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Author(s): Maria Marta Cigliano and Carlos E. Lange

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Phylogenetic relationships of *Eremopachys*Brancsik (Orthoptera: Tristiridae: Tropidostethini)

Maria Marta Cigliano

Departamento Científico de Entomología, Museo de Ciencias Naturales, Paseo del Bosque S/N, 1900 La Plata, Argentina email: cigliano@museo.fcnym.unlp.edu.ar

CARLOS E. LANGE

Centro de Estudios Parasitológicos y de Vectores (CEPAVE). Calle 2 Nro. 584, 1900 La Plata, Argentina.

ABSTRACT

The Tropidostethini are the only tristirids found in the Nothofagus forest, at the southern part of the South American continent along the Andes. Within this tribe, Eremapachys bergi Brancsik, the only known species of Eremapachys, occurs in the chilean patagonia mostly in the open steppe areas with Mulinum spinosum. Males of this species were unknown until recently, when specimens of this sex were found in the vecinity of the "Torres del Paine" National Park. The description of the male characteristics of this species is provided and the phylogenetic relationships for the genus Eremapachys are proposed based on a cladistic analysis performed for the subfamily Tristirinae.

INTRODUCTION

Tristirids are an endemic South American family considered to be a monophyletic group based on the uniqueness of their male genitalia (Cigliano 1989a, b). The species included in the tribe Tropidostethini are the only tristirids found in the Nothofagus forest, at the southern part of the South American continent along the Andes ("Subantartic" biogeographic province as defined by Cabrera & Willink, 1973). Within this tribe, Eremopachys bergi Brancsik, the only known species of Eremopachys Brancsik, occurs in the chilean patagonia mostly in the steppe with Mulinum spinosum, in the open areas of Nothofagus forest. When the revisionary study and cladistic analysis of the family were performed (Cigliano 1989a, b) males of E. bergi were unknown, and thus the genus was not included in the analysis. Eremopachys was considered (Cigliano 1989a) closely related to Tebacris Cigliano, based on characters from the external morphology, and provisionally included in the Tropidostethini. Recently, males of E. bergi were found in the vecinity of the "Torres del Paine" National Park. The examination of its male genitalia allowed us to corroborate its placement in the Tropidostethini and to elucidate its phylogenetic relationships.

The objectives of this paper are to describe the male characteristics of *Eremopachys begi* and to analyze the taxonomic relationships of the genus.

MATERIAL AND METHODS

Depositories.— Specimens examined for this study are deposited in the "Museo de Ciencias Naturales, La Plata, Argentina" (LA PLATA), Academy of Natural Sciences of Philadelphia (PHILADELPHIA), "Museo Nacional de Historia Natural, Santiago, Chile" (SANTIAGO).

Cladistic analysis. —The Tristiridae family is a monophyletic group of genera distinguished from other families of Acridoidea by synapomorphies of the phallic complex (Cigliano 1989a). At present it comprises 18 genera and 25 species included in the subfamilies Tristirinae and Atacamacridinae. The sixteen genera of Tristirinae (Cigliano 1989a) for which males are known are considered as terminal taxa. The taxa used as terminals in the analysis are reviewed in Cigliano (1989a). The characters used in the anlaysis are partly modified from Cigliano (1989b), and new information has being included (Appendix 1). Trees were rooted and character polarity was determined using the outgroup method (Nixon & Carpenter 1993). Atacamacris Carbonell & Mesa, the only genus included in Atacamacridinae, was used to root the tree.

Thirty eight characters were used, twenty from the external morphology (characters 1-19 and 38 in Appendix 1), five from the female genitalia (characters 20-24 in Appendix 1) and sixteen from the phallic complex (characters 25-37 in Appendix 1). Multistate characters were treated as non-additive (=unordered). Appendix 2 contains the data matrix used, which was analyzed with Hennig86 version 1.5 (Farris 1988) applying the implicit enumeration option for calculating trees (ie*), algorithm that finds all trees of minimal length. Consistency (Kluge and Farris 1969) and retention (Farris 1989) indices were calculated excluding autapomorphies. The Bremer support index (Bremer 1994), a measure of clade support was calculated. Goloboff's parsimony based program NONA (1993) was used to calculate the support. NONA was run using heuristic searches with random addition sequences, swapping by tree-bisection reconnection ("mult" N; max" in NONA). Trees with 5 steps longer were retained in memory to calculate the Bremer support. Optimization of characters (fast optimization) was performed using WINCLADA Beta version (Nixon 1999-2000).

TAXONOMY

EREMOPACHYS Brancsik

Eremopachys Brancsik 1901: 188-189; Kirby 1910: 296; Liebermann 1939: 133; 1958: 22; Rehn 1942: 51-52 (type species designation); Amedegnato 1974: 197, 1977: 48, 55, 58; Eades & Kevan 1974: 260; Cigliano 1989: 87, Otte 1995: 19; Elgueta et al. 1999: 28. Type species: Eremopachys bergi Brancsik.

Eremopachys bergi Brancsik Fig. 1

Eremopachys bergi Brancsik 1901: 190; Rehn 1942: 52; Liebermann 1939: 169; 1958: 36; Cigliano 1989a: 87-88 (=Eremopachys simplex Brancsik 1901: 189); Kirby 1910: 296; Liebermann 1939: 169; Rehn 1942: 52. Neotype: female, Chile, Magallanes, Lag. Azul, 5-1955, Dettlef, LA PLATA.

Male description.—Medium sized (22.0-23.0 mm.) dark ochraceous insects with fastigial margin and body granulations rubescent. Body depressed, tegument with granulations and rugosities coarser on head and pronotum. Head broad with small globose eyes, fastigium widely trigonal, with carinated margin, front of face vertical in side view; lateral foveolae without delimiting borders; frontal costa with contiguous lateral carinae except bellow median ocellum, where they diverge. Antennae filiform with flagellum of six segments, the last one clavate. Prosternum between front legs having a transverse arcuate ridge. Pronotum short, not extending onto mesonotum, trapezoidal, with straight anterior and posterior margins; lateral margins with an irregular ridge cut by the transverse sulcus, lateral carinae of pronotum only weakly indicated on anterior two thirds of pronotal disk. Meso and metanotum with mediolongitudinal sulcus; posterior margin of metanotum emarginate. Hind femur compressed with dorsal carina straight and ventral carina expanded; proximal upper and lower lobes widely separated. Posterior tibiae with external apical spine. Subgenital plate short and globose, epiproct with transverse ridge, medio-longitudinally sulcated, distal half trigonal. Cercus short and thick. Phallic complex: epiphallus with wide denticulated bridge, anchorae lobulated, lateral plates well developed, lophi acute, oval sclerites small. Cingulum reaching tip of aedeagus, with sclerotization reduced caudally; apodemal plates widely extended laterally; rami short, laminar. Pseudoarch not developed. Endophallus: distal portions of endophallic sclerites lanceolate.

Distribution.—Eremopachysbergi is known from the chilean patagonia, in the western edge of the Andes mountain range in the Magallanes Region. It mostly occurs in the open areas of the Nothofagus forest in the steppe with Mulinum spinosum.

Examined material.—Two males, Chile, Magallanes, Lag. Verde, in the vecinity of "Torres del Paine" National Park, "Hostería El Mirador del Paine" ex Estancia Lazo, 01-III-2000, Cigliano & Lange col., LA PLATA; 1 female, Chile, Magallanes, SANTIAGO; 2 juv. female, Chile, Magallanes, "Torres del Paine" National Park, Lago Lazo, 12/13-I-1986, Patagonian steppe, M. Elgueta col., SANTIAGO; 1 female neotype, Chile, Magallanes, Lago Azul, 5-1955, Dettleff, LA PLATA; 1 female, Magallanes, PHILADELPHIA.

CLADISTIC ANALYSIS RESULTS AND DISCUSSION

Three most parsimonious trees were found with Hennig86, each of 108 steps long (a consistency index of 0.70 and retention index of 0.79). Cladograms were stable to successive weighting. The same trees were

found when NONA was run treating trees as dichotomous (poly-). When NONA was run treating trees as polytomous only one tree was found (Fig. 2) that corresponds to the strict consensus of the three equally parsimonious cladograms. Optimization of characters (slow optimization) (Fig. 2) was performed using WINCLADA Beta version (Nixon 1999-2000). Except for the basal polytomy, and for the relationship inside the Tropidestethini clade (including Tebacris, Eremopachys, Tropidostethus, and Elysiacris), the tree obtained is highly congruent with the previous analysis performed for the whole family (Cigliano 1989b). The Tropidostethini is a well supported group and has a rather high Bremer support score (Fig. 2). It is founded on five synapomorphies from the phallic complex and one from the external morphology (character 19). Inside this clade Tropidostethus and Elysiacris come out as a very well supported clade and has the highest Bremer support score. *Eremopachys* is undoubtedly included in the tribe and it is related to Tebacris based on characters mostly from the external morphology (6 and 38). Previous analysis (Cigliano 1989b) showed Elysiacris to be the sister genus to Tebacris, in the cladogram here obtained these taxa share homoplasies from the phallic complex. Characters mostly from the external morphology characterize the sister genera relationships, while those from the male genitalia define the tribe. From this distribution of characters it might be hypothesized that in the tribe differentiation of the phallic complex preceded those of the external morphology.

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Appendix 1. Characters and character states used in the cladistic analysis of Trisitirinae.

- Longitudinal carina on dorsal head: not developed (0), present on vertex (1), present on vertex and fastigium (2).
- 2. Shape of fastigium: little salient (0), triangulate, wide (1), triangulate, narrow (2), elongate trigonal (3).
- Fastigium laterally: declivent (0), horizontal (1), ascending dorso-cephalad
 (2).
- 4. Fastigio-facial angle: lacking fastigio-facial angle (0), acute (1), truncated (3).
- 5. Frontal costa above median ocellum: broad (0), intermediate (1), narrow (2).
- 6. Lateral foveolae of fastigium: not developed (0), with ventral margin (1), without ventral margin (2), replaced by a convex area (3).
- 7. Fastigial ridges: un-cleaved (0), cleaved and without accessory carinula (1), cleaved and with accessory carinula (2).
- 8. Front of face: vertical (0), slanted (1), concave (2).
- 9. Lateral carinae of pronotal disk: absent (0), present on prozone (1), present on prozone and metazone (2).
- 10. Relationship between prozone-metazone: metazone not indicated (0), metazone as long as prozone (1), metazone longer than prozone (2).
- 11. Posterior margin of pronotal disk: entire (0), lobulate (1).
- 12. Posterior edge of pronotal disk: straight (0), obtusely angular (1), acutely angular (2).
- 13. Pronotal disk in transverse section: plane (0), ogival (1), dome-shaped (2).

- 14. Transverse sulci in pronotal disk: absent (0), one sulcus (1), two sulci (2), three sulci (3).
- 15. Sides of pronotal disk: rounding onto lateral lobes (0), with definite shoulders (1).
- Tegmina: not developed (0), subapterous (1), micropterous (2), macropterous (3).
- 17. Tympanum: absent (0), present (1).
- 18. Proximal lobes of hind femur: superior lobe larger than inferior (0), superior lobe as long as inferior (1), superior lobe smaller than inferior (2).
- 19. Apical spine on external margin of posterior tibia: absent (0), present or vestigial (1).
- 20. Espermatheca: apical diverticulum tubular, without pre-apical diverticulum (0), apical diverticulum S-shaped, without pre-apical diverticulum (1), apical diverticulum C-shaped, with small pre-apical diverticulum (2), apical diverticulum S-shaped with small pre-apical diverticulum (3).
- 21. Egg –guide / posterior edge of subgenital plate in ventral view: not surpassing or scarcely surpassing (0), highly surpassing (1).
- Hemispheric sclerite in terminal portion of spermathecal duct: absent (0), present (1).
- 23. Columellas on female subgenital plate: absent (0), few (1), numerous (2).
- 24. Length of spermathecal duct: short (0), intermediate horse-shoe shaped (1), long (2).
- Rami: rod-like (1), laminar (2), laminar dorsally, rod-like ventrally (3), laminar, dorsally lobular (4), strongly sclerotized (0).
- 26. Lateral sclerite of ectophallic ventral lobe: not developed (0), developed without covering the rami (1), developed, covering the rami (2).
- 27. Type of cingulum: capsule-like (0), with two caudal plaques (1), with sclerotization caudally reduced (2).
- 28. Pseudoarch: absent (0), reduced (1), prominent, capsule-like (2), prominent, rectangular (3).
- 29. Apical lobe of rami: absent (0), reduced (1), largely developed (2).
- 30. Aedeagus: without development of the distal portion of endophallic sclerites (0), aedeagus constituted by the apex of the ventral endophallic sclerites, covered by an ectophallic sheath (1), aedeagus constituted by the distal portion of the dorsal and ventral endophallic sclerites covered by an ectophallic sheath (2).
- 31. Gonopore process: reduced (0), short and wide (1), long and narrow (2).
- 32. Middle portion of endophallic sclerites: narrow, straight (0), narrow and curved (1), broad, reduced laterally (2), broad, prominent laterally (3).
- 33. Proximal portion of dorsal endophallic sclerites: laterally compressed (0), bent dorsoventrally (1), with hemispheric apodeme reduced (2), with hemispheric apodeme well developed (3).
- 34. Ventral margin of ventral endophallic sclerites: uncleaved (0), cleaved (1).
- Epiphallus bridge: convex in frontal view (1), wide (2), wide and short (3), narrow (0).
- Epiphallus with rugosities: absent (0), present (1).
- 37. Sheath of edeagus with rugosities: absent (0), present (1).
- 38. Fastigium slighty concave dorsally: absent (0), present (1).

Appendix 2. Data matrix used in the cladistic analysis of Tristirinae.

Taxa	Characters 123456789111111111112222222222333333333 01234567890123456789012345678		
		——————————————————————————————————————	000000000000000000000000000000000000000
		Tristira	01010120210000000003001211110123211010
Circacris	21001120210000000003001212110123211010		
Punacris	12001101210000000002010122120123201000		
Incacris	1211210111001100000??0??22120123201000		
Crites	1322220101001100000??0??22120123201000		
Paracrites	1311210111001100000?000?22120123001000		
Moluchaeris	22100111110000100001011211122123201000		
Peplacris	12112111110000100001011211121123201000		
Tropidostethus	13212202110021000010102041100212103000		
Elysiacris	13212202010021000010102041130212103100		
Tebacris	01000300010000000010002041130212103101		
Eremopachys	01000300110000100210012041100212103001		
Bufonacris	00000000000000100003001211110123211010		
Iretacris	01000000021102010100002031200001102000		
Elasmoderus	00000000021203021100002031100001102000		
Enodisomacris	00000000021203031100002031200001102000		

Note: Entries scored as ? were unknown of inapplicable. Outgroup taxon is denoted with an asterisk.

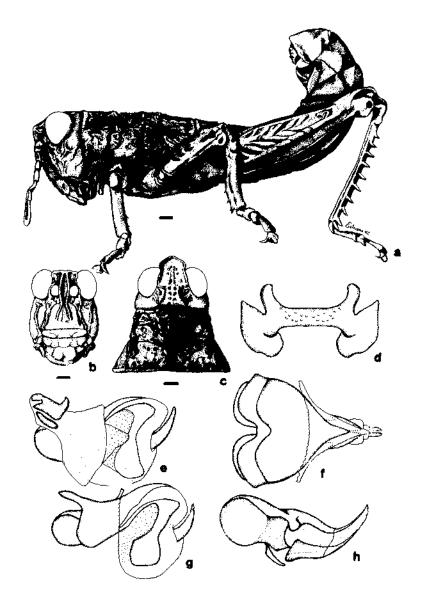


Fig. 1. Eremopachys bergi Brancsik. a-c, male specimen, d-h, phallic complex. a, lateral view, b, head, frontal view, c, head and pronotum, dorsal view; d, dorsal view of epiphallus; e, lateral view of phallic complex; f, dorsal view of cingulum and endophallus; g, lateral view of cingulum and endophallus; h, lateral view of endophallus.

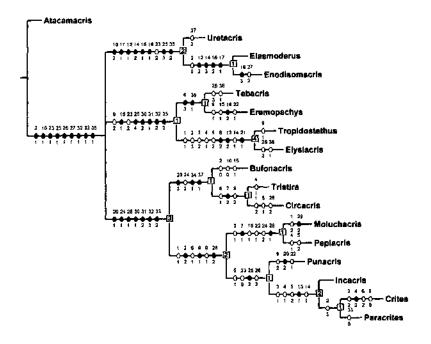


Fig. 2. Cladogram showing character optimization for Tristirinae. Solid circles represent non-homoplastic characters, open circles represent homoplastic characters. Numbers in squares indicate Bremer support values.