Phylogenetic analysis of the scorpion genus *Brachistosternus* (Arachnida, Scorpiones, Bothriuridae)

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A phylogenetic analysis of the scorpion genus *Brachistosternus* Pocock (Bothriuridae) is presented. The analysis is based on a data set including 38 of the 41 described species of *Brachistosternus* plus eight outgroup representatives of seven additional bothriurid genera and one buthid, scored for 116 morphological characters. The cladistic analysis of this matrix under implied weighting results in four most parsimonious trees. The monophyly of genus *Brachistosternus* is well supported; its subgeneric subdivision is redefined: the subgenera *Brachistosternus* Pocock and *Ministernus* Francke are considered valid, whereas *Leptosternus* Maury is synonymized with *Brachistosternus*. Illustrations of diagnostic structures are provided. The hemispermatophores of *Brachistosternus peruvianus* Toledo-Piza and *Brachistosternus pegnai* Cekalovic are illustrated for the first time. A key to species of *Brachistosternus* and maps with the distribution of the subgenera and main groups of species are provided.
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Introduction

The genus *Brachistosternus* is the most diverse of the family Bothriuridae, with 41 described species, all of them known from arid and semi-arid regions in South America, from southern Patagonia to central Ecuador (Cekalovic 1969; Ojanguren-Affilastro 2003a). The genus is especially diverse in the coastal deserts in Chile and Peru (Ochoa 2002; Ojanguren-Affilastro 2002a, 2005a; Ochoa & Ojanguren-Affilastro 2007; Ojanguren-Affilastro *et al.* 2007a,b), and in high altitudes on the Andes, up to 4500 m (Ochoa & Acosta 2002; Ojanguren-Affilastro 2003b; Ojanguren-Affilastro & Mattoni 2006). Members of the genus *Brachistosternus* were reported as the dominant scorpion species in these areas, reaching about 70% of the scorpion population (Agusto *et al.* 2006).

Despite being so diverse and abundant, most species (24 out of 41; Table S1 in the Supporting Information) were described within the last 10 years. Several factors have favoured this scarce knowledge of the group. Because all the species are fossorial, until the use of the UV detection became a usual technique of collection, the genus was poorly represented in collections. In addition, most of the species have a rather uniform external morphology, making very difficult their identification. Finally, some species with wide geographical distribution display considerable intraspecific variation, demanding a large number of specimens to clearly establish their limits.

Several diagnostic characters of *Brachistosternus* are unusual in Bothriuridae (see diagnosis below), the most remarkable being the great complexity of the hemispermatophores (first described by San Martín 1969), which are among the most complex in the entire order. The shape and development of their internal structures varies between species and are very useful in the systematics of the genus. These and other characteristics led Maury (1973a) to separate this genus in its own subfamily Brachistosterninae, but subsequent phylogenetic analyses (Prendini 2000, 2003) did not support this proposal.

Maury (1973b) published a short revision of the 15 species of *Brachistosternus* known at that time, and described three different trichobothrial patterns for the genus. Based on these patterns, he divided the genus in three subgenera, *Brachistosternus* Pocock, *Leptosternus* Maury and *Microsternus* Maury. *Microsternus* was preoccupied by a beetle, and was later replaced by *Ministernus* Francke (1985). Maury based this subgeneric division almost exclusively on the trichobothrial pattern. Many species have been described since Maury's revision, some of them with quite different trichobothrial patterns from those originally described by Maury.

Prendini (2003) established the phylogenetic position of *Brachistosternus* in the family Bothriuridae in a phylogenetic

analysis of the family; according to him the closest genera to *Brachistosternus* are *Tehuankea* Cekalovic and *Centromachetes* Lönnberg. This is intriguing because both genera are endemic to the forests of southern Chile, being morphologically very different from *Brachistosternus* which occurs, almost exclusively, in arid environments. The relationships between species of the genus are still unsolved, and most of the characters used by Prendini are not informative within the genus. In the present revision we present a phylogenetic analysis of the genus, and test its subgeneric classification. We also take the opportunity to provide a key to species, and distribution maps for the subgenera and main species groups.

Methods

Descriptive terminology follows Maury (1974) for the hemispermatophores, Vachon (1973) for the trichobothria, Cekalovic (1973a) for the androvestigia (a pair of glands situated on the dorsal surface of metasomal segment V in adult males of most species), Roig-Alsina & Maury (1981) for the male telson gland, and Stahnke (1970) for the metasomal carinae, which are abbreviated as follows: DL, dorsolateral; LIM, lateral inframedian; LSM, lateral supramedian; PL, paralateral; PM, paramedian; VL, ventrolateral; VM, ventromedian. Terminology for pedipalp carinae are according to Prendini (2000), and are abbreviated as follows: DI, dorsal internal; DE, dorsal external; VI, ventral internal; VE, ventral external. Illustrations were produced using a Leitz stereomicroscope with camera lucida. Measurements were taken with an ocular micrometer. Hemispermatophores were dissected from surrounding tissues and observed in 80% ethanol. Specimens examined are listed in Appendix S3. Abbreviations of collections from which material was studied are as follows: AMNH, American Museum of Natural History, New York; ARA, Arturo Roig Alsina personal collection, Buenos Aires, Argentina; CDA, Cátedra de Diversidad Animal I, Universidad de Córdoba, Argentina; FKCP, Frantisek Kovařík Personal collection; LEULS, Laboratorio de Entomología, Universidad de La Serena, Chile; MACN-Ar, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', National Arachnological Collection, Argentina; MUSM, Museo de historia Natural, Universidad Nacional Mayor de San Carlos, Lima, Perú; MHNC, Museo de Zoologia de la Universidad San Antonio Abad, Cusco, Peru; MZUC, Museo Zoológico del Instituto de Biología de la Universidad de Concepción, Chile Scorpion tissue samples are stored (in the vapour phase of liquid nitrogen at −150 °C) in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH.

Terminals

Ingroup. We have included all species of *Brachistosternus* available to us (38 out of 41; Table S1). Systematic criteria

used to identify *Brachistosternus* species follow: Ochoa (2002); Ochoa & Acosta (2002); Ochoa & Ojanguren-Afilastro (2007); Ojanguren-Afilastro (2002a, 2003a,b; 2004b, 2005a); Ojanguren-Afilastro & Mattoni (2006); Ojanguren-Afilastro *et al.* (2007a,b). Three nominal species were not available, as detailed below.

Brachistosternus holmbergi Carbonell 1923 was described from Jujuy province, in northern Argentina (Carbonell 1923). The holotype is presumably lost (Ojanguren-Afilastro 2005b). The original description does not match any of the known species from northern Argentina or southern Bolivia. The short description and the published photograph of the holotype suggest that it could be a specimen of *B. ehrenbergii* (Gervais 1841). However, this species is known from coastal deserts in northern Chile and Peru, but not in Argentina or any other locality east of the Andes. *Brachistosternus holmbergi* is here considered *nomen dubium*.

Brachistosternus castroi Mello-Leitão 1940 was described from Copiapó in northern Chile (Mello-Leitão 1940). We have studied a specimen identified by Mello-Leitão as *B. castroi*, most probably the one used by him to redescribe the species in his revision of 1945. This specimen does not correspond to any of the other species known from the area. We have preferred not to include this specimen in our analysis because it is a poorly preserved female juvenile, in which about a 70% of the characters used in our matrix cannot be scored. More specimens from the type locality should be collected in order to clarify the taxonomic position of this species.

Brachistosternus simoneae Lourenço 2000, was described from Serranopolis (Goias), in an area of Cerrados vegetation in central Brazil (Lourenço 2000). We could not study the female holotype and only known specimen of the species. Lourenço (2000) only reports as diagnostic some characters that would distinguish this species from its closest relative, *B. ferrugineus* (Thorell 1876). However, these characters (11 ventral trichobothria on the pedipalp chela; absence of a reticular pigmented spot on the dorsal surface of the chelicerae) are known to occur in specimens of *B. ferrugineus* (Maury 1974; Ojanguren-Afilastro 2005b), which is a highly variable species. *Brachistosternus ferrugineus* is one of the most abundant species of Chaco and Espinal biogeographical provinces from Argentina, Bolivia and Paraguay, and very common in environments highly modified by human activity, thus its presence in Brazil seems plausible. Maury (1974) mentioned the presence of *B. ferrugineus* in Brazil, based on a specimen from Campo Grande that was originally identified by Bücherl (1959) as *Brachistosternus intermedius* Lönnberg 1902. Maury has never examined this material; he based his identification on some comments from Vera Von Eickstedt. A decision on the validity of *B. simoneae* is pending until the holotype is examined and males from the type locality are available. We have preferred not to include this species in

our analysis based on the original description, because most of the characters used in our matrix are not included in such description.

Outgroups and rooting. We selected as outgroups the following bothriurid species: *Bothriurus flavidus* Kraepelin 1911, *Orobothriurus alticola* (Pocock, 1899), *Timogenes sumatranus* Simon 1880 and *Urophonius brachycentrus* (Thorell 1876); we have chosen these genera because they represent very well the morphological variability of the family, and the identity of the selected species is clearly established. We have also included *Tehuankea moyanoi* Cekalovic 1973 and *Centromachetes pococki* (Kraepelin 1894), which according to Prendini's analysis (2003) are closely related to genus *Brachistosternus*. We have also included *Thestylus aurantiuturus* Yamaguti & Pinto da Rocha 2003 because according to Prendini's analysis (2000, 2003) genus *Thestylus* is the most basal South American genus of Bothriuridae.

We have also selected as outgroup the Buthid *Tityus confluens* Borelli 1899, and we have used this species to root the tree.

Systematic criteria used to identify outgroups follow: Ojanguren-Affilastro (2005b) for *Bothriurus flavidus*, *Orobothriurus alticola*, *Urophonius brachycentrus*, *Timogenes sumatranus* and *Tityus confluens*; Cekalovic (1973b) for *Tehunakea moyanoi*; Yamaguti & Pinto da Rocha (2003) for *Thestylus aurantiuturus*. To identify *C. pococki* we have used a redescription of the type material (E. A. Maury unpublished data).

Cladistic analysis

Analyses were performed with TNT 1.0 (Goloboff *et al.* 2003–2006). All commands and instructions for output files were stored in script files for better documentation and accurate reproduction of results.

Heuristic tree searches. Heuristic searches were performed using random addition sequences (RAS) followed by tree bisection–reconnection branch swapping (TBR), iterating with cycles of the Parsimony Ratchet (Nixon 1999a). We performed 100 replicates of RAS followed by 200 iterations of TBR-Ratchet (string of commands *ratchet: iter 200; mult = ratchet repl 100 tbr hold 10;*). This sequence converges in the same minimum length in 50–100% of the replicates, depending on the weighting regime (see below). With so many hits it is likely the optimal tree was found.

Sensitivity to weighting regimes. We analysed the data set under weighting regimes against homoplasy, using implied weighting (Goloboff 1993). We assessed the sensitivity of the results to variations in the strength of the weighting function, with integer values of the constant of concavity $K = 1-9$, and under equal weights. For each group in the preferred tree, we report the frequency in which it is monophyletic under these

weighting regimes (from 1 to 10). The sensitivity of groups to changes in the analysis parameters also provides an insight to the support of groups (Goloboff *et al.* 2008; see also Prendini 2000, 2003; Giribet 2003; Prendini *et al.* 2003).

Synapomorphies. We produced synapomorphy lists taking into account only the unambiguous changes in ancestral states (e.g. $0 \rightarrow 1$, but not $01 \rightarrow 1$; $01 \rightarrow 2$, but not $01 \rightarrow 12$). Because synapomorphy lists for polytomies in consensus representations are dependent on the optimal resolutions, we calculated all optimal dichotomous trees and produced lists of synapomorphies that are common to all of them, using a heuristic search without branch collapsing, followed by the Common Synapomorphies command in TNT (string of commands *ratchet: iter 50; collapse 0; mult = ratchet repl 10 tbr hold 10; bb = fillonly; apo[-]*). Plotting of synapomorphies (Fig. 2) was produced with WINCLADA (Nixon 1999b) and manually edited to conform to the results given by TNT (WINCLADA does not have a common synapomorphies option).

Bremer support. Bremer support values (BS) (Bremer 1994), were heuristically estimated by TBR swapping from the optimal trees, retaining suboptimal trees with increasing bounds, up to 32 000 trees. BS values are expressed in terms of fit, under concavity constant $K = 6$. First, we used rough searches to estimate a maximum value of BS, which were about 1.6 units of fit. Then we run 16 cycles, increasing the tree buffer in 2000 trees each cycle. The suboptimal bound was increased in 0.1 units each time (from 0 to 1.6).

Resampling measures. We also estimated support values using group frequencies under jackknifing (see Goloboff *et al.* 2003). We used a probability of alteration $P = 0.36$. The absolute frequencies are reported over the optimal preferred tree, thus all values are reported (even below 50%). We performed 1000 pseudoreplicates, of 10 random sequence additions each followed by TBR swapping, keeping up to 10 trees (string of commands *mult: noratchet repl 10 tbr hold 10; resample jak repl 1000 freq from 0 [mult]*, where '0' is the consensus of the optimal trees). In addition to jackknifing, we similarly calculated group frequencies under bootstrap and symmetric resampling, expressed as absolute frequencies or frequency differences (GC) (Goloboff *et al.* 2003) (not shown). Because all these values were highly correlated, we only report the jackknifing values here (Fig. 1).

Transformation costs for multistate characters. Multistate characters were considered ordered (additive) when the states were interpreted as internested homologies; this is not intended to express assumptions on the evolution of characters, but merely reflects degrees of similarity (Lipscomb 1992; Goloboff 1997). Morphoclines were interpreted as internested homologies.
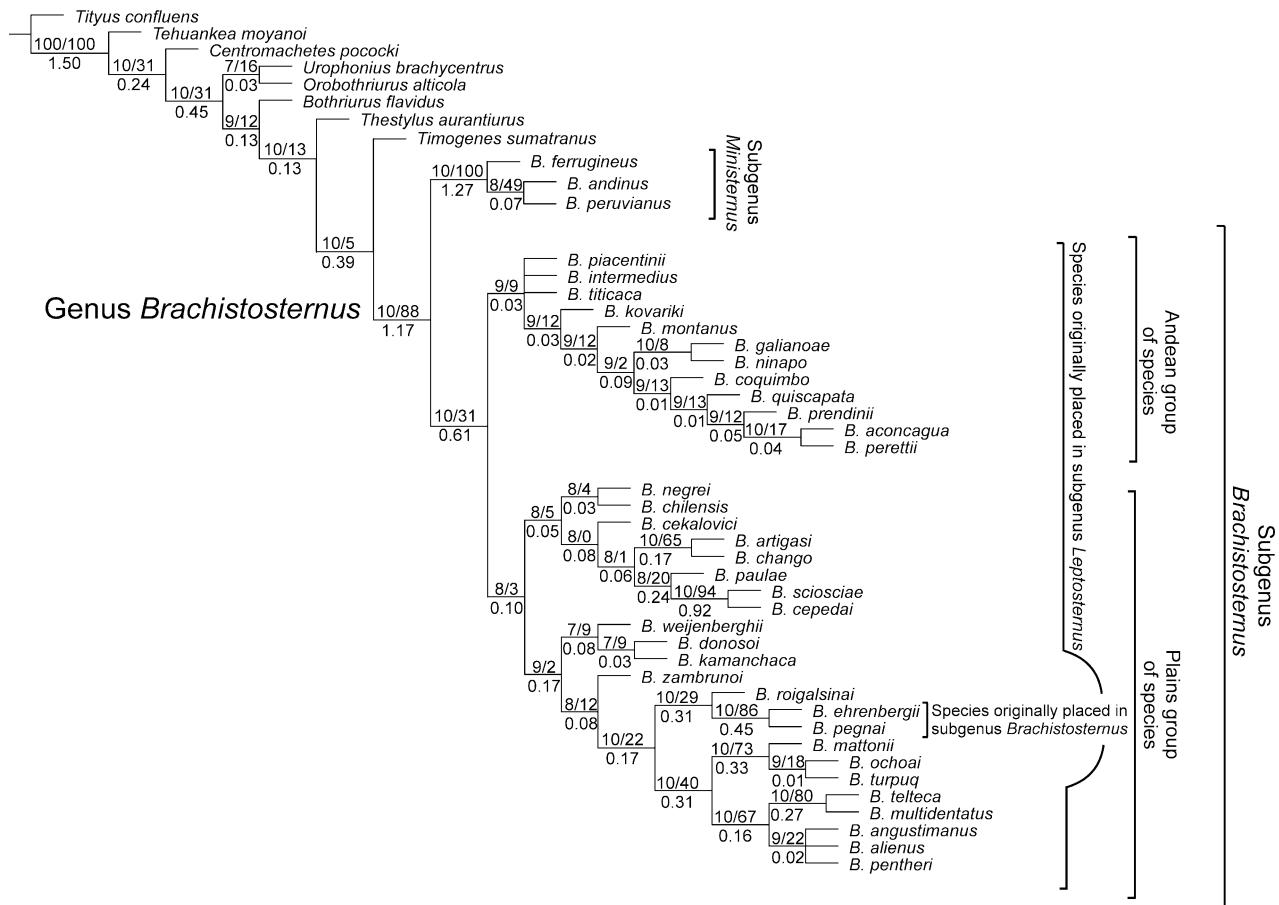
Fig. 1 Strict consensus of the four most parsimonious trees obtained under implied weights with concavity values *K* = 5–8 (Fit = 103.8 under *K* = 6, length = 500). Numbers above branches are Jackknife percentages (right) and sensitivity frequencies (left). Numbers below branches are Bremer support values in units of fit.

Character indices. Character indices were calculated exporting basic statistics (steps, minimum and maximum character lengths) from TNT to a spreadsheet. Consistency index (CI) and retention index (RI) were calculated for all characters. For each character system we have also calculated the average CI and RI, excluding uninformative characters.

Data set. The characters used in the cladistic analysis are described in Appendix S1, and the data matrix is listed in Appendix S2.

Results and discussion
Phylogenetics
Our preferred tree (Figs 1 and 2) corresponds to a range of mild concavities (*K* = 5–8). Ramírez (2003) and Lopardo (2005) found that mild concavity values produced higher topological congruence indices, a result that was recently confirmed by Goloboff *et al.* (2008) as a consistent trend for

many morphological and molecular data sets. We present the sensitivity to concavity changes in Fig. 1. All groups were stable in at least 7 of the 10 explored weighting regimes, and in general, the sensitivity of groups to changes in weighting regime is correlated with support measures (jackknifing and Bremer support, Fig. 1).

Brachistosternus appears as strongly supported, with many synapomorphies. The relationships between *Brachistosternus* and the rest of the genera of Bothriuridae are different to those from Prendini's analysis. In our analysis *Tehuankea* and *Centromachetes* appear as basal genera of Bothriuridae, and *Timogenes* appears as the most closely related genus to *Brachistosternus*. According to this topology *Thestylus* is not a basal genus of the family, but a derived genus, related with *Timogenes* and *Brachistosternus*.

The subgenera *Ministernus* and *Brachistosternus* (Figs 1 and 2) are also strongly supported with many synapomorphies. The subgenus *Brachistosternus* is here relimited to include the
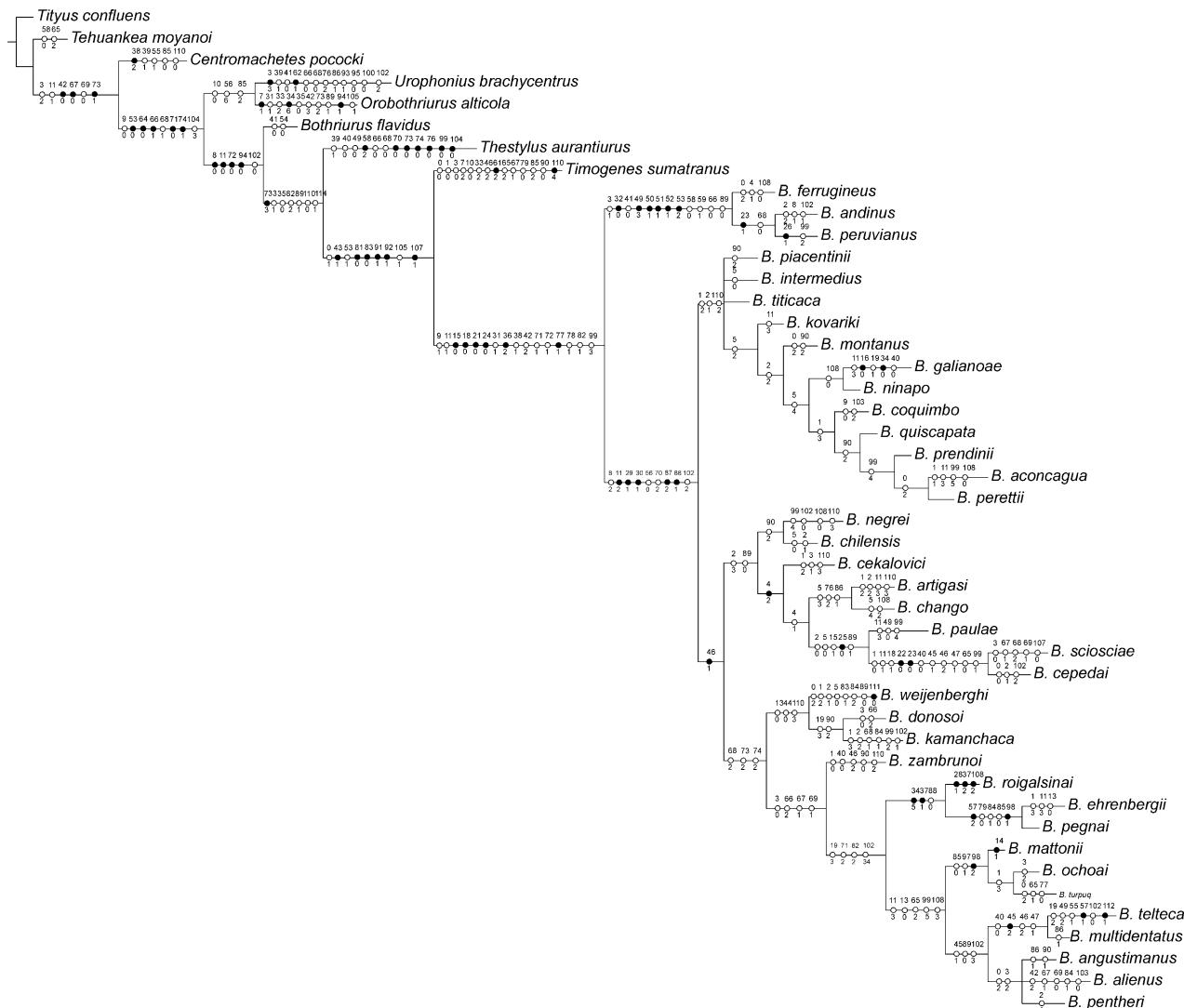
Fig. 2 Strict concensus of the four most parsimonious tree obtained under implied weights with concavity values *K* = 5–8, with unambiguous character optimizations shown for every branch. Empty and filled hashmarks represent homoplasious and nonhomoplasious transformations, respectively, with characters on top and states below.

larger subgenus *Leptosternus* as a junior synonym (Fig. 1), as the two species originally included in it are nested within *Leptosternus*.

For comparative purposes, we present the consensus tree obtained under equal weights (Fig. S2A). We also present the results of considering all characters as non-additive (Fig. S2B,C). We do not endorse the treatment of continuous characters as non-additive, but their treatment as non additive may help estimate the impact of additive characters in the analysis. Although the interactions are complex, the overall effect of changes in weighting and additivity is that those groups with higher Bremer and jackknifing scores are the

ones that survive alterations in the parameters of analysis and ordering of states.

In previous contributions (Ojanguren-Affilastro 2002a, 2003b, 2005a; Ojanguren-Affilastro & Mattoni 2006; Ojanguren-Affilastro *et al.* 2007a,b) we have suggested that there where at least two groups of species in the subgenus *Leptosternus*, one including the species from arid plains in Argentina, Chile and Peru, and the other including the Andean species. The results of our present analysis support this view. The species from the arid plains of coastal deserts in northern Chile and southern Peru are closely related with the species from plains of the Monte and Patagonia biogeographical regions in

western Argentina, while the species of the former subgenus *Leptosternus* occurring above 2000 m in the Andes are closely related to each other.

The results obtained using parameters different from those of our preferred tree (Fig. S2A–C) support only partially these groups of species. In the analyses considering all characters as non additive (Fig. S2B,C), or not using implied weighting (Fig. S2A,C), the position of *Brachistosternus* in Bothriuridae, and the subgeneric division remains similar to that of our preferred tree, but the Andean group of species, as well as part of the plains group of species collapse in smaller groups. In view of this dependence on parameters of analysis, together with the absence of clear synapomorphies and low support values, we delay the proposal of formal subgeneric status for those groups until additional data sources from ongoing molecular projects are examined.

Character systems and homoplasy levels

The homoplasy levels (expressed as CI) and the homoplasy retained as synapomorphies (RI) are not homogeneously distributed across character systems. The trichobothrial pattern and the structures of hemispermatophore are the less homoplasious character systems, with high retention indices as well (Fig. S1A,B). Due to its complexity, the hemispermatophore of *Brachistosternus* provides many characters that strongly support our results. The fact that many of these complexities are inapplicable or absent in the outgroups, partially explains the low homoplasy levels found here. The pigment pattern ('Colour') is the most homoplasious character system; this is not surprising, as these patterns are highly variable in Bothriuridae, even intraspecifically. The characters from pedipalp and metasomal ornamentation, also quite homoplasious, are more useful in other genera of Bothriuridae (Prendini 2000, 2003), but not very well represented in *Brachistosternus*.

Patterns of distribution

The species of subgenus *Brachistosternus* occur from southern Argentinean Patagonia (*Brachistosternus paulae* Ojanguren-Affilastro 2003a), to central Ecuador (*Brachistosternus pegnai* Cekalovic 1969) (Fig. S4A). There are two monophyletic groups of species with distinctive patterns of distribution. The Andean species occur from central Argentina to Southern Peru (Fig. S4A), from 2000 to 4500 m, in a sector of the Andes which includes the higher peaks, and receives fewest precipitations. This area corresponds to the Altoandina Scorpiological Area (Acosta & Maury 1998) or Andean Domain (Maury 1979). A second group includes most of the species from the plains, mostly restricted to extremely xeric areas at both sides of the Andes. East to the Andes they occur in the Argentinean Patagonia and Monte biogeographical provinces (Cabrera & Willink 1980), approximately from parallel 27°

to 47° (Fig. S4A) in an area that corresponds to the Sub-Andina or Monte Scorpiological Area (Acosta & Maury 1998) or Central and Patagonic Domains (Maury 1979). West to the Andes they are distributed in the Pacific coastal desert, from southern Ecuador to central Chile, between parallels 3° and 38°. This last group of species is present in the Atacama Desert, one of the most arid areas of Earth, while the southernmost Chilean species (*Brachistosternus negrei* Cekalovic 1975) occurs in grasslands and small open areas within *Nothofagus* and *Araucaria* humid forests. The disjunct distribution of the plains group of species could be explained by an ancestral continuous distribution of the group, previous to the raising of the Andes as proposed by Ochoa (2005). This mountain chain is a biogeographical barrier that most probably could not be surpassed by this very specialized group of species. The notorious similitude between the species at both sides of the Andes, despite their supposed long time of separation, could be due to their high adaptation to the similar environments that can be found at both sides of the Andes, as well as to the stability of these environments.

The species of subgenus *Ministernus* have a disjunct distribution as well. Two Andean species, *Brachistosternus andinus* Chamberlin 1916 and *Brachistosternus peruvianus* Toledo Piza 1974, are restricted to high altitude Andean valleys in southern Peru, in Cusco, Apurimac and Ayacucho provinces (Ochoa 2005), whereas *B. ferrugineus*, plus, probably *Brachistosternus simoneae* Lourenço 2000, occur in a wide area of the Espinal, Chaco and Cerrados in Argentina, Bolivia, Brazil and Paraguay (Lourenço 2000; Ochoa 2005) (Fig. S4B). *Brachistosternus ferrugineus* is the most widespread species of the genus inhabiting in several different habitats, from shrub steppes of southern Buenos Aires province in Argentina, to, the dry woods of northern Chaco Biogeographyc Province (Cabrera & Willink 1980) of northern Paraguay. This area corresponds to the Chaco Scorpiological Area (Acosta & Maury 1998) or Chaco District (Maury 1979), as well as to the ecotonal area of the Espinal (Acosta & Maury 1998). The disjunct distribution of subgenus *Ministernus* could be explained by a previous continuous distribution of the group, the raising of the Andes favoured a more humid environment of tropical forests in the lower areas of eastern Peru and northern Bolivia, where the genus *Brachistosternus* is not present, isolating both populations.

The high diversity of *Brachistosternus* contrasts with most genera of Bothriuridae, which are poorly diversified. This could be explained as a result of a specialization to the substratum (a concept proposed by Prendini 2001). This seems to be the case in northern Chile and in the Andes, where this genus has achieved the highest radiation, as well as with the ultrapsammophilous species of both sides of the Andes. However, most species in the eastern side of the Andes have wide areas of distribution, usually occurring in areas with
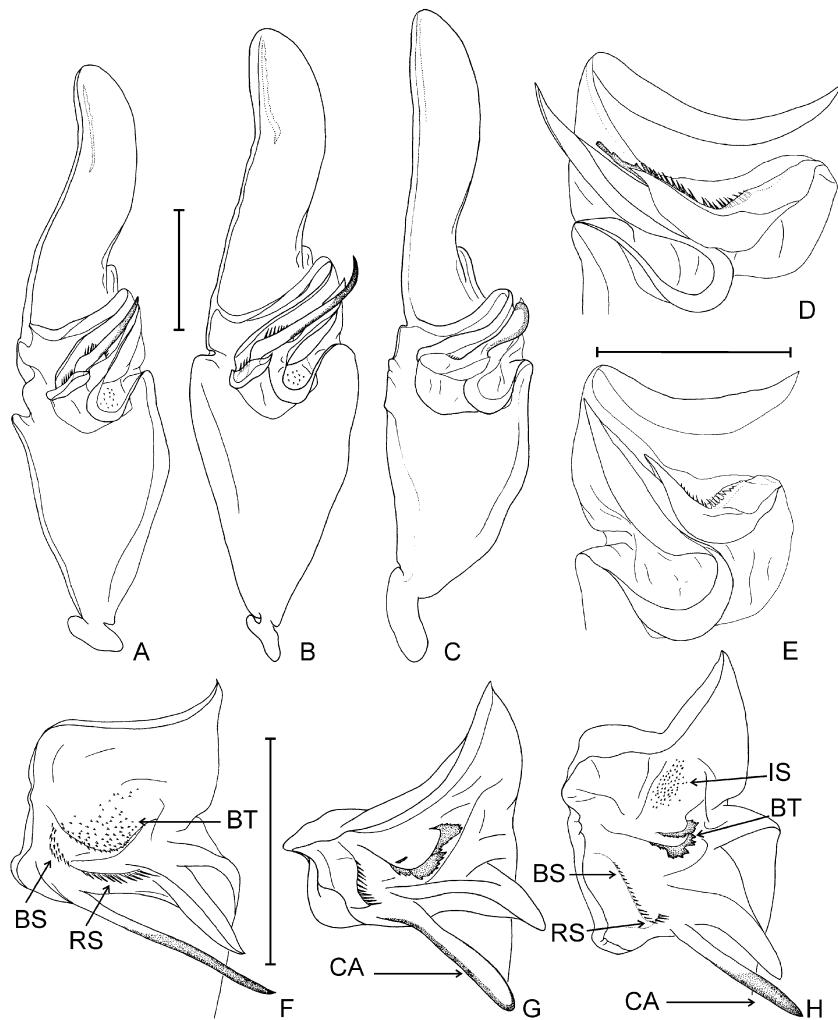
Fig. 3 A–H. Hemispermatophores of *Brachistosternus* species. —A. *Brachistosternus andinus* Chamberlin 1916, left hemispermatophore, ventral view. —B. *Brachistosternus peruvianus* Toledo Piza 1974, left hemispermatophore, ventral view. —C. *Brachistosternus pegnai* Cekalovic 1975, left hemispermatophore, ventral view. —D. *Brachistosternus roigalsinai* Ojanguren-Affilastro 2002, right hemispermatophore, detail of the lobe region. —E. *Brachistosternus multidentatus* Maury 1984, right hemispermatophore, detail of the lobe region. —F. *Brachistosternus peruvianus*, left hemispermatophore, detail of the lobe region, unfolded, showing internal structures. —G. *Brachistosternus pegnai*, left hemispermatophore, detail of the lobe region, unfolded, showing internal structures. —H. *Brachistosternus multidentatus*, left hemispermatophore, detail of the lobe region, unfolded, showing the internal structures. Scale bars = 1 mm. Abbreviations: BS, basal spines; RS, row of spines; IS, internal spines; BT, basal triangle; CA, cylindrical apophysis.

different substrata, as *B. ferrugineus* or *B. weijenberghi* (Thorell 1876) (Ojanguren-Affilastro 2002d, 2005b).

Systematics

The monophyly of genus *Brachistosternus* is well supported in all the analyses, similarly as obtained in previous phylogenetic studies (Prendini 2000, 2003). Our results support two well defined groups (Figs 1 and 2). One is the subgenus *Ministernus*, and the other includes the subgenera *Brachistosternus* and *Leptosternus*. The two members of the former subgenus *Brachistosternus* (*B. ehrenberghii* and *B. pegnai*) are deeply nested within the subgenus *Leptosternus*, hence, according to our analysis, we synonymize *Leptosternus* with *Brachistosternus*.

Genus Brachistosternus *Pocock 1893. Figs 1–5; S1–S4*

Brachistosternus Pocock 1893: 402–403; type species by original designation *Scorpio ehrenbergii* Gervais 1841. For a complete synonymic list see Lowe & Fet (2000).

Diagnosis. Brachistosternus can be distinguished from the rest of the genera of Bothriuridae by the complex hemispermatophore with several internal structures (Fig. 3F–H) that are not present in the rest of Bothriuridae, by having long setae on the lateral sides of the telotarsi (Fig. 5A–C), instead of spiniform setae, and by the intermedial lamellae of the pectines arranged in two or three rows of subcircular small lamellae, instead of a single row of squared medium-sized lamellae. In addition, males of most species bear two conspicuous glands on metasomal segment V (Fig. S3A–D); otherwise present in *Timogenes*.

Description. Medium to large size (30–110 mm), with slender appearance. Base colour light yellow, usually with brown spots on the carapace, tergites and metasoma. Carapace without carinae, with slight median projection on anterior margin. Chelicerae with one or two subdistal teeth on movable finger. Trichobothrial pattern neobothriotaxic Type C (Fig. 4A–H),
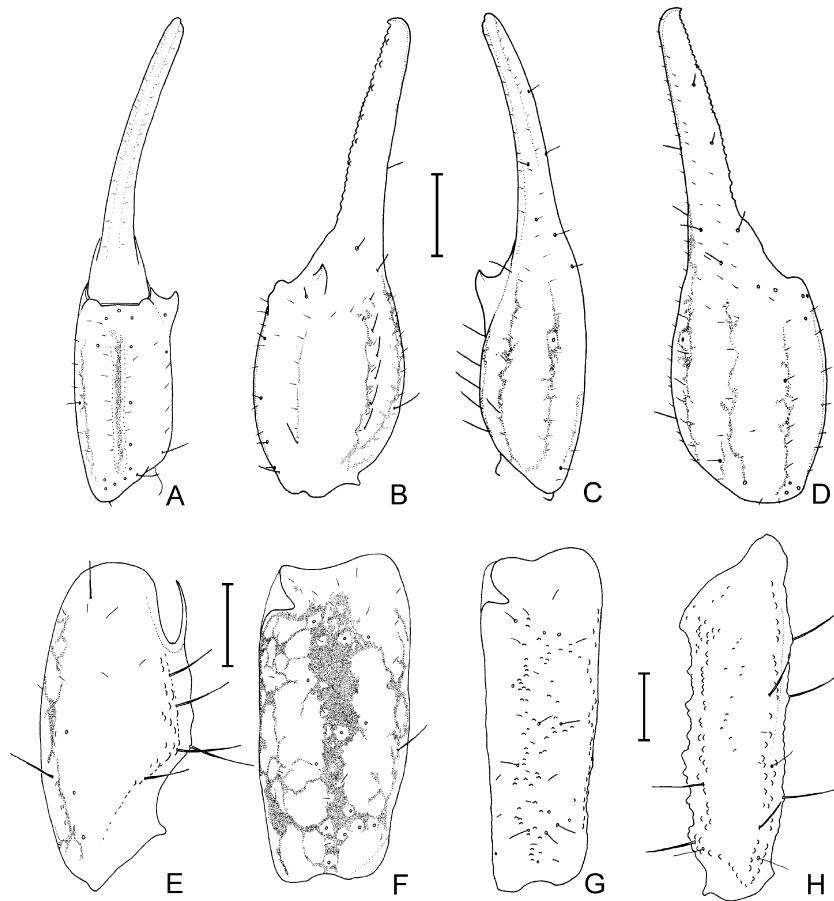
Fig. 4 A–H. Pedipalp of genus *Brachistosternus*. —A–D. *Brachistosternus artigasi* Cekalovic 1974 right pedipalp chela. —A. Ventral aspect. —B. Prolateral aspect. —C. Dorsal aspect. —D. Retrolateral aspect. —E–F. *Brachistosternus artigasi* right pedipalp patella. —E. Ventral aspect. —F. Retrolateral aspect. —G–H. *Brachistosternus multidentatus* Maury 1984. —G. Right pedipalp patella, retrolateral aspect. —H. Right pedipalp femur, dorsal aspect. Scale bars = 1 mm.

except in *B. paulae*, orthobothriotaxic Type C. Legs slightly elongated, with scattered setae; telotarsi laterally compressed, with abundant setae (Fig. 5C). Pedipalps slender, with scarce granulation. Carinae of femur and patella usually well developed (Fig. 4G,H), reduced in some species to pigment stripe or row of setae (Fig. 4E,F). Carinae of pedipalp chela always reduced to rows of setae or pigment stripes (Fig. 4A–D), except for the VM carinae, usually well developed (Fig. 4A). Internal surface of pedipalp fingers with median row of teeth, and four to nine pairs of accessory teeth. Males with conic apophysis on internal surface of pedipalp chela (Fig. 4A–C). Tergites usually granular in males, smooth in females, without carinae in segments I–VI, with four longitudinal carinae on segment VII; *B. ehrenbergii* and *B. pegnai* with a medial stridulatory organ on pretergites (Fig. 5G). Sternites usually granular in males and smooth in females; spiracles narrow, partially occluded by small internal denticles. Metasoma (Fig. 5H) with poorly developed DL, LSM and LIM carinae in segments I–V; segment V usually with well developed VM and VL longitudinal carinae (Fig. 5D), VSM carinae always absent; males usually with well developed paired dorsal glands (androvestigia) in segment V (Fig. S3A–D). Telson

well developed, vesicle globose; males usually with a gland on the dorsal surface, which can be completely or partially divided into halves; aculeus with same length as vesicle. Hemispermatophore lameliform (Fig. 3A–H), distal lamina slightly curved on its median part, usually similar in length to the basal portion, with well-developed distal crest on the apex, and distal lobe on anterior margin; lobe region usually with three groups of spines (Fig. 3F–H), internal spines, basal spines and row of spines. Hemispermatophores asymmetrical, left with basal lobe more developed (compare Fig. 3A–C, F–H with 3D,E) and a cylindrical apophysis (Fig. 3A,B,F,H).

Subgenus Brachistosternus *Pocock*

Brachistosternus Pocock 1893: 402–403; type species by original designation *Scorpio ehrenbergii* Gervais 1841. For a complete synonymic list see Lowe & Fet (2000).
Leptosternus Maury 1973b; type species by original designation *Telogonus weijenberghii* Thorell 1876, new synonymy.

Diagnosis. Subgenus *Brachistosternus* can be distinguished from subgenus *Ministernus* by the following characters: Pedipalp chela with four to six ventral trichobothria, instead of 9–12.
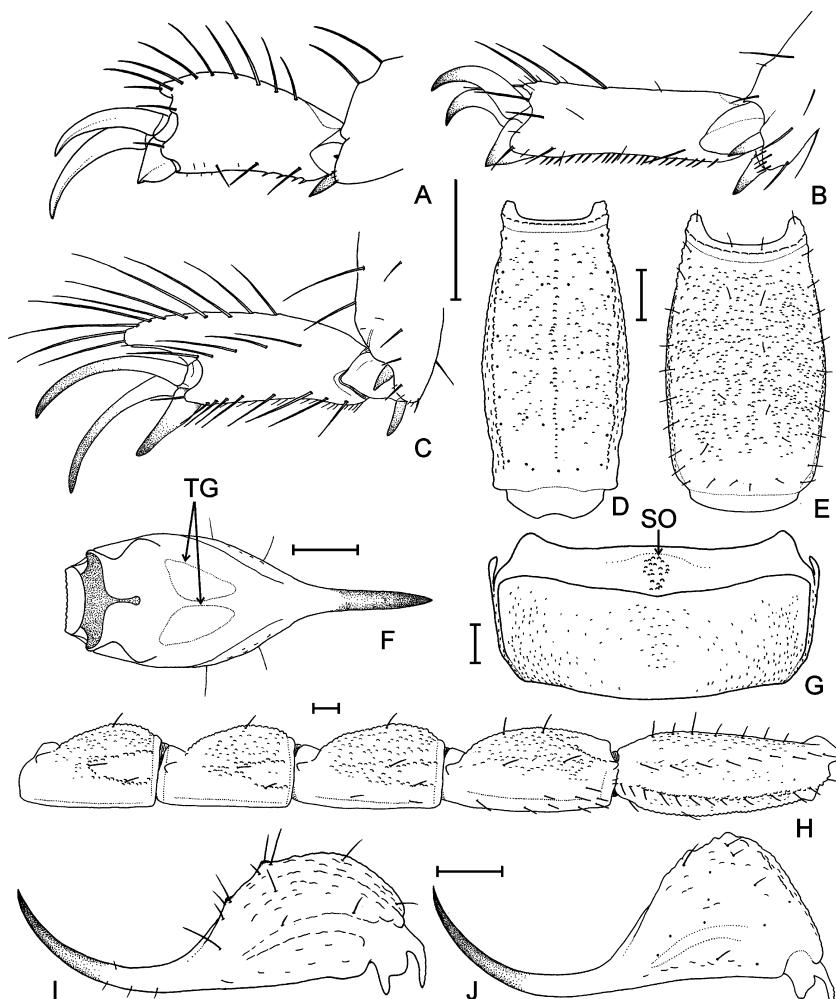
Fig. 5 A–J. —A. *Brachistosternus cepedai* Ojanguren-Affilastro *et al.* 2007b, right telotarsus I, prolateral view. —B. *Brachistosternus ferrugineus,* (Thorell 1876) right telotarsus IV, prolateral view. —C. *Brachistosternus multidentaus* Maury 1984, right telotarsus IV, prolateral view. —D. *Brachistosternus coquimbo* Ojanguren-Affilastro *et al.* 2007b, metasomal segment V, ventral aspect. —E. *Brachistosternus aconcagua* Ojanguren-Affilastro & Scioscia 2007, metasomal segment V, male, ventral aspect. —F. *Brachistosternus negrei* Cekalovic 1975, telson, male, dorsal aspect, showing the telson gland (divided into halves). —G. *Brachistosternus ehrenbergii* (Gervais 1841), fourth tergite, dorsal aspect, showing the stridulatory organ on the pretergite. —H. *Brachistosternus multidentatus*, metasoma, lateral aspect. —I. *Brachistosternus weijenberghi* (Thorell 1876), telson, male, lateral aspect, (only two of the four more developed granules of the ventral surface can be observed). —J. *Brachistosternus telteca* Ojanguren-Affilastro 2000, telson, male, lateral aspect. Scale bars = 1 mm. Abbreviations: SO, stridulatory organ; TG, telson gland.

Basal spines of hemispermatophore contiguous with the spines in a row, instead of separated into two groups by the cylindrical apophysis. Chelicerae with two subdistal teeth on movable finger, instead of only one.

Species included (36). *Brachistosternus aconcagua* Ojanguren-Affilastro & Scioscia 2007; *Brachistosternus angustimanus* Ojanguren-Affilastro & Roig Alsina 2001; *Brachistosternus alienus* Lönnberg 1898; *Brachistosternus artigasi* Cekalovic 1974; *Brachistosternus castroi* Mello-leitão 1940 *Brachistosternus cepedai* Ojanguren-Affilastro, Agusto, Pizarro-Araya & Mattoni; *Brachistosternus cekalovici* Ojanguren-Affilastro 2005a; *Brachistosternus chango* Ojanguren-Affilastro *et al.* 2007a; *Brachistosternus chilensis* Kraepelin 1911; *Brachistosternus coquimbo* Ojanguren-Affilastro *et al.* 2007b; *Brachistosternus donosoi* Cekalovic 1974; *B. ehrenbergii*; *Brachistosternus galianoae* Ojanguren-Affilastro 2002c; *Brachistosternus intermedius* Lönnberg 1902; *Brachistosternus kamanchaca* Ojanguren-Affilastro *et al.* 2007a; *Brachistosternus kovariki* Ojanguren-Affilastro 2003b; *Brachistosternus mattonii* Ojanguren-Affilastro 2005; *Brachistosternus montanus* Roig-Alsina 1977; *Brachistosternus multidentatus* Maury 1984; *B. negrei*, *Brachistosternus ninapo* Ochoa 2004; *Brachistosternus ochoai* Ojanguren-Affilastro 2004b; *B. paulae*; *B. Pegnai*; *Brachistosternus pentheri* Mello-Leitão 1931; *Brachistosternus perettii* Ojanguren-Affilastro & Mattoni 2006; *Brachistosternus piacentinii* Ojanguren-Affilastro 2003b; *Brachistosternus prendinii* Ojanguren-Affilastro 2003b; *Brachistosternus quiscapata* Ochoa & Acosta 2002a; *Brachistosternus roigalsinai* Ojanguren-Affilastro 2002a; *Brachistosternus sciosciae* Ojanguren-Affilastro 2002a; *Brachistosternus telteca* Ojanguren-Affilastro 2000; *Brachistosternus turpuq* Ochoa 2002; *Brachistosternus titicaca* Ochoa & Acosta 2002; *B. weijenberghi*; *Brachistosternus zambrunoi* Ojanguren-Affilastro 2002b.

Synonymy. *Leptosternus* Maury 1973b = *Brachistosternus* Pocock 1893, new synonymy. According to our phylogenetic analysis,

the two former members of subgenus *Brachistosternus* (*B. ehrenbergii* and *B. pegnai*) are deeply nested within *Leptosternus*, and closely related with *B. roigalsinai*, in a group including most of the species from the arid plains of northern Chile, Southern Peru and Argentina.

Subgenus Ministernus *Francke*

Microsternus Maury, 1973. 248, 249, 251; type species by original designation *Telogonus ferrugineus* Thorell 1876. Preoccupied by Lewis, 1887 (a coleopteran).
Ministernus Francke 1985. 4, 6, 10, 15 (replacement name). For a complete synonymic list see Lowe & Fet (2000).

Diagnosis. Subgenus *Ministernus* can be distinguished from subgenus *Brachistosternus* by the following characters: Pedipalp chela with 9–12 ventral trichobothria, instead of four to six. Basal spines of hemispermatophore not contiguous with row of spines, separated by the cylindrical apophysis. Chelicerae with one subdistal tooth on movable finger, instead of two.

Species included (4). *Brachistosternus andinus*; *B. ferrugineus*; *B. peruvianus*; *B. simoneae*.

Notes. Species of subgenus *Ministernus* integrate a clearly delimited clade, strongly supported in all our analyses. The two Andean species (*B. andinus* and *B. peruvianus*) form a monophyletic group, sister to the Chacoan species *B. ferrugineus* (plus, probably, *B. simoneae*). The original descriptions of *B. andinus* and *B. peruvianus* are vague, and the specimens in collections are still scarce; Maury (1978) redescribed *B. andinus* and suggested that *B. peruvianus* could be a junior synonym. Ochoa (2005), in his revision of the scorpion fauna of southern Peru, considers both as valid species. We have had access to most of the specimens studied by Maury plus others recently collected, and founded conspicuous differences between the species, especially in the hemispermatophores (Fig. 3A,B,F), thus corroborationg Ochoa's results. A complete redescription of these species is in preparation by J. A. Ochoa (personal communication). See terminals above for notes on *B. simoneae*.

Key to species of Brachistosternus *with patterns of distribution*

Andean species of this genus have a very uniform morphology, and in some cases they are very difficult to distinguish from each other, especially the females, which in certain species are almost indistinguishable. Because none of the extremely similar species occur in sympatry, the distribution data provided with this key should be useful to separate these species.

1 Pedipalp chela with four to six ventral trichobothria, pedipalp patella with two *Esb* trichobothria, chelicerae with two subdistal teeth, row of spines of the hemispermatophore, if present, contiguous with the basal spines (Fig. 3H). . . . . Subgenus *Brachistosternus* 2

1′ Pedipalp chela with 9–12 ventral trichobothria, pedipalp patella with one *Esb* trichobothrium, chelicerae with one subdistal tooth, row of spines of the hemispermatophore not contiguous with basal spines (Fig. 3F). . . . . Subgenus *Ministernus* 36

2 Pedipalp patella with 5–7 ventral trichobothria, cylindrical apophysis of hemispermatophore flattened (Fig. 3C,G). 3

2′ Pedipalp patella with 3–4 ventral trichobothria, cylindrical apophysis of hemispermatophore not flattened (Fig. 3H) 4

3 Pedipalp chela length/height ratio 2.67–3.09 in males, 2.79–3.03 in females, length/width ratio 3.23–3.86 in males, 3.38–3.78 in females. Basal denticle of median internal row of teeth on pedipalp chela strongly developed, two or three times larger than the rest (Pacific coastal desert, northern Chile and Southern and central Peru, up to 2000 m). . . . . *Brachistosternus (Brachistosternus) ehrenbergii*

3′ Pedipalp chela length/height ratio 3.25–3.39 in males, 2.92–3.08 in females, length/width ratio 3.94–4.32 in males, 3.84–3.93 in females; basal denticle of median internal row of teeth on pedipalp chela slightly larger than the rest (Pacific coastal desert, northern Peru, Southern Ecuador) . . . . *Brachistosternus (B.) pegnai*

4 Pedipalp patella with four ventral trichobothria, pedipalp chela with six ventral trichobothria, posterior margin of the vesicle of telson almost straight (Fig. 5J) (Central western Argentina, in northern Mendoza and southern San Juan provinces, exclusively in dunes) . . . . *Brachistosternus (B.) telteca*

4′ Pedipalp patella with three ventral trichobothria, pedipalp chela with four or five ventral trichobothria, posterior margin of the telson curved (Fig. 5I) 5

5 Pedipalp chela with four ventral trichobothria (Southern Argentinean Patagonia, in Santa Cruz province). . . . . *Brachistosternus (B.) paulae*

5′ Pedipalp chela with five ventral trichobothria. 6

6 Basal triangle and row of spines of hemispermatophore absent. 7

6′ Basal triangle and row of spines of hemispermatophore present (Fig. 3H) 8

7 Metasomal segment V, VM carina present in posterior half of segment; androvestigia absent (Northern Chile, in Atacama region, exclusively in dunes) . . . .*Brachistosternus (B.) sciosciae*

7′ Metasomal segment V, VM carina extending the entire length of segment; androvestigia small (Northern Chile, in northern Coquimbo region, in coastal dunes . . . . *Brachistosternus (B.) cepedai*

8 Distal lamina of the hemispermatophore narrow, strongly curved on its median part, basal spines poorly developed or vestigial (Bolivian central Andes, in Oruro department, between 4300 and 4500 m, restricted to areas where the substratum is volcanic sand) . . . . *Brachistosternus (B.) galianoae*

8′ Distal lamina of hemispermatophore slightly curved or straight, basal spines well developed. 9

9 Pedipalp femur with two macrosetae associated with *d* and *e* trichobothria 10

9′ Pedipalp femur with one macroseta associated with *d* and *e* trichobothria (Fig. 4H) 11

10 Metasomal segments I–IV, ventral surface with pair of VSM stripes (Fig. S3G); segment V of males with very large androvestigia, occupying > 50% of dorsal surface (Fig. S3C) (Central Chile, in northern Valparaiso and Southern Coquimbo regions, arid environments near the coast). . . . . *Brachistosternus (B.) chango*

10′ Metasomal segments I–IV, ventral surface with single VM stripe (Fig. S3E,F); segment V of males with medium-sized androvestigia, occupying < 50% of dorsal surface (Fig. S3B) (Northern Chile, in Coquimbo region, near the coast, in diverse arid environments, occasionally in dunes) . . . .*Brachistosternus (B.) artigasi*

11 Androvestigia occupying almost the entire dorsal surface of metasomal segment V (Fig. S3C), distal lobe of hemispermatophore very well developed reaching the median part of the distal lamina, basal triangle elongated (Northern Chile, in Antofagasta, Atacama and Coquimbo regions, in diverse arid environments, occasionally in dunes). . . . .
. . . .*Brachistosternus* (B.) *roigalsinai*

11′ Androvestigia always small (Fig. S3A) to medium-sized (Fig. S3B), occupying < 60% of dorsal surface of metasomal segment V, distal lobe of hemispermatophore poorly developed, occupying less than a quarter of the distal lamina, basal triangle not elongated 12

12 Ventral surface of metasomal segments I–IV with two VSM and two VL stripes (Fig. S3G). 13

12′ Ventral surface of metasomal segments I–IV without VSM stripes. 14

13 Metasomal segment V, VM carina extending through entire length of segment (Fig. 5D) (Northern Chile, Coquimbo region, in diverse arid environments, sometimes in dunes) . . . . *Brachistosternus (B.) cekalovici*

13′ Metasomal segment V, VM carina absent (Fig. 5E) (Central and Southern Chile, in Santiago, Maule and Bio-Bio regions, in grasslands, and in open areas in woods) . . . .*Brachistosternus (B.) negrei*

14 Telotarsal median dorsal lobe of leg IV elongated (Fig. 5C) (Central Argentina, in Mendoza and San Juan provinces, and in southern Buenos Aires province, exclusively in dunes) . . . .*Brachistosternus (B.) multidentatus*

14′ Telotarsal median dorsal lobe of leg IV not elongated (Fig. 5A) 15

15 Metasomal segment V with 18 or more ventral macrosetae 16

15′ Metasomal segment V with 17 or fewer ventral macrosetae 17

16 Metasomal segment V, VM carina absent (Fig. 5E); telson gland well developed, divided into separate halves (Fig. 5F) (Chilean central Andes, in Coquimbo region, between 3000 and 3600 m) . . . . *Brachistosternus (B.) perettii*

16′ Metasomal segment V, VM carina only present on posterior half of segment; telson gland poorly developed, not divided into separate halves (Chilean Northern Andes, in Antofagasta region, between 2800 and 3200 m) . . . .
. . . .*Brachistosternus (B.) prendinii*

17 Telson with four granules conspicuously more developed than the rest (Fig. 5I) (Central and north Western Argentina, in Mendoza, San Juan, La Rioja, Catamarca, Tucumán and Salta provinces, between 600 and 2900 m, in diverse arid environments) . . . .*Brachistosternus (B.) weijenberghi*

17′ Telson with all granules of similar size 18

18 Hemispermatophore with internal spines (Fig. 3H). 19

18′ Hemispermatophore without internal spines (Fig. 3G) 26

19 Androvestigia medium-sized, not elongated (Fig. S3B) 20

19′ Androvestigia narrow, elongated (Fig. S3D). 21

20 Metasoma unpigmented; tergites unpigmented or with lateral margins faintly spotted, VM carina of metasomal segment V extending through entire length of segment (Fig. 5D) (Northern Chile, in Tarapacá region, in arid environments, most usually in areas of woods of *Prosopis tamarugo* Philippi) . . . . *Brachistosternus (B.) donosoi*

20′ Metasoma with single VM stripe and a pair of VL stripes, at least on segments III–V; tergites I–VI with transverse stripe, or three dark spots; VM carina of metasomal segment V restricted to second half of segment (Northern Chile, in Atacama

and Coquimbo regions, in arid environments, most usually in areas of Lomas biotope) . . . . *Brachistosternus (B.) kamanchaca*

21 Metasomal segment IV densely granular (male), slightly granular (female) 22

21′ Metasomal segment IV smooth or slightly granular (male), smooth (female) 24

22 Tergites I–IV and carapace unpigmented, or with lateral margins faintly spotted; internal spines of hemispermatophore well developed and divided in two groups (Northern Chile, in Antofagasta region, in coastal arid environments) . . . . *Brachistosternus (B.) mattonii*

22′ Tergites I–IV and carapace densely pigmented; internal spines of hemispermatophore poorly developed 23

23 Metasomal segment V with single VM stripe and a pair of VL stripes, carapace densely pigmented, with unpigmented triangle from ocular tubercle to the anterior margin (Northern Chile, in Atacama region, in diverse coastal arid environments). . . . .*Brachistosternus (B.) ochoai*

23′ Metasoma unpigmented, carapace completely pigmented . . . . *Brachistosternus (B.) turpuq*

24 VM carina of metasomal segment V poorly developed, almost indistinguishable; total length 30–43 mm (Argentinean central and northern Patagonia, in Chubut, Río Negro, and Neuquén provinces). . . . . *Brachistosternus (B.) alienus*

24′ VM carina of metasomal segment V extending through entire length of segment, well developed, total length 45–90 mm 25

25 Length/height ratio of pedipalp chela 2.91–3.43 in males, 2.80–3.20 in females, ventral setae of meosomal segment V usually arranged in two rows of two setae each (Central and northern Argentina, in Monte and Espinal biogeographical provinces, in very diverse arid environments (from coastal dunes to dry woods of *Prosopis*); in Buenos Aires, La Pampa, Mendoza, San Juan, San Luis, La Rioja, Catamarca, and Salta Provinces; from sea level to 2000 m) . . . . *Brachistosternus (B.) pentheri*

25′ Length/height ratio of the pedipalp chela 3.47–4.14 in males, 3.40–3.63 in females, ventral setae of metasomal segment V usually arranged in two to five rows, basal row with four setae, the rest with two setae each (Argentinean central and northern Patagonia, in Chubut, Río Negro, and Neuquén provinces) . . . .*Brachistosternus (B.) angustimanus*

26 Carapace, tergites and metasoma unpigmented. Basitarsi I and II, prolateral pedal spurs vestigial or absent (Fig. 5A) (Northern Argentina, in Catamarca and Salta provinces, exclusively in dunes of the 'Valles Calchaquies', between 1500–2000 m). . . . . *Brachistosternus (B.) zambrunoi*

26′ Carapace, tergites and metasoma densely pigmented. Basitarsi I and II prolateral pedal spurs well developed, equal to retrolateral pedal spur (Fig. 5B,C). 27

27 Telson of males without glands (Central Chile, in Valparaiso and Metropolitana regions) . . . .*Brachistosternus (B.) chilensis*

27′ Telson of males with glands 28

28 VM stripe of metasoma joining with the VL stripes in all segments (Fig. S3F) 29

28′ VM stripe of metasoma not joining with the VL stripes at least on metasomal segments I–III (Fig. S3E) 32

29 Metasomal segment V without VM carina (Fig. 5E) (Central Chilean Andes, (Valparaiso region), between 1600 and 2100 m). . . . .*Brachistosternus (B.) aconcagua*

29′ Metasomal segment V with a well developed VM carina extending through entire length of segment (Fig. S3D). 30

30 Distal lamina of hemispermatophore almost straight, metasomal segment V with 4–9 ventral setae (Southern Peruvian Andes, (Arequipa and Tacna departments), between 2900 and 4000 m) . . . . *Brachistosternus (B.) ninapo*

30′ Distal lamina of hemispermatophore slightly curved, metasomal segment V with 10–17 ventral setae. 31

31 Pedipalp chela length/width ratio 4.70–5.09 in males, 4.33 in the only studied female (Chilean central Andes, (Coquimbo region), between 2850 and 3000 m) . . . . *Brachistosternus (B.) coquimbo*

31′ Pedipalp chela length/width 3.70–3.90 in males, 3.80–4.50 in females (Andean sector of Northern Chile (Tarapacá region) and southern Peru (Tacna department); between 2800 and 3400 m). . . . . *Brachistosternus (B.) quiscapata*

32 Metasomal segment V, length/width ratio 1.50–1.65 33

32′ Metasomal segment V, length/width ratio 1.70–1.95 34

33 VM stripe of metasoma only joining with the VL stripes in metasomal segment V; 7–8 dorsal setae on telotarsus III (Andean sector of central Bolivia (La Paz departamatent) and southern Peru (Puno department), in the Titicaca plateau; between 3800 and 4200 m). . . . . *Brachistosternus (B.) titicaca*

33' VM stripe of metasoma not joining with the VL stripes; 9–10 dorsal setae on telotarsus III (Andean sector of southern Bolivia (Oruro, Chuquisaca and Potosí Departments) and northern Argentina (Catamarca, Tucumán, Salta and Jujuy Provinces), between 2500 and 4000 m). . . . . *Brachistosternus (B.) intermedius*

34 Pedipalp chela length/width ratio 4–4.37 in males, 3.90–4.16 in females (Argentinean central Andes, (Mendoza and San Juan Provinces), between 2700 and 3500 m) . . . . *Brachistosternus (B.) montanus*

34' Pedipalp chela length/width ratio 3.46–3.88 in males, 3.59–3.95 in females. 35

35 Length/width ratio of metasomal segment V 1.70–1.80, androvestigia very small, occupying less than a third of dorsal surface of metasomal segment V, distal lamina of hemispermatophore broad, shorter than the basal portion, VM carina of metasomal segment V restricted to the second half of the segment (Andean sector of Central Bolivia (Oruro department) and Northern Chile (Tarapacá region), between 4000 and 4500 m) . . . .*Brachistosternus (B.) piacentinii*

35' Length/width ratio of metasomal segment V 1.80–1.95, androvestigia medium-sized, occupying almost a half of the dorsal surface of metasomal segment V, distal lamina of the hemispermatophore narrow, similar in size to the basal portion, VM carina of metasomal segment V extending through entire length of the segment (Chilean northern Andes, (Antofagasta region), between 3200 and 3600 m) . . . . *Brachistosternus (B.) kovariki*

36 Basal triangle of hemispermatophore with sclerified crests (as in most species of subgenus *Brachistosternus*, Fig. 3G–H) (Central and northern Argentina, Paraguay, South western Bolivia, and probably southern Brazil) . . . . *Brachistosternus (M.) ferrugineus*

36' Basal triangle of hemispermatophore with small spines (Fig. 3F) 37

37 Cylindrical apophysis of hemispermatophore slightly curved, longer than the laminar apophysis (Fig. 3B) (Peruvian Southern Andes, in Apurimac, (Cusco and Ayacucho departments); between 1900 and 2700 m) . . . . *Brachistosternus (M.) peruvianus*

37' Cylindrical apophysis of hemispermatophore almost straight, similar in size to laminar apophysis (Fig. 3A) (Peruvian Southern Andes, (Cusco department), between 2700 and 3400 m) . . . .*Brachistosternus (M.) andinus*

References

Acosta, L. E. & Maury, E. A. (1998). Scorpiones. In J. J. Morrone & S. Coscaron (Eds) *Biodiversidad de Artrópodos Argentinos* (pp. 545–559). Argentina: La Plata.

Agusto, P. C., Mattoni, I., Pizarro-Araya, J., Cepeda-Pizarro, J. & López-Cortes, F. (2006). Comunidades de escorpiones (Arácnida. Scorpiones) del desierto costero transicional de Chile. *Revista Chilena de Historia Natural*, *79*, 407–421.

Bremer, K. (1994). Branch support and tree stability. *Cladistics*, *10*, 295–304.

Bücherl, W. (1959). Escorpiones e escorpionismo no Brasil. X. Cátalogo da coleção escorpionica do Instituto Butantan. *Memórias Do Instituto Butantan*, *29*, 255–275.

Cabrera, A. L. & Willink, A. (1980). *Biogeografía de América Latina. Monografía 13*. Washington D.C.: Serie Biología. Organización de Estados Americanos.

Carbonell, J. J. (1923). Una nueva especie de escorpión. *Physis*, *6*, 358–359.

Cekalovic, K. T. (1969). *Brachistosternus pegnai* n. sp. de escorpión para el Ecuador (Scorpionida-Bothriuridae). *Boletín de la Sociedad Biológica de Concepción*, *41*, 163–171.

Cekalovic, K. T. (1973a). Nuevo carácter sexual secundario en los machos de *Brachistosternus* (Scorpiones, Bothriuridae). *Boletín de la Sociedad de Biología de Concepción*, *46*, 99–102.

Cekalovic, K. T. (1973b). *Tehuankea moyanoi* n. gen y n. sp. de escorpión chileno (Scorpiones: Bothriuridae). *Boletín de la Sociedad Biológica de Concepción*, *46*, 41–51.

Cekalovic, K. T. (1974). Dos nuevas especies del género *Brachistosternus* (Scorpiones, Bothriuridae). *Boletín de la Sociedad Biológica de Concepción*, *47*, 247–257.

Cekalovic, K. T. (1975). *Brachistosternus (Leptosternus) negrei* n. sp. de escorpión de Chile (Scorpiones, Bothriuridae). *Brenesia*, *6*, 69–75.

Chamberlin, R. V. (1916). Results of the Yale Peruvian expedition of 1911. The Arachnida. *Bulletin of the Museum of Comparative Zoology*, *60*, 177–299.

Francke, O. (1985). *Conspectus genericus scorpionorum*. 1758–1982 (Arachnida. Scorpiones). *Occasional Papers, Museum of Texas Tech. University*, *98*, 1–32.

Gervais, P. M. (1841). Arachnides. In Eydoux, Souleyet (Eds) *Voyage autour du monde exécuté pendant les annés 1836 et 1837 sur la corvette La Bonite, commandée par M. Vaillant*. Publié par ordre du roi sous les auspices du Département de la Marine. Zoologie. Apteres. Paris. Arthus Bertrand, 281–285.

Giribet, G. (2003). Stability in phylogentic formulations and its relationtshp with nodal support. *Systematic Biology*, *52*, 554–564.

Goloboff, P. A. (1993). Estimating character weigting during tree search. *Cladistics*, *9*, 83–91.

Goloboff, P. A. (1997). Self-weighted optimization: character state reconstructions and tree searches under implied transformation costs. *Cladistics*, *13*, 225–245.

Goloboff, P. A., Farris, J. S., Källersjö, M., Oxelman, B., Ramírez, M. J. & Szumik, C. (2003). Improvements to resampling measures of group support. *Cladistics*, *19*, 324–332.

Goloboff, P. A., Farris, J. & Nixon, K. (2003–2006). TNT*: Tree Analysis Using New Technology*. Program and documentation avaliable from the authors at <www.zmuc.dk/public/phylogeny>.

Goloboff, P. A., Carpenter, J. M., Arias, J. S. & Miranda Esquivel, D. R. (2008). Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, *24*, 1–16.

Kraepelin, K. (1911). Neue Beiträge zur Systematik der Gliederspinnen. *Mitteilungen aus dem Naturhistorischen Museum* (2, Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 1910), *28*, 59–107.

Lewis, G. (1887). On the new genus of Erotyilidae. *Entomologist's Monthly Magazine*, *24*, 3.

Lipscomb, D. L. (1992). Parsimony, homology and the analyisis of multistate characters. *Cladistics*, *8*, 45–65.

Lönnberg, E. (1898). On the scorpions obtained during the Swedish expedition to Tierra del Fuego 1895. *Svenska Expeditionen Till Magelländersna*, *2*, 45–48.

Lönnberg, E. (1902). On some scorpions collected in northwestern Argentina and Bolivia by Baron Erland Nordenskiöld. *Entomologisk Tidskrift*, *23*, 253–256.

Lopardo, L. (2005). A phylogenetic revision of the spider genus *Negayan* (Aranae, Anyphaenidae, Amaurobioidinae). *Zoologica Scripta*, *34*, 245–277.

Lourenço, W. R. (2000). Confirmation de la présence de genre *Brachistosternu*s Pocock (Scorpiones, Bothriuridae) au Brésil et description d'une espèce nouvelle. *Revue Arachnologique*, *13*(6), 93–100.

Lowe, G. & Fet, V. (2000). Family bothriuridae simon, 1880. In V. Fet, W. D. Sissom, G. Lowe & M. E. Braunwalder (Eds) *Catalog of the Scorpions of the World (1758–1998)* (pp. 17–53). New York: New York Entomological Society.

Maury, E. A. (1973a). Essai d'une classification des sous familles de scorpions Bothriuridae. *5th International Congress of Arachnology. Brno*, *1971*, 29–36.

Maury, E. A. (1973b). Las tricobotrias y su importancia en la sistemática del género *Brachistosternus* Pocock, 1893 (Scorpiones, Bothriuridae). *Physis (Buenos Aires) C*, *32*, 247–254.

Maury, E. A. (1974). Escorpiofauna Chaqueña. 1. La verdadera identidad de *Brachistosternus* (*Microsternus*) *ferrugineus* (Thorell 1876) (Bothriuridae). *Physis (Buenos Aires), Sec. C*, *33*, 73–84.

Maury, E. A. (1978). Escorpiones y escorpionismo en el Perú. VII: nuevos hallazgos y redescripción de *Brachistosternus (Microsternus) andinus* Chamberlin, 1916 (Bothriuridae). *Revista Peruana de Entomología*, *21*, 23–26.

Maury, E. A. (1979). Apuntes para una zoogeografía de la escorpiofauna argentina. *Acta Zoológica Lilloana*, *35*, 703–719.

Maury, E. A. (1984). Una nueva especie de *Brachistosternus* de la Argentina (Scorpiones, Bothriuridae). *Revista de la Sociedad Entomológica Argentina 41*, 113–118.

Mello-Leitão, C. de. (1931). Notas sôbre os Bothriuridae Sul-Americanos. *Arquivos Do Museu Nacional*, *33*, 75–105.

Mello-Leitão, C. de. (1940). Arácnidos de Copiapó (Atacama) y Casablanca. *Revista Chilena de Historia Natura*, *44*, 231–235.

Mello-Leitão, C. de. (1945). Escorpioes sul-americanos. *Arquivos Do Museu Nacional*, *40*, 7–468.

Nixon, K. C. (1999a). The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, *15*, 407–414.

Nixon, K. C. (1999b). WINCLADA. Published by the author, Ithaca, NY (v. 1.00.04). Available at <http://www.cladistics.com/about_winc.htm>.

Ochoa, J. A. (2002). Nueva especie de *Brachistosternus* Pocock (Scorpiones. Bothriuridae) del sur del Perú. *Revista Peruana de Biologia*, *9*, 55–63.

Ochoa, J. A. (2004). *Brachistosternus ninapo* una nueva especie (Scorpiones: Bothriuridae) de los Andes occidentales en el sur del Perú. *Revista Peruana de Biología*, *11*, 139–148.

Ochoa, J. A. (2005). Patrones de distribucion de escorpiones de la región andina en el sur peruano. *Revista Peruana de Biologia*, *12*, 49–68.

Ochoa, J. A. & Ojanguren-Afflastro, A. A. (2007). Systematics and distribution of *Brachistosternus (Brachistosternus) ehrenbergii* (Gervais, 1841) with the first record of stridulation in this genus *Brachistosternus* (Scorpiones. Bothriuridae). *Studies on Neotropical Fauna and Environment*, *41*, 79–85.

Ochoa, J. A. & Acosta, L. E. (2002). Two new Andean species of *Brachistosternus* Pocock (Scorpiones. Bothriuridae). *Euscorpius*, *2*, 1–13.

Ojanguren-Afflastro, A. A. (2000). *Brachistosternus telteca* (Scorpiones, Bothriuridae), una nueva especie de la República Argentina. *Revista Del Museo Argentino de Ciencias Naturales*, *2*, 157–160.

Ojanguren-Afflastro, A. A. (2001). Sistemática y distribución de *Brachistosternus alienus* Lönnberg (Scorpiones, Bothriuridae). *Revista Del Museo Argentino de Ciencias Naturales*, *3*, 169–174.

Ojanguren-Afflastro, A. A. (2002a). Aportes al conocimiento del género *Brachistosternus* en Chile, con la descripción de dos nuevas especies (Scorpiones, Bothriuridae). *Boletín de la Sociedad de Biología de Concepción*, *73*, 37–46.

Ojanguren-Afflastro, A. A. (2002b). *Brachistosternus zambrunoi*, una nueva especie del noroeste argentino (Scorpiones, Bothriuridae). *Revista Ibérica de Aracnología*, *5*, 33–38.

Ojanguren-Afflastro, A. A. (2002c). *Brachistosternus galianoae* una nueva especie de Bolivia. *Revista del Museo Argentino de Ciencias Naturales*, *4*, 105–109.

Ojanguren-Afflastro, A. A. (2002d). Sistemática y distribución de *Brachistosternus weyenberghi* Thorell. *Revista del Museo Argentino de Ciencias Naturales*, *4*, 203–208.

Ojanguren-Afflastro, A. A. (2003a). The genus *Brachistosternus*. Argentina, with the description of a new species from Patagonia (Scorpiones, Bothriuridae). *Journal of Arachnology*, *31*, 317–331.

Ojanguren-Afflastro, A. A. (2003b). Las especies andinas de *Brachistosternus (Leptosternus)*, con la descripción de tres nuevas especies (Scorpiones, Bothriuridae). *Revista Ibérica de Aracnología*, *8*, 23–36.

Ojanguren-Affilastro, A. A. (2004a). Sistemática y distribución de *Brachistosternus (Leptosternus) intermedius* Lönnberg (Scorpiones, Bothriuridae). *Physis, (Buenos Aires), Sec. C, 59*, 29–35.

Ojanguren-Affilastro, A. A. (2004b). Un nuevo *Brachistosternus* Pocock 1893 del norte de Chile (Scorpiones, Bothriuridae). *Revista Ibérica de Aracnología, 10*, 69–74.

Ojanguren-Affilastro, A. A. (2005a). Notes on the genus *Brachistosternus* (Scorpiones, Bothriuridae) in Chile, with the description of two new species. *Journal of Arachnology, 33*, 175–192.

Ojanguren-Affilastro, A. A. (2005b). Estudio monográfico de los escorpiones de la República Argentina. *Revista Ibérica de Aracnología, 11*, 75–241.

Ojanguren-Affilastro, A. A. & Mattoni, C. I. (2006). A new species of *Brachistosternus* from Chilean central Andes (Scorpiones. Bothriuridae). *Studies on Neotropical Fauna and Environment, 41*, 79–85.

Ojanguren-Affilastro, A. A. & Roig Alsina, A. (2001). *Brachistosternus angustimanus*, una nueva especie del norte de la Patagonia, Argentina (Scorpiones, Bothriuridae). *Physis, (Buenos Aires), Sec. C, 58*, 15–22.

Ojanguren-Affilastro, A. A. & Scioscia, C. L. (2007). New data about genus *Brachistosternus* in Chile (Scorpiones: Bothriuridae). *Journal of Arachnology, 35*, 102–113.

Ojanguren-Affilastro, A. A., Mattoni, C. I. & Prendini, L. (2007a). The genus *Brachistosternus*. Chile (Scorpiones: Bothriuridae), with the description of two new species. *American Museum Novitates, 3564*, 1–44.

Ojanguren-Affilastro, A. A., Agusto, P., Pizarro Araya, J. & C. I. Mattoni (2007b). Two new scorpion species of genus *Brachistosternus* (Scorpiones: Bothriuridae) from northern Chile. *Zootaxa, 1623*, 55–68.

Pocock, R. I. (1893). Contributions to our knowledge of the arthropod fauna of the West Indies. Part. I. Scorpiones and Pedipalpi, with a supplementary note about the freshwater Decapoda of St. Vincent. *Journal of the Linnean Society, 24*, 374–409.

Prendini, L. (2000). Phylogeny and classification of the superfamily Scorpionoidea Latrielle 1802 (Chelicerata, Scorpiones). an exemplar approach. *Cladistics, 16*, 1–78.

Prendini, L. (2001). Substratum specialization and speciation in southern African scorpions. The Effect Hypothesis revisited. In V. Fet & P. A. Selden (Eds), Scorpions 2001. In *Memoriam* Gary A. Polis. (pp. 113–138). Burnham Beeches, UK: British Arachnological Society.

Prendini, L. (2003). A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology, 28*, 149–172.

Prendini, L., Crowe, T. M. & Wheeler, W. C. (2003). Systematics and biogeography of the family Scorpionidae Latreille, with a discussion of phylogenetic methods. *Invertebrate Systematics, 17*, 185–259.

Ramírez, M. J. (2003). The spider subfamily Amaurobioidinae (Aranae, Anyphaenidae): a phylogenetic revision at generic level. *Bulletin of the American Museum of Natural History 277*, 1–262.

Roig-Alsina, A. H. (1977). Una nueva especie de escorpión andino en Mendoza, República Argentina. *Physis (Buenos Aires) C, 37*, 255–259.

Roig-Alsina, A. H. & Maury, E. A. (1981). Consideraciones sistemáticas y ecológicas sobre *Brachistosternus (Leptosternus) borellii* Kraepelin, (1911). (Scorpiones, Bothriuridae). *Physis (Buenos Aires), Sec. C, 39*, 1–9.

Roig-Alsina, A. H. & Maury, E. A. (1984). Sistemática y distribución geográfica de *Brachistosternus (L.) pentheri* Mello-Leitão, (1931). (Scorpiones, Bothriuridae). *Physis (Buenos Aires), Sec. C, 42*, 17–21.

San Martín, P. R. (1969). Estudio sobre la compleja estructura del esqueleto esclerificado del órgano paraxial del género *Brachistosternus* (Bothriuridae. Scorpionida). *Boletín de la Sociedad Biológica de Concepción, 41*, 13–30.

Stahnke, H. L. (1970). Scorpion nomenclature and mensuration. *Entomological News, 83*, 121–133.

Thorell, T. (1876). Études corpiologiques. *Atti Della Società Italiana Di Scienze Naturali, 19*, 75–272.

Toledo Piza, Jr S. de. (1974). A new Scorpion from Peru. (Bothriuridae) *Revista de Agricultura, 49*, 155–156.

Vachon, M. (1973) [1974]. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. *Bulletin du Muséum national d'histoire naturelle (Paris), Series, 3*, 857–958.

Yamaguti, Y. H. & Pinto Da Rocha, R. (2003). Taxonomic review of the genus *Thestylus* Simon (1880) (Scorpiones, Bothriuridae). *Revista Ibérica de Aracnología, 7*, 157–171.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Character statistics through character systems from the cladistic analysis, calculated from optimal trees under implied weights with concavity value $K = 6$. All characters have the same statistics on any of the four optimal trees. —A. Consistency index (CI). —B. Retention index (RI). Black bars are individual values for each character; white bars are averages for character systems, excluding uninformative characters.

Fig. S2 —A. Consensus of 40 trees obtained under equal weights. —B. Single tree obtained under implied weighting with $K = 6$, considering all characters as non additive. —C. Consensus of 40 trees obtained under equal weights, considering all characters as non additive.

Fig. S3 —A. *Brachistosternus cekalovici* Ojanguren-Affilastro 2005, metasomal segment V, male, dorsal aspect, showing the androvestigia. —B. *Brachistosternus kamanchaca* Ojanguren-Affilastro *et al.* 2007a, metasomal segment V, male, dorsal aspect, showing the androvestigia. —C. *Brachistosternus chango* Ojanguren-Affilastro *et al.* 2007a, metasomal segment V, male, dorsal aspect, showing the androvestigia. —D. *Brachistosternus mattonii* Ojanguren-Affilastro 2005, metasomal segment V, male, dorsal aspect, showing the androvestigia. —E. *Brachistosternus chilensis* Kraepelin 1911, metasoma, pigmentation pattern, ventral aspect. —F. *Brachistosternus aconcagua* Ojanguren-Affilastro & Scioscia 2007, metasoma,

pigmentation pattern, ventral aspect. —G. *Brachistosternus negrei* Cekalovic 1975, metasoma, pigmentation pattern, ventral aspect. Scale bars = 1 mm. Abbreviation: AV, androvestigia.

Fig. S4 Approximate distribution of *Brachistosternus* subgenera and main species groups in South America. —A. Subgenus *Brachistosternus*, with the distribution of the Andean and Plains groups of species. —B. Subgenus *Ministernus*.

Table S1 List of species of *Brachistosternus* and descriptive references.

Appendix S1 Characters used in the cladistic analysis.

Appendix S2 Data matrix.

Appendix S3 List of studied specimens, collections and collection numbers.

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