanded (11,12)	0	0	1	1	0	0	0	0	0	0
7.2.3)	with small ventral tip (11, 12)	0	0	1	1	0	0	0	0	0	0
7.3)	<i>Hinge orientation</i>										
7.3.1)	longitudinal (9, 16)	0	0	0	1	1	1	1	1	1	1
7.3.2)	horizontal (11, 12)	0	1	1	1	0	0	0	0	0	0
7.4)	<i>Size of hinge</i>										
7.4.1)	rather enlarged (8)	0	1	0	0	0	0	0	0	0	0
7.4.2)	distinctly enlarged (11,12)	0	1	1	0	0	0	0	0	0	0
7.5)	<i>Apical membranous lobe</i>										
7.5.1)	absent (8, 9, 11-15)	1	1	1	1	1	1	1	0	0	0
7.5.2)	present (16-18)	0	0	0	0	0	0	0	1	1	1
<b>8) BODY SHAPE\COLOR</b>											
8.1)	<i>Shape</i>										
8.1.1)	rather oval	1	0	S	0	S	0	0	S	S	S
8.1.2)	more parallel sided	0	1	S	S	S	0	0	S	S	S
8.1.3)	tapering posteriorly	0	0	0	S	S	1	1	S	S	S
8.2)	<i>Color</i>										
8.2.1)	darker	1	1	1	1	1	0	0	1	1	1
8.2.2)	lighter	0	0	0	0	0	1	1	1	1	1
8.2.3)	with tranverse band	S	0	S	S	S	S	S	S	S	S

Table 2.

Range of measurements (mm) for total length (TL), greatest width (GW) and ratio of total length to greatest width (TL/GW) for specimens of each species of *Laccornis*.

	Total length Min/Max	Greatest width Min/Max	TL/GW
<i>L. kocai</i>	3.30–3.35	1.69–1.84	1.82–1.95
<i>L. oblongus</i>	4.30–4.69	2.00–2.15	2.15–2.18
<i>L. pacificus</i>	4.69–4.92	2.23–2.38	2.07–2.10
<i>L. conoideus</i>	4.23–4.58	2.15–2.46	1.86–1.97
<i>L. latens</i>	5.23–5.62	2.46–2.62	2.13–2.14
<i>L. deltoides</i>	6.26–6.60	3.23–3.46	1.91–1.94
<i>L. nemorosus</i>	7.00–7.23	3.54–3.69	1.96–1.98
<i>L. difformis</i>	5.60–6.15	2.69–3.08	2.00–2.08
<i>L. etnieri</i>	5.23–6.00	2.62–2.92	2.00–2.01
<i>L. schusteri</i>	5.35–6.10	2.63–3.00	2.00–2.03

#### CLASSIFICATION

Laccornini, New Tribe

*Type genus.*— *Laccornis* Gozis, 1914.

*Diagnosis.*— Members of Laccornini are diagnosed among Hydroporinae by common presence of the following character states of adults: mandibles without a ventral, medial row of setae (Fig. 7A), base of metafemur extending distally and contacting metacoxal lobes (Fig. 6Q), and the metathoracic episternum contacting the mesocoxal cavity.

Most previous workers assigned members of *Laccornis* to the tribe Hydroporini of the subfamily Hydroporinae [except Arnett (1960) who placed *Laccornis* in Agabini of Colymbetinae]. However, Hydroporini with *Laccornis* is polyphyletic (Wolfe 1985, 1989). Creation of Laccornini therefore assists in creating a more natural classification of Hydroporinae.

**Description.**— The rationale for division of characters among tribal, generic and species level is given above under Materials and Methods.

**Head.** Cypeus not thickened. Labrum (Fig. 7C) with transverse, dense row of setae along medial 1/3 of anterior edge. A dense, somewhat elliptical patch of thick setae located on ventral, anteromedial portion of labrum, these setae not more spine-like in anterior portion of elliptical patch. A transverse row of 4-7 spines located ventrally on each side in anterolateral region of labrum, spines approximately 4 times longer than wide and separated by 1 to 3 times their width. Epipharynx (Fig. 7C) with a distinct but small, lobe-like structure on each side of middle in anterior region; lobes with sparse, peg-like sensilla. Surrounding each lobe are dense microtrichia that extend posteriorly on each side of middle; intermixed with microtrichia and only just posterior to the lobes are sparsely placed, short sensilla each with an expanded base. Three, long, seta-like sensilla located on each side of epipharynx in anterolateral region and a group of placiform-like sensilla (Fig. 7D) located on each side in posterolateral, epipharyngeal region. Labium (Fig. 7J) with long setae located anteromedially on ventral surface, distinctly denser laterally so that two patches of dense setae are evident. Dorsally, mentum (Fig. 7I) with an anterior, transverse row of spines, more laterally placed spines distinctly longer than medial ones, lateral spines in some specimens appearing as a double row; anterior to the transverse row is a group of about 5, short, peg-like spines; mentum with dorsal surface distinctly elevated posteriorly, elevated area with a sparse group of very short sensilla. Labial palp (Figs. 7I-L) 4-segmented; palpomere 2 not cleft anteriorly; palpomere 3 anteroapically produced, apex with a group of about 5 to 6 sensilla, 1 or 2 long and hair-like, at least one short spine, the others peg-like; palpomere 4 not apically emarginate and with only one dense patch of sensilla (Figs. 7K, L); palpomeres 3 and 4 otherwise with short, stout irregularly placed spines. Maxilla (Figs. 7E-H) concealed in repose. Maxillary cardo (Fig. 7F) with two long setae apicolaterally and a group of irregularly placed, very short spines just posterior to long setae. Stipes (Fig. 7F) with a posteromedial group of 3 to 4, closely placed setae and one long seta in anteromedial region. Lacinia basolaterally somewhat furrowed, galea 2-segmented (Figs. 7E, G) and articulated within furrow; maxillary palp placed just behind galea. Galeomere 2 with short coniform, irregularly placed sensilla along entire length, apex with a cluster of about 5-7 sensilla, two of these larger and broader than others. Lacinia curved, tapering to blunt point, scythe-like in shape; basomedial, oval sclerite evident (Figs. 7E, G); dorsomedial row of at least 4 spines, posterior ones longer and thinner than anterior ones; posterior to dorsal medial row is an elongate patch of very short, stout spines. Medial lacinial edge with a row of about 15 long, curved, stout spines (Figs. 7G, H); these medial spines separated into an apical (4 spines) and basal (16 spines) group by a medial gap; on basal sclerite there are 8 spines on dorsal medial edge and 4 spines on alternate side; sub-apex of lacinia with one, medially placed, more slender, seta-like spine; apex of lacinia (Fig. 7H) with elongate digitiform sensilla; one short spine on ventromedial surface. Maxillary palp (Fig. 7E) 4-segmented, maxillomere 1 not distinctly cleft medially, maxillomere 4 with 2 dense patches of sensilla at apex; apicolaterally with oval series of digitiform sensilla. Mandibles (Fig. 7A) without dorsolateral groove; apex truncate, with 2-3 retinacular teeth, retinacular teeth of left mandible smaller than those of right mandible. No ventromedial, mandibular setae evident; apical patch of setae present or not.

**Prothorax.** Prosternum and prosternal process in different plane.

**Pterothorax.** Metasternal process interlocked onto mesosternum. Metafurca (Figs. 7N, O) expanded into a triangularly shaped, broad, flat plate on each side; anteromedial portion with two pairs of distinct concave depressions for muscle insertion; another pair of less distinct depressions in anterolateral region, one on each side; anterodorsal edge of basal portion of metafurca cleft (in dorsal view) but cleft portion not projecting anteriorly between anterolateral extensions of metafurca. Flight wing (Fig. 7M) with M4 vein not connected to oblongum cell; subcubital binding patch very distinct. Elytral apex evenly rounded, not acute. Proventriculus (Fig. 7B) of typical hydroporine type; each oval crushing lobe with transverse medial tooth, each valve-like inner lobe with anterior ciliate flap.

**Legs.** Natatory setae observed on each (Figs. 6A-P) of: dorsal edge of profemur (Fig. 6B) and mesofemur (Fig. 6D); dorsal and ventral edge of protibia (Figs. 6E-G), mesotibia (Figs. 6H-J), and metatibia (Fig. 6L); natatory setae sparse on ventral edge of protibia; dorsal surface of protarsus and mesotarsus and dorsal and ventral surface of metatarsus. Some species additionally with elongate setae on meso- and metafemora (Figs. 6O, P) of males, otherwise no sexual



differences in placement of elongate setae. Profemur with a shallow ventroapical sinuation which has a row of closely placed, short spines (Fig. 6A); anterior, dorsal edge with a longitudinal row of spines and another row just below this; irregularly placed spines on lower 1/2 of anterior profemoral surface, longer and more dense posteriorly and ventrally. Ventral edge with fewer (but longer) spines than dorsal edge. Posterior, profemoral surface (Fig. 6B) with fewer spines than anterior surface; an irregular, longitudinal row of short spines about 1/4 of length from dorsal edge; a more or less transversely arranged group of small spines at medial and distal end. Protibia (Figs. 6E-G) with a row of spines along dorsal edge on each side of elongate setae but extending only 3/4 of length; ventral edge with a dense row of very closely placed spines extending almost to apex, just beside this is another, more irregularly arranged, more sparse row; anterior face with scattered, short spines becoming stouter and more numerous apically; ventral surface with fewer spines than anterior surface, arranged primarily longitudinally in ventral 1/3; apical edge of protibia with a row of very stout spines, 4 to 6 of these prolonged at dorsoapical and ventroapical edge. Chaetotaxal characteristics of midlegs (Figs. 6C, D, H, I, J) generally as for anterior legs but spines larger and stouter; anterior apical sinuation absent; an extra, sublateral row of 7 to 15 widely spaced spines evident. Metafemur (Figs. 6N-P) with sparse, randomly arranged, short setae, some specimens with a discernable, short row of setae evident in apical 1/3. Metatibia (Figs. 6K, L) with sparse row of distinct, short and stout spines. Ventral surface with two rows of short spines, one in anterior 1/3 and the other in posterior 1/3; dorsal surface with short spines more randomly placed than on ventral side; apex of metatibia ringed with a row of short, proximally placed spines, spines at anteroapical and posteroapical edge longer, ventroapical spines longest. Each metatarsomere (Fig. 6M) with 2 distinct longitudinal rows of short spines along anterior and posterior margins of ventral edge, one row on each side of ventral, elongate setae; posteroventral row progressively more abbreviated on tarsomeres 2-5; posterodorsal, apical edge of tarsomeres 1-4 with transverse row of closely placed spines; metatibial claws equal in length.

### Genus *Laccornis* Gozis

*Laccornis* Gozis 1914a:111 [Erected as subgenus of *Hydroporus* Clairville. Type species, *Hydroporus oblongus* Stephens 1835:437, fixed by subsequent monotypy of Gozis 1914b:146]; Zimmermann 1930:94; Guignot 1932:283, 419; Zimmermann 1933:190, Balfour-Browne 1934:225; Houlbert 1934:43, 71; Zaitzev 1953:125, 177; Leech and Chandler 1956:309; Leech and Sanderson 1959:992; Arnett 1960:195, 198; Wewalka 1969:49; Schaefflein 1971:20, 46; Malcolm 1971:16, 22; Larson 1975:257, 325; Brigham 1982:10.53, 10.57; White *et al.* 1984:385.

*Agaporus* Zimmermann 1919:147, 160, 194. [Type species, *Hydroporus oblongus* Stephens 1835:437, fixed by subsequent designation in Zoological Record for 1923, volume 60 (11):132, published in 1925]; Zimmermann 1920:134; Fall 1923:6, 121.

*Taxonomic history*.— Sharp (1882) in his key to species-groups of *Hydroporus*, diagnosed members of his species-group 9 on the form of the metacoxal processes. To this species-group he assigned one Palearctic species, *H. oblongus* Stephens, one Nearctic species, *H. difformis* LeConte, two Neotropical species, *H. lugubris* Aubé and *H. copelatoides* Sharp, and an African species, *H. advena* Sharp.

Gozis (1914a, b) described *Laccornis* as a subgenus of *Hydroporus* and assigned to it only *H. oblongus*. Apparently unaware of this Zimmermann (1919: 147, 160, 194) provided the name *Agaporus* for most of Sharp's group 9 except that he transferred *H. advena* to his new genus *Canthyporus* Zimmermann. As with most of Zimmermann's new genera he did not designate a type species for *Agaporus*.

Fall (1923) discussed the characteristics of *Agaporus* in his revision of Nearctic species and described one new species, *A. deltoides*. Later Fall (1937) described another North American species, *A. latens*. Zimmermann (1930) first noted synonymy of *Agaporus* and *Laccornis* and elevated *Laccornis* to generic

level. Generic status was maintained by Guignot (1932) and Balfour-Browne (1934, 1938 and 1940a, b). The latter reviewed many of the structural features which distinguish the majority of the members of *Laccornis*, although he limited his discussion to *L. oblongus*.

In 1935, Gschwendtner described a species from Austria which he named *Hydroporus brevisculus*. This species was later transferred to *Laccornis* by Gschwendtner (1939) and subsequently found (Wewalka 1969) to be a junior, subjective synonym of *L. kocai* (Ganglbauer) which had been assigned variously to *Hydroporus* Clairville or *Graptodytes* Seidlitz.

As listed above, the first designation of the type species that we can find for *Agaporus* is in the Zoological Record 6 (11):132 (1925) for 1923. This appears to be an inadvertent error. However, according to Article 69 (iv) of ICZN (1985), this type designation is valid and therefore *Agaporus* is a junior, objective synonym of *Laccornis* Gozis. Subsequently, Balfour-Browne (1940b:205) writes of *Agaporus* "...type, sole species cited = *oblongus* Steph." As noted above, Zimmermann (1919:160) clearly included more taxa within his concept of *Agaporus* and Zimmermann did not indicate a type species although he does formally describe only *A. oblongus* (Zimmermann 1919:192). Also in 1940, Leech described another North American species, *L. pacificus*.

Guignot (1955) described an African species which he assigned to *Laccornis*, *L. sigillatus*, however, this species was transferred to *Canthyporus* by Wewalka (1981). Wolfe and Spangler (1985) described two additional species, *L. etnieri* and *L. schusteri*, from the eastern United States. Wolfe (1985, 1989) presented a phylogenetic analysis of plesiotypic members of Hydroporinae and provides much of the rationale for recognizing *Laccornis* as belonging to a distinct tribe. Roughley and Wolfe (1987) have erected a new genus, *Laccornellus*, to receive the two Neotropical species previously placed in *Laccornis*.

**Diagnosis.**— Members of *Laccornis* are characterized by the short rather broad prosternal process (Figs. 4B-G), presence of enlarged setae on ventral surface of protarsomere 3 (Fig. 5B) and the presence of valvifer in adult females (Fig. 10).

**Description.** —

**Size and shape.** Total length of body from 3.30 to 7.3 mm. Greatest width from 1.69 to 3.69 mm. Shape of outline of body short and broad, to parallel, to elongate (Total length/greatest width = 1.87 - 2.18). Head, pronotum and elytron in continuous outline; posterolateral corner of pronotum not distinctly angulate.

**Head.** Without cervical carina behind eye.

**Microsculpture.** Microreticulation of most specimens hexagonal-pentagonal (Figs. 1A-J). Three types of punctures: compound, eccentric punctures; compound, concentric punctures with thickened walls; and simple punctures, in which about nine, reticulate lines radiate out from each puncture so that arrangement of sculpticels around it has a rosette-like appearance (Fig. 1J).

**Prothorax.** Lateral, pronotal bead distinct, maximum width about 1/2 width of terminal antennomere. Prosternal process broad, length to width ratio at least 2.5; laterally margined; declivity not distinctly protuberant; apex broadly rounded (Figs. 4B-G). Prosternal process reaching metasternal process and interlocking with apical, metasternal notch. Pronotum without plicae.

**Pterothorax.** Elytron with lateral edge almost straight in lateral view, not ascending anteriorly, without humeral carina; ventral, elytral ridge evident but not distinctly elevated or ligulate posteriorly. Metacoxal process medially incised (in ventral view, Fig. 6Q) but not recessed (in posterolateral view).

**Coloration.** Primarily brownish to blackish dorsally and ventrally, some specimens with a lighter transverse band across elytral base.

**Protarsus.** Protarsus with 2 to 4 modified palettes on each of tarsomeres 1-3 (Figs. 5A-B). Protarsomere 4 with 2 short spines.

**Female genitalia.** Valvifer present (Fig. 10). Genital valve with short apodeme; lateral edge, apicomedial edge and apex with dense setae of variable length. Vulval sclerite with a row of setae along posterior edge.

**Sexual dimorphism.**— Males of most taxa have modified antennae and protarsi. Additionally, males of some species have elongate setae on the meso- and/or metafemora.

**Geographic distribution and habitat.**— The genus as now constituted is restricted to the Holarctic region. Except for the enigmatic *L. kocai* (see below), most specimens of *Laccornis* are collected in woodland pools. Many of these pools are temporary in nature and exist only in spring and into early summer.

#### Key to Adults of Species of *Laccornis*

A key to most of the North American species of *Laccornis* is given in Wolfe and Spangler (1985). That key extensively uses sexual characteristics of male specimens. However specimens of many species of *Laccornis* exhibit a large degree of sexual dimorphism and this makes a key which is effective for both sexes, simultaneously, difficult to construct. Therefore in the following key the sexes are separated beyond couplet 3. Confident determination of specimens is best accomplished with male specimens. Identification of female specimens is much less confidently accomplished in the key below because of use of fewer and less reliable characters such as colour, size and distribution. Therefore female specimens are best identified by association with males; the key may be helpful in corroborating the identification of some female specimens.

- |    |      |   |    |
|----|------|---|----|
| 1  |      | Palaearctic specimens .....   | 2  |
| 1' |      | Nearctic specimens .....  | 3  |
| 2  | (1)  | Shorter specimens, TL=3.30-3.50 mm; body shape oval, TL/GW=1.82- 1.95; distribution more southern (Fig. 20C)....  |    |
|    |      | ..... <i>L. kocai</i> (Ganglbauer), p. 308  |    |
| 2' |      | Longer specimens, TL=4.30-4.69 mm; body shape more elongate, TL/GW= 2.15-2.18; distribution more northern (Fig. 20C) .....  |    |
|    |      | ..... <i>L. oblongus</i> (Stephens), p. 309   |    |
| 3  | (1') | Protarsomeres 1 to 3 ventrally each with four, enlarged palettes (Fig. 5B); antennomere 4, at least, of most species enlarged and/or of different shape from subapical antennomeres (Figs. 3A- H); anterior protarsal claw modified and of different shape from posterior claw. Male specimens..... | 4  |
| 3' |      | Protarsomeres 1 to 3 ventrally with all setae of about same size; antennomere 4 not modified, similar in shape to subapical antennomeres; anterior protarsal claw not modified, similar in shape to posterior claw. Female specimens .....  | 12 |
| 4  | (3)  | Metacoxa with punctation coarse (Figs. 2B-D), appearing subrugose; shorter specimens, TL less than 5.1 mm (TL=4.23-5.00 mm) .....   | 5  |
| 4' |      | Metacoxal punctation fine (Figs. 2A, E-G); longer specimens, TL more than 5.1 mm (TL=5.23-7.23 mm).....   | 7  |
| 5  | (4)  | Anterior protarsal claw without medial tooth (Fig. 5D); meso- and metafemur (Fig. 6N) without elongate setae on posterior margin.....   |    |
|    |      | ..... <i>L. oblongus</i> (Stephens), p. 309   |    |

5'	Anterior, protarsal claw with medial tooth (Figs. 5E-F); meso- and metafemur (Fig. 6O) with elongate setae on posterior margin .....	6
6 (5')	Shorter specimens, TL less than 4.60 mm (TL=4.23-4.58 mm); anterior, protarsal claw with medial tooth shorter (Fig. 5E); distribution transcontinental but predominantly east of Rocky Mtns. (Fig. 20C)..... <i>L. conoideus</i> (LeConte), p. 312	
6'	Longer specimens, TL more than 4.6 mm (TL=4.69-4.92 mm); anterior, protarsal claw with medial tooth longer (Fig. 5F); distribution western, predominantly west of Rocky Mtns. (Fig. 20C) .....	<i>L. pacificus</i> Leech, p. 313
7 (4')	Metacoxa without evident strigations (Fig. 2F); longer specimens, TL more than 6.2 mm (TL=6.28-7.23 mm); protarsomere 5 with apex with anterolateral ridge (Fig. 5P); elytral punctation fine (Figs. 1A, F) .....	8
7'	Metacoxa with evident strigations (Figs. 2E-G); shorter specimens, TL less than 6.2 mm (TL=5.23-6.15 mm); protarsomere 5 with apex symmetrical (Fig. 5P); elytral punctation coarse (Fig. 1B, G-I) .....	9
8 (7)	Longer specimens, TL more than 6.8 mm (TL=7.0-7.23 mm); aedeagus more expanded apically (Fig. 15C); distribution more southern (Fig. 20B)..... <i>L. nemorosus, n.sp.</i> , p. 317	
8'	Shorter specimens, TL less than 6.8 mm (TL=6.26-6.60 mm); aedeagus less expanded apically (Fig. 14C); distribution more northern (Fig. 20B).....	<i>L. deltoides</i> (Fall), p. 316
9 (7')	Metafemur without elongate setae (Fig. 6N) on posterior margin; antennomere 4 scarcely enlarged (Fig. 3A); aedeagus parallel-sided medially, apex reflexed (Fig. 13 A-C) .....	<i>L. latens</i> (Fall), p. 315
9'	Metafemur with elongate setae (Fig. 6P) on posterior margin; antennomere 4 evidently enlarged (Fig. 3B); aedeagus broadly expanded medially, apex bent but not reflexed (Figs. 16A-C - 18A-C) .....	10
10 (9')	Anterior protarsal claw with apex placed medially (Fig. 5J)..	<i>L. difformis</i> (LeConte), p. 319
10'	Anterior protarsal claw with apex placed laterally (Figs. 5K, L).....	11
11 (10')	Anterior protarsal claw with long, anterolateral process, notch absent (Fig. 5K). .....	<i>L. schusteri</i> Wolfe & Spangler, p. 320
11'	Anterior protarsal claw with short, anterolateral process, notch present (Fig. 5L).....	<i>L. etnieri</i> Wolfe & Spangler, p. 316
12 (3')	Metacoxa with evident strigations (Figs. 2E-G).....	17
12'	Metacoxa without evident strigations (Fig. 2F).....	13
13 (12')	Metacoxa with punctation coarse (Figs. 2B-D), appearing subrugose; TL less than 5.0 mm (TL=4.23-4.92 mm); body in dorsal aspect relatively rounded posteriorly .....	14
13'	Metacoxa with punctation fine (Figs. 2A, F); TL more than than 6.0 mm (TL=6.26-7.23 mm); body in dorsal aspect relatively attenuate posteriorly .....	16

- 14 (13) TL/GW >2.13 (TL/GW=2.15-2.18); most specimens with elytra not distinctly paler basally; known from northwestern North America (Fig. 20C) ..... *L. oblongus* (Stephens)  
 14' TL/GW <2.13 (TL/GW=1.86-2.10); most specimens with elytra distinctly paler basally; distribution transcontinental including northwestern North America (Fig. 20C) ..... 15  
 15 (14') TL less than 4.63 mm (TL=4.23-4.58); distribution transcontinental with most records from east of Continental Divide (Fig. 20C) ..... *L. conoideus* (LeConte), p. 312  
 15' TL more than 4.63 mm (TL=4.69-4.92 mm); distribution western with most records from west of Continental Divide (Fig. 20C) ..... *L. pacificus* Leech, p. 313  
 16 (13') Longer specimens, TL more than 6.8 mm (TL=7.0-7.23 mm); distribution more southern (Fig. 20B) .....  
 ..... *L. nemorosus*, n.sp., 317  
 16' Shorter specimens, TL less than 6.8 mm (TL=6.26-6.60 mm); distribution more northern (Fig. 20B) .....  
 ..... *L. deltoides* (Fall), p. 316  
 17 (12) Prosternal process narrower (Fig. 4F) .....  
 ..... *L. latens* (Fall), p. 315  
 17' Prosternal process broader (Fig. 4G) ..... 18  
 18 (17') Distributed primarily on the Atlantic coastal plain (Fig. 20A) .....  
 ..... *L. difformis* (LeConte), p. 319  
 18' Distributed primarily to the west of the Atlantic coastal plain (Fig. 20A) ..... 19  
 19 (18') Distribution more eastern and/or more northern (Fig. 20A) ...  
 ..... *L. etnieri* Wolfe & Spangler, p. 320  
 19' Distribution more western and/or more southern (Fig. 20A) ...  
 ..... *L. schusteri* Wolfe & Spangler, p. 320

*Laccornis kocai* (Ganglbauer)

(Figs. 1A, 4B, 5A, 5C, 6J, 9A-D, 10, Map, Fig. 20D)

*Hydroporus kocae* Ganglbauer 1906:352 [Type locality-- Vinkovci, eastern Croatia, Yugoslavia.

Type repository-- NMW], Zimmermann 1920:88.

*Graptodytes kocae*; Zimmermann 1932:70; Csiki 1946:623.

*Laccornis brevisculus* Gschwendtner 1935:2 [Type locality-- Zurndorf, Burgenland, Austria.

Information about type specimens in Wewalka (1969). Types not re-examined. Type

repository-- Oberösterreichischen Landesmuseum in Linz, Austria], Gschwendtner

1939:17; Csiki 1946:627; Zaitzev 1953:178.

*Laccornis kocae* Wewalka 1969:46. *Laccornis kocai*; Schaefflein 1970:89 [Justified emendation],

1971:47.

*Type information and taxonomic notes.*— The type was examined by GWW and it is a female. It is deposited in NMW and bears the following label information: Vinkovci, Slav 74900 G. kocai/*Hydroporus kocae* Gangl. Typ/TYPUS/Coll Mus. Vin. dob./*Laccornis kocae* Gangl. det Wewalka 68. Although we did not re-examine the type of *L. brevisculus*, we accept Wewalka's (1969) conclusion that *L. brevisculus* is a junior, subjective synonym of *L. kocai*.

*Diagnostic combination.*— The short body length (TL=3.30-3.50mm) and southern European range (Fig. 20D) should easily separate specimens of both

sexes from all other species of *Laccornis*. In addition, male specimens have the aedeagus bisinuate in lateral view and the tip deflexed in the opposite direction (Fig. 9) to that of all other extant *Laccornis*.

*Description*.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process illustrated in Fig. 4B; elytral punctation, Fig. 1A; metacoxal punctation, Fig. 2A; male protarsus, Fig. 5A; male protarsal claws, Fig. 5C; male genitalia, Fig. 9; female genitalia, Fig. 10.

*Sexual dimorphism*.— Males have unmodified antennomeres. The male protarsus is scarcely broader than that of the female and there are only two, enlarged palettes on each of protarsomeres 1 to 3 of males (Fig. 5A). The male, anterior, protarsal claw is slightly shorter than the posterior and has a distinctive, basal lobe (Fig. 5C). Wewalka (1969) mentioned also that abdominal sterna 2 and 3 are more distinctly strigate in males than in females.

*Natural history*.— There is little biological information published on this species. Adults were collected in a cold, spring-fed pond at Moosbrunn, 40 km south of Vienna (Wewalka 1969), and one specimen was collected in the margin of rushes of the Neusiedler See, Austria (Schaefflein 1979). Up to 1970 only 22 specimens were known from six localities in Austria, Hungary and Yugoslavia (Geiser 1978). Subsequently however more than 100 specimens were taken in a flooded meadow at St. Margarethen, Burgenland, Austria (Geiser 1978, Schaefflein 1983). This meadow is frequently dry by late summer but specimens were collected from the larger ditches in association with other tyrphophilic or tyrphobiontic species (Geiser 1978).

*Distribution*.— (Fig. 20D). This species is known from only one or a few localities in each of Austria, Hungary and Yugoslavia. The map of its known distribution was compiled from locality information provided by Wewalka (1969) and Schaefflein (1979, 1983). The known range is completely allopatric to all other species of *Laccornis*.

*Phylogenetic relationships*.— *Laccornis kocai* represents the sister lineage to all other members of *Laccornis* (Fig. 19).

*Laccornis oblongus* (Stephens)  
(Figs. 1B, 2B, 4C, 4H, 5D, 8A-E; Maps, Figs. 20C-D)

*Hydroporus oblongus* Stephens 1835:437 [Type locality-- Cambridge, England. Type not examined. Type repository-- BMNH. **Note**--a complete catalogue of *H. oblongus*, *H. nitidus* and *H. bohemani* is given in Zimmermann (1920:134) and is not repeated here].

*Hydroporus nitidus* Sturm 1835:38, plate 207 [Type locality-- Lappland. Type not examined. Type repository-- ZSM].

*Hydroporus bohemani* Thomson 1856:198 [Type locality-- Lappland. Type not examined. Type repository-- ZM].

*Laccornis oblongus*; Gozis 1914b:146, Guignot 1932: 420, Zimmermann 1933:190, Balfour-Browne 1934:225, Houlbert 1934:71, Balfour-Browne 1938:36, 1940a:361, Leech 1940:127, Csiki 1946:626, Guignot 1947:125, Balfour-Browne 1953:19, Zaitzev 1953:177, Schaefflein 1971:46, Wolfe and Spangler 1985:71.

*Agaporus oblongus* Zimmermann 1919:192, 1920:134; Fall 1923:121.

*Type information and taxonomic notes*.— We have not examined the type of this well-known species and have followed European taxonomists in recognizing *H. nitidus* and *H. bohemani* as junior, subjective synonyms of *L. oblongus*. Confusion between this species and *L. conoideus* is discussed more fully in the treatment of latter.

*Diagnostic combination*.— Palearctic specimens are easily determined because they are longer (TL=4.30-4.69 mm), the body shape is more elongate

(TL/GW=2.15-2.18 and the distribution is more northern and/or more eastern (Figs. 20C-D) compared to that of the only other Palearctic species, *L. kocai*. In the Nearctic region, the size of specimens and phylogenetic characters group *L. oblongus* with *L. conoideus* and *L. pacificus*. Males of the latter two species, however, have the anterior, protarsal claw toothed medially and antennomere 4 is distinctly widened. Females of *L. oblongus*, *L. pacificus*, and *L. conoideus* are difficult to separate; however, most female specimens of *L. oblongus* are not as long as those of *L. pacificus* and have a distinctly narrower more parallel sided shape than those of *L. conoideus*.

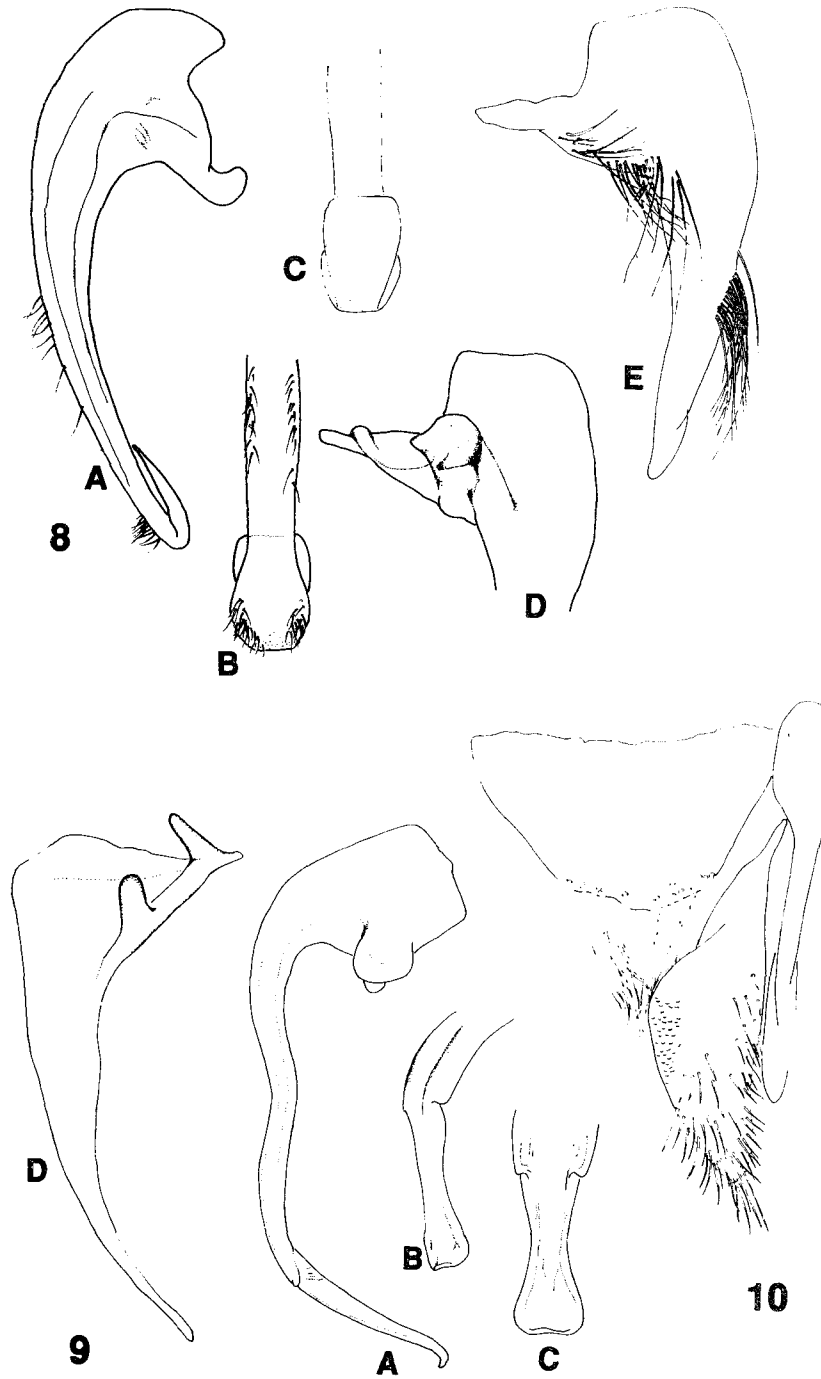
*Description*.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process illustrated in Fig. 4C; elytral punctation, Fig. 1B; metacoxal punctation, Fig. 2B; male protarsal claws, Fig. 5D; male genitalia, Fig. 8.

*Sexual dimorphism*.— Male specimens of *L. oblongus* have antennomere 4 only slightly widened/modified and antennomere 4 has the reticulation of the ventral surface little modified. The anterior, protarsal claw of males is scarcely thicker than the posterior claw (Fig. 5D) and the claws are almost equal in length. Except for *L. kocai*, *L. oblongus* is the least sexually dimorphic species of *Laccornis*.

*Natural history*.— In the British Isles this species is known to overwinter, as an adult, in ponds under ice and its "...normal habitat is mossy, peaty or rushy pools and swamps of clear water, but it also occurred...less frequently in muddy and swampy dykes in which the water was thick with ordinary fresh-water vegetation..." (Balfour-Browne 1940a:364). From his experience in northern France, Guignot (1947) adds an affinity for pools with decomposing leaves. In a survey of water beetle habitats in south-central Finland, Koskinen (1960) collected adult *L. oblongus* only from field pools formed by snow melt or rain. It is described as tyrophophilous species and it occurs among coarse organic debris of aquatic vascular plants (Schaefflein 1971, Cuppen and Dettner 1987). The specimens from Siberia, which we examined were collected from small ponds on the taiga, overgrown with *Hypnum* (Poppius 1905). The life history and larval instars are described by Cuppen and Dettner (1987).

*Distribution*.— (Figs. 20C-D). This is the only Holarctic species of *Laccornis*. It occurs across northern Europe, Siberia and into northwestern North America. In Fig. 20C, which illustrates only the European distribution, filled circles indicate localities from which we examined specimens and the approximate limits of the range (solid line) are generalized from Borchert (1938), Lindroth *et al* (1960), Balfour-Browne (1960) and Nilsson (1983). Extralimital to this map we saw specimens from Shigansk, (=Zigansk, 66°45'N 123°20'E) and Ust Aldan, in Siberia, USSR. The single North American specimen is from Tununuk, NWT (Wolfe and Spangler 1985) and this locality is indicated in Fig. 20D. However, this species is probably more widespread in the Nearctic portion of Beringea, as Hamilton (1894a) records *L. oblongus* from Unalaska, Alaska although Hamilton may have been examining specimens of *L. conoideus* which he considered to be a synonym of *L. oblongus*.

*Phylogenetic relationships*.— *Laccornis oblongus* is the sister species to *L. conoideus* + *L. pacificus* (Fig.19). This relationship is established by synapotypic character states of male antennomeres and genitalia.



Figures 8A-E, 9A-D, 10. Fig. 8. *Laccornis oblongus*, male genitalia. A-C. Aedeagus (150x). A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-E. Paramere (150x). D) Posteromedial view, showing enlarged, modified hinge, E) Lateral view. Fig. 9. *L. kocai*. male and female genitalia. A-C. aedeagus (200X). A) lateral view, B) apicodorsal, lateral view, C) dorsoapical view, D) paramere, medial view. Fig. 10. *L. kocai* (200x). Female genitalia, vulval sclerite, ovipositor, and valvifer.



*Laccornis conoideus* (LeConte)  
(Figs. 1C, 2C, 3E, 3H, 5E, 12A-F; Map, Fig. 20C)

*Hydroporus conoideus*; LeConte 1850:216 [Type locality-- Eagle Harbor, Lake Superior. Type repository-- MCZ], LeConte 1855:292, Crotch 1873:396. *Hydroporus oblongus*; Sharp 1882:485, *ex parte* Hamilton 1894a:13, 1894b:357, *ex parte* Wickham 1895:76, *ex parte*, Hamilton 1889:100, *ex parte* (nec Stephens 1835).

*Agaporus conoideus*; Zimmermann 1919:192, 1920:134, Fall 1923:122. *Laccornis conoideus*, Leech 1940:126, Hatch 1953:215, Wewalka 1969:49, Wallis and Larson 1973:106, Larson 1975:326, Wolfe and Spangler 1985:70.

*Type information and taxonomic notes.*— The holotype is a male with the following label information: [light greenish, circular tag]/3405/type 6037 [red label, black type]/*H. conoideus* Lec. [hand written]. The type locality, although not recorded on labels, is known to be Eagle Harbor, Michigan (see LeConte 1850).

Sharp (1882) was the first author to consider *L. conoideus* as a junior synonym of *L. oblongus*. Most European authors, thereafter, have recorded *L. oblongus* as occurring in North America. Fall (1923) re-established the current usage of these two names.

*Diagnostic combination.*— Except for those of *L. pacificus*, males of *L. conoideus* are recognized easily by the unique modifications of antennomeres 3-7 (Figs. 3E, H), medially toothed, anterior, protarsal claw (Fig. 5E), and elongate setae on meso- and metafemora. Males of *L. conoideus* are separated from those of *L. pacificus* by the less distinctly toothed, anterior, protarsal claw. Males and females both can be separated from those of *L. pacificus* by presence of slightly denser and finer elytral punctation (compare Figs. 1C, D), shorter total length of the body (Table 2), and the more northern and eastern distribution (Fig. 20C).

*Description.*— Taxonomically important character states are presented in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. oblongus* in Fig. 2C; elytral punctation, Fig. 1C; metacoxal punctation as in Fig. 4C; male antenna, Figs. 3E, H; male protarsal claws, Fig. 5E; male metafemur with elongate setae as in *L. pacificus*, Fig. 60, and mesofemur with elongate setae; male genitalia, Fig. 12.

*Sexual dimorphism.*— The distinctive modifications of male antennae, protarsal claws, and presence of elongate setae on meso- and metafemora establish this species and *L. pacificus* as the most sexually dimorphic species among *Laccornis*.

*Natural history.*— The majority of our records of *L. conoideus* are from the boreal biome where it is collected predominantly from quite cold, shallow pools or ponds dominated by *Carex* or by *Carex* and *Sphagnum* (Larson 1975:327, pers. obs.). Therefore this is probably the most typical habitat of *L. conoideus*. However, specimens also occur in snowmelt ponds in parkland regions and in non- to low salinity ponds in grassland areas (Larson 1975:326). These relatively temporary ponds provide an additional biotype for *L. conoideus* and apparently exist just long enough for them to complete larval development.

We collected specimens from shaded portions of a drying streambed and a calcareous bog in southern Ontario, from shaded margins of a large *Carex* marsh, small depressions in the *Sphagnum* mat of a cedar and black spruce bog, and dense moss in a non-acidic bog surrounded by larch in Manitoba, as well as from a richly vegetated, permanent pond north of Old Crow, Y.T. In the sandhills region of Nebraska, three specimens were collected in a small, possibly

semipermanent pond which was partially shaded by saplings. Specimens from Colorado were taken at 9,000 ft. elevation.

The larva of this species was described by Watts (1970) and Alarie (1989). Teneral adult specimens were examined from (arranged approximately south to north): 20/v/1937 (Wisconsin), 10/vi/1969 (Minnesota), 18/vi/1933, 21/vi/1978 and 2/vii/1978 (Ontario), 21/viii/1935 (Quebec), and 10/viii/1920 (Manitoba). Larson (1975) recorded teneral specimens from July to late August in Alberta.

*Distribution (Fig. 20C).*— As noted above under *L. oblongus*, Hamilton's (1894a) record of *L. oblongus* from Unalaska, Alaska may represent either *L. oblongus* or *L. conoideus*. It is difficult to assign this record to either species without re-examining his specimens which we were unable to find. Even without this record, *L. conoideus* has a large range. It extends from the northern Yukon Territory east to Newfoundland and the most southern records are from northern Colorado and Nebraska in the midwestern United States. In North America, *L. conoideus* is probably allopatric to *L. oblongus*, however, they may be sympatric within Beringia. The distribution of *L. conoideus* is parapatric to that of *L. pacificus* (Larson 1975). In the northeastern United States, *L. conoideus* is sympatric with *L. latens* and *L. deltoideus* although some range overlap with *L. difformis* is possible, (compare Figs. 20A and Fig. 20C).

*Phylogenetic relationships.*— *Laccornis conoideus* is the sister species to *L. pacificus* (Fig. 19).

*Laccornis pacificus* Leech  
(Figs. 1D, 2D, 5F, 60, 11A-E; Map, Fig. 20C)

*Hydroporus oblongus*; Sharp 1882:485, *ex parte* (*nec* Stephens 1835).

*Agaporus conoideus*; Fall 1923:122, *ex parte* (*nec* LeConte 1850).

*Laccornis pacificus* Leech 1940:123 [Type locality-- Salmon Arm, British Columbia. Type repository-- CNC], Hatch 1953:215, Wewalka 1969:49, Larson 1975:327, Wolfe and Spangler 1985:70.

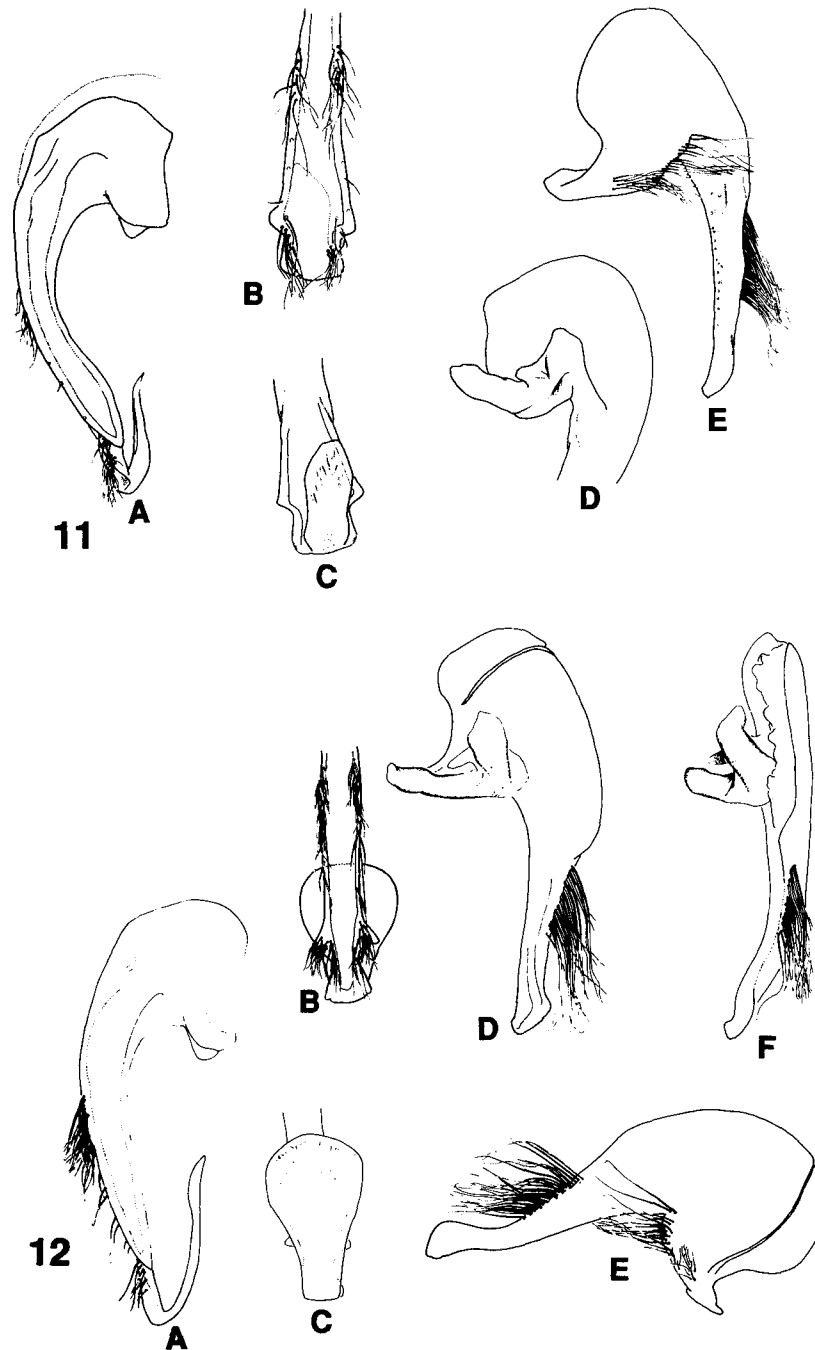
*Type information and taxonomic notes.*— Full data about types is presented in Leech (1940) and the label data of the holotype male is given in Ruetie (1970:42). We examined the holotype as well as numerous paratypes from various collections. Prior to 1940, specimens of *L. pacificus* were confused with *L. conoideus* or *L. oblongus*.

*Diagnostic combination.*— This species is most similar to *L. conoideus* and is discussed under the above species treatment.

*Description.*— Taxonomically important character states are presented in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. oblongus* in Fig. 4C; elytral punctation, Fig. 1D; metacoxal punctation, Fig. 2D; male antenna as in *L. conoideus*, Figs. 3E, H; male protarsal claws, Fig. 2D; male antenna as in *L. conoideus*, Fig. 3H; male protarsal claws, Fig. 5F; male metafemur with elongate setae, Fig. 60, and mesofemur with elongate setae; male genitalia, Fig. 11.

*Sexual dimorphism.*— The distinctive modifications of male antennae, protarsal claws, and presence of elongate setae on meso- and metafemora establish this species and *L. conoideus* as the most sexually dimorphic species among *Laccornis*.

*Natural history.*— As with *L. conoideus*, this species is found in a wide variety of habitats. Leech (1940) commonly collected specimens from a small, temporary pond in an open meadow and mentioned that as pools dried, specimens were found in damp soil under a log. He records, also, specimens from



Figures 11 A-E, 12 A-F. Male genitalia (150X). Fig. 11. *Laccornis pacificus*. A-C. Aedeagus. A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-E. Paramere. D) Posteromedial view, E) Lateral view. Fig. 12. *Laccornis conoideus*. A-C. Aedeagus. A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-F. Paramere. D) Medial view, E) Lateral view, F) Dorsal view. D and F show enlarged modified hinge of paramere.

a cold spring, from a small stream at 1170 ft. elevation and from elevations up to 4,300 ft. (Copper Mountain, B.C.). We examined only one teneral specimen which is from British Columbia and it is dated 24/v/1939.

*Distribution* (Fig. 20C).— This is the only species occurring west of the Rocky Mountains. It is allopatric to all other species of *Laccornis* but its distribution is proximate to that of *L. conoideus* in southeastern Alberta (Larson, 1975).

*Phylogenetic relationships*.— *Laccornis pacificus* is the sister species to *L. conoideus* (Fig. 19).

*Laccornis latens* (Fall)

(Figs. 1E, 2E, 3A, 4F, 5I, 5O, 7A, 7J, 7N, 13A-D; Map, Fig. 20B)

*Agaporus latens* Fall 1937:10 [Type locality-- Sherborn, Massachusetts. Type repository--MCZ].  
*Laccornis latens*; Leech 1940:126, Wolfe and Spangler 1985:70.

*Type information and taxonomic notes*.— Fall (1937) reported that six specimens were used to compile the original description. Only two specimens are in the MCZ type collection. The male holotype has the following label data: Sherborn, Mass. 1934 VI-18 CA Frost/N.B. XIII p. 94/*latens* /Type M.C.Z. 23695 [black type on red label]HC. Fall Collection/. Prior to Fall's (1937) description of *L. latens*, specimens were confused with those of *L. difformis*.

*Diagnostic combination*.— Both sexes of *L. latens* are longer than those of *L. kocai*, *L. oblongus*, *L. conoideus* and *L. pacificus* and shorter than those of *L. deltoideus* and *L. nemorosus*. Male and female *L. latens* have strigate metacoxae which are absent from the above taxa. These characters place *L. latens* in a complex which includes also *L. difformis*, *L. schusteri* and *L. etnieri*. Within this complex females can be identified conclusively only by association with males; however specimens of *L. latens* do have a narrower prosternal process (compare Figs. 4F to 4G). Males of *L. latens* are recognized by scarcely modified antennomere 4 (Fig. 3A) and absence of meso- and metafemoral elongate setae. The anterior, protarsal claw of male specimens of *L. latens* (Fig. 5I) is distinctive; it is similar to that of *L. difformis* (Fig. 5J) but lacks any indication of a lateral notch.

*Description*.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated in Fig. 4F; elytral punctation, Fig. 1E; metacoxal punctation, Fig. 2E; male antenna, Fig. 3A; male protarsal claws, Fig. 5I; male genitalia, Fig. 13.

*Sexual dimorphism*.— This species is relatively more sexually dimorphic than *L. kocai* or *L. oblongus*, however, the sexual dimorphism is less developed than in any of the other species of *Laccornis*. Although the male, anterior, protarsal claw is dramatically contorted and broadened, males lack elongate, femoral setae and distinctly enlarged antennomeres.

*Natural history*.— We collected specimens in southern Ontario from a small pond almost completely shaded by maple trees and from a small depression in a *Sphagnum* mat. The general area around these habitats was dominated by a more boreal flora, typical of the Canadian Shield. Specimens were collected in central New Jersey in small, completely shaded pools that were drying remnants of a seasonally, more extensively flooded, deciduous forest. At all of the above sites, vascular aquatic plants were scarce to absent and the bottom substrate was composed primarily of decaying leaves. These habitats are in marked contrast to specimens collected at Douglas Lake, Michigan, where specimens were taken

from exposed beach pools with a sand substrate and dense growths of *Chara* and *Carex*.

*Distribution.* (Fig. 20B).— Specimens of *L. latens* are known from the Great Lakes region, northeastern United States (New York, Massachusetts, Connecticut and New Jersey) and eastern Canada (Ontario to New Brunswick). It is sympatric with more species of *Laccornis* than is any other single species in the genus.

*Phylogenetic relationships.*— *Laccornis latens* is the sister species to *L. difformis* + *L. etnieri* + *L. schusteri* (Fig. 19).

*Laccornis deltoides* (Fall)  
(Figs. 14 A-D; Map, Fig. 20C)

*Agaporus deltoides* Fall 1923:123 [Type locality--Beaver Creek, Illinois. Type repository--MCZ].

*Laccornis deltoides*; Leech 1940:127, Wolfe and Spangler 1985:70.

*Type information and taxonomic notes.*— Fall (1923) stated that his description was based on four specimens from the University of Illinois Collection and that all were labelled with the number 1331. According to Fall, accession records indicated that this number refers to material taken in 1883 by H.A. Peters at Beaver, Illinois. Malloch (in Fall 1923) stated that the locality should be interpreted as Beaver Creek, Illinois. Fall (1923) indicated that "The type is a male in my own collection; paratypes in the University of Illinois Collection". There are two specimens (one male and one female) deposited in MCZ. The holotype male was examined and it has the following label information: Beaver (Creek)? Ill H.A. Peters 1883/TYPE *deltoides*/M.C.Z. Type 23964/HC. Fall Collection. The references to *L. deltoides* in Folkerts and Donavan (1974) and Folkerts (1978) from Alabama are referred to *L. nemorosus* below.

*Diagnostic combination.*— Except for specimens of *L. nemorosus*, all specimens of *L. deltoides* can be separated easily from those of all other species of *Laccornis* by their substantially greater length of 6.28 to 6.60 mm. The outline of the body is distinctly tapering posteriorly and specimens are light brown in colour. Members of *L. deltoides* are a little shorter than those of *L. nemorosus* (7.00 to 7.23 mm) and the prosternal process is slightly more convex medially. Nevertheless genitalic characteristics of males should be used for conclusive identification. The apex of the aedeagus of males of *L. deltoides* is less expanded than is that of *L. nemorosus*.

*Description.*— Taxonomically important characters are given in Table 1; measurements in Table 2. This is the rarest species of *Laccornis* and no specimens were used for SEM. However, below, we indicate characteristics that are very similar. Prosternal process a little more convex medially than in Figs. 4D, E; elytral punctation as in Fig. 1F; metacoxal punctation as in Fig. 2F; male antenna modified as in Figs. 3C, D, G; male protarsal claws as in Fig. 5I; male genitalia, Fig. 14.

*Sexual dimorphism.*— Among members of species-group III, males of *L. deltoides* have the most modified antennae but the least modified, anterior, protarsal claws and are without elongate, femoral setae.

*Natural history.*— The label information about the type locality may indicate that members of *L. deltoides* occur in stream or stream-associated habitats.

*Distribution* (Fig. 20B).— *Laccornis deltoides* is sympatric with *L. latens* but the distribution of the former is centered a little further south. This species is known from about 10 specimens and more specimens and/or more knowledge of the preferred habitat are needed to document its range more fully.

*Phylogenetic considerations*.— *Laccornis deltoides* is the sister species to *L. nemorosus*. These two species together form the sister clade to *L. latens* + *L. difformis* + *L. schusteri* + *L. etnieri*.

*Laccornis nemorosus* NEW SPECIES

(Figs. 1F, 2F, 3C, 3D, 3G, 4D, 4E, 4I, 4P, 5G, 5H, 15A-D; Map, Fig. 20C)

*Type information and taxonomic notes*.— The holotype, allotype, and paratypes are all from the same locality. The holotype is a male and has the following label information: *L. cf. deltoides* 4 May 76 Reelfoot Lk. Lake Co. Tn GWW 70/*Laccornis nemorosus* Holotype. The holotype is deposited in NMNH

Specimens of *L. nemorosus* previously were confused with those of *L. deltoides*. We examined one of the specimens from Alabama, referred to as *L. deltoides* by Folkerts and Donavan (1974) and Folkerts (1978), and consider it to be *L. nemorosus*.

*Etymology*.— The name of this species is derived from a Latin word for a "wooded" or "shady" place. This name is used in reference to the habitat characteristics of the type locality.

*Diagnostic combination*.— This is the longest species of *Laccornis*. Members of *L. nemorosus* can be confused only with those of *L. deltoides*. Characteristics distinguishing among these two taxa are discussed in treatment of the latter.

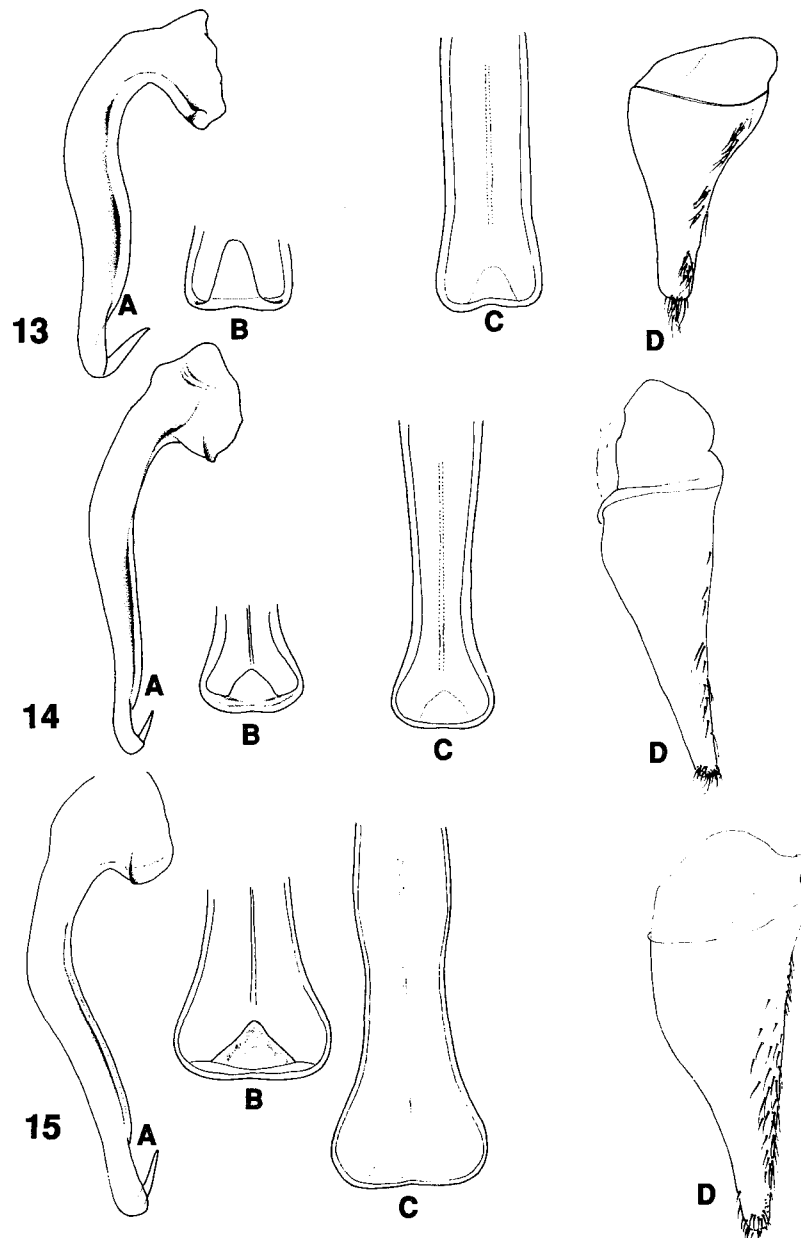
*Description*.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated in Figs. 4D, E; elytral punctation, Fig. 1F; metacoxal punctation, Fig. 2F; male antenna, Figs. 3C, D; male protarsal claws, Fig. 5G, H; male genitalia, Fig. 15.

*Sexual dimorphism*.— Males of *L. nemorosus* have the antennae extremely modified. The anterior protarsal claws are not as modified as among other members of species-group III and elongate, femoral setae are absent.

*Natural history*.— Folkerts and Donavan (1974) reported collecting a specimens from root masses along the margins of a small, gravel-bottom stream. At the type locality, GWW collected approximately 30 specimens, some of which are teneral, in small woodland pools that appeared to be the remnants of a formerly, more extensively flooded area. There was little vascular vegetation and decaying leaves were the predominant substrate.

*Distribution* (Fig. 20B).— *Laccornis nemorosus* is known only from one locality in each of Tennessee and Alabama. We predict that its distribution is more widespread, that it is centered in the southeastern U.S. and allopatric to that of *L. deltoides*. Folkerts and Donavan (1974) report *L. deltoides* from Alabama and Florida. The Bullock Co., Alabama specimen is a teneral male that we have tentatively assigned to *L. nemorosus*; we did not examine the specimen recorded from Calhoun Co., Florida.

*Phylogenetic relationships*.— *Laccornis nemorosus* is the sister species to *L. deltoides*. These two species together are the sister clade to *L. latens* + *L. difformis* + *L. schusteri* + *L. etnieri* (Fig. 19).



Figures 13A-D, 14A-D, 15A-D. Male genitalia (150X). A-C. Aedeagus. A) Dorsal view, B) Ventroapical view, C) Dorsoapical view, D) Lateral view of paramere. Fig. 13. *Laccornis latens*. Fig. 14. *L. deltoides*. Fig. 15. *L. nemorosus*.

*Laccornis difformis* (LeConte)

(Figs. 1G, 3F, 5J, 5Q, 6A-I, 7B-I, 7M-O, 17A-C; Map, Fig. 20A)

*Hydroporus difformis* LeConte 1855:292, 298 [Type locality-- Georgia. Type repository-- MCZ], Crotch 1873:396, Sharp 1882:484, Wickham 1895:76.*Agaporus difformis*; Zimmermann 1920:134, Fall 1923:124 *ex parte*.*Laccornis difformis*; Leech 1940:126, Malcolm 1971:22, Brigham 1982:10.57, Wolfe and Spangler 1985:61.

*Type information and taxonomic notes.*— LeConte (1855) specifically mentioned that only one specimen was available at the time he described *L. difformis*; that specimen is therefore the holotype. The only locality information provided is "Georgia". The holotype male in MCZ was examined and it is labelled as follows: [orange circle]/3412/Type 6036 [black type on red label]/*H. difformis* LeC./ The type is teneral and very fragile; the protarsus was removed and placed in a microvial on the pin.

*Diagnostic combination.*— Males of *L. difformis* are recognized by the enlarged antennomere 4 (Fig. 3F and as in *L. schusteri*, Fig. 3B), apex of anterior, protarsal claw located medially and with a minute lateral notch (Fig. 5J), and the presence of elongate, metafemoral setae (as in *L. etnieri*, Fig. 6P). Female specimens of *L. difformis* cannot be reliably separated from those of *L. schusteri* and *L. etnieri*; however, most females of *L. difformis* are longer and the prosternal process is a little broader than in those of *L. latens*.

*Description.*— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 1G; metacoxal punctation as in *L. schusteri*, 2G; male antenna, Fig. 3F; male elongate, metafemoral setae as in *L. etnieri*, Fig. 6P; male protarsal claws, Fig. 5J; male protarsomere 5, Fig. 5Q, male genitalia, Fig. 17.

*Sexual dimorphism.*— Specimens of *L. difformis* are more sexually dimorphic than members of either the *L. latens* or *L. deltoides*-complexes because of presence of elongate, metafemoral setae. However, the anterior, protarsal claw of male *L. difformis* is not as modified as that of either *L. etnieri* or *L. schusteri*.

*Natural history.*— This species apparently is restricted to woodland habitats, especially temporary pools. We collected specimens in New Jersey and North Carolina. At both sites specimens were in small pools that were remnants of a seasonally, more extensively flooded area. Some moss was present, there was scarcely any vascular vegetation, and the substrate was dominated by leaves. Leech (1941) reported that many specimens were taken by placing leaf debris from the shoreline of pools onto a sheet and then waiting for specimens to become active as this material dried.

*Distribution* (Fig. 20A).— *Laccornis difformis* is restricted primarily to the Atlantic coastal plain. The most southern record is that of the holotype and is not exactly known other than that it is in Georgia. To the north, *L. difformis* extends off of the coastal plain but still proximate to the coast into northeastern USA; the exact northern limits are uncertain. Fall (1923) mentions specimens from Marquette, Michigan; however, he later (Fall 1937) described them as *L. latens*. Malcolm (1971) mentions specimens from Maine but we were unable to locate them. Two female specimens from Rhode Island are probably this species. The range of *L. difformis* is proximate to that of *L. etnieri* in Maryland.



*Phylogenetic relationships.*— *Laccornis difformis* is placed as the sister species to *L. etnieri* in Fig. 19; however, the relationship among *L. difformis*, *L. etnieri*, and *L. schusteri* requires further study (see Reconstructed Phylogeny).

*Laccornis etnieri* Wolfe and Spangler  
(Figs. 11, 5L, 6P, 16A-F; Map, Fig. 20A)

*Laccornis etnieri* Wolfe and Spangler 1985:67 [Type locality -- Jefferson Co., Tennessee. Type repository -- NMNH].

*Type information and taxonomic notes.*— Full label data for the types is given in Wolfe and Spangler (1985). Members of this species were probably confused with *L. difformis* formerly.

*Diagnostic combination.*— Males of *L. etnieri* are recognized by presence of enlarged antennomere 4 (as in *L. schusteri*, Fig. 3B), apex of anterior, protarsal claw located laterally and with a minute lateral notch (Fig. 5L), and the presence of elongate, metafemoral setae (Fig. 6P). Female specimens of *L. etnieri* cannot be separated from those of *L. difformis* and *L. schusteri* based on structural characters. Most female specimens of *L. etnieri* are longer and the prosternal process is a little broader than in *L. latens*.

*Description.*— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 11; metacoxal punctation as in *L. schusteri*, Fig. 2G; male antenna as in *L. schusteri*, Fig. 3B; male with elongate, metafemoral setae, Fig. 6P; male protarsal claws, Fig. 5L; male genitalia, Fig. 16.

*Sexual dimorphism.*— This species is the most sexually dimorphic in species-group III based on the quite derived condition of the male anterior protarsal claw.

*Natural history.*— We have collected this species on several occasions in Tennessee. At one locality, there was a temporary pond (about 6m x 6m) in an open field that was partially shaded by trees at the margin and there was abundant vascular vegetation. At several other sites the habitat was peripheral pools at the margins of extensively flooded forest (e.g., Goose Pond, Tennessee) where it appeared that flooding was seasonal.

According to Wolfe and Spangler (1985), the larva described as *L. difformis* by Spangler and Gordon (1973) is actually that of *L. etnieri*. We have examined teneral specimens captured on 11/xi/1921 (Maryland) and 12/iv/1976 (Tennessee).

*Distribution* (Fig. 20A).— The distribution of *L. etnieri* approaches that of *L. schusteri* at the northern end of its range; the distribution of *L. etnieri* is proximate to that of *L. difformis*.

*Phylogenetic relationships.*— *Laccornis etnieri* is probably the sister species to *L. difformis* (Fig. 19); however, *L. schusteri* is closely related to both of the above species and the relationships among all three species requires further study (see Reconstructed Phylogeny).

*Laccornis schusteri* Wolfe and Spangler  
(Figs. 1H, 2G, 3B, 4G, 5K, 18A-C; Map, Fig. 20A)

*Laccornis schusteri* Wolfe and Spangler 1985:68 [Type locality-- Cotrell Pond, Stewart Co., Tennessee. Type repository-- NMNH].

*Type information and taxonomic notes.*— Full information about types is given in Wolfe and Spangler (1985). Members of this species were probably confused with *L. difformis* formerly.

*Diagnostic combination*.— Males of *L. schusteri* are recognized by enlarged, antennomere 4 (Fig. 3B), anterior protarsal claw of male with apex placed laterally but without a minute lateral notch (Fig. 5K), and presence of elongate, metafemoral setae (as in *L. etnieri*, Fig. 6P). Females of *L. schusteri* are difficult to distinguish from females of *L. difformis* and *L. etnieri* based on structural characters. Most female specimens of *L. etnieri* are longer and the prosternal process is a little broader than in those of *L. latens*.

*Description*.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 1H; metacoxal punctation, 2G; male antennae as in *L. schusteri*, Fig. 3B; male with elongate, metafemoral setae as in *L. etnieri*, Fig. 6P; male anterior protarsal claws, Fig. 5K; male genitalia, Fig. 18.

*Sexual dimorphism*.— Except for specimens of *L. etnieri*, this is the most sexually dimorphic in species-group III.

*Natural history*.— This species has been collected only twice. At the type locality the habitat was a rather large, semipermanent pond surrounded by trees at the edge of a pasture. Specimens of *L. schusteri* were distinctly more abundant in the more shaded portions of the pond with little or no aquatic vegetation. The other locality was on the flood plain of the Obion River, Tennessee. At this latter site, there were numerous small pools in dense forest (completely shaded); the pools were unvegetated but with an abundance of decaying leaves. Teneral specimens were captured on 12/vi/1977.

In June 1979, an attempt was made to find pupal cells at Cotrell Pond. No pupae were found but third instar larvae were discovered about two meters above the water line, most abundantly at the base of a rotten log. Several larvae were trapped in spider webs at this spot. Attempts were made to rear larvae; unfortunately only one female successfully emerged.

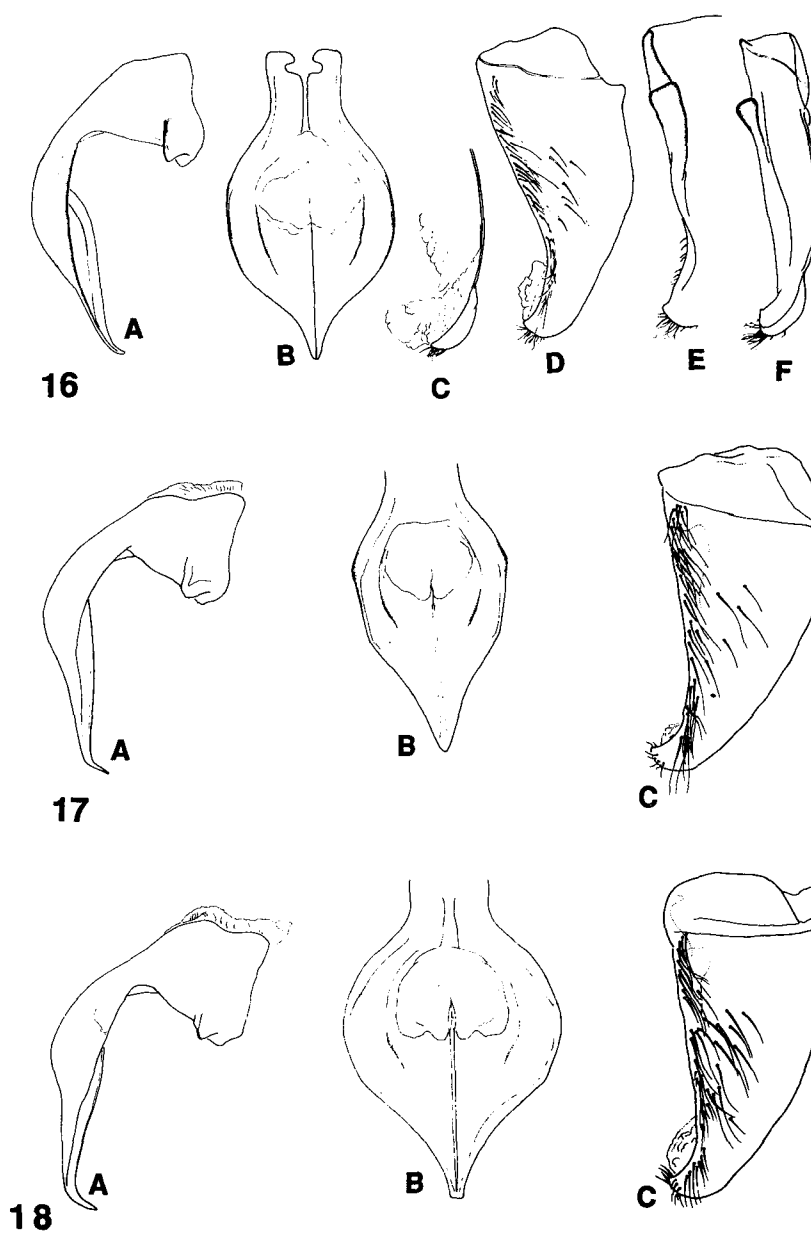
*Distribution* (Fig. 20A).— We have captured *L. schusteri* on the Gulf Coastal plain and Highland Rim in Tennessee. However, the Highland Rim locality was literally "within a stone's throw" of the coastal plain faunal region which extends up the Mississippi River to southern Illinois and includes western Tennessee. We predict therefore that the distribution of this species is centered on the Gulf Coast.

*Phylogenetic relationships*.— This species is very closely related to *L. etnieri* and *L. difformis*. Our analysis suggests that *L. etnieri* and *L. difformis* are sister species (Fig. 19); however, relationships among these three species requires further study (see Reconstructed Phylogeny).

#### RECONSTRUCTED PHYLOGENY

Our approach to reconstructing the phylogeny of members of *Laccornis* was to incorporate every noticeable difference of external structure that could be coded reliably and for which a moderate level of polarity could be demonstrated. This follows from our studies of structure in which representative specimens of each species, except the very rare *L. deltoides*, were disarticulated and for which all sclerites were examined.

Phylogenetic character state changes and polarities are shown in Table 3; the array of phylogenetic character states by taxon are shown in the matrix in Table 4. Table 5 shows phylogenetic character state changes by character and associated consistency index value; homoplasy and structural divergence are summarized in Table 6; change by lineage is shown in Fig. 19. If all characters are ordered, only one most parsimonious phylogeny can be constructed (Fig. 19).



Figures 16A-F, 17A-C, 18 A-C. Male genitalia, (150X). Fig. 16. *Laccornis etnieri*. A-B. Aedeagus. C-F. Paramere. A) Lateral view, B) Dorsal view, C) Dorsoapical view clearly illustrating membranous lobe, D) Lateral view, E) Ventromedial view, F) Dorsal view. E and F show hinge structure. Fig. 17. *L. difformis*. A) Aedeagus, lateral view, B) Aedeagus dorsal view, C) Paramere, lateral view. Fig. 18. *L. schusteri*. A) Aedeagus, lateral view, B) Aedeagus dorsal view, C) Paramere, lateral view.

The character state changes and justifications associated with our reconstructed phylogeny are described below. Also, overall patterns of structural divergence are discussed.

#### ***Laccornis* as a monophyletic unit**

Previous authors have defined *Laccornis* primarily by the fact that the metafemora contact metacoxal lobes (Fig. 7A) (e.g., Fall 1923 and Leech 1940). However, Wolfe (1985) and Roughley and Wolfe (1987) pointed out that that characteristic was shared with other hydroporines (Methlini, *Hydrovatus* Motschulsky, *Canthyporus* Zimmermann and *Laccornellus* Roughley and Wolfe) and that it is plesiotypic.

Information in Burmeister (1976) and Wolfe (1985) indicates that female members of *Laccornis* are unique among all hydroporines in their possession of a valvifer (=Tergum IX of Burmeister, 1976). Wolfe (1985) demonstrated that presence of a valvifer is plesiotypic and absence is derived among members of Hydroporinae.

There is only one demonstrable synapotypy for all members of *Laccornis*, if *L. kocai* is included; the prosternal process is broadened apically (see Figs. 4A vs 4B-G). This character is coded as PSTSHP in Tables 3-5 and on Fig. 19. We are not absolutely confident in the reliability of prosternal process shape. Several other hydroporine groups also possess a broadened prosternal process (notably, at least some members of *Canthyporus*). However, since all other known hydroporines have lost the valvifer and the most common prosternal shape among hydroporines is elongate and tapered, we retain *L. kocai* in *Laccornis* and we accept PSTSHP as a generic synapotypy.

Not used in the phylogenetic analysis is the presence of enlarged palettes on protarsomere 3 (Figs. 5A, B) which may be a synapotypy of *Laccornis*. Most hydroporines have these enlarged setae restricted to protarsomeres 1 and 2. This character state was not used because we have not examined a sufficient number of outgroup taxa to develop a firm hypothesis about the polarity of this character. The enlarged palettes are easily abraided and are difficult to see on most museum specimens (cf. Larson 1975).

#### **Species-group relationships**

Three species-groups are recognized within *Laccornis* for 10 species; each species-group is subdivided, where appropriate, into species-complexes as follows: i) species-group I monobasic, with *L. kocai*; ii) species-group II - two species-complexes, a) *L. conoideus*-complex with *L. conoideus* and *L. pacificus* and b) *L. oblongus*-complex - monobasic; iii) species-group III - three complexes; a) *L. deltoideus*-complex with *L. deltoideus* and *L. nemorosus*, b) *L. latens*-complex, monobasic, and c) *L. difformis*-complex with *L. difformis*, *L. etnieri* and *L. schusteri*.

*Species-group I.*—*Laccornis kocai* is the most plesiotypic member of *Laccornis*. Our analysis of characters suggests that it is a very unspecialized species. It is because of this that other species of *Laccornis* demonstrate a relatively high number of steps of change from *L. kocai* (Table 6) which we refer to as structural divergence.

In only two character states—form of anterior protarsal claw of males (3.9, Table 1) with basal lobe, and elytral punctation (4.1, Table 1) less coarse do members of *L. kocai* differ from a generalized ancestor of *Laccornis*. However these two character states are very difficult to polarize because a broad array of states is shown by a variety of hydroporines and they may be plesiotypic.

*Species-groups II + III.*— Four synapotypies suggest common ancestry of all members *Laccornis*, exclusive of *L. kocai*: 1) aedeagus distinctly reflexed (AEDREFL), 2) increased number of mesotibial spines in the anterior lateral row (MSTSPIN), 3) increased number of protarsal palettes (PROPALE), and 4) form of ventral sensilla of protarsomere 4 (PROVSEN).

Of these four characters, the least reliable is probably the number of mesotibial spines in the anterolateral row (MSTSPIN). This character is partitioned into two states but distinction among these two states is not well defined. However, specimens of *L. kocai* are clearly at the low end of MSTSPIN number and despite variation in this character a low number of spines almost surely is plesiotypic (Wolfe 1985).

We are not certain about the phylogenetic value of the number of enlarged palettes; among hydroporines in general the most common state is two per row, however, in many species of a variety of genera there is an increase in number of palettes per row (cf. Larson 1975). We judge such increases as probably secondary development. Our recognition of increased number of enlarged palettes as apotypic within *Laccornis* is justified based on the comparison to the state present among members of Methlini, or *Laccornellus* (outgroup representatives).

The presence of hair-like setae on protarsomere 5 (PROVSEN) is interesting because the difference between the state in *L. kocai* and all other members of *Laccornis* is marked and the condition of *L. kocai* clearly is present in the outgroup. Because this character is distinctly dichotomous and easily interpreted by outgroup comparison we give it considerable weight.

Of the four synapotypies uniting species-groups II and III, the aedeagal reflexed character (AEDREFL) is the only one that is not perfectly consistent [CI (consistency index) = .667]. However, aedeagal structure is probably the most well studied character among members of Hydroporinae and the reflexed aedeagal condition is very rare (as far as we know, otherwise only known in some males of *Canthyporus* and *Hydrovatus*). The decreased CI value results from secondary loss among the members of the *L. difformis*-complex of species-group III.

In order to search for biases with this character (AEDREFL) system in our analysis, phylogenies were constructed under several premises: 1) all character states unordered, 2) all character states associated with aedeagal reflex unordered, 3) all characters ordered. When characters were considered fully ordered, generally we hypothesized that they changed from less developed to more developed (i.e., aedeagal apex not reflexed, e.g., *L. kocai*, to maximally reflexed and ligulate, e.g., *L. conoideus*). If characters were considered unordered no sequence is specified *a priori*. If either all characters, or only the states associated with AEDREFL, were unordered the character state change preceding divergence of species-groups II and III was from state 0 to state 4, with successive subsequent loss in species-group III. By ordering all characters, the analysis obviously is biased in favor of generating phylogenies with taxa with the less reflexed aedeagal condition in more basal (plesiotypic) positions. However, even under this latter premise the character state change preceding divergence of species-groups II and III was 0 to 3 with successive loss only in the *L. difformis*-complex (Fig. 19). Therefore, under any of the above premises, a change took place in AEDREFL early in the evolution of this group with subsequent loss of the reflexed condition only in members of species-group III.

With ordered characters, only one most parsimonious tree was obtained (Fig. 19) and in that hypothesis five other characters clearly establish the monophyly of both the *L. difformis*-complex and species-group II. Therefore, we are

confident that the reflexed aedeagal condition (state 0 or 3) is a reliable synapotypy for species-groups II + III.

Evolution has independently tended towards increased sexual dimorphism in species-groups II and III, primarily in modifications to antennae, protarsal claws, and elongate setae of meso- and metafemora of males. Modifications within species-group II involve enlargement, change in shape, and ventral reticulation of antennomeres 3-7, development of a medial tooth on the anterior protarsal claw, and presence of meso- and metafemoral elongate setae. These modifications all are maximally evident in the *L. conoideus*-complex. Within species-group III, elongate femoral setae occur only on metafemora; anterior protarsal claws are without a medial tooth, rather the claws are progressively contorted and foliately expanded. Only antennomeres 3-5 are modified, and of these only antennomere 4 is distinctly developed. Parallel trends toward sexual dimorphism therefore occur within species-groups II and III, but by different and independently derived modifications of the same structures (antennae and anterior protarsal claws).

*Species-group II.*— Six synapotypies suggest monophyly of species-group II. Four are genitalic: 1) aedeagal reflexed condition (AEDREFL) maximally developed, 2) dorsolateral aedeagal setae present (AEDSETA), 3) paramere setation altered into a unique configuration (PARASET), and 4) paramere shape altered (PARASHP). Additionally among males, antennomeres 3-7 are modified (ANTTYP2) and metafemoral setae are present (METASET). Within species-group II, *L. conoideus* and *L. pacificus* are clearly sister species based on more extensive modification of genitalic (AEDSETA) and antennal (ANTTYP2) characters. Additionally, the anterior lateral processes (AEDALPR) are developed at the apex of the aedeagus, mesofemoral setae (MESOSET) are present, and anterior protarsal claws are medially toothed (CLTOOTH). The anterior lateral aedeagal process is maximally distinct in *L. conoideus* and the medial tooth of anterior protarsal claw is most developed in males of *L. pacificus*.

The modifications associated with the aedeagus, parameres, mesofemoral setae and protarsal claws are unique within *Laccornis*; antennal modifications are also unique as long as our hypothesis concerning its independent origin in species-groups II and III is correct. Presence of metafemoral setae occurred independently in the *L. difformis*-complex. The aedeagal reflex is not homoplastic within species-group II; however, this character is secondarily lost in members of the *L. difformis*-complex of species-group III.

Overall species-group II is very distinctive and exhibits a high degree of structural divergence (Table 6) and we are very confident about the species relationships within it, especially concerning the sister species status of *L. conoideus* and *L. pacificus*.

*Species-group III.*— Monophyly of species-group III is based on claw shape (CLSHAPE), antennal structure (ANTTYP1), and presence of a prosternal pore (PSTPORE). Presence of a prosternal pore (Fig. 4I) in this clade is interesting. The notched condition (Fig. 4H) of all other members of *Laccornis* exists in the more plesiotypic hydroporines so far examined, such as members of *Canthyporus*, Methlini and Hydrovatini (Wolfe 1985, 1989). The pore is present in more apotypic hydroporines both in the northern and southern hemisphere (Wolfe 1985). Antennal and claw structural modifications each form a morphocline. Successively more apotypic stages of development are synapotypies for lineages in this species-group as shown in Fig. 19.

The *L. deltooides*-complex is the sister-group to all other members of species-group III. *Laccornis deltooides* and *L. nemorosus* are extremely similar in size, shape, and coloration. They are grouped together based on maximal development of antennomere 4 (ANTTYP1), protarsal structure (PRORIDG), and more distinctly concave condition of the prosternal process (PSTPRCV).

Monophyly of the *L. latens* - and *L. difformis*-complexes is based on derived shape of spines on protarsomere 4 (PRO4SPI), presence of coxal strigae (CXSTRIG) and more foliate anterior protarsal claws (CLSHAPE). However, there is a loss in degree of antennomere development in the *L. latens* -complex and this is the direct cause for decreased CI of this character (.750) in species-group III.

The *L. difformis*-complex is the most structurally divergent in the genus (Table 6). Six synapotypies suggest monophyly of this group. One of the six is a character loss (AEDREFL). The aedeagus becomes non-reflexed although the apex still is distinctly deflected ventrally in two of the three species (Figs. 16-18). Other synapomorphies are associated with the aedeagus (AEDBASE, AEDSHAPE), presence of membranous lobe of apex of paramere (PARAMEM) and presence of distinctly evident metafemoral setae (METASET). The CI for the aedeagal reflex and claw shape is decreased because of partial character loss in males of *L. difformis* and *L. etnieri* respectively. The CI for metafemoral setae is .750 because it arose twice in the genus (species-group II and *L. difformis*-complex) as discussed above.

Relationships within the *L. difformis*-group are a little ambiguous. If all characters are ordered, *L. difformis* and *L. etnieri* are sister species based on presence of asymmetrical ventral lobe of protarsomere 5 (PROLOBE), and presence of at least a subtle notch on the anterior claw (CLNOTCH). If all characters are unordered, it is equally parsimonious that *L. etnieri* could be considered the sister species to *L. schusteri*. Unordering of all phylogenetic characters is perhaps too unrealistic; however, it is interesting to note that even under this condition only relationships within the *L. difformis*-group are altered.

We have considered the possibility that *L. latens* is the sister species to all other members of species-group III based on the less evidently modified antenna of members of that species (Figs. 3A vs 3B). That hypothesis was rejected for three reasons. First, while reversing the positions of the *L. deltooides*- and *L. latens* -complexes eliminates inconsistency in antennal structure, a new reversal would be introduced with respect to anterior protarsal claw structure. Although the anterior protarsal claw of both members of the *L. deltooides*-complex is contorted, it is distinctly less foliately expanded than it is in males of *L. latens*; thus if *L. latens* diverged first there would have to be partial character loss accepted with respect to claw structure. Second, additional homoplasy involving metacoxal striga and shape of sensilla of protarsomere 4 is introduced if the position of *L. latens* and the *L. deltooides*-complex are switched. Third, we think it ill advised to weigh the antennal structural changes more than anterior protarsal claw changes because antennal modifications similar to those of members of *Laccornis* are known in numerous other hydroporine taxa. There is a noticeable tendency for this character to be homoplastic among hydroporines and indeed among various groups of Dytiscidae in general (*cf.* Larson 1975). On the other hand, the type of protarsal claw modification (contorted and foliate) present in members of species-group III is unique and unknown in any other dytiscid group. Therefore, if we were to weight any character in our analysis of species-group III members, it would be claw structure (which already in part is contributing strongly to the more parsimonious resolution).

Table 3.

Phylogenetic characters, their abbreviations, character states, character state changes, polarities, and consistency index used for phylogenetic analysis of species of *Laccornis*. See Fig. 19 for arrangement of characters by lineage. 0 - plesiotypic state, higher numbers indicate progressively more apotypic conditions. Numbers in parentheses refer to figure numbers.

CHARACTER	Changed		Along branch	CI
	from	to		
Leg characters.				
1) Claw tooth (CLTOOTH)				
not toothed (5 G-L).....0	0	1	12-11	
toothed (5E).....1	1	2	11- <i>pacificus</i>	1.000
distinctly toothed (5F).....2				
2) Claw shape (CLSHAPE)				
not foliate (5C-F).....0	0	1	18-17	
contorted (5G,H).....1	1	2	17-15	
foliate (5I-L).....2	2	3	15-14	
foliate and apically				
truncate (5K-L) .....3	3	2	13- <i>difformis</i>	0.750
3) Claw notch (CLNOTCH)				
absent (5K).....0	0	1	13-12	
slightly evident (5J) .....1	1	2	12- <i>etnieri</i>	1.000
distinctly evident (5L).....2				
4) Protarsal palettes (PROPALE)				
maximum of two enlarged (5A).....0	0	1	19-18	1.000
four enlarged (5B).....1				
5) Shape of apicolateral lobe of protarsomere 5 (PROLOBE)				
symmetrical (5M, N).....0	0	1	14-13	1.000
not symmetrical (5Q) .....1				
6) Sensilla of protarsomere 5 (PROVSEN)				
sensilla spine-like (5M).....0	0	1	19-18	1.000
sensilla seta-like (5N, O, P) .....1				
7) Spines of protarsomere 4 (PRO4SPI)				
long, slender (5M).....0	0	1	17-15	1.000
short, cone-like (5O).....1				
.....			(continued on next page)	



Table 3 (continued)

CHARACTER		Changed from to		Along branch	CI
8)	Ridge of protarsomere 5 (PRORIDG)				
	ridge absent (5M, N) .....	0	1	17-16	1.000
	ridge present (5P) .....				
9)	Mesotibial spines (MSTSPIN)				
	anterior lateral row with less than eight spines (6O) .....	0	1	19-18	1.000
	anterior lateral row with nine or more spines (6H) .....				
10)	Mesofemoral elongate setae (MESOSET)				
	absent .....	0	1	18-12	1.000
	present .....				
11)	Metafemoral elongate setae (METASET)				
	absent (6N) .....	0	2	15-12	
	present (6O) .....	0	1	12-11	0.667
	distinctly present (6P) .....				
Genitalic characters.					
12)	Aedeagal ventrally bent/reflexed (AEDREFL)				
	not vent. bent/reflexed (9) .....	0	3	19-18	
	slightly bent (16) .....	3	2	15-14	
	distinctly bent (17-18) .....	3	4	18-12	
	reflexed (13-15) .....	2	1	13-etnieri	0.667
	reflexed and ligulate (8, 11, 12) .....				
13)	Aedeagal base (AEDBASE)				
	not enlarged (8, 9, 11-15) .....	0	1	15-14	1.000
	enlarged (16-18) .....				
14)	Aedeagal setae (AEDSETA)				
	absent (9, 13-18) .....	0	1	18-12	
	present, not long .....	1	2	12-11	1.000
	and dense (8) .....				
	present, long dense (11-12) .....				
	.....				

(continued on next page)

Table 3 (continued)

CHARACTER		Changed from to		Along branch	CI
15)	Aedeagal shape (AEDSHAP)				
	not distinctly expanded (8-15).....0	0	1	15-14	1.000
	broadly expanded (16-18).....1				
16)	Aedeagal lateral projections (AEDALPR)				
	absent.....0	0	1	12-11	
	present (11).....1	1	2	11- <i>conoideus</i>	1.000
	distinctly present (12).....2				
17)	Paramere shape/hinge (PARASHP)				
	gradually tapering; hinge				
	horizontally oriented (16).....0	0	1	18-12	
	abruptly narrowed apically;.....1	2	2	12-11	1.000
	hinge enlarged and vertically				
	oriented (8).....1				
	as in state 1 but hinge with ventral				
	apodeme and apex w/slightly				
	expanded tip (11, 12).....2				
18)	Paramere setation (PARASET)				
	one ventral setal series.....0	0	1	18-12	1.000
	ventral and dorsal series.....1				
19)	Paramere membrane (PARAMEM)				
	not enlarged apically				
	(8-9, 11-15).....0	0	1	14-13	1.000
	enlarged (16-18).....1				
Antennal characters.					
20)	Antenna - morphotype 1 (ANTTYP1)				
	no modification.....0	0	2	18-17	
	4th slightly enlarged,.....	2	3	17-16	
	slightly concave (3 A).....1	2	1	15- <i>latens</i>	0.750
	4th evidently enlarged, 3rd and 5th				
	slightly; 4th slightly concave;				
	post edge with setae (3 B, F)....2				
	.....(continued on next page)				

Table 3 (continued)

CHARACTER		Changed from to		Along branch	CI
4th distinctly enlarged, 3rd and 5th scarcely; 4th distinctly concave; ant. and post. edge w/setae, vent. reticulation effaced (3 C-E, G, H, 4I) .....					3
21)	Antenna - morphotype 2 (ANTTYP2)				
	no modification.....	0	1	18-12	
	3-7 scarcely modified, vent.....	1	2	12-11	1.000
	surface slightly rugose.....				1
	3-5 distinctly enlarged, 6 and 7 slightly; 3-5 asymmetrically shaped, ventral surface convex sinuate and distinctly rugose.....				2
Prosternal characters.					
22)	Prosternal pore (PSTPORE)				
	absent, cleft/notch present (4H)....	0	1	18-17	1.000
	pore present (4I) .....				1
23)	Prosternal process shape (PSTSHP)				
	elongate (4A).....	0	1	generic	
	broad (4B-G).....			synapotypy	
24)	Prosternal convexity (PSTPRCV)				
	evident (4B, C, F, G).....	0	1	15-14	1.000
	reduced (4D, E).....				1
Metacoxal characters.					
26)	Metacoxal strigae (CXSTRIG)				
	absent (2A-D, F) .....	0	1	17-15	1.000
	present (2E, G) .....				1

Table 4

Matrix of phylogenetic character states used for reconstruction of phylogeny of species of *Laccornis* (Fig. 19). Character abbreviations (*i.e.* column designations) are listed and explained in Table 5.

	C	C	C	P	P	P	P	P	M	A	A	A	A	A	P	P	P	A	A	P	P	P	C	M	M
	L	L	L	R	R	R	R	R	S	E	E	E	E	E	A	A	A	N	N	S	S	S	X	E	E
	T	S	N	O	O	O	O	O	T	D	D	D	D	D	R	R	R	T	T	T	T	T	S	S	T
Charac.	O	H	O	P	L	V	4	R	S	R	B	S	S	A	A	A	A	T	T	P	S	P	T	O	A
	O	A	T	A	O	S	S	I	P	E	A	E	H	L	S	S	M	Y	Y	O	H	R	R	S	S
	T	P	C	L	B	E	P	D	I	F	S	T	A	P	E	H	E	P	P	R	P	C	I	E	E
Species	H	E	H	E	E	N	I	G	N	L	E	A	P	R	T	P	M	1	2	E		V	G	T	T
<i>L. kocai</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>L. conoideus</i>	1	0	0	1	0	1	0	0	1	4	0	2	0	2	1	2	0	0	2	0	1	0	0	1	1
<i>L. pacificus</i>	2	0	0	1	0	1	0	0	1	4	0	2	0	1	1	2	0	0	2	0	1	0	0	1	1
<i>L. oblongus</i>	0	0	0	1	0	1	0	0	1	4	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0
<i>L. latens</i>	0	2	0	1	0	1	1	0	1	3	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
<i>L. difformis</i>	0	2	1	1	1	1	1	0	1	2	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
<i>L. etnieri</i>	0	3	2	1	1	1	1	0	1	1	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
<i>L. schusteri</i>	0	3	0	1	0	1	1	0	1	2	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
<i>L. deltoides</i>	0	1	0	1	0	1	0	1	1	3	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
<i>L. nemorosus</i>	0	1	0	1	0	1	0	1	1	3	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.

Observed character state changes (alphabetically arranged by character abbreviation) and consistency index (CI) for each character used in reconstructed phylogeny of species of *Laccornis* (Fig.19). See Table 3 for hypothesized transformation series; see Fig. 19 for arrangement of character states by lineage.

CHARACTER	Changed			CI
	from	to	Along branch	
AEDALPR - Development of anterolateral process of aedeagus.	0	1	12 – 11	1.000
	1	2	11 – <i>conoideus</i>	
AEDBASE - Enlargement of aedeagal base.	0	1	14 – 13	1.000
AEDREFL - Aedeagus more reflexed.	0	3	19 – 18	0.667
	3	2	15 – 14	
	3	4	18 – 12	
	2	1	13 – <i>etnieri</i>	
AEDSETA - Increased distinctiveness of aedeagal setae	0	1	18 – 12	1.000
	1	2	12 – 11	
AEDSHAP - Aedeagus medially expanded.	0	1	15 – 14	
ANTTYP1 - Progressive development antennal morphotype 1.	0	2	18 – 17	0.750
	2	3	17 – 16	
	2	1	15 – <i>latens</i>	
ANTTYP2 - Progressive development antennal morphotype 2.	0	1	18 – 12	1.000
	1	2	12 – 11	
CLNOTCH - Distinctiveness of claw notch.	0	1	13 – 12	1.000
		2	12 – <i>etnieri</i>	
CLSHAPE - Claw shape modification.	0	1	18 – 17	0.750
	1	2	17 – 15	
	2	3	15 – 14	
	3	2	13 – <i>difformis</i>	

(continued on next page)

Table 5 (continued)

CHARACTER	Changed		Along branch	CI
	from	to		
CLTOOTH - Progressive development of claw tooth.	0 1	1 2	12 – 11 11 – <i>pacificus</i>	1.000
CXSTRIG - Coxal strigae present.	0	1	17 – 15	1.000
MESOSET - Mesofemoral elongate setae.	0	1	18 – 12	1.000
METASET - Metafemoral elongate setae present.	0 0	2 1	15 – 14 12 – 11	0.667
MSTSPIN - Density of anterior lateral row of mesotibial spines.	0	1	19 – 18	1.000
PARAMEM - Development of paramere membrane.	0	1	14 – 13	1.000
PARASET - Pattern of setation of paramere altered.	0	1	18 – 12	1.000
PARASHP - Progressively more tapered shape of paramere.	0 1	1 2	18 – 12 12 – 11	1.000
PROLOBE - Protarsal lobe asymmetrical.	0	1	14 – 13	1.000
PROPALE - Increased number of protarsal palettes.	0	1	19 – 18	1.000
PRORIDG - Anterodistal ridge of protarsomere 5.	0	1	17 – 16	1.000
PRO4SPI - Spines of protarsomere 4 more cone-shaped.	0	1	17 – 15	1.000
PROVSEN - Protarsal ventral sensilla more hairlike.	0	1	19 – 18	1.000

(continued on next page)

Table 5 (continued)

CHARACTER	Changed		Along branch	CI
	from	to		
PSTPORE - Prosternal pore present.	0	1	18 – 17	1.000
PSTPRCV - Prosternal process more concave.	0	1	15 – 14	1.000
PSTSHP - Prosternal process shape broader.	0	1	Generic Synapotypy	1.000

Table 6.

Summarization of phylogenetic character change, homoplasy, and structural divergence in reconstructed phylogeny of species of *Laccornis* (Fig. 19); see text for explanation.

	Steps changed from <i>L. kocai</i>	Number of homoplasies	Divergence from <i>L. kocai</i> (First column minus second column)
1) <i>L. conoideus</i>	19	0	19
2) <i>L. pacificus</i>	19	0	19
3) <i>L. oblongus</i>	12	0	12
4) <i>L. latens</i>	14	2	12
5) <i>L. difformis</i>	24	4	20
6) <i>L. etnieri</i>	25	4	20
7) <i>L. schusteri</i>	21	2	19
8) <i>L. deltoides</i>	12	0	12
9) <i>L. nemorosus</i>	12	0	12

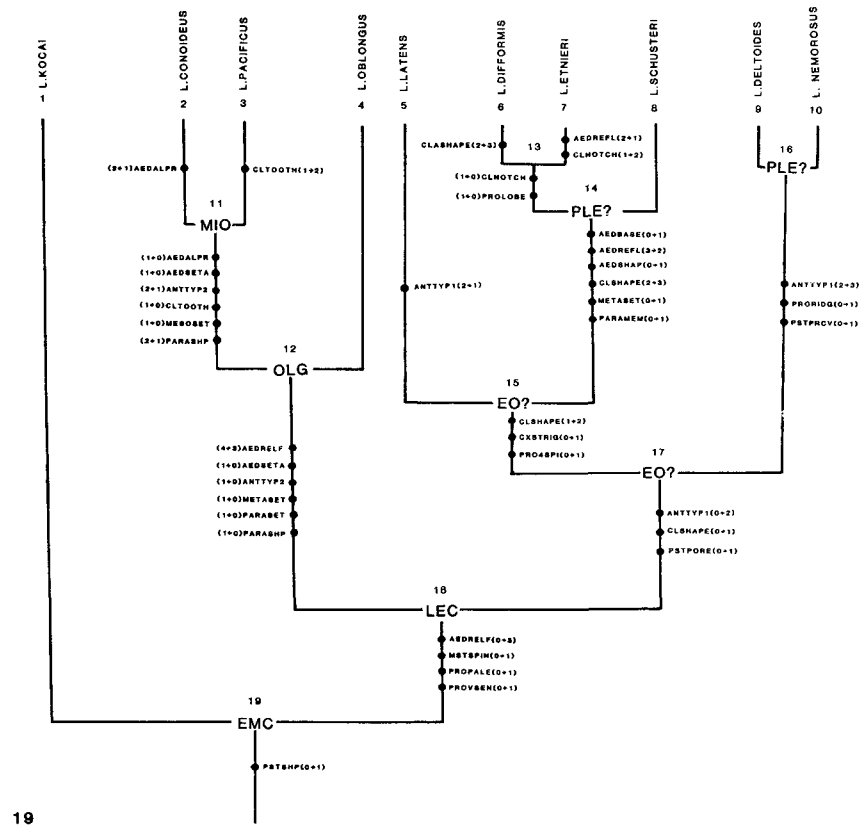


Figure 19. Proposed phylogeny of species of *Laccornis*. EMC-early to middle Cretaceous, LEC-late Cretaceous to early Cenozoic, OLG-Oligocene, MIO-Miocene, PLE-Pleistocene, EO-Eocene.



**Homoplasy.**— Within *Laccornis* only one character has independently arisen twice and that is elongate metafemoral setae. Three character losses are recognized (see Table 6): i) antennal development in *L. latens* reverts to state 1 from state 2, ii) claw shape changes back to state 2 from state 3 in *L. difformis*, and iii) the aedeagus becomes progressively less reflexed in the *L. difformis*-complex. All losses occur in species-group III and mostly they occur within the *L. difformis*-complex.

**Conclusion.**— Parallel trends in modification of secondary Sexual characteristics could be interpreted as homoplasy but by careful re-evaluation of character states this potential problem was resolved. Nine of 10 species of *Laccornis* are remarkably divergent in terms of structural characters from their nearest relative (Table 6). Examination of Fig. 19 suggests that there were irregular episodes of structural divergence, followed by diversification of closely related and similar taxa within the *L. conoideus*-, *L. difformis*- and *L. deltoides*-complexes.

## ZOOGEOGRAPHY

### Introduction.

The distribution of species of *Laccornis* is interpreted by means of vicariance biogeography. The elements of vicariance biogeography are discussed in Nelson and Platnick (1981), Platnick (1976), Rosen (1978) and Humphries and Parenti (1987). Excellent reviews of land configuration, global climates and timing of vicariant events in the Northern Hemisphere are provided by Matthews (1979), Allen (1983), and Noonan (1986, 1988) and we have relied on these references extensively when developing our biogeographic hypotheses.

Several investigators (Coope 1979, Matthews 1977) have demonstrated that many (most?) extant species of beetles existed prior to Pleistocene glacial episodes. Matthews (1977) specifically indicated that the earliest fossil deposits with substantial numbers of extinct species are of late Miocene age. Thus based on fossil evidence (albeit none of which include *Laccornis*), it does not seem tenable to explain speciation within *Laccornis* exclusively in terms of Pleistocene events. Primarily because of this and the inferred age of origin of *Laccornis*, we assume that older geological events were important in the zoogeographic history of the taxa included within this genus.

However, we do invoke Pleistocene divergence of extremely similar species which all occur allopatrically within the southeastern United States. We are more tentative about this assumption compared to the ages postulated for earlier vicariant events.

We rely exclusively on a vicariant model of allopatric speciation. As pointed out by Kavanaugh (1979), this model depends on the assumption that structural divergence among taxa is positively correlated with: 1) genetic differentiation, 2) degree of reproductive isolation, and 3) length of period of geographical isolation. Although these assumptions are not without exception, the phylogenetic position of Laccornini within Hydroporinae combined with extensive amount of structural divergence of certain clades represented in Fig. 19 supports our view that *Laccornis* constitutes an ancient lineage among hydroporine dytiscids.

Kavanaugh (1979) suggested that slow rates of speciation would be more apparent in beetle taxa of lowland habitats as compared to higher rates of speciation for taxa occurring in montane habitats. Members of *Laccornis* are

predominantly lowland and the moderate diversity of species (10), we think, adds credibility to our assumption of antiquity of origin.

*Distributional patterns.*— Distributional ranges are illustrated in Figs. 20 A-D and these are generalized into patterns in Figs. 21A-D.

At the species level, generalized patterns of distribution tend to be allopatric, especially when closely related taxa are compared. No known species is sympatric with its sister species [compare ranges of *L. conoideus* - *L. pacificus* (2, 3 in Fig. 21A), *L. deltoideus* - *L. nemorosus* (9, 10 in Fig. 21A) and *L. difformis* - *L. etnieri* (6, 7 in Fig. 21A). However, the distributions of members of some species pairs are virtually proximate (*L. difformis* - *L. etnieri* and *L. conoideus* - *L. pacificus*). Collections from areas of maximum proximity in Maryland/eastern Virginia and southern British Columbia/Alberta of the respective species pairs have failed to demonstrate any evidence of parapatry and/or hybridization. *Laccornis latens* is the sister lineage to the *L. difformis*-complex and these two lineages are largely allopatric (compare 5 to 6+7+8 in Fig. 21A); as is that of *L. oblongus* and the *L. conoideus*-complex (compare 4 to 2+3 in Fig. 21A).

Often distributions are irregularly shaped and they are often imperfectly known. One way to factor out such vagaries is to use the center of endemism approach of Kavanaugh (1980). To conduct such an analysis we drew circles, approximately scaled to the size of the long-axis length of the distribution of each species. The circle representing each species was located on the map so that its center approximated the center of the "real" distribution (Fig. 21B). It is obvious immediately that there is no center of endemism based on concentric overlap of circles. As a matter of fact with this approach, "allopatry" is even more evident in the genus. Only circles of *L. difformis* and *L. etnieri* (6, 7 in Fig. 21B) narrowly overlap and only circles of *L. nemorosus* and *L. schusteri* (8, 10 in Fig. 21B) overlap completely.

Species-complexes show more distributional overlap than do species-groups (Figure 21C). The distribution of the *L. latens* -complex is completely contained in that of the *L. conoideus*-complex. The *L. difformis*- and *L. deltoideus*-complexes each are narrowly sympatric at their independent northern limits with the *L. latens* - and *L. conoideus*-complexes. The *L. deltoideus*- and the *L. difformis*-complexes are allopatric towards the north with respect to each other but are largely sympatric in the south on the Gulf Coast based on the speculation that *L. schusteri* extends onto the Gulf Coastal Plain, as discussed above.

A somewhat generalized composite picture of species-group distributions (except *L. kocai*, endemic to southeastern Europe) is shown in Fig. 21D. Generalizations about these patterns are as follows. 1) Species-group I (*L. kocai*) has the most restricted range (Fig. 20D). As discussed above, the limited distribution of *L. schusteri* and *L. nemorosus* is probably artificial and both almost surely occur throughout the Gulf Coastal Plain. 2) Species-group II (Fig. 21D) occurs in both the northern Nearctic and Palearctic areas; it is circumboreal. 3) Species-group III is restricted to eastern North America, primarily south of the Great Lakes Region. Therefore, species-group distributions are allopatric, except for narrow overlap between species-groups II and III in eastern North America.

Based on these distribution patterns we feel that our assumption of allopatric speciation is justified and that this group is amenable to interpretation by vicariant zoogeography. Similarly because these distributions are allopatric

and because we are confident in the time of origin of *Laccornis* we added the timing of vicariant events to the cladogram (Fig. 19).

*Age of origin of the genus Laccornis.*— Wolfe (1985), based on a phylogenetic analysis of primitive lineages of the subfamily Hydroporinae, suggested that the genus *Laccornis* represented either the sister group to all other Hydroporinae, or, at least, the sister group to hydroprine genera with centres of diversity in the Northern Hemisphere. It was proposed that the initial break-up of Pangea in mid-Jurassic [about 170 million years before present (mybp)] separated the faunas of the Northern and Southern Hemispheres and that the northern isolate included the common ancestor of *Laccornis* as well as that of the hydroporine genera which are most diverse there today. There is no reason to challenge this conclusion at the present time.

*Historical analysis.*— After origin of the genus *Laccornis* on Laurasia (Wolfe 1985), the first vicariant event was the dichotomization of the common ancestors of species-group I (*L. kocai*) and species-groups II + III (all other species of *Laccornis*). The first major vicariant event within Laurasia was division into Euramerica and Asiamerica by the development of the Turgai Straits which existed from mid-Jurassic up to Oligocene times (Hallam 1981). This broad saltwater barrier would have been an effective isolating mechanism. The ancestral species to species-group I could have been isolated within western Asiamerica. If so it probably dispersed southeastward to its present range some time after regression of the Turgai Straits. Alternatively it may have remained in Euramerica but was disjunct from the common ancestor of species-groups II + III. Maps of continental land mass configuration of Jurassic and Late Cretaceous times provided by Noonan (1988:42) suggest that small isolated areas existed within the Turgai Straits and such areas may have provided a refuge for the ancestor of *L. kocai*. This vicariant event occurred in Early to Middle Cretaceous or prior to 100 million years before present.

An important element of this scenario is the phylogenetic position of *L. kocai* which is the sole member of species-group I. We interpret it as being a member of *Laccornis* and therefore of having diverged early in the history of *Laccornis*. If *L. kocai* represents an undescribed genus which is the sister group to *Laccornis* our scenario will remain accurate. However, if *L. kocai* is misplaced and it is not a close relative to *Laccornis* then our scenario would be misconstrued by virtue of polyphyly. It should be emphasized that there is only one relatively weak synapotypy linking *L. kocai* with the remainder of *Laccornis* and that the amount of structural divergence among it and members of species-groups II+III is considerable. However, until evidence from other sources (*e.g.*, immature stages) is presented to the contrary, *L. kocai* should be considered correctly assigned.

The common ancestor of species-groups II + III was probably a widespread species occurring at least in Euramerica but more likely it was distributed among eastern Asiamerica and Euramerica if these land masses were indeed continuous at high latitudes. The formation of the Mid-Continental Seaway through central North America led to the divergence of species-groups II + III. Species-group II was thus isolated in Asiamerica.

Our historical, zoogeographic hypothesis requires a vicariant zone across Beringia which isolated Eurasian populations (*L. oblongus*-complex) from the North American populations (*L. conoideus*-complex). Considering the amount of divergence between the members of these two complexes, we suspect that the vicariant event involved is relatively old.

Asiamerica was broadly connected by a Beringian land bridge from Cretaceous through Pliocene times (Matthews 1979). Several climatically induced filters to dispersal across Beringia have been proposed that could have impeded faunal interchange; however, the evidence supporting their existence is equivocal (Matthews 1979). Matthews (1979) indicated that Beringia was maximally eroded in the early Oligocene and this may have provided a barrier to dispersal. However, it is certain that sometime between the late Miocene and early Pleistocene times, Beringia was breached and Siberia and Alaska were separated until the late Pliocene-Pleistocene.

We propose that the vicariant event which vicariated the two complexes of species-group II pre-dates the late Miocene-Pliocene inundations of Beringia and that it probably corresponds to the maximal reduction of the land bridge in the Oligocene which may have provided enough of a filter effect to allow divergence of Eurasian and North American populations. Kavanaugh (1986) proposed a similar (also somewhat vague by his own admission) vicariant event at Beringia at approximately the same time for members of *Amphizoa* LeConte (Coleoptera: Amphizoidae).

Beginning in the late Miocene, mountain building and orogenic activity in northwestern North America was sufficient to cause divergence of floras on the eastern and western sides of the developing continental divide (J.A. Wolfe 1969). Kavanaugh (1986) and Perkins (1980) each have proposed this region as a vicariant zone for amphizoids and hydraenid water beetles respectively. We think that this uplift was the event that divided the range of the ancestor of the *L. conoideus*-complex and led to the divergence of *L. pacificus* and *L. conoideus*.

The distribution of the members of the eastern North American species-group III do not suggest distinct geographic areas or paleogeological events with vicariant attributes/effects. Species-group III is composed of three sets of species: *L. latens* -, *L. deltoides*- and *L. difformis*-complexes. Within the latter two complexes the taxa are quite similar. However, there has been significant structural divergence of the common ancestor of the *L. difformis*-complex from that of *L. latens*. Similarly the ancestor of this *L. deltoides*-complex is moderately distinct from that of the *L. latens* - + *L. difformis*-complexes.

The amount of structural divergence among the complexes of species-group III suggests an early divergence which is at least pre-Pleistocene. It has been demonstrated that divergence of eastern North American and European floras and faunas was accentuated during the Eocene. Perhaps the factors influencing the North American flora/fauna in general at that time affected the ancestors of the species-complexes of species-group III.

Perkins (1980) suggests a vicariant zone in eastern North America for hydraenids (his vicariance zone 6) that very approximately coincides with the distributions of the *L. latens* - and *L. difformis*-complexes. Perkins (1980) was unable to associate this vicariant zone with a paleogeological event; however, he did support its existence with distributional evidence of three synvicariads. He interpreted this vicariant event as occurring within the Pleistocene. We propose, as an alternative explanation, that if these-groups occupied a common area and were divided by a common event that it was pre-Pleistocene in age and probably Eocene as discussed above.

The members of the *L. difformis*- and *L. deltoides*-complexes are quite similar in structure. This suggests that divergence and speciation within these complexes were induced by Pleistocene glacial episodes.

*Rate of speciation within Laccornis.*— Askevold (1988) provided a cogent discussion of rates of speciation in certain groups of Chrysomelidae

(Coleoptera) based on phylogeny and zoogeography. This provides an interesting analogy to the rate of speciation within *Laccornis*.

Overall, and assuming that *Laccornis* originated 100+ mybp and that it includes 10 extant species then the average rate of speciation for the genus is one extant species/10 my. This is within the range of 0.01 to 0.06 species/my of the groups examined by Askevold (1988). However, as pointed out by Whitehead (1972) and Askevold (1988) speciation rates so derived are not meant to be taken as constants, but rather as averages to allow comparisons of speciation rates among clades of equal age and of similar macrohabitats (e.g., temperate lowlands).

Our zoogeographic/phylogenetic analysis indicates that rates of speciation within *Laccornis* is unequal (Fig. 19). For instance, our hypothesis suggests that the division of species-group I (one species) and species-groups II + III (nine species) occurred 70 mybp. Therefore, it is safe to assume that within this overall pattern of slow rates of speciation there have been times of relatively rapid diversification.

*Evolution with respect to habitat.*— Members of *Laccornis* have been collected from a variety of habitats in North America. In this section we use this information to generalize the preferred habitat of members of the genus *Laccornis* from a phylogenetic perspective.

In total, the habitat valence is quite broad. Specimens were collected from extensive sedge marshes (Alberta and Manitoba), extensive marshes and swamps (Ontario and Tennessee), small or medium sized temporary woodland pools (Ontario and Tennessee), permanent ponds with little shade (Yukon), and temporary ponds that are partially shaded in open fields (New Jersey and Tennessee). Also there are some few records of *Laccornis* from lotic habitats (e.g., *L. conoideus* and *L. nemorosus*).

Despite this array of habitats, we believe that the members of *Laccornis* occur most often and most abundantly in temporary, vernal pools that are heavily shaded by forests. See Wiggins *et al* (1980) for a discussion of the features of this habitat. Within this broad category specimens of *Laccornis* are known from cooler pools with less daily temperature variation. Below we refer to temporary, vernal pools as the preferred habitat. Our conclusions on the preferred habitat are based on three lines of evidence: 1) most specimens were collected in this habitat, 2) collecting at more extensive habitats (e.g., marshes, swamps and fens) has yielded more specimens from shaded, marginal areas that are isolated from the main body of water, and 3) within a single partially shaded pond, specimens are most abundant in areas with shade for the majority of the day. The occurrence of specimens in such habitats as streams probably indicates accidental occurrence; however in many low gradient streams subject to high water in the spring time, conditions in marginal pools could be appropriate. There are other features of this preferred habitat which may be important. One of these is that these habitats normally have very little vegetation. There is very little to no wave action within these pools and this may be important in that adults and larvae tend to crawl on the pool substrate rather than swimming actively.

These pools exist until mid-summer. The shallow and temporary or seasonally flooded habitats contain water for only a short time and food resources may be abundant for only a restricted period of time corresponding to larval development. Adults of *Laccornis* presumably aestivate in the substrate of the dry pond (cf. Leech 1940, Cuppen and Dettner 1987). Another aspect of these pools may be a reduction of predators such as fish (Wolfe 1985) and/or odonates.

When examining this analysis with respect to the reconstructed phylogeny (Fig. 19) two distinct trends are evident. Members of species-groups I + II + *L. latens* -complex, in general, are moss-associated species (tyrphophilic/tyrphobiotic, Hebauer 1974) whereas the remaining members of species-group III are woodland pool specialists (acidophilic, Hebauer 1974). Tyrphophilic and tyrphobiotic species very often uses mosses such as *Sphagnum* or *Drepanocladus* as a substrate within which to crawl. Many other species of dytiscids also use this habitat type and therefore the number of co-occurring species may be quite high (cf. Larson 1987).

The members of species-group II use a wider variety of habitats and present the greatest known divergence from the narrow definition of preferred habitat given above (see Natural history for *L. oblongus*, *L. conoideus* and *L. pacificus*). The distribution of those three species generally is more northern than is that of other members of *Laccornis*. Interestingly, members of these species appear to occupy fewer kinds of habitats in the southern portion compared to those used in the more northern portions of their ranges.

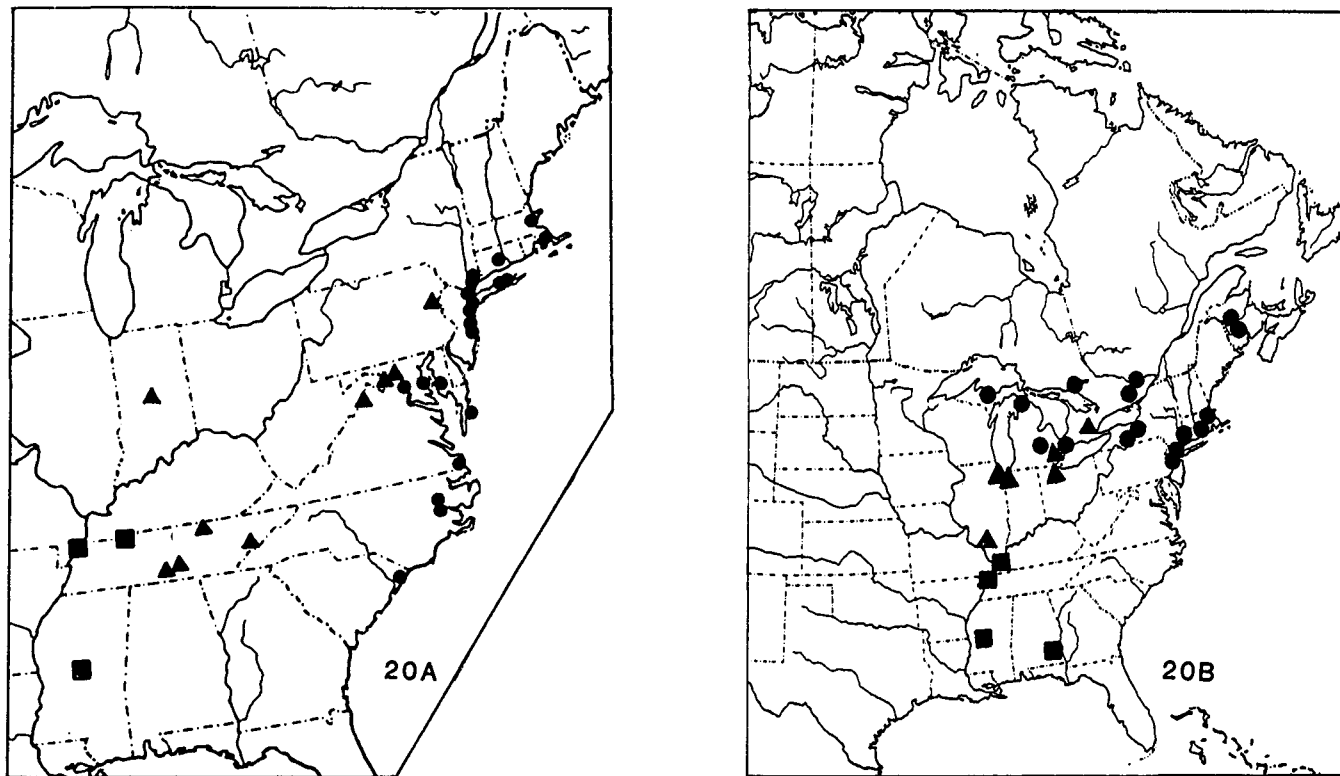
Members of the *L. difformis*- and *L. deltoideus*-complexes of species-group III tend to prefer temporary woodland pools in which the substrate is composed of dead leaves from surrounding trees. Within the spectrum of this habitat type the members of these complexes occur at the more austere end of the range, based on our own field collections throughout eastern North America and in particular the southeastern United States. Such pools are without the diversity of niches and food resources associated with other habitat types. Diversity of species, including other groups of dytiscids, is very low. This may explain, in part, why so few specimens are known of many of the species within these complexes; the number of invertebrates collected per unit of effort is extremely low but such low return is often an indicator that it is a good pool for collecting specimens of *Laccornis*.

In summary, the three species-groups each prefer temporary pools and they are adapted to aquatic sites in which the water has cooler temperatures. An important question is whether or not the habitat and temperature preferences are positively correlated and follow the historical development of the genus. We believe that the preferred habitat referred to above has always represented the preferred habitat of members of *Laccornis* since the origin of the genus. The habit has existed continuously through time and there is no evidence to suggest that any other habitat was used by ancestral members of *Laccornis*.

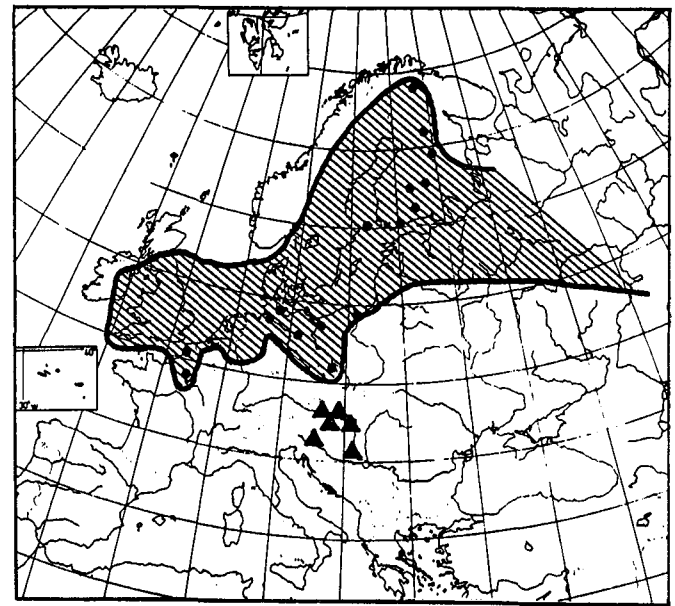
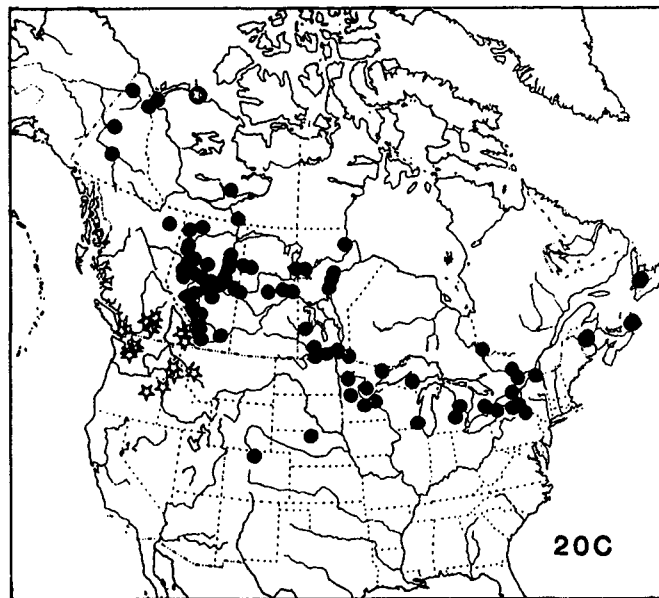
Adaptations to cooler temperatures are more difficult to analyze. There are two equally viable hypotheses. As we are unable to choose among these they are both presented below.

*Hypothesis 1.*— Adaptations to cooler temperatures occurred independently in each of the ancestors of species-groups I, II and III. Above we postulated that the genus *Laccornis* arose at least by the start of the Cretaceous.

This becomes important when we overlay global climate onto the cladogram. Warm temperate climates (analogous to modern climates) existed in the Northern Hemisphere since early Cretaceous which includes the time of origin of *Laccornis*. However, during the Eocene when the common ancestors of species-groups I to III were present there was a distinct, upward pulse of temperature; even climates at very high latitudes at this period were nearly tropical in nature (J.A. Wolfe 1969); however, small areas of cooler temperate habitats may have co-existed with the more warm temperate and subtropical biota and then become more widespread during Eocene/Oligocene cooling (Noonan 1986, 1988). Nevertheless, if the three lineages of *Laccornis* were



Figures 20A-B. Distribution maps of species of *Laccornis*. A) circles-*Laccornis difformis*, triangles- *L. etnieri*, squares-*L. schusteri*, B) circles-*L. latens*, triangles-*L. deltoides*, squares-*L. nemorosus*.



Figures 20C-D. Distribution maps of species of *Laccornis*. C) circles-*L. conoideus*, stars-*L. pacificus*, star in circles-*L. oblongus*, D) triangles-*L. kocai*, circles and cross-hatched area-*L. oblongus*.



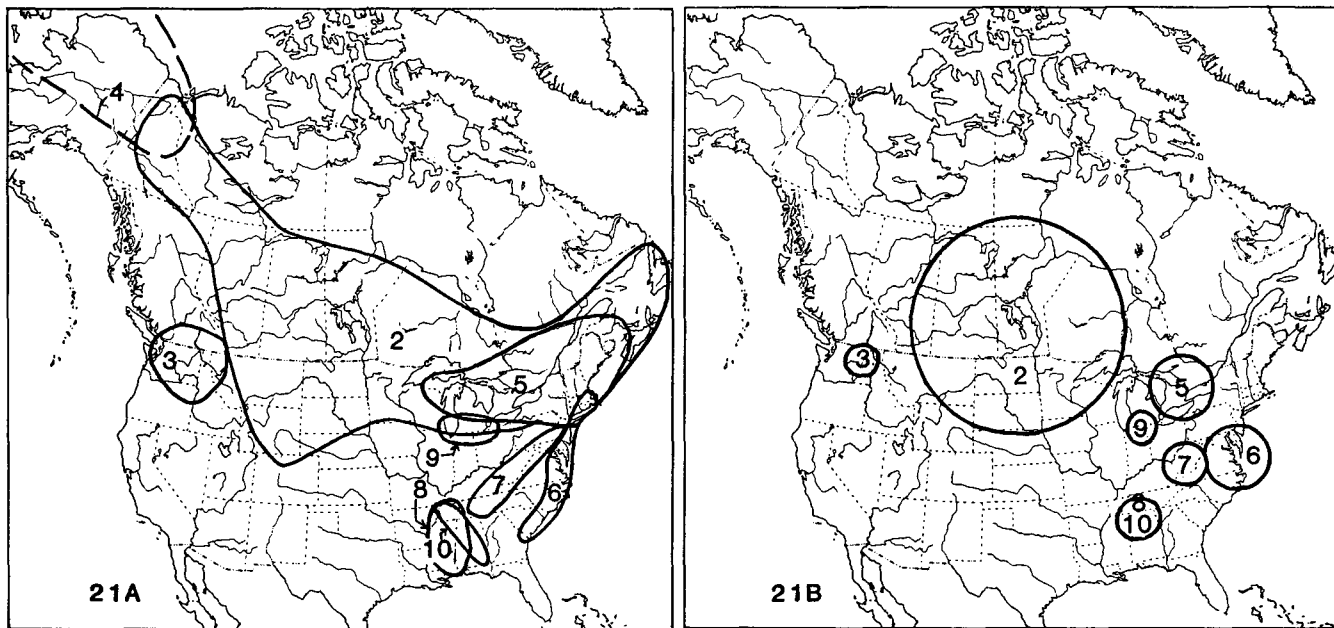
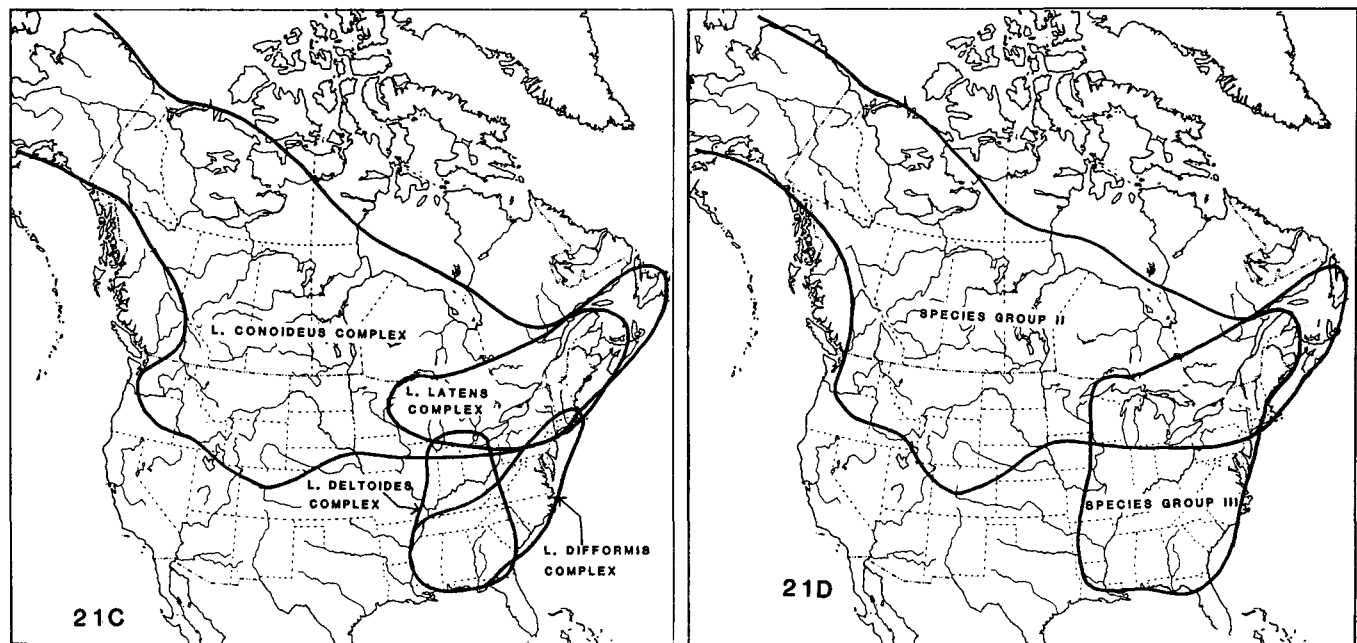


Figure 21A-B. Generalized distributional patterns. A) Generalized Nearctic distributions. Numbers coincide with species numbers within reconstructed phylogeny (Fig. 19); 2=*Laccornis conoideus*, 3=*L. pacificus*, 4=*L. oblongus*, 5=*L. latens*, 6=*L. difformis*, 7=*L. etnieri*, 8=*L. schusteri*, 9=*L. deltooides*, 10=*L. nemorosus*. B) Species ranges scaled down to demonstrate centers of endemism.



Figures 21C-D. Generalized distributional patterns. C) Generalized distribution of species-complexes within *Laccornis*, D) Generalized distribution of species-groups within *Laccornis*.

adapted to cooler habitats since the early Cretaceous it is difficult to explain how such a geographically widespread group could have survived. In this hypothesis, then the cool temperature adaptations would have occurred after climates returned to a more temperate regime.

*Hypothesis 2.*— Adaptations to cooler temperatures are a ground plan feature of *Laccornis*. This hypothesis is similar to the above except that it assumes that preference for cooler water habitats has always been a feature of *Laccornis* since the origin of the genus. This requires that the lineages became widespread during the Cretaceous in part because they were well adapted to the temperate environment. The diversification which occurred in the Cenozoic could be a direct result of the warming that occurred during the Eocene. The geographical ranges of the formerly widespread ancestral lineages would have been disrupted by the warming trend. During this period, isolated populations of the ancestors could have survived (and diverged) within isolated refugia in which cooler temperatures prevailed.

A clear choice between these two hypotheses cannot be made on available evidence. Nevertheless, it is interesting to note that speciation in *Laccornis*, in the phylogeny that we propose (Fig. 19), increased markedly after the post-Eocene cooling trend which resulted once again in more widespread temperate conditions.

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