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PHYLOGENETIC RELATIONSHIPS OF *SCOTUSSA* AND *LEIOTETTIX* (ORTHOPTERA: ACRIDIDAE)

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Abstract — A cladistic analysis of the South American grasshopper genera *Scotussa* and *Leiotettix* was performed in order to test the monophyly of these genera. *Eurotettix, Chlorus* and the *Dichroplus bergi* species group were included as terminal taxa. The genus *Atrachelacris* was used to root the tree. Twenty-nine characters from external morphology, male genitalia and female ovipositor were used in the analysis. In order to test for association between the structural change that occurred in the ovipositor valves of *Scotussa* and the functional change of the oviposition habits, the data matrix was partitioned and two analyses were performed. Characters from the female ovipositor were excluded from the data set used in the first analysis and another analysis was performed where all the characters were included in the analysis. Information on oviposition habits was then mapped on the cladogram, to determine the transformation for performance. Both analyses yielded only one most parsimonious tree and produced congruent results, confirming the monophyly of *Leiotettix* and *Scotussa* and corroborating their close relationship. Characters from the female ovipositor valves were informative not only at the species level but also at higher levels in the cladogram. The results also support the hypothesis of association between the structural change that occurred in the ovipositor valves of *Scotussa* with the functional change in the oviposition habits. However, this association did not seem to be correlated with the adaptive radiation in the genus.

Introduction

Scotussa Giglio-Tos and *Leiotettix* Bruner constitute a monophyletic group within the Dichroplini together with *Atrachelacris* Giglio-Tos, *Eurotettix* Bruner, *Chlorus* Giglio-Tos and the *bergi* species group of the polyphyletic genus *Dichroplus* Stal (Ronderos and Cigliano, 1990). This group of genera, referred to as "paranense-pampeano", is based on characteristics of the phallic complex (i.e. apical valves of penis without mid-longitudinal furrow diverging caudally, sheath of penis simple with middle lobes or slot and lateral lobes developed). Following Cabrera and Willink's (1973) biogeographic scheme, the group is distributed in the Chaqueño domain (mainly Pampas and Chaqueño provinces) and in the Amazonian domain (mainly the Paranense and Cerrado provinces).

Mesa and Zolessi (1968) suggested that *Scotussa delicatula* Liebermann, *S. lemniscata* (Stal), *S. cliens* (Stal) and *S. daguerrei* Liebermann should be included in the genus *Leiotettix*. However, Cigliano and Ronderos (1994) considered that the peculiar characteristics of the ovipositor valves of *Scotussa* justified the genus including

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those species, while they redefined *Leiotettix* based on a unique combination of derived attributes of the male phallic complex.

Most Acridoids oviposit in soil (hypodaphic). However, exceptions to this general rule are known (Uvarov, 1977). Within the Dichroplini, oviposition on the exposed surface of plants has been recorded only for *Scotussa* species, *S. cliens*, *S. liebermanni* Mesa and Zolessi and *S. daguerrei* oviposit on the surface of plants (epiphytic), mainly on species of the genera *Eryngium* and *Panicum* (Liebermann, 1951; Zolessi, 1958; pers. obs.), and *S. lemniscata* on the bases of grass (epidaphic, pers. obs.). Although some authors (Liebermann, 1958; Mesa and Zolessi, 1968; Cigliano and Ronderos, 1994) suggested that the structural change that occurred in the ovipositor valves of *Scotussa* species seems to be correlated with a functional change in the oviposition habits of the genus, this hypothesis has never been tested.

The appearance of a particular structural change correlated to a given functional change was listed by Coddington (1988) as one of the criteria useful to recognize an adaptive radiation. At the population level and below, methods to document the role of adaptation have been developed (Maynard-Smith, 1978; Oster and Wilson, 1978). However, the importance of adaptation as an explanation at higher taxonomic levels remained quite speculative until recently when some authors developed cladistic tests of adaptational hypotheses (Coddington, 1988, 1990; Carpenter, 1989; Brooks and McLennan, 1991). The use of tests of evolutionary scenarios by reference to a phylogeny is increasingly recognized as a pertinent approach in comparative studies (Wanntorp et al., 1990; Baum and Larson, 1991; Armbuster, 1992; Miles and Dunham, 1993; Wenzel and Carpenter, 1994). The development of cladograms independently of process theories makes tests of such theories possible. Patterns predicted from process theories may be compared with the general patterns predicted by cladograms, which summarize genealogical evidence (Carpenter, 1989). Under this context, adaptations can be interpreted as one possible explanation of observed synapomorphies (Coddington, 1988).

Our main objective was to conduct a phylogenetic analysis for *Leiotettix* and *Scotussa* in order to test the hypothesis of monophyly of these taxa. We were also interested in testing for association between the structural change that occurred in the ovipositor valves of *Scotussa* and the functional change in the oviposition habits. Finally, we wanted to see if this association has had some relevance in the adaptive radiation of the genus.

Materials and Methods

The methodology for constructing the phylogenetic hypotheses for *Leiotettix* and *Scotussa* follows the theoretical framework advocated by Hennig (1966) and reviewed in its operational aspects by Eldredge and Cracraft (1980), Nelson and Platnick (1981), and Forey et al. (1992), among others.

To test the hypothesis on the evolutionary sequence of the ovipositor structure we followed Baum and Larson's (1991) definition of adaptation and the phylogenetic approach to adaptation (Coddington, 1988, 1990; Carpenter, 1989; Brooks and McLennan, 1991; Miles and Dunham, 1993). Baum and Larson (1991)

described a general protocol for discerning adaptations that synthesized and refined a phylogenetically based definition of adaptation. In their description, an adaptation is a trait that must have current utility and that was generated historically through action of natural selection for its current biological role. Losos and Miles (1994) summarized the phylogenetic approach to adaptation. They noted that the historical approach to adaptation has three features:

(1) The identification of those lineages in which a trait transformation is evident. This is necessary for the comparison of the historical antecedent state.

(2) Mapping of functional capacity on the phylogeny to determine the transformation sequence for performance.

(3) Determination of the shift in the environment with respect to the genealogical relationships of the taxa as portrayed in the phylogeny. The hypothesized environmental change may be related to alterations in the "selective regime" experienced by the taxa.

The emphasis of this protocol is to delimit the occurrence of shifts in the selective regime, where in the phylogeny the selective regime changed, and whether it is concordant with the transformation of the trait and its function. Adaptations may thus be autapomorphic or synapomorphic, but must show a concordant shift in performance. Because the direction of trait change is known, relevant traits that may be adaptations are more easily identified using the historical approach.

Table 1
Taxa included in the cladistic analysis of *Scotussa* and *Leiotettix*, their geographic distribution, oviposition habits and acronyms

Taxa	Geographic distribution	Oviposition habits	Acronyms
Leiotettix viridis Bruner	Chaco, Cerrado, Paranense	—	vir
Leiotettix sanguineus Bruner	Chaco, Cerrado, Paranense Pampas (north of parallel 34°S)	hypodaphic	san
Leiotettix flavipes Bruner	Pampas (north of parallel 34°S)	hypodaphic	fla
Leiotettix pulcher Rehn	Chaco, Paranense, Pampas	hypodaphic	pul
Leiotettix politus Rehn	Paranense, Pampas (north of parallel 34°S)	hypodaphic	pol
Leiotettix hastatus Rehn	Paranense	—	has
Scotussa impudica G. Tos	Paranense, Chaco, Pampas	epiphytic	imp
Scotussa liebermanni Mesa and Zolessi	Pampas	epiphytic	lie
Scotussa cliens (Stal)	Chaco, Paranense, Pampas	epiphytic	cli
Scotussa lemniscata (Stal)	Paranense, Pampas	epidaphic	lem
Scotussa daguerrei Liebermann	Pampas	epiphytic	dag
Scotussa delicatula Liebermann	Chaco	—	del
Scotussa brachyptera Cigliano and Ronderos	Cerrado, Chaco	—	bra
Dichroplus bergi species group	Paranense, Pampas (mostly north of parallel 34°S)	hypodaphic	ber
Chlorus Giglio-Tos	Chaco, Cerado, Paranense	hypodaphic	Chl
Eurotettix Bruner	Paranense	hypodaphic	Eur
Atrachelacris Giglio-Tos	Chaco, Paranense, Pampas (mostly north of parallel 34°S)	hypodaphic	Atr

TAXA

The cladistic analysis includes all *Scotussa* and *Leiotettix* species considered valid by Cigliano and Ronderos (1994). It also includes the genera *Eurotettix*, *Chlorus* and the *Dichroplus bergi* species group as terminal taxa. Table 1 lists the species, genera, their geographical distributions and oviposition habits.

CHARACTERS

The selection of characters was based on a morphological study of the genitalia and external morphology (Cigliano and Ronderos, 1994) and on a re-analysis of the female ovipositor valves of the taxa under study (Figs 1 and 2). Twenty-nine characters were used, 14 from the external morphology (characters 1–14 in Table 2), eight from the male genitalia (characters 15–22 in Table 2), and seven from the female external genitalia (characters 23–29 in Table 2). Apomorphic character states were identified by the outgroup comparison method (Watrous and Wheeler, 1981; Nixon and Carpenter, 1993). The genus *Atrachelacris* was taken as the outgroup.

Table 2
Characters and character states used in the cladistic analysis of *Scotussa* and *Leiotettix*

Character	Character state and codification
1. Relation head / pronotum	as wide as (0); wider (1)
2. Eyes: shape	subcircular (0); oval (1)
3. Head: shape	subglobose (0); conical (1)
4. Fastigium excavated	absent (0); present (1)
5. Fastigium: development	barely prominent (0); prominent (1)
6. Fastigium: lateral carinae	absent (0); present (1)
7. Interocular space: width	wide (0); narrow (1)
8. Vertex: lateral view	lower than eyes (0); as high as eyes (1)
9. Pronotum: dorsal view	expanding caudally (0); subcylindrical (1); with expanded metazone (2)
10. Pronotum constricted at the middle	absent (0); present (1)
11. Posterior margin of pronotal disk	angulate (0); rounded (1)
12. Transverse sulci of pronotal disk	deeply impressed (0); shallowly impressed (1)
13. Tegmina development	macropterous (0); brachypterous (1); brachypterous and macropterous (?)
14. Tip of male cerci: shape	conical (0); obliquely truncated (1)
15. Sheath of penis: width	wide (0); narrow (1); very narrow (2)
16. Epiphallus: anterior process	normal (0); highly expanded (1)
17. Epiphallus: lophi development	prominent (0); barely prominent (1)
18. Epiphallus: lophi shape	rectangular (0); largely horizontal (2); prominent rounded (1)
19. Sheath of penis: middle lobes	developed (0); not developed (1)
20. Apical valves of penis: dorsal view	diverging caudally (0); spiral shape (1); straight (2)
21. Apical valves of penis: shape	subcylindrical (0); lanceolate (1); flat (2)
22. Apical valves of penis: apices	entire (0); divided (1)
23. Dorsal ovipositor valves: apical tooth	with one apical tooth (0); with two apical teeth (1)
24. Relation dorsal / ventral ovipositor valves	as long as ventral (0); twice as long as ventral (1)
25. Dorsal ovipositor valves: superior margin	low serrulate (0); serrate (1); prominently serrate (2); prominent teeth on distal portion (3); prominent teeth all over the margin (4)
26. Ventral ovipositor valves: external apical tooth	very prominent (0); not prominent (1)
27. Ventral ovipositor valves: width	very narrow (0); very wide (1); wide (2)
28. Dorsal valves: dorsal view	convergent (0); divergent (1)
29. Ovipositor valves: lateral view	curve (0); straight (1)

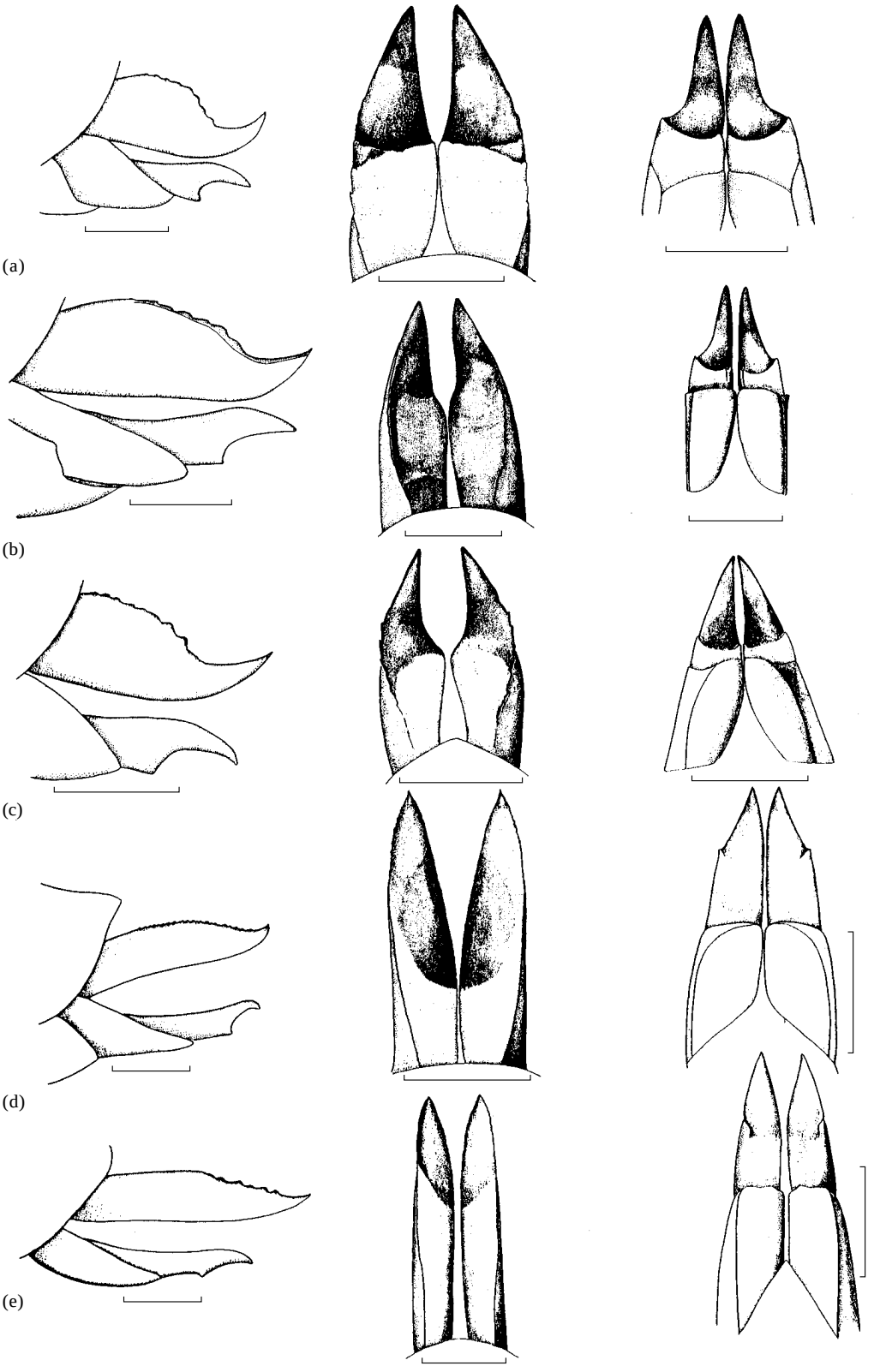

Fig. 1. Lateral, dorsal and ventral view of ovipositor valves of (a) *Atrachelacris olivaceus*, (b) *Dichroplus bergi*, (c) *Leiotettix pulcher*, (d) *Scotussa impudica*, (e) *Scotussa liebermanni*.

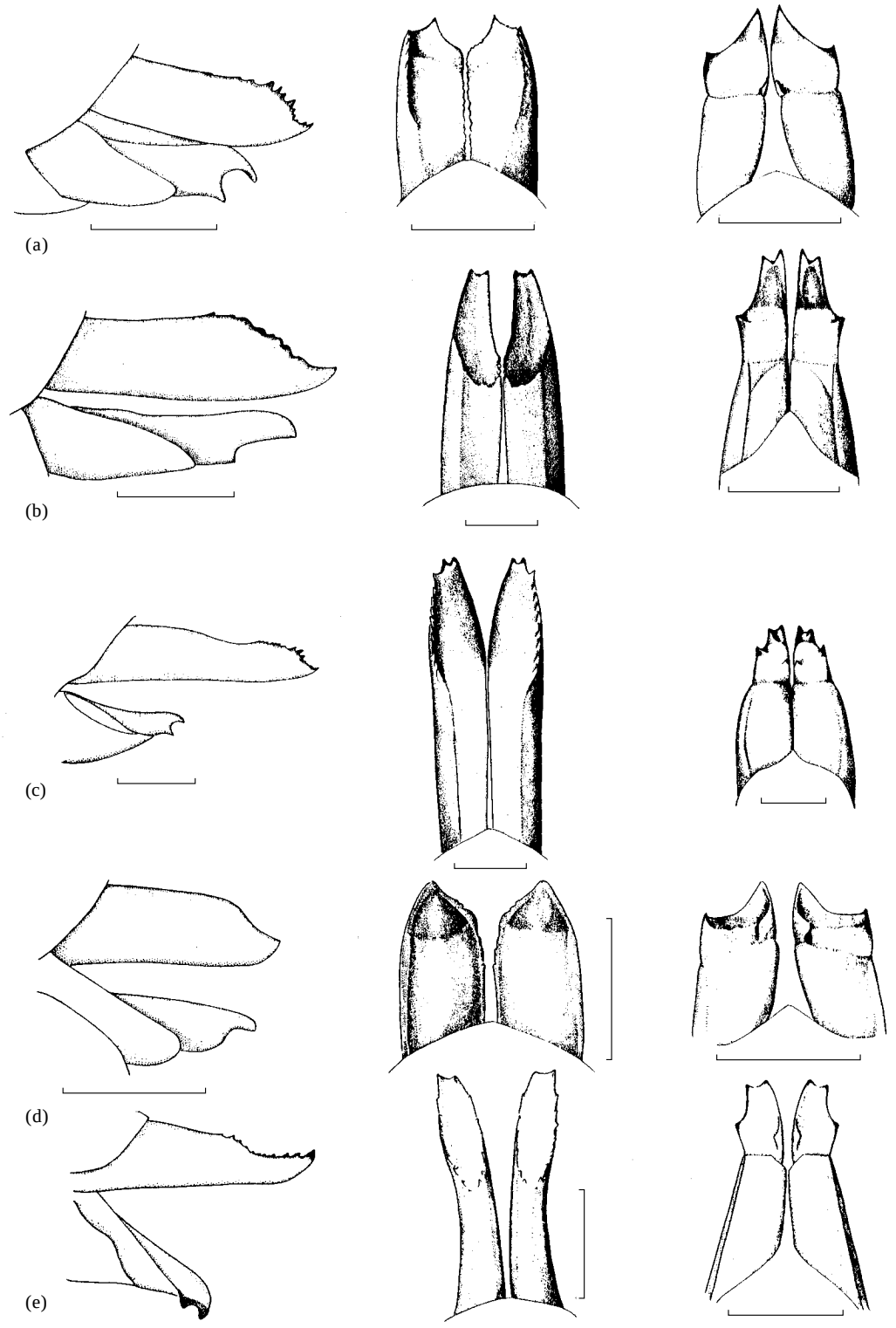

Fig. 2. Lateral, dorsal and ventral view of the ovipositor valves of (a). *S. daguerrei*, (b) *S. lemniscata*, (c) *S. cliens*, (d) *S. brachyptera*, (e) *S. delicatula*.

In order to check the performance of the characters from the female ovipositor two analyses were performed, one where characters from the female ovipositor were excluded from the analysis, and another where all the characters were included in the analysis.

The information on the oviposition habits (Table 1) was then mapped on to the final cladogram, to determine the transformation sequence for performance.

Coding and Analysis

Multistate characters were treated as non-additive. Table 3 contains the data matrix used, which was analysed using HENNIG86 version 1.5 (Farris, 1988), applying the ie option for calculating trees, algorithm that finds all trees of minimal length (Farris, 1988; Platnick, 1989). Consistency (Kluge and Farris, 1969) and retention (Farris, 1989) indices were calculated excluding autapomorphies. The genus *Atrachelacris* was used to root the tree.

In order to check if any of the ovipositor characters could be parsimoniously optimized in more than one way, CLADOS' version 1.1 (Nixon, 1992) Ctrl-O and O optimizations (accelerated and delayed) were used.

Results

Cladogram Based on the Data Set Excluding Characters from the Ovipositor

The analysis of the data matrix excluding characters from the ovipositor yielded one most parsimonious cladogram of 40 steps, a consistency index of 0.67 and a retention index of 0.80 (Fig. 3). The cladogram confirms the monophyly of *Scotussa* and *Leiotettix* as well as their close relationship. *Scotussa* and *Leiotettix* share the "vertex as high as the eyes in lateral view" (8), "pronotum subcylindrical" (9_1), and

Table 3
Data matrix used in the cladistic analysis of *Scotussa* and *Leiotettix*

	Characters																											
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Atr	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	0	0	0	0
Eur	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chl	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0	0
ber	0	0	0	1	0	1	1	0	2	1	0	0	?	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
vir	1	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0
san	1	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
pul	1	0	0	0	0	0	0	1	1	1	0	1	0	1	2	0	0	2	0	0	1	0	0	0	0	0	0	0	0
fla	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
has	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
pol	1	1	1	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
imp	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	1
lie	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	1	1	0	1	1
lem	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1
del	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	1	1
cli	0	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	3	0	2	1	1
dag	0	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	4	0	1	1	1
bra	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1

"transverse sulci of pronotal disk shallowly impressed" (12). The monophyly of *Scotussa* is supported by "prominent fastigium" (5). *Leiotettix* is characterized by "head wider than pronotum" (1, paralleled at *S. delicatula*), "sheath of penis narrow" (15_1), "tip of male cerci obliquely truncated" (14, reversing in *L. hastatus*) and "valves of penis lanceolate" (21_1). *Scotussa* species are grouped into two clades. The clade constituted by the pair *S. impudica* and *S. liebermanni* is supported by the "lophi barely prominent" (17), "anterior process of epiphallus highly expanded" (16), and "apical valves of penis spiral shape" (20_1). The other clade defined by the "sheath of penis without middle lobes" (19), comprises the pair of species *S. daguerrei, S. cliens* (defined by "oval eyes" (2) and "conical head", 3) and the polytomy *S. lemniscata, S. delicatula, S. brachyptera*.

Leiotettix species are related in the following phylogenetic sequence: *L. politus, L. sanguineus, L. viridis, L. pulcher, L. flavipes* and *L. hastatus*.

Cladogram Based on the Data Set Including Characters from the Ovipositor

The combined data sets gives one tree of length 52, consistency index 0.71 and retention index 0.82 (Fig. 4). This tree has almost the same topology as the one on Fig. 3, except for the resolution of the polytomy involving *S. brachyptera, S. delicatula, S. lemniscata* and the pair *S. cliens, S. daguerrei*.

Characters from the ovipositor valves were parsimoniously optimized in only one way when the different optimization procedures (accelerated and delayed) were implemented (Fig. 4). These characters only show apomorphies in the clade constituted by *Scotussa* species.

The characters "dorsal valves of ovipositor divergent in dorsal view" (28), and "ovipositor valves straight" (29) define the genus *Scotussa* together with character 5. The relation between *S. impudica* and *S. liebermanni* is supported by characters 16, 17, and 20_1, and corroborated by the following characters from the ovipositor: "dorsal valves with superior margin serrate" (25_1, Fig. 1d, e) and "ventral valves with external apical tooth not prominent" (26, Fig. 1d, e). The pair *S. delicatula, S. lemniscata* is defined by "dorsal ovipositor valves with two apical teeth" (23, paralleled in *S. cliens* Fig. 2b, c, e). *S. brachyptera* is related to *S. daguerrei* and *S. cliens* based on "ventral ovipositor valves very wide" (27, Fig. 2a, c, d).

Most of the taxa included in the analysis are characterized by autapomorphies mostly from the external morphology and from the ovipositor in *Scotussa* species.

Cladogram with the Information on the Oviposition Habits

The information on the oviposition habits (Table 1) was mapped onto the final cladogram (Fig. 5). The cladogram shows that the appearance of the structural change that occurred in the ovipositor valves of *Scotussa* is correlated with a shift in the oviposition habits, from hypodaphic to epiphytic (Fig. 5). Thus, the synapomorphies "ovipositor valves straight in lateral view" (29), and "dorsal valves of ovipositor divergent in dorsal view" (28) show a concordant shift in performance.

Discussion

Our foregoing analyses support several conclusions, the first of which is taxonomic. *Leiotettix* and *Scotussa* are monophyletic genera. *Leiotettix* is defined based

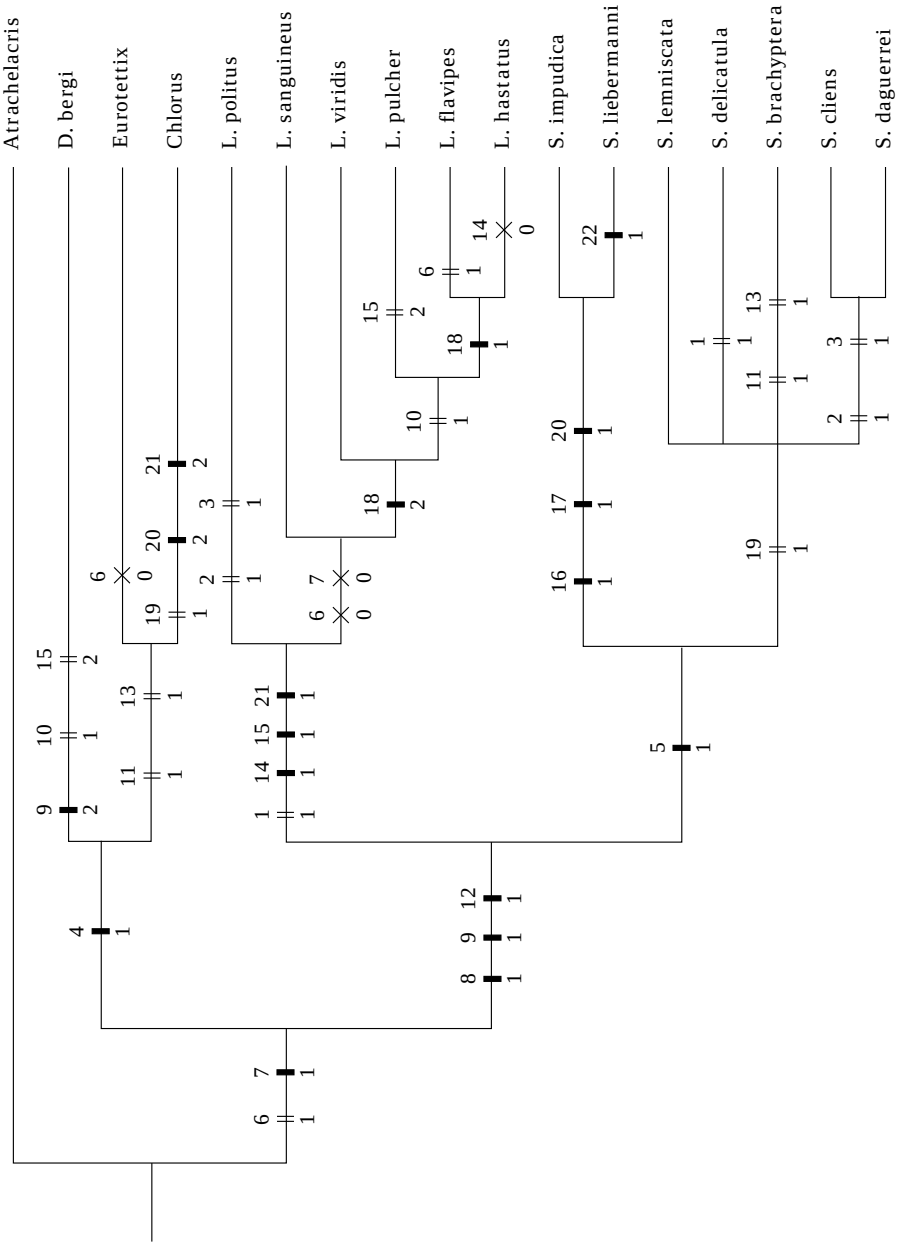

Fig. 3. Cladogram based on the data set excluding characters from the ovipositor valves. Simple lines indicate synapomorphies, double lines parallelisms, and X reversals.

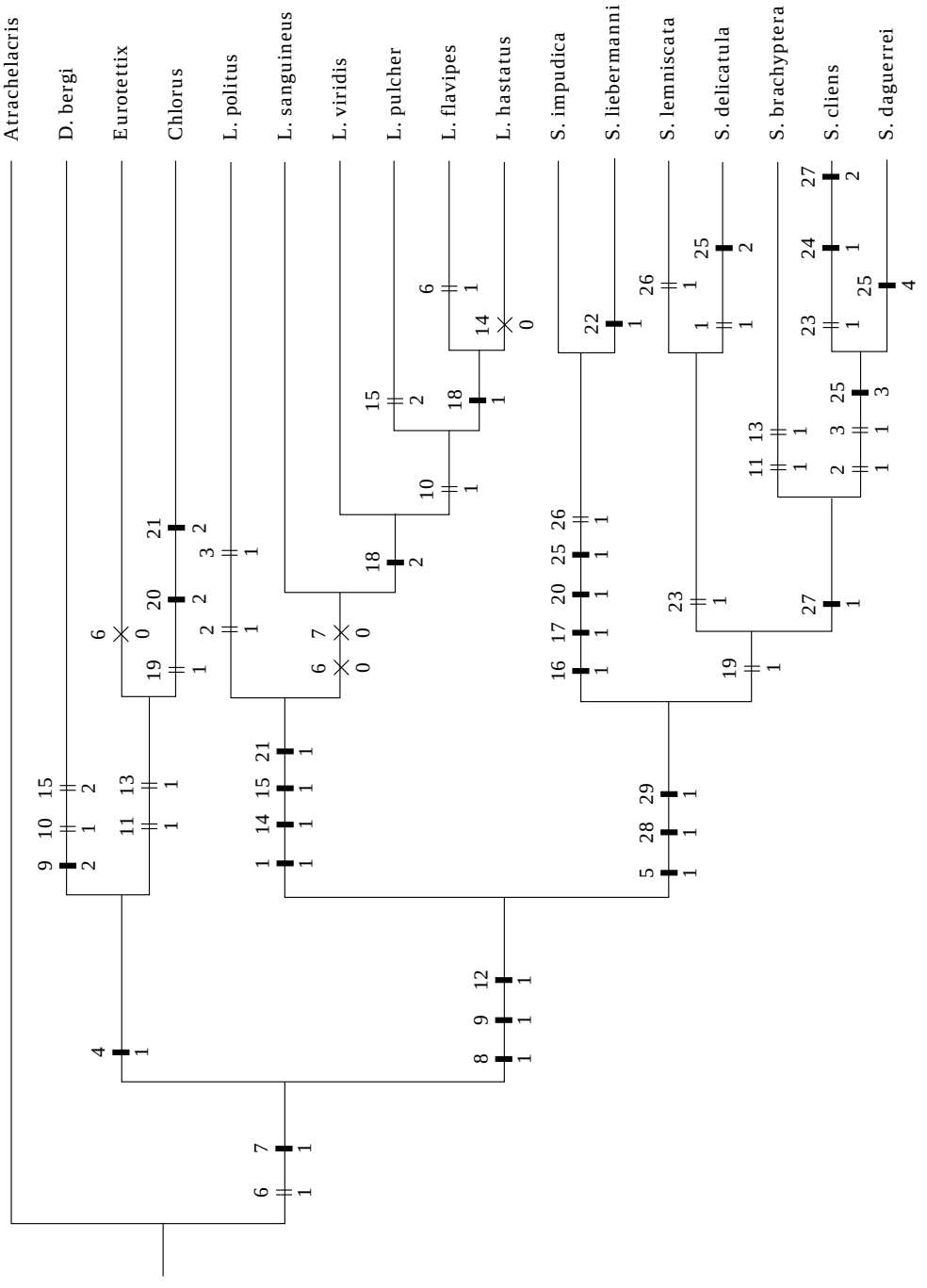

Fig. 4. Cladogram based on the data set including characters from the ovipositor valves. Simple lines indicate synapomorphies, double lines parallelisms, and X reversals.

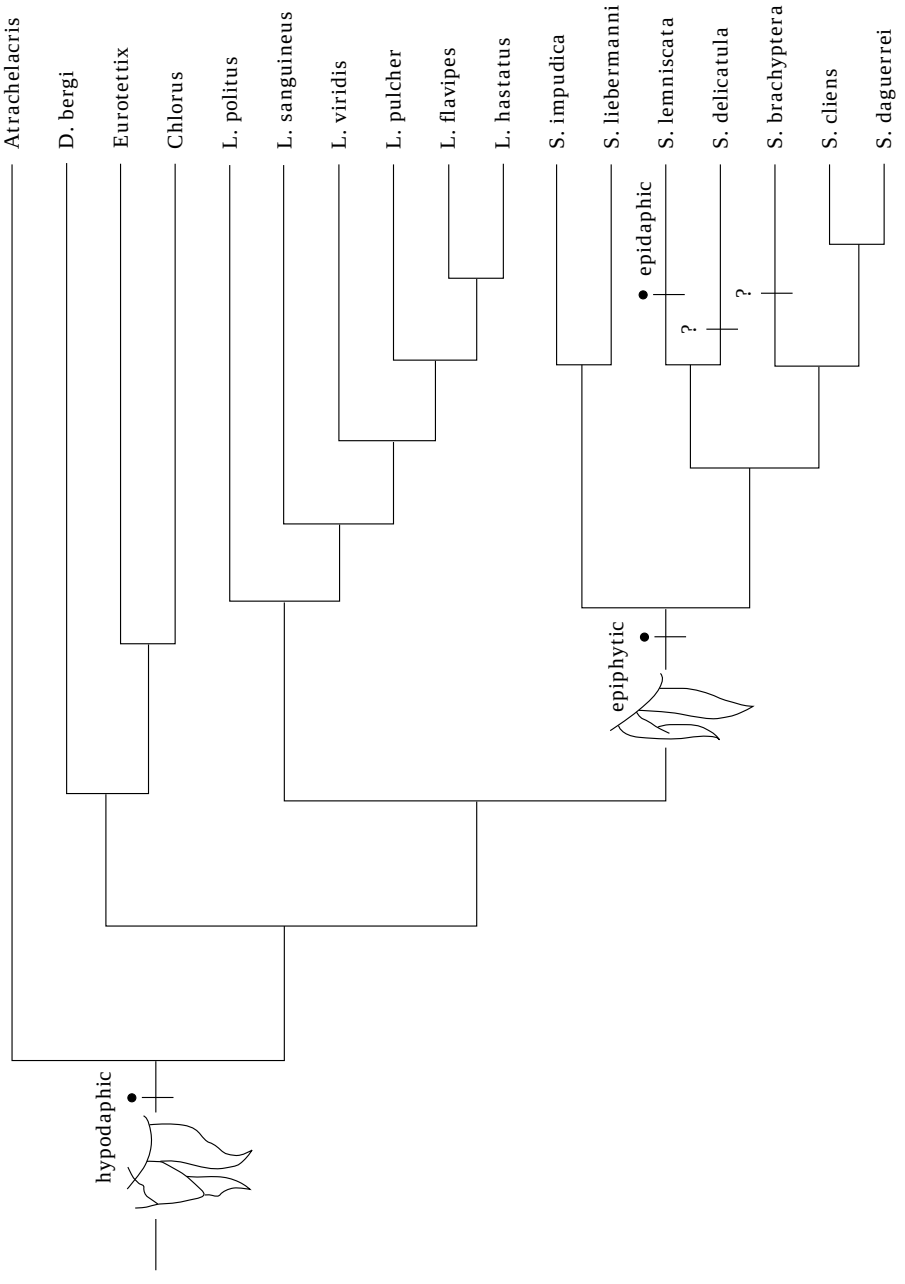

Fig. 5. Cladogram with the information on oviposition habits.

on characters from the phallic complex and the male external genitalia, while *Scotussa* is mostly defined on synapomorphies of the ovipositor structure. Second, the analysis corroborates the close relationship between these genera based on the synapomorphies "vertex as high as the eyes in lateral view" (8), "pronotum subcylindrical" (9_1), and "transverse sulci of pronotal disk shallowly impressed" (12). Finally, the results support the hypothesis of association of the structural change that occurred in the ovipositor valves of *Scotussa* (from a curve ovipositor with dorsal valves dorsally convergent to a straight ovipositor with dorsal valves dorsally divergent) with the functional change in the oviposition habits (from hypodaphic to epiphytic). However, such association does not seem to have any relevance in the adaptive radiation of the genus, if this concept is equated with speciation rates per se.

Brooks and McLennan (1991) postulated that adaptive changes early in the ancestry of a group might constitute the step that led to an unusually high speciation in descendant species. The result would be a species-rich clade whose members share a "key innovation" which would explain the success of the group. Cracraft (1982 a, b) considers a key innovation to be any novel feature characterizing a clade that is correlated with its adaptive radiation. Coddington (1988) expanded the criteria for assessing adaptive evolution to incorporate functional, morphological and ecological information. The development of a particular structural change correlated to a given functional change was listed by Coddington (1988) as one of the criteria useful to distinguish an adaptive radiation event. In *Scotussa*, the structural change that occurred in the ovipositor valves was correlated with a functional change in the known oviposition habits of the species of *Scotussa*. The structural diversification that occurred in the ovipositor valves of the species of the genus (Fig. 1d, e and Fig. 2) is contrasted with the structural homogeneity found in the ovipositor of the remaining taxa included in the analysis (Fig. 1a–c). However, this evolutionary novelty in *Scotussa* is not correlated with an unusually high species diversity when compared with its sister group, the genus *Leiotettix*.

Although it is apparent that the ovipositor valves in each species of *Scotussa* represent a unique combination of those characters (autapomorphies), some of them (synapomorphies) showed to be informative at higher levels in the cladogram, resolving the polytomy *S. brachyptera, S. delicatula, S. lemniscata* (Fig. 2).

Finally, it is interesting to note that although *Scotussa* is sympatric for most of its range with the remaining taxa included in this analysis, it reaches more southern latitudes, extending well in the Pampas south of parallel 34 S where it is largely diversified (Table 1).

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