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Kipling WILL

Systematics and zoogeography of the genus *Lophoglossus* Leconte (Coleoptera Carabidae Pterostichini)

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Abstract. A phylogenetic hypothesis for the genus *Lophoglossus* LeConte is developed based on the results of a cladistic analysis using 21 characters from adult morphology of the six species in the genus. The *substrenuus* group (*L. substrenuus* + *L. vernix)*, *scrutator* group (*L. scrutator)* and *tartaricus* group (*L. tartaricus* (*L. haldemanni* + *L. gravis*)) are designated as species groups and cladistic diagnoses and descriptive notes are presented for each. A key to species and notes on biology, distribution and phenology are provided. A zoogeographical scenario involving glacial cycles and vicariance of population east and west of the Appalachian Mountain barrier explains the present distributions of species given their cladistic relationships.

Резюме. На основании результатов кладистического анализа 21 признака имагинальной морфологии шести видов рода *Lophoglossus* LeConte разработана филогенетическая гипотеза. Выделены группы видов *substrenuus* (*L. substrenuus* + *L. vernix)*, *scrutator* (*L. scrutator)* и *tartaricus* (*L. tartaricus* (*L. haldemanni* + *L. gravis*)), представлены кладистические диагнозы и описания каждой из них. Приводятся определительная таблица видов и замечания по биологии, распространению и фенологии. Зоогеографический сценарий, включающий циклы оледенения и викарирование популяций на востоке и западе барьера гор Аппалачи, объясняет современное распространение видов с учетом их кладистических взаимоотношений.

Key words: Carabidae, *Lophoglossus*, morphology, cladistic analysis, species key.

INTRODUCTION

LECONTE (1852: 248-49) circumscribed *Lophoglossus* to include three species, *L. haldemanni* LeConte, *L. tartaricus* (Say) and, *L. scrutator* LeConte. He distinguished these taxa from other *Pterostichus* by the form of the ligula, though he was doubtful of the distinctiveness of the genus. LECONTE (1873: 316-317) later expanded the genus to include *L. gravis* LeConte and *L. tartaricus* (Say), and developed a key to species. CASEY (1913) described three additional forms and devised a key for the genus (excluding *gravis*). Casey's subsequent publication (CASEY, 1918) included *Lophoglossus* in a key to genera of Pterostichini, and therein he designated *Feronia tartarica* Say as the type for the genus. Others authors, such as CHAUDOIR (1868: 331), CSIKI (1930: 627), LINDROTH (1968: 497), and HORN & LECONTE (1883: 32) considered *Lophoglossus* as a weak subgeneric group within *Pterostichus* s.l. BOUSQUET & LAROCHELLE (1993) recognized *Lophoglossus* as a distinct genus including the six species treated here. I concur with Bousquet and Larochelle's recognition of generic status for *Lophoglossus*, which is substantiated by generically distinct autapomorphic characteristics of adults as discussed below and characteristics of larvae (BOUSQUET, 1985). Whether the large Holarctic genus *Pterostichus* is made paraphyletic by recognizing *Lophoglossus* as a distinct genus is beyond the scope of this paper. Species within the genus are recognized by the criteria established by NIXON & WHEELER (1990).

Material and methods

Taxonomic material

Approximately 380 adult specimens of *Lophoglossus* species and all holotypes, 30 specimens of *Piesmus submarginatus* (Say) and 15 specimens of *Pterostichus (Hypherpes) lama* (Ménétriés) from the collections listed in the acknowledgments below are the basis for this study. All *Lophoglossus* species where represented by large series except *Lophoglossus vernix* Casey, which is known only from fewer than 20 specimens.

Specimen preparation and measurement

External structures were examined using a dissecting stereo-microscope at magnification of 100X or less. Smaller structures and microsculpturing of legs, mouth parts and elytra were examined using a Hitachi 4500 scanning electron microscope. Overall length was standardized using the sum of lengths; 1. base of labrum to the cervical collar, 2. apex to base of pronotum along the midline, 3. base of scutellum to apex of left elytron.

Methods used for preparation of male and female genitalia and reproductive tracts are outlined by Will (1998). Drawings were made using an ocular grid or camera lucida. Nomenclature of female reproductive tract structures follows Liebherr & Will (in press). Nomenclature of endophallic structures follows Noonan (1991).

Phylogeny reconstruction

Morphological characteristics that could be coded as cladistic characters (Hennig, 1966) were placed into a taxa x character matrix using the computer program DADA (Nixon, 1995). The most parsimonious branching pattern was found by submitting the matrix to the tree searching program NONA (Goloboff, 1993b) (default settings used). The resulting cladogram and the distribution of character states were examined using the tree viewing program ClaDOS (Nixon, 1993).

The cladistic parsimony methodology is an assumption minimizing program, however, several assumptions are necessary to derive the cladogram and then make the leap between the observed pattern and interpreting that pattern as the reconstructed history of a lineage. Herein I apply the following: 1. Many generations of taxonomists have shown that historical relationships (natural groups) of most extant taxa are best represented by a hierarchy (e.g. Darwin, 1859; Strickland, 1841). 2. The hierarchical branching pattern is found assuming that character weight, or the relative importance, of all characters is equal. All current methods for differential weighting require the inclusion of some arbitrary element(s) thereby increasing the implied or explicit assumptions in pattern construction (Farris, 1969; Goloboff, 1993a). Characters that pass the congruence test, confirming the initial hypotheses of homology of states (de Pinna, 1991) are used to group taxa. These data are best explained by common ancestry (Hennig, 1966).

Two outgroup taxa were selected for this analysis. *Piesmus submarginatus* was selected as the distant outgroup given the apparently less derived morphological characteristics found in both adults and larvae (Will, unpublished data). *Pterostichus (Hypherpes) lama* was selected because of the very similar form of the female reproductive tract in *Lophoglossus* species and *P. lama*. The outgroup method (Nixon & Carpenter, 1993) was implemented using the two outgroup taxa, The root was then placed between *Piesmus submarginatus* and *Pterostichus lama* + *Lophoglossus*. Alternative rooting, between an ingroup clade and the outgroup or with either of the outgroups at the root, does not affect character optimizations. A test of a possible relationship of *Lophoglossus* and *Pterostichus*, or some subset of *Pterostichus*, as the genus is presently conceived, is beyond the scope of this study and will be the topic of future works.

Characters

Twenty-one potentially informative characters of the adult external and internal morphology were coded. Two multi-state characters were treated as unordered. Characters, states and the coding are listed below. Table 1 provides the taxa x character states matrix.

Table 1. Characters 1 – 21.

	1 5 10 15 20
	| | | | |
Piesmus submarginatus	00000000000000000000
Pterostichus lama	00000001110000000010
L. substrenuus	01001000011010100011
L. vernix	01001000010010100011
L. scrutator	01101101000201011 0001
L. tartaricus	10111111100211011 1101
L. haldemanni	10121111102111111101
L. gravis	10121111101111111101

Character list:

1. latero-basal seta of pronotum: width of socket or less from margin (0), Figs 1-3; more removed from margin (1), Figs 4-6.

2. meso tibial subapical spine (male): absent (0), Figs 14-15; present (1), Figs 12-13.

3. meso tibial apical spine (male): absent (0), Fig. 12; present (1), Figs 13-15.

4. meta tibial spine (male): absent (0), Figs 7-8; long (1), Fig. 9; short (2), Figs 10-11 [nonadditive].

5. ventral abdominal tip (male): rounded (0); emarginate (1).

6. abdomen tip thickened internal edge (male): absent (0); present (1). The inner margin, internally, with a distinct thickened rim, either simple or sulcate.

7. abdomen tip internal inner processes (male): absent (0); present (1). A second thickened ridge, internal and strongest laterally.

8. meso/meta-thorax ventral: impunctate (0); punctate (1).

9. elytral microsculpturing: transverse (0); isodiametric (1).

10. elytral sculpticells: flat/shiny (0), Fig. 16; convex/dull (1), Fig. 17.

11. elytral tip: uniform (0); depressed (1).

12. median tergite depigmented area (female): obsolete (0); shallow (1); deep (2) [nonadditive].

13. aedeagus tip (male): flat (0), Figs 18-20; hooked dorsally (1), Figs 21-24.

14. aedeagus basal process (male): absent (0); present (1), Figs 24-25.

15. right paramere (male): narrow (0), Fig. 26a; wide (1), Fig. 27a.

16. left paramere (male): simple (0); notched (1), Figs 26-27.

17. left basal sacculus (male): short (0); elongate (1), Fig. 28a.

18. left basal sacculus sclerite (male): absent (0); present (1), Fig. 28a.

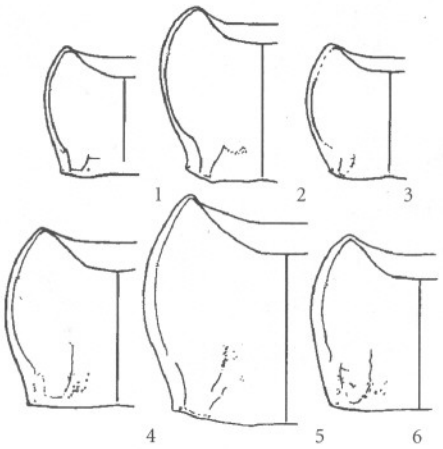
19. endophallus trichoid field (male): absent (0); present (1), Fig. 28a.

20. gonocoxite II ensiform setae (female): subequal/robust (0), Figs 29, 31; basal seta reduced/absent (1), Fig. 30.

21. bursal sclerites (female): absent (0); present (1), Fig. 29.

Taxonomic methods

I do not redescribe the species of *Lophoglossus* in detail, rather, I focus on synapomorphies in the cladistic diagnoses and discuss general habitus, variation and autapomorphies in the descriptive notes. I provide a more complete account of character systems that were not covered, incompletely treated or incorrectly interpreted by previous authors. Although each monophyletic clade and each species is discussed in turn, three species groups are designated that seem to represent significant character evolution and are therefore worthy of particular attention.



Figs 1-6. Pronota: 1, *L. vernix*; 2, *L. substrenuus*; 3, *L. scrutator*; 4, *L. tartaricus*; 5, *L. haldemanni*; 6, *L. gravis*.

Result of cladistic analysis

A single most parsimonious cladogram was found (Fig. 32) with RI= 79 and CI=85 and length 29 . These scores show that grouping information is quite strong and homoplasy low for this set of taxa and characters. Specific characters for each clade are discussed in cladistic diagnoses below.

Taxonomic treatment

Key to the species of *Lophoglossus*

1. Ventral sclerites of the meso and meta thorax punctate laterally (questionable *L. scrutator* covered in both halves) 2

1'. Ventral sclerites of the meso and meta thorax impunctate[1] 7

2(1). Elytral microsculpture reticulate or granular, generally duller (same sex compared); male without subapical mesotibial spine, apical spine present (Figs 14-15). 3

2'. Elytral microsculpture weak or obsolete, if present stretched, shinier (same sex compared); male with subapical mesotibial spine, apical spine small (Fig. 13). . . . . .*L. scrutator* (LeConte)

3(2). Pronotal hind angles obtusely rounded (Fig. 6). . . . . .*L. gravis* LeConte

3'. Pronotal hind angles approximately right angled (Figs 1-5). 4

4(3'). Males, expanded protarsi 5

4'. Females, protarsi simple 6

5(4). Metatibia with process over apical spur smaller, length less than 1.5 x width (Fig. 11). . . . . *L. haldemanni* (LeConte)

5'. Metatibia with process over apical spurs elongate, greater than 2 x width (Fig. 9). . . . . .*L. tartaricus* (Say)

6(4'). Elytral microsculpture granulate, dull; very large species 21 to 25mm[2] . . . . . .*L. haldemanni* (LeConte)

6'. Elytral microsculpture smooth, rather shiny, never granulate; smaller, 16 to 20mm. . . . . .*L. tartaricus* (Say)

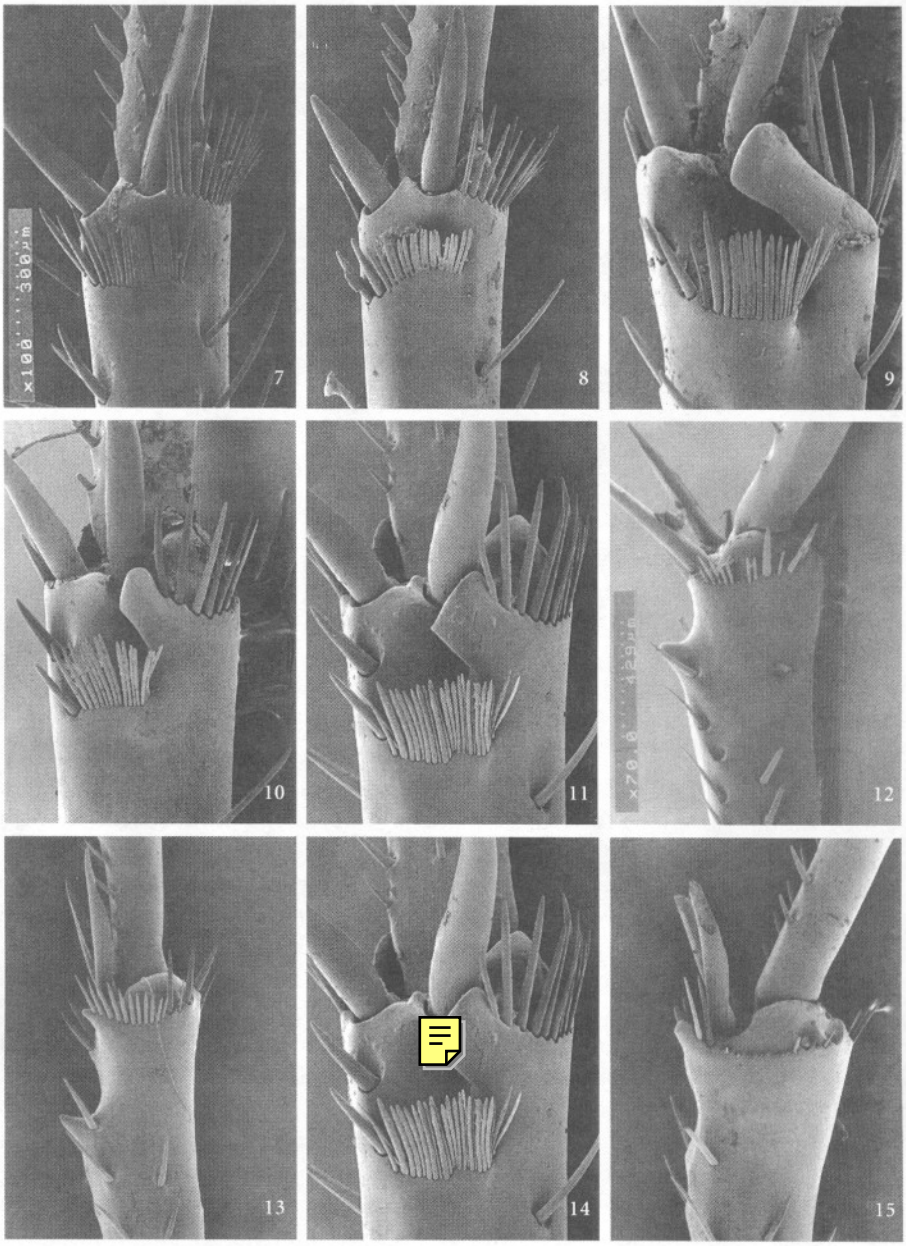
7(1). Elytra with depressed area at the apexes of stria 3-5. 8

7'. Elytra without depressed area at the apex, stria 3-5 uniformly convex, males with small apical and large subapical mesotibial spines (Fig. 13). . . . . .*L. scrutator* (LeConte)

8(7'). Outer basal impression of the pronotum sharply delimited against a convex area along the explanate laterally margin (Fig. 1); hind trochanter usually with distinct euventral flattened area . . . . . *L. vernix* Casey

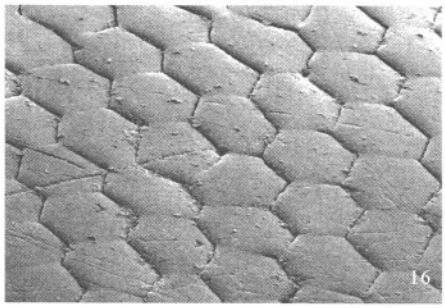
[1] A single individual from Indiana was found to have a few weak punctures on the metasternum.

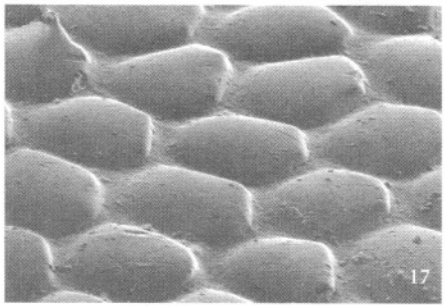
[2] A single deformed male measured 18.6 mm.



Figs 7-15. 7-11. Ventral view metatibia, scale in 7: 7, *L. substrenuus*; 8, *L. scrutator*; 9, *L. tartaricus*; 10, *L. gravis*; 11, *L. haldemanni*. 12-15. Lateral view mesotibia, scale in 12: 12, *L. substrenuus*; 13, *L. scrutator*; 14, *L. tartaricus*; 15, *L. gravis*.

8'. Outer basal impression of the pronotum without a sharp demarcation laterally, broadly flattened to the explanate lateral margin (Fig. 2); hind trochanter usually cylindrical or with a small and poorly defined flat euventral area. . . . . *L. substrenuus* (Csiki)





Figs 16-17. Scanning electron micrograph of cuticle on the dorsum on of the elytron at the third interval, 1.80k x magnification: 16, *L. tartaricus*; 17, *L. gravis*.

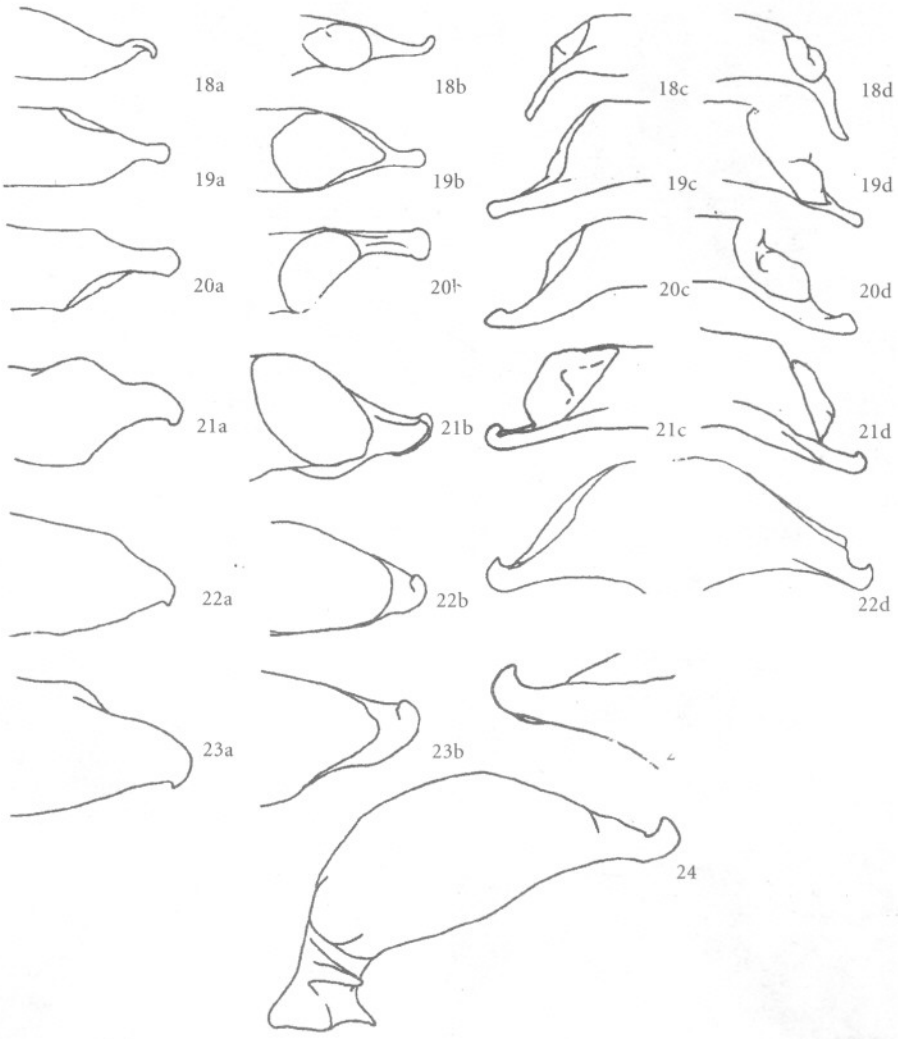
Genus *Lophoglossus* LeConte

Lophoglossus LeConte 1852: 248. Type species: *Feronia tartarica* Say, 1823, designated by CASEY (1918: 324).

CLADISTIC DIAGNOSIS. (Characters 2, 5, 14, 16, 21; Fig. 32). Two of the synapomorphies for the genus are character states not known from any other pterostichine genus; lateral process on the median lobe of the aedeagus (Figs 24-25) and the prominent apophysis of the left paramere. This apophysis is likely homologous to a less developed apophysis found in other genera of Pterostichini (Y. Bousquet pers. comm.). However, the shape of the apophysis in *Lophoglossus* is unlike any other pterostichine taxa studied. Females have two small bursal sclerites on the dorsal wall of the bursa. A similar condition is found in females of some *Cyclotrachelus* Chaudoir and *Myas* Dejean species. However, there is little other character evidence suggesting a close relationship among these taxa. Males have an emargination of ventrite VI, a synapomorphy for the genus but parallel occurrences are found in other pterostichine groups. Presence of a subapical mesotibial spine in the males is considered the primitive condition for the genus. This spine is absent in the *tartaricus* group species. The presence of the spine can be equally optimized as a two parallel gains or as a gain and loss. The latter is preferred given that the occurrence of such spines is exceedingly rare in Pterostichini.

The larvae are unique among Pterostichini s. str., with the cervical groove reaching beyond the pore Pab. Second and third instars have additional secondary setae on abdominal segments I-V (BOUSQUET, 1985). The elongate cervical groove is also known from *Loxandrus* LeConte (Loxandrini), however, this is likely a convergence as there is little else common between these two widely separated genera.

DESCRIPTIVE NOTES. Habitus typical for large Pterostichini, overall color deep black to piceous, head and pronotum shiny. Mandibles heavy, right with a sharp anterior retinacular tooth and a prominent posterior retinacular tooth and molar. Ligula moderately to strongly carinate ventro-medially, mentum tooth strongly bifid. Male genitalia of all species of *Lophoglossus* (Figs 18-25) with a strongly developed process at base of median lobe on left lateral face (Figs 24-25). Foramen is small and apical two-thirds of median lobe inflated. Left paramere (Figs 26b, 27b) with thickened process at base, and a notch in the dorsal edge. Apex of median lobe variously modified. Ostium slightly deflected to the left. Endophallus (Fig. 28)



Figs 18 –24. Tip of aedeagus: a, ventral view; b, dorsal view; c, right lateral view; d, left lateral view. 18, *L. vernix*; 19, *L. substrenuus*; 20, *L. scrutator*; 21, *L. tartaricus*; 22, *L. gravis*; 23, *L. haldemanni*; 24, Left lateral view of median lobe, parameres removed, *L. haldemanni*.

with three sacculi, basal left sacculus, basal dorsal sacculus (in some almost basal right) and, basal right sacculus (in some nearly basal ventral). Female reproductive tract (Fig. 29) with gonocoxae well developed, dimeric. Gonocoxite I with 3-5 prominent apical/subapical setae. Gonocoxite II with two ventral and one dorsal ensiform seta, ventro-basal seta reduced or absent in some (Fig. 30), two nematiform setae in apical furrow. Bursa copulatrix large, heavily thickened and cup shaped. Junction of spermatheca, common oviduct and bursa with a complex arrangement of three structures. 1. spherical body (sb, fig. 29), consisting of a cluster of tightly packed, radiating fibers connected to the base of the spermatheca, 2. a thin sclerite along the wall of the common oviduct (scl, fig. 29) that subtends 3. a thickened, fibrous structure at the base of the common oviduct (fb, fig. 29).

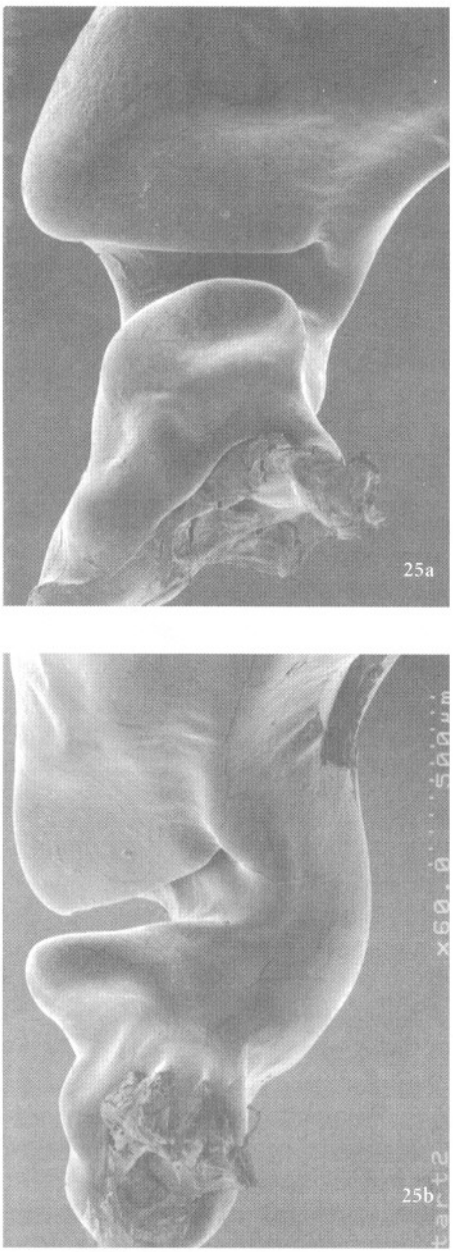


Fig. 25. Scanning electron micrograph of base of median lobe of *L. tartaricus* showing lateral process: a, left lateral view; b, ventral view.

Spermatheca unmodified tube. Appended gland elongate, subtended by ampulla and connected to spermatheca by a long duct. The junction of duct and spermatheca in the basal third of spermatheca. Flight wing full in all species (Fig. 33) with venation as in most flighted Carabidae (WARD, 1979).

NOTES ON RANGE AND LIFE HISTORY. Specimens are known from North America ranging from the Central Plains to the East Coast, southern Canada to the Gulf Coast. All species of the genus are hygrophilus and are frequently collected under flotsam near slow moving and still waters. Collection records indicate that in most species the adults are bimodally active although the northern species have scattered records through the summer months. All species have well-developed flight wings and probably can readily fly to escape rising water. However, no observations of flight or collection records from lights were found.

(*substrenuus* + *vernix*): *substrenuus*-group

CLADISTIC DIAGNOSIS. Two synapomorphies define this clade; the elyral tip with a depressed area near apex on striae 3-5 (character 11, Fig. 32) and the basal ensiform setae of gonocoxite II reduced or absent (character 20, Fig. 32). The latter character is a reduction that has occurred numerous times in Pte-rostichini, e.g. the outgroup taxon *Pterostichus lama*. However, considering the morphological homogeneity of *Lophoglossus* species it is reasonable to consider this as a reliable character for grouping within the ingroup.

DESCRIPTIVE NOTES. Other characteristic of the group are plesiomorphic or at one end of an apparent continuum within the genus. Hind angles of pronotum generally

minutely denticulate and set slightly forward of base (Figs 1, 2). In males, subapical mesotibial spine strongly developed and mesotibiae lack apical spine. Metatibia unmodified at apex (Fig. 7). Ventrally the meso and metatho-rax glabrous. Prothorax moderately to weakly punctate ventrally. Microsculpture weak or absent throughout, or when present transverse causing iridescence. Median lobe of aedeagus attenuated (markedly in *L. vernix)* without the development of a hooked tip. Tip of right paramere narrow peg. Endophallus lacks defined scleritized regions and spine fields weak. Left lateral sacculus small.

Figs 26-27. Parameres: a, right paramere; b, left paramere. 26, *L. tartaricus*; 27, *L. haldemanni.*

Lophoglossus substrenuus (Csiki, 1930)

Pterostichus strenuus LeConte 1852: 249 (secondary homonym of *Pterostichus strenuus* (Panzer, 1797)).

Pterostichus substrenuus Csiki 1930: 627 (replacement name for *Pterostichus strenuus* LeConte, 1852).

TYPE INFORMATION: ♂ (MCZ) labeled with a pink disk, Red label «Type 5643», «*L. strenuus* Lec.»

DESCRIPTIVE NOTES. Overall length 16.3-18.6 mm. Depressed, very shiny. In addition to the characters in the key and in the group diagnosis above the median lobe of the aedeagus (Fig. 19) is characteristic. The tip is simple, flat with an expanded tip.

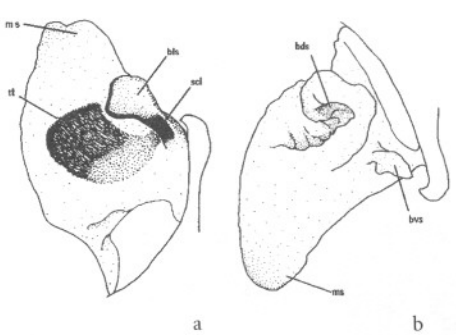


Fig. 28. Everted endophallus of *L. haldemanni*: a, left lateral view; b, right lateral view; bds, basal dorsal sacculus; bls, basal lateral sacculus; bvs, basal ventral sacculus; ms, median sacculus; scl, sclerite; tf, tricoid field.

NOTES ON RANGE AND LIFE HISTORY. Type locality: Here designated, Odenten, Ann Arundel Co., Md; Range (Fig. 34) upper Mississippi drainage south to Florida and north along East Coast to New York. New records for this species for the following states: **Florida**, Liberty Co., Apalachicola; **Indiana**, Posey Co., Hovey Lake; **Kentucky**, Henderson Co., Henderson; **Missouri**, Boone Co., Ashland; **Mississippi**, George Co., Pascagouloa R.; **New Jersey**, Passaic Co., Riverdale; **South Carolina**, Richland Co., Congaree National Monument.

Collected together with *L. gravis* in hardwood swamp in Richland Co. South Carolina. Adults records from February to October, tenerals in August and October.

Lophoglossus vernix Casey, 1913

Lophoglossus vernix Casey 1913: 146.

TYPE INFORMATION: ♂ (USNM) dissected with genitalia vial, labelled «Lyme Conn VIII.5.1911, vernix Csy, Casey bequest 1925, [Orange label] Type 47098, [Red and white label] lectotype *vernix* Csy By C.H.Lindroth».

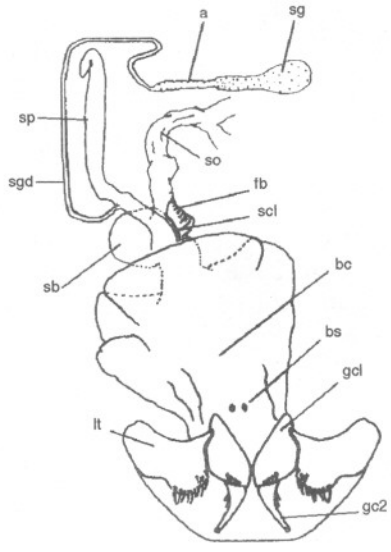


Fig. 29. Ventral view of female reproductive tract in *L. tartaricus*: a, ampula; bc, bursa copulatrix; bs, bursal sclerites; co, commmon oviduct; fb, fibrous body; gc1, gonocoxite 1; gc2, gonocoxite 2; lt, lateral tergite IX; sb, spherical body; scl, sclerite; sg, spermathecal gland; sgd, spermatheca gland duct; sp, spermatheca.

DESCRIPTIVE NOTES. Overall length 13.7-14.0 mm. Relatively small and convex, very shiny. In addition to characters in the key and group diagnosis above, median lobe of aedeagus (Fig. 18) very characteristic. Tip strongly attenuated, ostium small. Sacculi and spine fields of endophallus very weakly developed. Head large relative to pronotum. Pronotum glabrous, basal and lateral impressions sharply engraved.

NOTES ON RANGE AND LIFE HISTORY. Type locality Lyme, Ct. original designation by CASEY (1913). Range (Fig. 36), East Coast from Virginia to New Hampshire. New records for this species for the following state: **Virginia**, no further data (USNM!); **Massachusetts**, Middlesex Co. Sherbon.

Least common species in the genus. Habitat destruction along the eastern coast of North America may have extirpated this species from much of its original range. Adult collection records from April, May and August, September and December.

(*scrutator*)+((*tartaricus*)(*haldemanni* + *gravis*))

CLADISTIC DIAGNOSIS. These taxa share a number of significant synapomorphies (Characters 3, 6, 8, 12, 17, Fig. 32). Mesotibia apical spine present (Figs 13-15). Last visible tergite distinctly thickened internally along apical margin. Left lateral sacculus of endophallus elongate (Fig. 28a). Meso and metathorax punctured ventrally. The plesiomorphic state for this character is ambiguous for the genus. Probably both glabrous and punctate states have been achieved independently in Pterostichini *s.l.* many times. In either case this character separates this clade from the *vernix*-group. Except for *L. gravis*, all species of this clade have a deep V-shaped depigmented area medially on tergite VIII.

Figs 30-31. Left gonocoxae, ventral view: 30, *L. substrenuus*; 31, *L. tartaricus*.

(*scrutator*): *scrutator*-group

Herein the *scrutator*-group of *Lophoglossus* refers only to *L. scrutator* and is not equivalent to

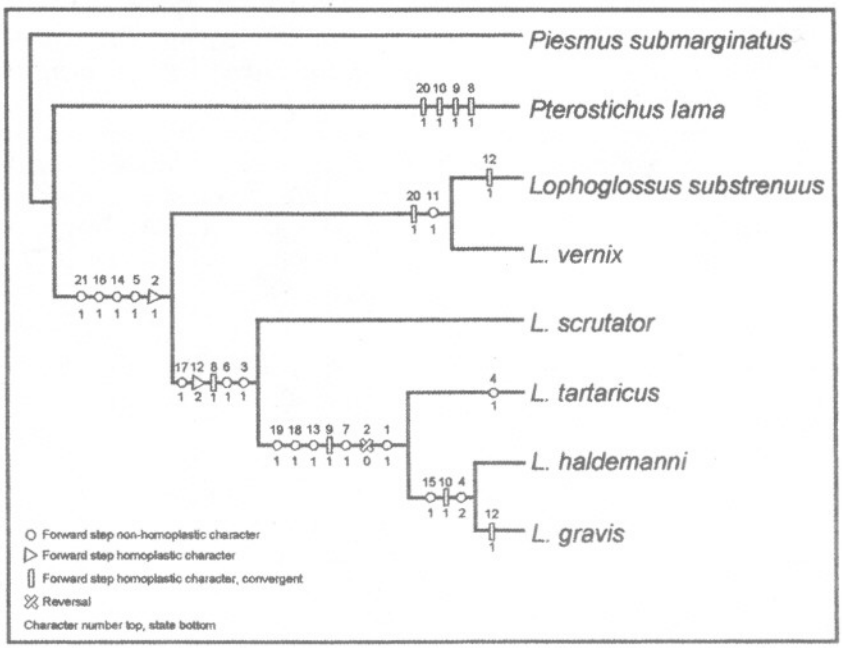


Fig. 32. Cladogram of *Lophoglossus* species with character state transformations.

Lindroth's (LINDROTH, 1968: 497) *scrutator*-group of *Pterostichus* that also included *L. vernix.*

Lophoglossus scrutator (LeConte, 1848)

Lyperus scrutator LeConte, 1848: 342.
Feronia canadensis Chaudoir, 1868: 331.
Lophoglossus illini Casey, 1913: 145.
Lophoglossus bispiculatus Casey, 1913: 146.

TYPE INFORMATION: ♀ (MZC), labelled with a yellow disk, Red Label «Type 5644», «*L. scrutator* Lec.», Orange label «Lectotype *Lyperus scrutator* Le Conte Des. by Y.Bousquet'91».

DESCRIPTIVE NOTES. Overall length 13.8-15.6 mm. In general form *Lophoglossus scrutator is* very similar to *L. vernix*, relatively small, very shiny and somewhat convex. *Lophoglossus scrutator* shares several plesiomorphic traits with the *substrenuus*-group: Mesotibia with strong subapical spine (Fig. 13), tip of median lobe not hooked (Fig. 19), base of left lateral sacculus of endophallus lacks sclerotised field and, basal setae of pronotum close to lateral margin (Fig. 3). Form of pronotum also similar with hind angles often denticulate and turned slightly forward, though varying in this character. In many respects the morphology of this species is intermediate between the more derived *tartaricus*-group and the basal *substrenuus*-group. The apical spine of

Fig. 33. Flight wing of *L. tartaricus*

mesotibia (Fig. 13) much smaller than that of *tartaricus*-group species (Figs 14-15), while the subapical spine is developed as in the *substrenuus*-group. Although the ventral surface of nearly all specimens examined were clearly puncture, the ventral surface several specimens from the eastern Great lakes region had only three or four punctures on the meso and metas-ternum and were otherwise glabrous as in the *substrenuus* group. Tip of aedeagus (Fig. 19) moderately attenuated, similar to *L. substrenuus*, and tip slightly reflexed (but not hooked). The character evidence shows clearly that *L. scrutator* is the adelphotaxon to the *tartaricus* group but is much less modified then any member of that group.

The larva is know for this species (Bousquet, 1985).

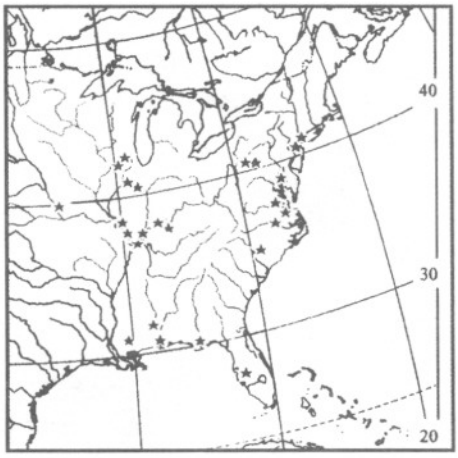


Fig. 34. Collection records for *L. substrenuus*.

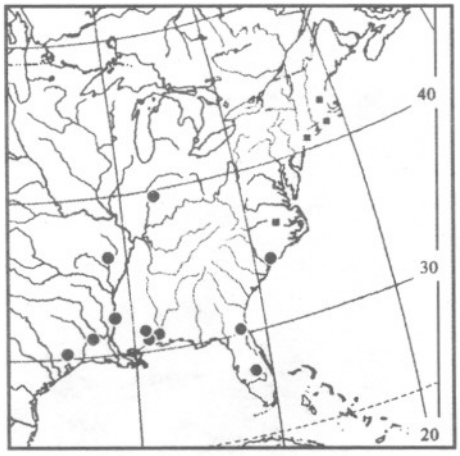


Fig. 35. Collection records for *L. gravis*, *L. scrutator* and *L. haldemanni*.

Notes on range and life history. Type locality: Cleveland, Ohio, designated by LeConte (1852). This is an exclusively northern species, ranging from Wisconsin and Iowa east to the coastal states (Fig. 30). Adults collected May to September, tenerals in May and August. New records for this species for the following state: **West Virginia**, Preston Co., Cranesville Swamp Preserve.

Adults were collected under rotten logs in low lying wet forest on Pelee Is., **On** (see Will et al., 1995 for associated taxa).

((*tartaricus*)(*haldemanni* + *gravis*)): *tartaricus*-group

Cladistic diagnosis. Seven synapomorphies group these three closely related taxa (Characters 1, 2, 7, 9, 13, 18, 19, Fig. 32); seta at hind angle of pronotum distant from the lateral margin (Figs 4-6), loss of apical spine of mesotibia in males (Figs 14-15), male abdomen with additional internal process, tip of aedeagus dorsally hooked (Figs 21-24), endophallus with sclerotized region at base of left lateral sacculus and well developed tricoid field (Fig. 28a), elytral microsculpture isodiametric; and right paramere broad and blunt.

Descriptive notes. Ventral sclerites strongly punctured. Males with strongly developed apical mesotibial spines.

Males of this group have the most extremely developed secondary sexual characteristics of the legs and abdomen. The complex shape of left paramere very similar among these three species (Fig. 26), relatively broader and more depressed than in other species of *Lophoglossus*.

Lophoglossus tartaricus (Say, 1823)

Feronia tartarica Say, 1823: 44.
Feronia complanata Dejean, 1828: 281.

TYPE INFORMATION: ♂ (MCZ), dissected with genitalia in vial, Labeled- «H.P. Löding, Mobile, Ala.; Frederick Blanchard Collection; *Pterostichus tartaricus* Say, det. Lindroth 68; MCZ Neotype 32963; Neotypus *Feronia tartarica* Say desig. Lth; ♂»

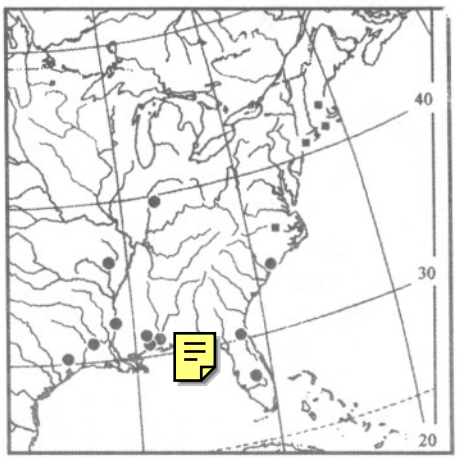


Fig. 36. Collection records for *L. vernix* and *L. tartaricus*.

DESCRIPTIVE NOTES. Overall length 16.5-20.2mm. Large, subdepressed and shiny. Elytral microsculpture reti-culate, sculpticells flat and smooth (Fig. 16). Several autoapomorphies isolate this species from other members of the *tartaricus* group. Most of these unique character states involve modification of the male secondary characteristics. Median lobe of aedeagus has a strong ventrolateral carina (Fig. 21). Modification of inner edge of last visible tergite very pronounced. Male meso and metatibial spines very large (Figs 9, 14).

Both LECONTE (1873) and CASEY (1913) had apparently misinterpreted the condition of the spine on the mesotibia. LECONTE's key (1873: 316) states that *L. tartaricus* males have «an obtuse subapical tooth and a large acute apical process». In fact, *L. tartaricus* completely lacks the subapical spine (Fig. 14). Apparently following LeConte's key Casey confused specimens of *L. substrennus* from New York with *L. tartaricus* (Casey Collection USNM!). Thus, Casey was lead to incorrectly synonymize *L. substrenuus* with *L. tartaricus* (CASEY, 1913: 144).

NOTES ON RANGE AND LIFE HISTORY. Type locality, here designated, Mobile, Mobile Co., Alabama. This species is known from the upper Mississippi drainage to the Gulf Coast, west into Texas and east to the southern East Coast (Fig. 36). New records for this species for the following states: **Indiana**, Marion Co., Foster Falls; **Louisiana**, Winn Co. Chestnut; **South Carolina**, Georgetown Co., Hobcaw Barony; **Texas**, Brazos Co.

This species is sympatric with *L. haldemanni*, *L. gravis* and, *L. substrenuus*. Synchronic/syntopic collection of adults of *L. tartaricus* and *L. haldemanni* are common. This species favors very wet swamp woods or backwater areas.

(*haldemanni* + *gravis*)

CLADISTIC DIAGNOSIS. Three synapomorphies for these taxa distinguish them from all congeners (Characters 4, 10, 15, Fig. 32). Elytra dull due to granulate microsculpture (Fig. 17), male metatibial spine short (Figs 10-11) and, right

paramere is wide (Fig. 27a). The development of the trichoid fields on the endophallus and the shape of the median lobe of the aedeagus are very similar (Figs 22-24) between these two species.

Lophoglossus haldemanni (LeConte, 1848)

Lyperus haldemanni LeConte, 1848: 341.

TYPE INFORMATION: ♀ (MCZ) , Labeled with a yellow disk, Red Label «Type 5642»,

DESCRIPTIVE NOTES. Largest species of the genus, overall length 18.6-23.2 mm. Individuals below 20.0 mm rare. Form of pronotum similar to *L. tartaricus* (Fig. 5). Microsculpture of elytra dull. Males occasionally, slightly, smoother but never as shiny as *L. tartaricus*.

NOTES ON RANGE AND LIFE HISTORY. Type locality, Alabama, from LECONTE (1848, 1852), site here designated, Mobile, Mobile Co. CASEY (1913: 144) incorrectly listed St. Louis, Mo. This was probably based on a single male specimen from the Horn Collection [MCZ!] labeled «Mo». Known from the upper Mississippi drainage, west into Texas and south to Florida along the Gulf Coast (Fig. 35). Found together with *L. tartaricus* (see notes above). Adults collected February to April. New records for this species for the following state: **Kansas**, Douglas Co., Lawrence; **Texas**, Dallas; Trinity Co. 12mi sw Lufkin.

Lophoglossus gravis LeConte, 1873

Lophoglossus gravis LeConte, 1873: 316.

TYPE INFORMATION: ♀ (MCZ), Damaged specimen, glued to card with genitalia in vial. Labeled «*L. gravis* Lec.», «Horn Coll.», Red label «MCZ Type 34935».

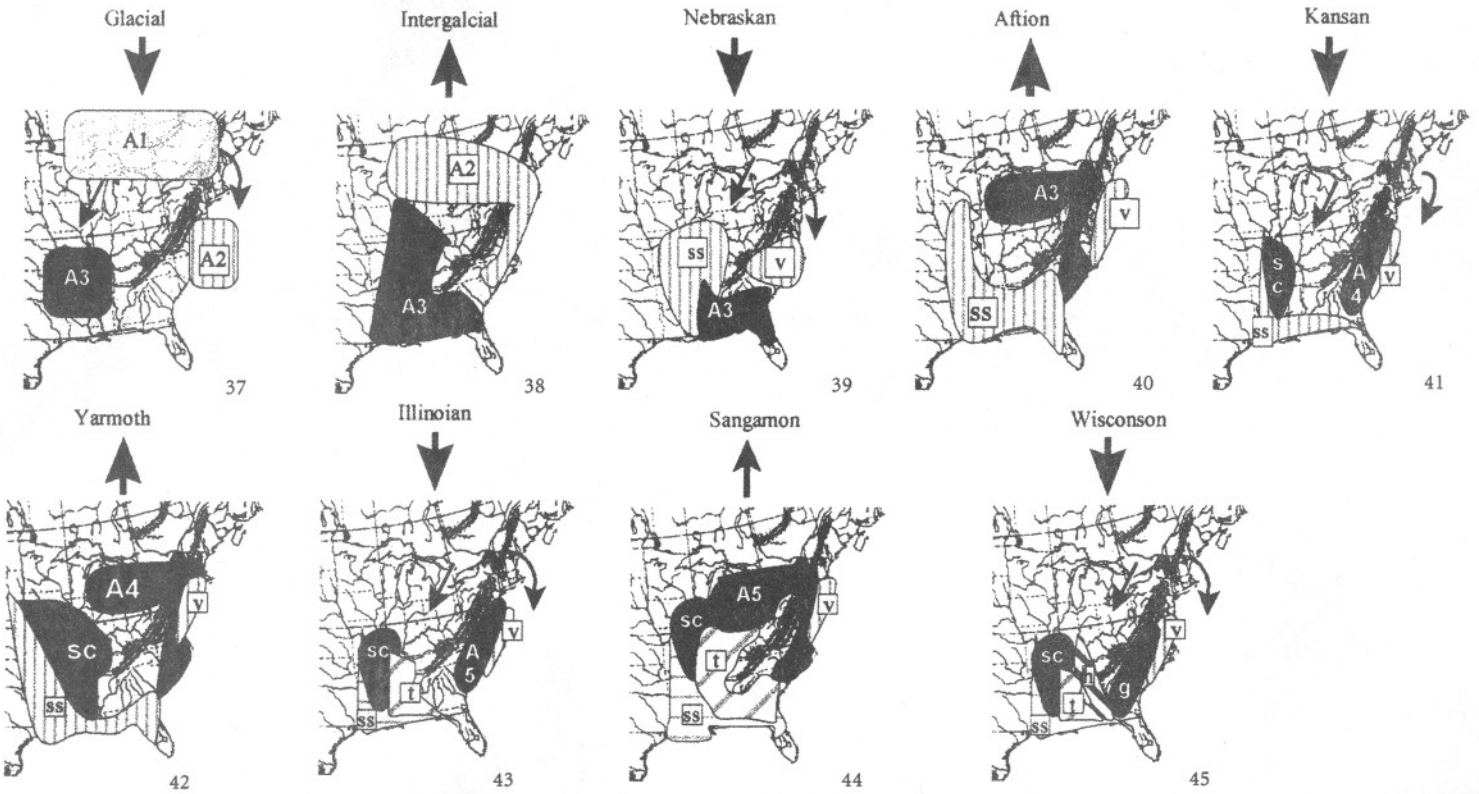
DESCRIPTIVE NOTES. Overall length 17.1-19.1 mm. The form of pronotum separates this species from all other species of *Lophoglossus* (Fig. 6). Elytra of both sexes are constantly dull from granulate microsculpture (Fig. 17). The duct of the appended gland of the female reproductive tract is very elongate. Relative to the length of the gland it is approximately twice as long as in other *Lophoglossus* species. This represents the only noticeable modification of the female reproductive tract in the genus.

NOTES ON RANGE AND LIFE HISTORY. Type locality, Pennsylvania, designated by LECONTE (1873). I have seen no further specimens from Pennsylvania and propose no specific site. Range from Maryland to Georgia (Fig. 35). New records for this species for the following states: **Maryland**, Kent Co.; **South Carolina**, Richland Co.,Congaree National Monument.

This species has been collected with *L. substrenuus*.

ZOOGEOGRAPHY

Given the cladistic relationships of the species of *Lophoglossus* and their distributions (Figs 46-47) it is possible to propose a plausible set of events by which the species could have originated and come to occupy their present ranges. Several carabid genera from eastern North America have been studied and zoogeography discussed, e.g., *Cyclotrachelus* Chaudoir (FREITAG, 1969), *Brachinus* Weber (ERWIN, 1970), *Diplocheila* Brullé (BALL, 1959), *Loxandrus* LeConte (ALLEN, 1972). The significance of the glacial-interglacial periods during the Pleistocene for North American carabid faunas is discussed in these works.



Figs 37-45. Hypothesized sequence of speciation and distributional changes in *Lophoglossus* species in response to glacial movements over the last 500,000 years: A1-A5, hypothetical ancestral population; ss, *L. substrenuus*; v, *L. vernix*; sc, *L. scrutator*; t, *L. tartaricus*; h, *L. haldemanni*; g, *L. gravis*. Species ranges are generalized and adjacency is shown for clarity. Species were probably in part sympatric as seen in the present.

Fig. 46. Present areas of endemism for *Lophoglossus* species.

Like the ancestors of *Cyclotrachelus*, *Brachinus* and *Diplocheila*, the lineage giving rise to *Lophoglossus* would have been established in eastern North America by the end of the Tertiary. No fossils of *Lophoglossus* are known so a minimum age for its differentiation from other pterostichines cannot be set. However, if the populations of *Lophoglossus* species responded to glacialinterglacial periods by shifting their ranges and differentiating then a minimum age can set by correlating the phylogenetic pattern with the sequence of glacial movements. Oxygen isotope measurements from ice cores have been used to estimate air temperatures during the Pleistocene and approximate dates of the glacial minimum and maximum (GATES, 1993) and are used here as central marks for periods of movement.

Prior to the Nebraskan glacial maximum (ca 500,000 ybp) an ancestral *Lophoglossus* population would have been established in Eastern North America (Fig. 37). When the glacier advanced (ca 450,000 ybp) the population would have been forced south and was divided into east and west populations by the intervening Appalachian Mountains. During the next interglacial a (ca 400,000 ybp) these populations expanded their ranges (Fig. 38), during the subsequent glacial period (Nebraskan, ca 375,000 ybp) they were again forced south, this time dividing the north+east population into two vicars that we now recognize as the *substrenuus*-group species (Fig. 39). The Aftion interglacial period allowed the ranges to expand northward, again establishing a broad east-west species in the north (Fig. 40). Figures 41 to 45 show how this process could be repeated and result in the present pattern of species distributions (Fig. 46). Similarly, the vicariance of populations of *Cylotrachelus* east and west of the Appalachian in response to the glacial advances and withdraws was proposed by (FREITAG, 1969) to explain the origin of species in the *spoliatus* and *sigillatus* groups and the split between *C. furtivus* (LeConte) and (*C. alternans* (Casey) + *C. iowensis* (Freitag)).

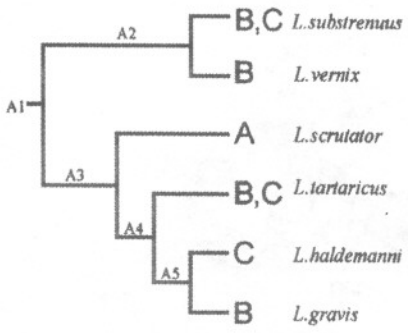


Fig. 47. Taxon area cladogram for *Lophoglossus* species. Hypothesized ancestors mapped on branches to show the relationship of the process illustrated in figures 37-46 to the phylogeny for the species.

The events proposed here are also consistent with the hypothesis that species in the far south are less likely to have been affected by the shifting glacial front

(ALLEN, 1972). By the process proposed here species move southward but new species are not generated unless the population spans the Appalachians, most likely via the Hudson River Valley. The glacier is a barrier to the north preventing species from circumventing the mountains. However, the Gulf Coast - East Coast habitat is a corridor that connects southern populations. Therefore, it is not the distance from the glacier but rather the presence of a suitable barrier (in this case the Appalachian Mountains) in conjunction with the glaciers' advance that affects northern populations. The lack of barriers in the south allows for an accretion of taxa generated by vicariance in the north.

The general area cladogram for the taxon area cladogram of *Lophoglossus* species (Fig. 47) would be (A(B+C)), where A is approximately the Great Lakes drainage (range of *L. scrutator)*, B the Mississippi River drainage + Gulf Coast (range of *L. haldemanni)*, and C the East Coast (ranges of *L. vernix* + *L. gravis*). This general applicability of these relationships is unclear given that area A was repeatedly unavailable during glacial maxima and areas B and C are not definitively separated in northern Florida. It is hoped that the narrative presented here will be tested with other taxa using rigorous cladistic biogeographic methods.

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