

CLASSIFICATION OF *LISTROPUS* PUTZEYS,
A SUBGENUS OF *SCHIZOGENIUS* PUTZEYS
(COLEOPTERA: CARABIDAE: SCARITINI)

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ABSTRACT

The Neotropical taxon *Listropus* Putzeys, until now treated as a genus of the subtribe Scapterina, is reclassified as a subgenus of *Schizogenius* Putzeys in the subtribe Clivinina; therefore, the subtribe Scapterina is not represented in the New World. *Listropus* includes 7 known species arrayed in 3 species groups; these are keyed and discussed, locality records of the 6 South American species are mapped, and phylogeny and zoogeography are briefly discussed. One species not treated elsewhere as a *Schizogenius*, *S. brevicornis*, is redescribed and figured. **New combinations** in *Schizogenius* are *S. brevicornis* (Brullé), *S. iridescens* (Putzeys), and *S. xanthopus* (Brullé). **New synonymies** (junior names parenthetic) are *S. iridescens* (= *S. jacarensis* Whitehead and *Listropus micans* Putzeys) and *S. xanthopus* (= *S. grossus* Whitehead).

During our independent studies of Neotropical Scaritini, we have been puzzled by the taxon *Listropus* Putzeys. Putzeys (1863, 1866) treated *Listropus* as a genus related to *Scapterus* and *Thlibops*; thus it has been listed as the only New World representative of the scaritine subtribe Scapterina. The only subsequent discussion of *Listropus* was that of Jeannel (1946): "Sans doute le genre américain *Listropus*, que Putzeys rapproche de *Thlibops*, doit-il appartenir à une autre lignée." Recently, Whitehead identified as *Schizogenius jacarensis* Whitehead a rather strange scaritine that Reichardt had tentatively identified as *Listropus iridescens* Putzeys. This apparent synonymy, which prompted us to investigate the status of *Listropus*, proved to be correct.

In this paper the subgenus *Listropus* is recognized and defined, and member species are reclassified. This subgenus corresponds to the *jacarensis* and *optimus* groups of *Schizogenius* s. str. as defined by Whitehead (1972); Whitehead had been tempted to erect a subgenus for these groups but for reasons of conservatism did not do so.

Putzeys and later authors probably overlooked the relationship of *Listropus* to *Schizogenius* because they thought the median tooth of the mentum was absent. Two of the species included in *Listropus*, *L. brevicornis* (Brullé) and *L. xanthopus* (Brullé), are distinctive especially in their large size (*Listropus* originally included the huge, *Scarites*-like *L. brevicornis*, as *L. brevipennis* Putzeys), but their longitudinally carinate frons is

¹Deceased.

characteristic of *Schizogenius*: In these 2 species and in the closely related *S. bicolor* Whitehead, the submentum and mentum are fused, and the mentum tooth is reflexed and readily observed only in frontal view. In the smaller forms included in *Listropus*, however, the suture between the submentum and mentum is distinct, and the mentum tooth is conspicuous.

J. Mateu and H. Perrin, Museum National d'Histoire Naturelle, Paris (MNHP) sent all specimens of *Listropus* they could find, including some but not all of the type-specimens of species described as *Listropus*. Also, in addition to specimens previously reported by Whitehead (1972), we examined a few specimens from the Institut Royal des Sciences Naturelles de Belgique (IRSB); the Museu de Zoologia, Universidade de São Paulo (MZSP); and the United States National Museum of Natural History (USNM). We thank Terry L. Erwin (Smithsonian Institution) and Gordon Gordh and Kellie O'Neill (Systematic Entomology Laboratory) for constructive criticism of the manuscript, and we thank Candy Feller for preparing figs. 2-7.

GENUS *Schizogenius* PUTZEYS

Schizogenius Putzeys 1846:650; Whitehead 1972:142-143.

See Whitehead (1972) for full systematic treatment. In that paper, the genus was subdivided into 2 subgenera, *Genioschizus* Whitehead and *Schizogenius s. str.* Since *Listropus* Putzeys is here recognized as a third subgenus to include some forms previously assigned to *Schizogenius s. str.*, we give a revised key to subgenera, rediagnoses of *Schizogenius s. str.* and *Listropus* Putzeys, a key to species of *Listropus*, redescription of *S. brevicornis* (Brullé), and new synonymic and distributional data on other included species. Standard measurements and abbreviations are as in Whitehead (1972).

KEY TO SUBGENERA OF *Schizogenius*

1. Lateral channel of elytron flared near apex, with 1 or more deep subapical pits *Genioschizus* Whitehead
- 1'. Lateral channel of elytron narrowed near apex, without deep subapical pits 2
- 2(1'). Hind tarsus elongate, Ta/Ti 0.75 or more; paramedian frontal sulci not microsculptured; clypeal suture weakly engraved; elytral disc asetose or with setae on interval 3 only *Listropus* Putzeys
- 2'. Hind tarsi shorter, Ta/Ti under 0.75; paramedian frontal sulci microsculptured in most species; clypeal suture weakly to strongly engraved; elytral disc asetose or with setae on intervals 3, 3+5, or 3+5+7 *Schizogenius s. str.*

SUBGENUS *Schizogenius s. str.*

We here restrict this subgenus by transferring the *jacarensis* (= *iridescens*) and *optimus* groups to the subgenus *Listropus*. Since Whitehead's (1972) study was published, 2 new species have been discovered in Central America; these will be described by Terry L. Erwin in his Central American

ground beetle study, in preparation. South American members of this subgenus need a complete revision, a study beyond the scope of this paper.

Diagnostic combination. Lateral channel of elytron not flared near apex, without deep subapical pits; hind tarsus short, Ta/Ti under 0.75; paramedian ambulatory setae of sternum 7 absent in females except those of *basalis* group and *S. pluripunctatus*, present in males. Also: paramedian clypeal carinae tuberculate or not, clypeal field narrow to broad, clypeal suture feeble to sharply impressed; paramedian frontal sulci microsculptured in most species; antennae moniliform to filiform; paralateral pronotal sulci absent; front tarsi dilated in many species, especially in males; elytra asetose or with setae on intervals 3, 3+5, or 3+5+7; pygidium serrate or crenulate in females of many species; and male endophallus of many species with well-developed basal collar spines. No species sellate, maculate, or strongly metallic. Size, LE 1.65-4.00 mm.

Distribution and natural history. See Whitehead (1972).

SUBGENUS *Listropus* PUTZEYS, new status

Listropus Putzeys 1863:3, 13. Type-species.—*Listropus brevipennis* Putzeys 1863, by monotypy. Putzeys 1866:10 (descriptions of new species); Jeannel 1946:220 (comments on systematic position).

Diagnostic combination. Lateral channel of elytron not flared near apex, without deep subapical pits; hind tarsus elongate, Ta/Ti 0.75 or greater; paramedian ambulatory setae of sternum 7 absent in female, present or absent in males. Also: paramedian clypeal carinae tuberculate or arcuate, clypeal field broad, clypeal suture generally feebly impressed; paramedian frontal sulci not microsculptured; antennae moniliform; paralateral pronotal sulci absent; front tarsi slender in both sexes; elytra asetose or with setae on interval 3 only; pygidium not crenulate in either sex; and male endophallus without well-developed basal collar spines. Some species either sellate or maculate, or brightly metallic. Size, LE 2.75-7.00 mm.

Distribution. The aggregate range of known members of this subgenus extends from extreme southern Mexico to northern Argentina. See fig. 7 for distribution records of South American species.

Natural history. We have extremely little knowledge of *Listropus* in nature. The scarcity of specimens in collections, Whitehead's (1972) notes on collecting *S. optimus* in Mexico, the large body size, and (notably in *S. brevicornis*) the modified mouthparts all are tantalizing hints that the natural histories of members of *Listropus* are dissimilar from those of *Genioschizus* and *Schizogenius s. str.*

Taxonomic notes. Of the 4 species recognized by Putzeys (1866) in the genus *Listropus*, only 3 are valid. All have been named more than once. Only *Listropus brevicornis*, the type-species of *Listropus* and at 12 to 13 mm total length the giant among species of *Schizogenius*, has not been redescribed in *Schizogenius* under a different name.

This subgenus includes those forms treated by Whitehead (1972) as the *jacarensis* and *optimus* groups of *Schizogenius s. str.*; here, the *jacarensis* group is renamed the *iridescens* group because of synonymy, and the *optimus* group is subdivided into the *optimus* and *brevicornis* groups because of a different interpretation of relationships.

With placement of *Listropus* as a subgenus of *Schizogenius*, subtribe Clivinina, the subtribe Scapterina is not represented in the New World.

KEY TO SPECIES OF SUBGENUS *Listropus*

1. Paramedian pronotal sulci well developed; interval 3 of elytron bi- or trisetose; suture between mentum and submentum distinct (*iridescens* group)..... *S. iridescens* (Putzeys)
- 1'. Combination of characters not as above..... 2
- 2(1'). Paramedian pronotal sulci obsolete or nearly so; suture between mentum and submentum distinct (*optimus* group) 3
- 2'. Paramedian pronotal sulci well developed; suture between mentum and submentum indistinct (*brevicornis* group)..... 5
- 3(2). Elytral interval 3 asetose; southern Chiapas in Mexico to southern Costa Rica *S. optimus* Bates
- 3'. Elytral interval 3 bi- or trisetose; Panama and South America 4
- 4(3'). Elytra piceous, metallic; clypeal carinae straight, apices abbreviated; elytra ovate *S. dyschirioides* Putzeys
- 4'. Elytra brunneous, unmetallic; clypeal carinae arcuate, apices joined and extended by stem to median tooth; elytra elongate, not ovate *S. clivinoides* Putzeys
- 5(2'). Elytron with large sutural macula..... *S. xanthopus* (Brullé)
- 5'. Elytron not maculate 6
- 6(5'). Black; LE over 6.0 mm; mentum and submentum concave..... *S. brevicornis* (Brullé)
- 6'. Brunneous or castaneous; LE under 4.0 mm; mentum and submentum normal *S. bicolor* Whitehead

THE *optimus* GROUP

Discussion. The *optimus* group as defined by Whitehead (1972) is probably not monophyletic, and it is sufficiently diverse to warrant subdivision into 2 species groups here, the *optimus* and *brevicornis* groups. The *optimus* group is here restricted to include species with the paramedian pronotal sulci obsolete, pronotal front angles not lobate, and the mentum and submentum not fused. Included are the only members of the old *optimus* group having such features as elytral interval 3 setose, metallic coloration, or clypeal carinae fused in an arc and joined to median tooth by a common stem. Type-specimens of *S. dyschirioides* and *S. clivinoides* have not yet been located. This group contains those members of the subgenus *Listropus* treated by Putzeys as *Schizogenius* rather than *Listropus*, probably because of the prominent median mentum tooth.

Schizogenius optimus Bates

Distribution. See Whitehead (1972).

Schizogenius dyschirioides Putzeys

Distribution. See Whitehead (1972) and fig. 7. The following are new records:

BOLIVIA. La Paz: 24 km. W Coripata (1; USNM). ECUADOR. Napo: Limoncocha (2; USNM). PERU. Huánuco: Tingo Maria (1; USNM).

Schizogenius clivinoides Putzeys

Distribution. See Whitehead (1972) and fig. 7.

THE *iridescens* GROUP

Discussion. This is the *jacarensis* group of Whitehead; the name is changed to reflect the following synonymy of the only included species.

Schizogenius iridescens (Putzeys), **new combination**

Listropus iridescens Putzeys 1866:11-12. Type-locality "Amazone", here restricted to BRAZIL: Pará: Santarém; holotype in MNHP.

Listropus micans Putzeys 1866:12. Type-locality "Brésil"; holotype in MNHP. **New synonymy.**

Schizogenius jacarensis Whitehead 1972:172-173, figs. 77, 81. Type-locality BRAZIL: Mato Grosso: Jacaré, Parque Nacional do Xingu; holotype in Museum G. Frey, Tutzing, Germany. **New synonymy.**

Discussion. The holotype of *L. iridescens* is light brown, somewhat teneral; that of *L. micans* is dark. In the original description of the latter, Putzeys wrote "Il ne serait pas impossible que cet insecte fût le [male sign] du précédent. . . ." The specimen differs slightly from the *L. iridescens* specimen, especially in the sculpture of the head (weaker longitudinal carinae in *L. micans*), but there is no doubt that the 2 specimens are conspecific; hence these names are synonymous. The holotype of *L. iridescens* bears the label ". . . Amaz. Bates". Because a specimen from Bates' collection (MNHP) is labelled "Santarem Amaz.", we here fix Santarém as the type-locality of *L. iridescens*. *S. jacarensis*, originally based on 2 specimens from Jacaré in Mato Grosso and 1 from Santa Isabel in Goiás, was named in the absence of information about *Listropus*.

Distribution. Fig. 7. In addition to type-specimens as cited above, there are the following records:

BRAZIL. Pará: Santarém (1; MNHP). Mato Grosso: Barra do Tapirapés (1; MZSP); Parque Nacional do Xingu (1; MZSP); Jacaré, Parque Nacional do Xingu (2; MZSP).

THE *brevicornis* GROUP

Discussion. Members of this group are distinguished from those of the *optimus* group by having the paramedian pronotal sulci normal, pronotal front angles lobate, and mentum and submentum fused. Included are the only members of the old *optimus* group (*sensu* Whitehead 1972) with LE over 4.0 mm, maculate elytra, 4 rather than 3 posteroventral setae near base of front tibia, mentum and submentum concave, labrum fringed laterally with more than 10 pairs of setae, mentum tooth blunt and reflexed, or antennal articles 3 and 4 plurisetose rather than pubescent.

Schizogenius bicolor Whitehead

Distribution. See Whitehead 1972 and fig. 7. The following is a new record:

BRAZIL. Mato Grosso: Jacaré, Parque Nacional do Xingu (3; MZSP, USNM).

Schizogenius xanthopus (Brullé), **new combination**

Clivina xanthopus Brullé 1837:39, pl. 4, fig. 10. Type-locality "dans la province de Moxos, au mois de Mai, sur les bancs de sable du Mamoré"; type-specimens not found in MNHP. Putzeys 1846:654.

Listropus xanthopus, Putzeys 1866:11.

Listropus discophorus Chaudoir 1863:118. Type-locality BOLIVIA: Santa Cruz: Valle Grande; holotype in MNHP. Putzeys 1866:11 (proposed synonymy with *L. xanthopus*).

Schizogenius grossus Whitehead 1966:3. Type-locality BRAZIL: Amazonas (?): "Rio Madeira"; holotype in USNM. Whitehead 1972:176-177 (new records). **New synonymy.**

Discussion. Even though the holotype of *C. xanthopus* was not found in MNHP (its presumed depository), its description exactly fits *L. discophorus* and *S. grossus*. The type-locality of *C. xanthopus* is presumably the Rio Mamoré, Llanos de Mojos, Bení, Bolivia.

Distribution. See Whitehead (1966, 1972) and fig. 7. The following is a new record:

BRAZIL. Amazonas: Tefé (formerly Ega) (1; MNHP).

Schizogenius brevicornis (Brullé), **new combination**

Scarites brevicornis Brullé 1837:39, pl. 3, fig. 9. Type-locality "province de Santa-Cruz de la Sierra, sur les dunes de sable mouvant de la maison de Mercado, chemin de Santa-Cruz à Chuquisaca"; type-specimens not found in MNHP.

Listropus brevicornis, Putzeys 1866:10 (transferred to this genus).

Listropus brevipennis Putzeys 1863:13-16, figs. 10-12. Type-locality "deux exemplaires comme venant de la Plata. J'en ai vu un troisième, mais mutilé, dans la collection de M. Chevrolat"; type-specimens not found in MNHP or IRSB. Putzeys 1866:10 (proposed synonymy with *S. brevicornis*).

Diagnostic combination. This species is easily recognized by the large size, with LE over 6.0 mm; by the large tooth on the left mandible; and by the combination of black or piceous coloration and fused, concave mentum and submentum.

Description. Fig. 1. Similar to *S. xanthopus* (= *S. grossus* in Whitehead 1966) except as follows. Color piceous to black, antennae, palpi, and tarsi rufous. Fine isodiametric microsculpture on gena, gula, tibiae, anterior surfaces of front and middle femora and posterior surfaces of hind femur, basal 3rd of elytral epipleuron, and entire abdomen. Visible sterna 1 and 2 rugose laterally.

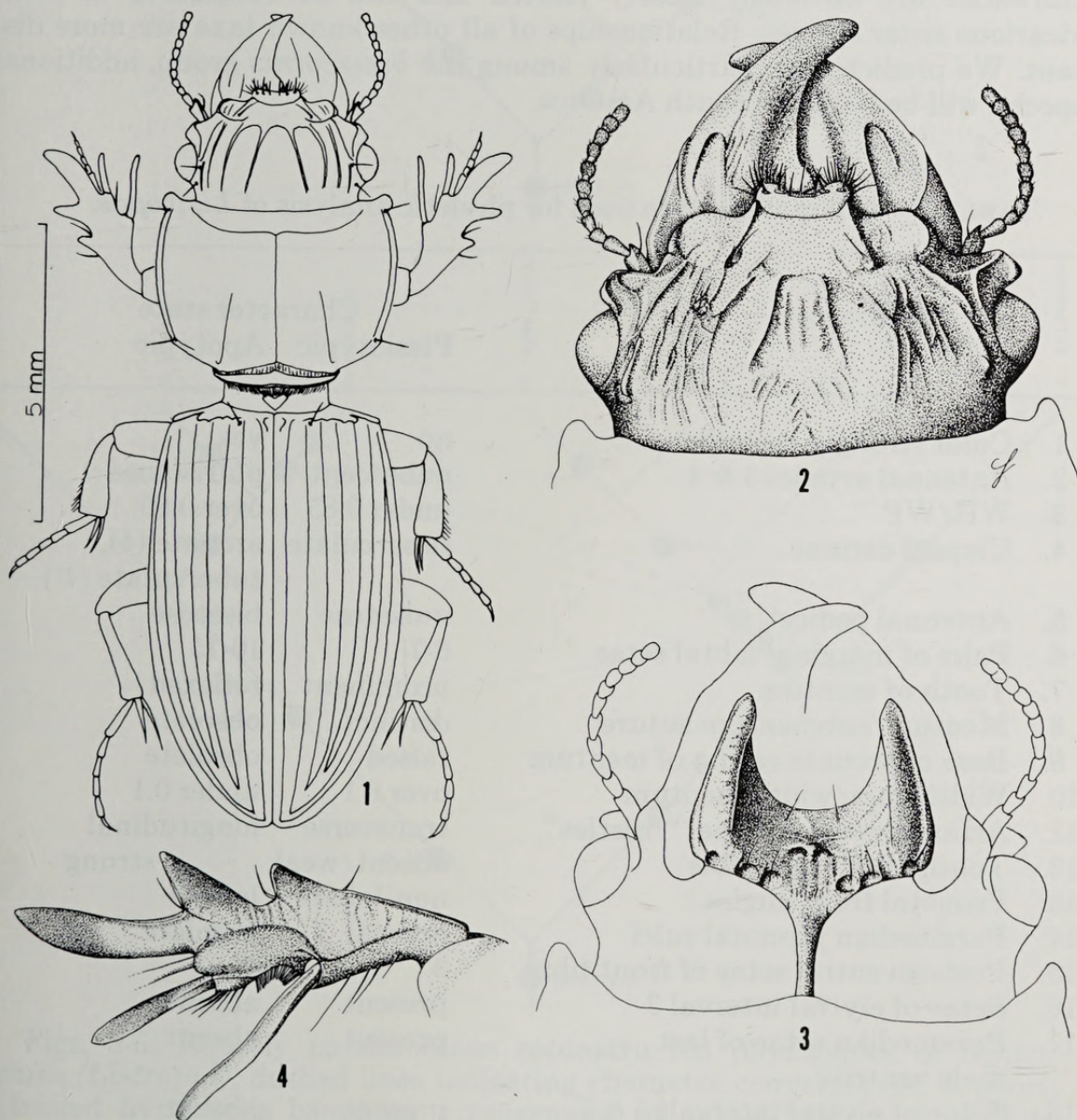
Head. Fig. 2. Labrum deeply emarginate. Clypeus with median tooth obsolete, paramedian carinae feebly. Clypeal suture deep (1 specimen) or obsolete (1 specimen). Frons with longitudinal carinae feeble, little more developed than longitudinal rugae and confused with them. Eyes proportionately smaller. Mentum and submentum (fig. 3) fused, concave; arcuate carina inconspicuous; median tooth of mentum short and broad, reflexed, visible only in anterior aspect; mandibles longitudinally rugose, left mandible with large tooth behind middle (fig. 2).

Pronotum more transverse, paramedian sulci shorter (PS/LP 0.50-0.55), anterior transverse impression smooth. Legs (fig. 4), elytra, and abdomen as in *S. xanthopus* except for color and microsculpture. Genitalia not examined.

Measurements and proportions, based on 2 specimens. TL, 10.27-10.80 mm; LE, 6.27-6.58 mm; WH, 3.11-3.42 mm; WP, 3.79-4.09 mm; WE, 3.91-4.22 mm; WF/WH, 0.79-0.80; LP/WP, 0.65-0.68; WP/WE, 0.63-0.66; Ta/Ti, 1.11-1.15.

Discussion. Unequivocal type-specimens of the 2 named forms were not found in IRSB or MNHP, but the 3 specimens that we examined agree with both descriptions. One specimen in IRSB bears the label, in Putzeys' hand, "*Listropus brevicornis* Boliv. (C. Chd.)"; though not here regarded as type-material, this specimen may have come to Putzeys from Brullé through Chaudoir.

Distribution. In the original description of *L. brevipennis*, Putzeys (1863) cited the type-specimens as from La Plata, Argentina. Later (1866:11) he wrote "cet insecte vient de la Bolivie et non de la Plata." We cannot determine what the range is, but assume that only the Bolivian records are correct (fig. 7). We examined the following specimens:



Figs. 1-4, *Schizogenius brevicornis*: 1, habitus; 2, dorsal view of head; 3, ventral view of head, detail of mentum and submentum; 4, posterior view of front tibia.

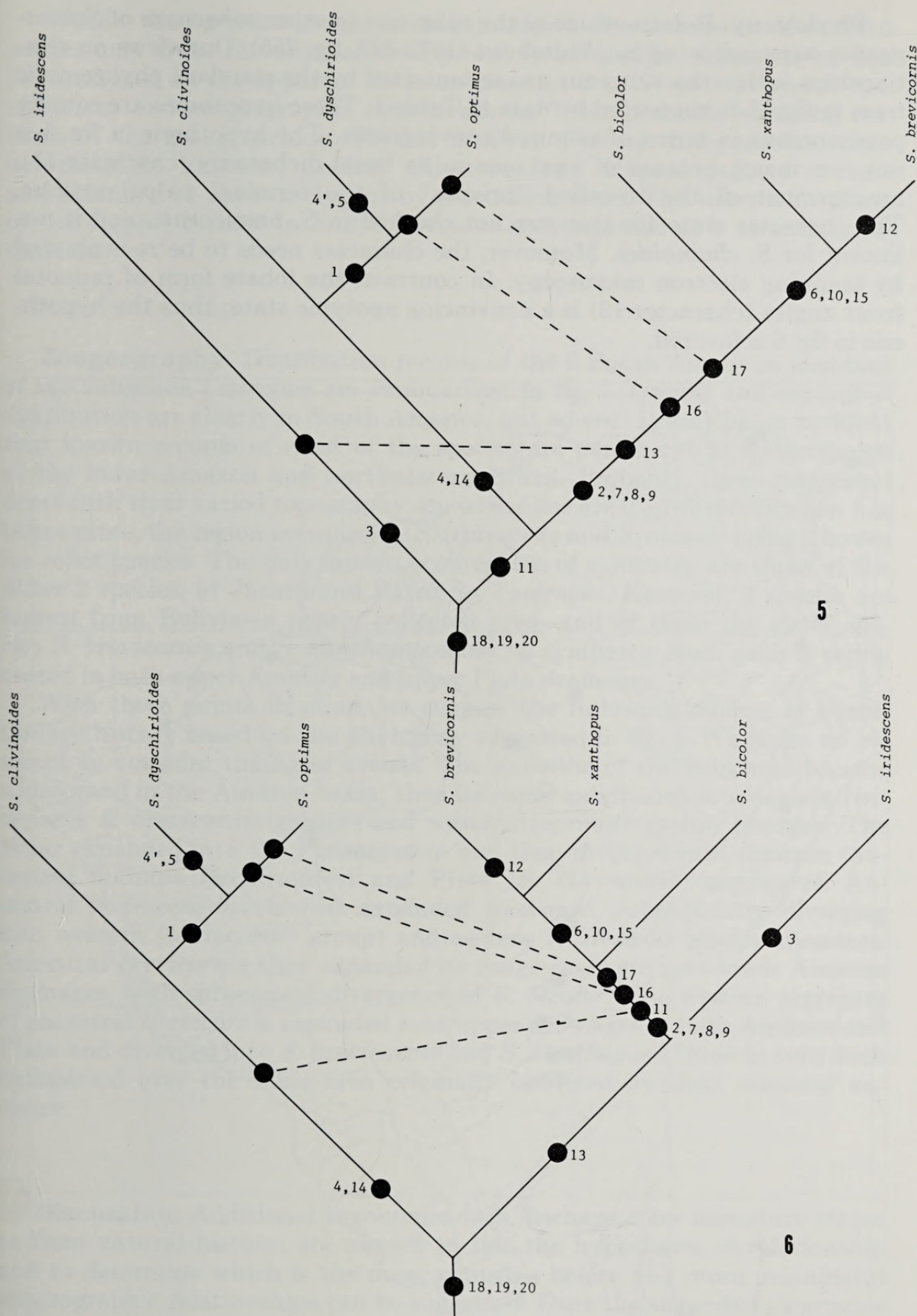
No locality (1; MNHP). BOLIVIA. Yuracary (?) (1; MNHP; this specimen might be from the Yuracares area of southwestern Bení or northwestern Santa Cruz, or from near Yura or Rio Yura, Potosí province); no locality (1; IRSB).

EVOLUTIONARY CONSIDERATIONS

The poor representation of species in collections, lack of adequate records of known species, and lack of knowledge of type-specimens of *S. dyschirioides* and *S. clivinoides* combine to make presumptuous a detailed discussion at this time. However, we think it desirable to summarize what we know about the phylogeny and zoogeography of this subgenus. The diversity of the group is unknown. However, the divergence is obviously great and thus so must be the antiquity of the group. Only *S. optimus* and *S. dyschirioides* are obviously closely related and can be considered as true, vicarious sister species. Relationships of all other known taxa are more distant. We predict that, particularly among the *brevicornis* group, additional species will be found in South America.

TABLE 1. Character states used for phyletic analysis of *Listropus*.

Character	Character state	
	Plesiotypic	Apotypic
1. Color strongly metallic	no	yes
2. Antennal articles 3 & 4	pubescent	plurisetose
3. WH/WP	under 0.85	over 0.85
4. Clypeal carinae	tuberculate	arcuate (4), tuberculate (4')
5. Antennal pedicel	unisetose	bisetose
6. Pairs of marginal labral setae	6-7	10-15
7. Tooth of mentum	prominent	reflexed
8. Mentum/submentum suture	distinct	obsolete
9. Base of arcuate carina of mentum	raised	obsolete
10. Width gula/width mentum	over 0.1	under 0.1
11. Arrangement of palpal "bristles"	transverse	longitudinal
12. Tooth of left mandible	absent/weak	strong
13. Pronotal front angles	non-lobate	lobate
14. Paramedian pronotal sulci	normal	obsolete
15. Posteroventral setae of front tibia	3	4
16. Setae of elytral interval 3	present	absent
17. Paramedian setae of last male ventrite	present	absent
18. Setae of elytral intervals 5 & 7	present	absent
19. Microsculpture of frontal sulci	present	absent
20. Ta/Ti	under 0.75	over 0.75



Figs. 5-6, Equally parsimonious reconstructed phylogenies of *Schizogenius* (*Listropus*), dashed lines indicating character convergences: 5, poorly defended hypothesis based on arrangement of palpal bristles; 6, well-defended hypothesis based on form of pronotal front angles. See table 1 and text for details.

Phylogeny. Relationships of the subgenus to other subgenera of *Schizogenius* were indicated by Whitehead (1972:323, fig. 255). Our views on relationships within the subgenus are summarized by the standard phylogenetic trees in figs. 5-6, supported by data in Table 1. These hypotheses are equally parsimonious in terms of required convergences. The hypothesis in fig. 5 is not convincing because of weakness in its basal dichotomy (character 11), arrangement of the so-called "bristles" of the terminal palpal articles. The character state for this was not checked in *S. brevicornis*, and is not known for *S. clivinoides*. Moreover, the character needs to be re-evaluated by scanning electron microscopy. In contrast, the lobate form of pronotal front angles (character 13) is a convincing apotypic state; thus the hypothesis in fig. 6 is favored.

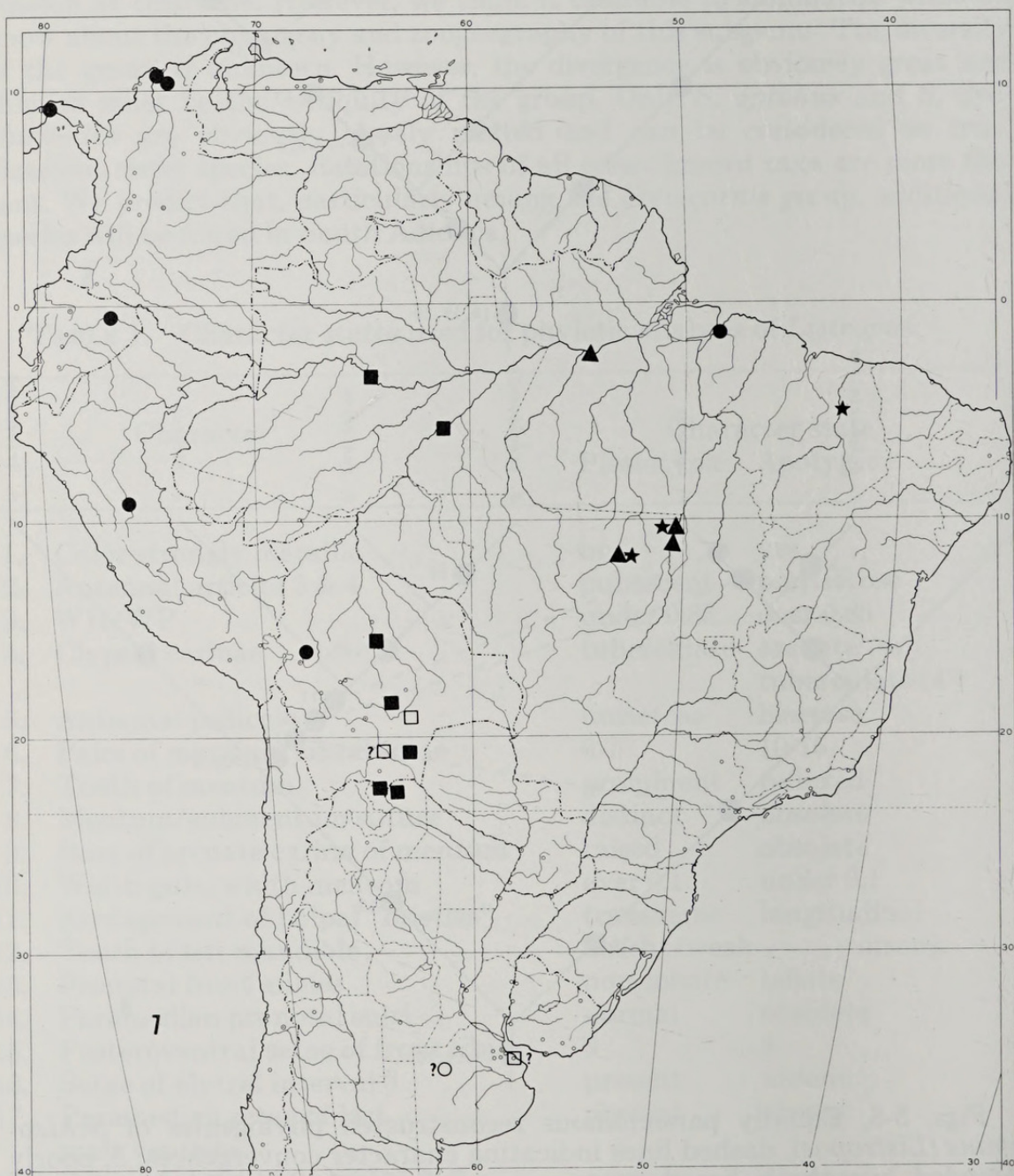


Fig. 7, Distribution records of South American members of *Schizogenius* (*Listropus*) (?=imprecise locality): Closed circle, *S. dyschirioides*; open circle, *S. clivinoides*; triangle, *S. iridescens*; star, *S. bicolor*; closed square, *S. xanthopus*; open square, *S. brevicornis*.

Within the *optimus* group, we can interpret characteristics of *S. clivinoides* only from the original description. Relationships suggested by figs. 5-6 are based on the apparent sister species status of *S. optimus* and *S. dyschirioides* and on geographic considerations. Thus, probable ancestral features of the group include: Elytral interval 3 setose; integumental color non-metallic; antennal pedicel unisetose; and clypeal carinae arcuate and extended to apex of clypeus by a common stem. The tuberculate form of the clypeal carinae in *S. dyschirioides* is interpreted as a secondary reduction.

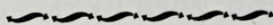
Zoogeography. Distribution records of the 6 South American members of the subgenus *Listropus* are summarized in fig. 7. Origins and centers of distribution are clearly in South America, but where? It may be no accident that known records of most of the species are peripheral to watercourses of the lower Amazon and northeastern Brazil. Probably, these peripheral areas with their varied topography are where the greatest diversification has taken place, the region occupied by *S. iridescens* and *S. bicolor* being a haven for relict species. The only known occurrences of sympatry are those of the latter 2 species, at Jacaré and Barra do Tapirapes. However, 3 species are known from Bolivia—a poorly collected area—and of these the sister species *S. brevicornis* and *S. xanthopus* must be sympatric since each is represented in both upper Amazon and upper Plata drainages.

With these points in mind, we suggest the following scheme of evolutionary history based on the phylogeny suggested in fig. 6. We make no attempt to consider timing of events. The ancestor of the subgenus became widespread in the Amazon basin; then its range subdivided into eastern (*iridescens* & *brevicornis* groups) and western (*optimus* group) lineages. The latter expanded into the Plata system and then diverged into Amazon (ancestral *optimus-dyschirioides*) and Plata (*S. clivinoides*) segregates. Ancestral *iridescens-brevicornis* expanded westward, subsequently diverging into western (*brevicornis* group) and eastern (*iridescens* group) ancestors. Ancestral *brevicornis* then expanded its range eastward into lower Amazon drainages, with subsequent divergence of *S. bicolor*. The western segregate of ancestral *brevicornis* expanded over upper drainages of both Amazon and Plata and diverged into *S. brevicornis* and *S. xanthopus*. These in turn each redispersed over the same area originally occupied by their common ancestor.

Discussion. Additional taxonomic data, perhaps from immature stages or from natural history, are needed to test the hypotheses of relationship and to determine which is the most plausible before any more meaningful zoogeographic relationships can be suggested. Does the suggested vicariance between upper and lower parts of the Amazon have any factual, historical basis? How do natural histories of these beetles affect their distributions? Can distributions be correlated, on a general or detailed level, with postulated Pleistocene refugial events (Haffer 1969; Vanzolini and Williams 1970; Whitehead 1976)? We hope that the introductory taxonomy done in this paper will stimulate the needed exploration.

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