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Systematic revision, cladistics and biogeography of the genus *Neogutierrezia* Martínez (Coleoptera : Scarabaeidae) and its phylogenetic placement in Rutelinae based on structural alignment of 28S rDNA sequences

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Abstract. The Argentinean endemic genus *Neogutierrezia* Martínez, 1953 (Scarabaeidae : Rutelinae) is revised and seven new species are described: *N. bicolor* Ocampo & Ruiz-Manzanos, sp. nov., *N. chelii* Ocampo & Ruiz-Manzanos, sp. nov., *N. galileoi* Ocampo & Ruiz-Manzanos, sp. nov., *N. lagosae* Ocampo & Ruiz-Manzanos, sp. nov., *N. payuniensis* Ocampo & Ruiz-Manzanos, sp. nov., *N. scutata* Ocampo & Ruiz-Manzanos, sp. nov. and *N. variabilis* Ocampo & Ruiz-Manzanos, sp. nov. Species status is proposed for *N. affinis* Martínez stat. nov., which was formerly considered as subspecies of *N. mirabilis* Martínez. The genus *Neogutierrezia* now includes 10 species distributed in the Monte biogeographic province in Argentina. In order to clarify the systematic placement of the genus *Neogutierrezia*, a molecular phylogenetic analysis was performed using structurally aligned 28S rDNA sequences (expansion segments D2 and D3) from 23 taxa in Scarabaeoidea, including two representative species of *Neogutierrezia*. This is the first report of an annotated secondary structure alignment of the D2 and D3 segments of 28S rRNA that spans a wide sample of scarabaeoids, providing a useful homology template for further phylogenetic reconstruction in these and closely related beetles. Results of the molecular parsimony analysis strongly indicate that the genus is closely related to members of the Rutelinae (Scarabaeidae), and thus *Neogutierrezia* Martínez is transferred from Melolonthinae: Pachydemini to Rutelinae, new placement. A morphological cladistic analysis of the genus was also undertaken, including all the 10 known species in the genus plus two outgroup taxa in Rutelinae, and based on 53 adult characters. The most-parsimonious cladogram provides evidence for the monophyly of the genus, which shows three main clades, distributed in Central Monte and Southern Monte. The adult morphology of the 10 species is described and a key is provided, along with illustrations of the diagnostic characters. The biogeography of species in the genus is discussed.

Introduction

The tribe Pachydemini (as was defined by Lacroix 2007; Evans 2003) is classified in the Melolonthinae (Scarabaeidae) and includes 118 genera and nearly 570 valid species worldwide. They are distributed in all major biogeographic regions except India and Australia. In the Neotropics, the group is currently represented by 18 genera and 31 species without *Neogutierrezia* that is no more a Pachydemini but it is fair to assume that the group is more diverse, as recent taxonomic explorations resulted in new taxa discoveries (Ocampo and Smith 2006; Ocampo and Ruiz-Manzanos 2007). Neotropical scarabs currently placed in the tribe Pachydemini are mainly distributed in the Monte, Chacoan, Central Chile and Patagonian biogeographic provinces and most species are highly adapted to live in xeric conditions. The classification of the pachydemines is confused and taxonomic foundation to assign species to this group is weak (Sanmartín and Martín–Piera 2003), moreover, there is increasing evidence that the current concept of the tribe is polyphyletic (Evans 1988; Ruiz-Manzanos and Ocampo, unpubl. data). In most cases, genera are identified based on male external morphology and very few specimens, thus a solid basis for intrageneric variation and circumscription of genera is lacking. Females are rarely collected and are known for only a few species (10 species in the New World genera) and many genera present strong sexual dimorphism. A review of the Neotropical Pachydemini (*sensu lato*) is in progress (Ruiz-Manzanos and Ocampo, unpubl. data).

The genus *Neogutierrezia* Martínez 1953 was originally described for a single species, *Neogutierrezia mirabilis* Martínez 1953, from Río Negro Province in Argentina. Martínez placed the genus in the tribe Pachydemini (Scarabaeidae : Melolonthinae), indicating that *Neogutierrezia* is morphologicaly similar to *Acylochilus* Ohaus (Melolonthinae : Pachydemini), 'although very different from all other Pachydemini genera' (Martínez 1953). Later, Martínez (1973) provided a more detailed description of the genus and described a subspecies of *N. mirabilis*, *N. mirabilis affinis* Martínez, from the Atlantic coast of Río Negro province and a second species, *N. araucana* Martínez, from Neuquén province. In the same publication, Martínez provided a key to species and subspecies, illustrations of diagnostic characters and information about their biology. Martínez (1973) provided the description of

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the female of *N. araucana* based on two specimens. These are the only known female specimens of the genus. Martínez (1975) included *Neogutierrezia* in a key to genera of Neotropical Pachydemini.

The genus *Neogutierrezia* was later listed in catalogues by Evans (2003), Lacroix (2007, 2008) and Evans and Smith (2009).

The unusual external morphology of the genus *Neogutierrezia* makes it one of the most intriguing 'Pachydemini' taxa and has lead to classification problems. On the other hand, its peculiar morphology serves to characterise the genus and its species and supports the hypothesis of monophyly (hypothesis tested in this contribution). Species in this genus do not resemble any of the known taxa described in the tribe including the nominotypical genus, *Pachydema* Castelnau. Additionally, the genus *Neogutierrezia* does not clearly fit in any of the known phytophagous scarab subfamilies as they are currently defined (i.e. Melolonthinae, Dynastinae, Rutelinae and Cetoniinae). Characters that are traditionally used to define phytophagous scarab subfamilies are from the apex of the 5th tarsomere, tarsal claws, mandibles, antennal insertion, tibial spurs and male genitalia (based on Jameson and Ratcliffe 2002). In part, uncertainties of the classification of *Neogutierrezia* are linked with the lack of a natural classification for the Scarabaeidae and circumscription of monophyletic lineages (subfamilies, tribes, genera, etc.). The most recent studies suggest that the subfamily Melolonthinae (*sensu* Lawrence and Newton 1995; Ratcliffe *et al*. 2002; Ocampo and Ruiz-Manzanos 2008) is not a clade but a grade (Smith *et al*. 2006). On the other hand, there is morphological and molecular evidence that supports the close relationship between Dynastinae and Rutelinae (Howden 1982; Browne and Scholtz 1998; Jameson 1998; Smith *et al*. 2006), although the relationships among tribes within these two subfamilies, as well as the set of morphological characters defining them, remain unclear (Jameson 1998; Smith *et al*. 2006).

The purpose of this contribution is to clarify the systematic placement of the genus *Neogutierrezia* by means of a modern phylogenetic analysis using molecular data (28S rDNA, segments D2 and D3) and in turn, provide an annotated structure alignment of these rDNA markers from a wide sample of scarab beetles, clarify the relationships among the species within the genus based on morphological evidence, to provide a comprehensive revision of the genus including the description of seven new taxa, provide an illustrated key to species and discuss their natural history and biogeography.

Materials and methods

Molecular phylogenetic analysis

Taxon sampling

A total of 23 scarabaeoid taxa were included as terminals (see Table 1): two species of *Neogutierrezia*, 16 representatives of other major groups of Scarabaeidae, plus five taxa in related families of Scarabaeoidea (Pleocomidae, Geotrupidae, Hybosoridae, Ochodaeidae and Glaphyridae). The sample includes representatives of phytophagous scarabs (Melolonthinae, Dynastinae, Rutelinae, Cetoniinae, Aclopinae, Orphninae, Allidiostomatinae and Pachypodinae).

Table 1. Taxa used for the molecular phylogenetic analysis and accession numbers of sequences

Family/subfamily/ species	Voucher number	Depository	GenBank number
Pleocomidae			
Pleocoma rubiginosa	S31	UCRC	FJ000407
Geotrupidae			
Eucanthus lazarus	S514	UCRC	FJ000406
Glaphyridae			
Glaphyrus superbus	S521	UCRC	GU226582
Hybosoridae			
Hybosorus illigeri	S13	UCRC	GU226583
Ochodaeidae			
Cucochodaeus sparsus	S08	UCRC	GU226584
Scarabaeidae			
Scarabaeinae			
Scarabaeus deludens	FO42	UNSM	GU226585
Aphodiinae			
Aphodius aegrotus	Sx1	UCRC	GU226586
Aclopinae			
Aclopus sp.	S333	IAZA	GU226587
Neophaenognatha jenseni	FO06	IAZA	GU226573
Allidiostomatinae			
Allidiostoma hirtum	FO08	IAZA	GU226588
Orphninae			
Orphnus sp.	S579	UCRC	GU226574
Pachypodinae			
Pachypus caesus	Sx	UCRC	GU226575
Melolonthinae			
Melolontha melolontha	S574	UCRC	GU226589
Phyllophaga sp.	Robertson *et al*. (2004)		AY310662
Acylochilus sp.	FO59	IAZA	GU226576
Puelchesia gracilis	AS118	IAZA	GU226577
Neogutierrezia chelii	FO61	IAZA	GU226578
Neogutierrezia scutata	AS119	IAZA	GU226579
Rutelinae			
Rutela sanguinolenta	Sx2	UCRC	GU226590
Anomala carlsoni	S229	UCRC	GU226580
Popilia japonica	S45	UCRC	GU226581
Dynastinae			
Dynastes granti	Sx3	UCRC	GU226591
Cetoniinae			
Cetonia carthami	S551	UCRC	GU226592

Characters

The rDNA regions used in this study include the D2 and D3 expansion segments of the 28S rRNA. The estimated length of the sequences used ranges from 810 to 825 nucleotides. The 28S-D2, D3 sequences were chosen because they are among the most commonly used markers in molecular phylogenetic studies of insects (Gillespie *et al*. 2006), being highly informative at different taxonomic levels (Marvaldi *et al*. 2009). Although the region is difficult to align because of length variation, the use of structure information of the gene to perform the alignment makes it most meaningful for phylogenetic analyses (see Marvaldi *et al*. 2009 for a recent example with Phytophaga and related beetles). Except for the sequences that were already available in GenBank, the new ones from this study were obtained following the protocols as in

Ocampo and Hawks (2006*a*, 2006*b*) for DNA extraction, PCR amplification and sequencing.

Alignment

The 28S rDNA sequences were aligned with reference to secondary structure, a method that allows the identification of homologous positions within length-heterogeneous segments and objective delimitation of regions of ambiguous alignment (Kjer 1995; Gillespie *et al*. 2004). Concepts and instructions on how to perform a structural alignment of RNA sequence data are available at http://hymenoptera.tamu.edu/rna/methods.php, verified 7 April 2010. This method uses a biological criterion (covariation) for assigning positional nucleotide homology in RNA datasets, resulting in delimitation of stems, loops and regions where alignment is ambiguous. Regions that cannot be unambiguously aligned across all taxa, are explicitly excluded (bracketed in the data matrix) from primary homology statements. Basically, the methodology of structure alignment uses information of established secondary structure models (Gutell *et al*. 1994; Gillespie *et al.* 2004, 2006: http://www.rna.ccbb.utexas.edu, verified 7 April 2010) to first perform the alignment of conserved regions of the rRNA (converted from the sequenced rDNA) sequences. To align the 28S-D2 sequences of this study, a previous coleoptera alignment (Marvaldi *et al*. 2009: http://hymenoptera.tamu.edu/rna/models/phyt/index.php, verified 7 April 2010) was used as a starting template. Similarly, the alignment of the D3 segment was done using the predicted secondary structural model proposed for leaf-beetles and *Tenebrio* sp. (Gillespie *et al*. 2004: http://hymenoptera.tamu.edu/rna/models/gal/index.php, verified 7 April 2010). Then, paired regions that were more variable among taxa were aligned by searching for compensatory base changes, considering that a single base change (mutation) on one strand of a stem is compensated for by a change on the other strand, to maintain structure and ensure that bases on partner strands are complementary (Gutell *et al*. 1994; Kjer 1995; Gillespie 2004; Gillespie *et al*. 2004). Evidence for secondary structure mainly comes from observation of covarying positions, indicated by hydrogen-bonding base pairs: Watson–Crick pairs (A ↔ U and G ↔ C) and also by G ↔ U (permitted in RNA). After recognition of paired (co-evolving) stems and highly conserved unpaired (single-stranded) regions, the interspersed regions of ambiguous alignment were delimited (Kjer 1995). Gaps were treated as in Kjer *et al*. (2001), using outgroup comparisons to distinguish between insertions and deletions. The 'ancestrally-missing' condition was considered a fifth state (coded with asterisks *) and gaps were treated as missing data when representing deletions in the ingroup. Gaps within the bracketed alignment ambiguous regions were inserted to retain columnar homology assignment in the unbracketed regions, but they do not represent homologous columns as in the unambiguously aligned regions. In addition to the methodology just described, the repeatability of our results is ensured by presentation of the alignment (see results).

Phylogenetic analysis

A parsimony analysis was performed with PAUP* 4.0b10 (Swofford 1998) and with TNT (Goloboff *et al*. 2003) using a heuristic search, 1000 random addition sequences and TBR branch swapping. Node support was evaluated by bootstraping as implemented by PAUP*, using the heuristic search option with 500 bootstrap replicates.

Morphological phylogenetic analysis of the genus Neogutierrezia

Sampling of taxa

All species of *Neogutierrezia*, including those recently discovered as new, were included in the analysis and treated as ingroup taxa. In order to test their status, *N. mirabilis* subspecies (*N. mirabilis affinis* and *N. mirabilis mirabilis)* were treated as terminal taxa. To test monophyly of the genus, the following outgroup taxa were also included as terminals: *Acylochilus ottianus* Ohaus, *A. curvidens* Ohaus, *Pseudoliogenys flavidus* Moser, *Myloxena bruchiana* Ohaus (Melolonthinae : Pachydemini) and *Rutela lineola* (Linnaeus) and *Anomala testaceipennis* Blanchard (Rutelinae : Rutelini and Anomalini respectively). The genera *Acylochilus* and *Pseudoliogenys* were hypothesised to be sister taxa to *Neogutierrezia* by Martínez (1953).

Data matrix and character analysis

The program Mesquite 2.5 (Maddison & Maddison 2008) was used to create the data matrix and for reconstruction of ancestral states and character evolution based on the tree topologies that resulted from the phylogenetic analysis.

Morphological characters used in the phylogenetic analysis

A total of 53 adult characters were used. Of these, 29 are binary and 24 are multistate characters (Table 2). All characters had equal weight and were treated as unordered, except characters 6, 31, 43–45 that were considered additive. Inapplicable data were coded as '–' (dash) in the matrix for the analysis and was used when the structure is not present on the species (Appendix 1).

Phylogenetic analysis of morphological data

Parsimony searches and node support values were calculated as in the analysis of molecular data.

Systematic revision

Definition of taxonomic characters and character examination

Internal and external adult morphological characters formed the basis of this work. Specimens were examined using a dissecting microscope (6.5–40×) and fibre-optic lights. For measurements, we used an ocular micrometer. Internal sclerotised structures were dissected by relaxing the specimen in hot water. Heavily-sclerotised parts were soaked in a dilute solution (~15%) of potassium hydroxide and neutralised in a dilute solution (~15%) of acetic acid. For dissected specimens, wings and genitalia were card-mounted or placed in a glycerin-filled vial beneath the specimen.

Table 2. List of characters and character states used for the phylogeny of *Neogutierrezia*

Head

(*1*) *Frons setae*: (0) present, very dense; (1) present, moderately dense; (2) present, sparse; (3) glabrous

(*2*) *Frons surface*: (0) punctate; (1) rugopunctate; (2) rugose

(*3*) *Frontoclypeal suture, shape*: (0) complete, straight; (1) complete, convex towards apex (Fig. 6*A*); (2) incomplete, convex towards apex (Fig. 13*A*, *B*); (3) concave towards apex; (4) absent

(*4*) *Frons apex*: (0) flat; (1) slightly reflexed; (2) strongly reflexed, developed as carina

(*5*) *Clypeal shape*: (0) broadly rounded (Fig. 8*A*, *B*); (1) pentagonal (Fig. 14*A*, *B*); (2) subtriangular, narrowed at apex; (3) apically blunt

(*6*) *Clypeal lateral margins*: (0) strongly reflexed; (1) slightly reflexed; (2) not reflexed. This character was coded as ordered because althought the direction is not known, state 2 is morphologically intermediate between 0 and 1

(*7*) *Clypeal apical margin*: (0) reflexed, entire; (1) reflexed, bifid

(*8*) *Clypeal* '*shield*': (0) absent (Fig. 6*A*, *B*); (1) present, small (Fig. 10*A*, *B*); (2) present, well developed (Figs 3, 13*A*, *B*). This structure is present only in some species of *Neogutierrezia*. Even if it could seem an ordered character, it was coded as unordered because there is no evidence of small 'shield' being before of after the well developed 'shield'

(*9*) *Mandibles, margin*: (0) rounded; (1) angulose

(*10*) *Labral position relative to clypeus*: (0) hidden beneath clypeus (Fig. 6*B*); (1) slightly visible in dorsal view (Fig. 14*B*); (2) clearly visible in dorsal view (Fig. 8*B*). Hidden labra are common in Melolonthinae and Dynastinae whereas protruded labra are widespread on Rutelinae

(*11*) *Labral surface and margin*: (0) glabrous, or sparsely setose; (1) densely setose

(*12*) *Labral shape*: (0) triangular; (1) kidney-shaped

(*13*) *Maxillary palpomere 4, sensory area*: (0) basal, flat (Fig. 18*J*); (1) longitudinal, groove-like (Fig. 4*A*); (2) absent (Fig. 18*I*)

(*14*) *Maxillary palpomere 4, apical sensory area*: (0) strongly truncate (Fig. 18*F*); (1) rounded or slightly truncate (Fig. 18*J*); (2) pointy (Fig. 18*I*)

(*15*) *Eye shape*: (0) 1/3 of eye diameter visible on dorsal view; (1) 1/2 or more of eye diameter visible in dorsal view (diameter was measured on ventral lateral view, where the eye is fully exposed)

(*16*) *Eye canthus*: (0) well developed, shelf-like; (1) small, thumb-like

(*17*) *Eye canthus conformed, in part, by a projection of the clypeus*: (0) present; (1) absent. The clypeus usually ends at the frontoclypeal suture, but in some cases we observed that laterobasal angles of the clypeus are protruded and extended along the eye canthus. They might occur slightly on top of the eye canthus, or they might reach the apex on its dorsal surface. In spite of being fused, the sutures are visible

(*18*) *Number of antennomeres*: (0) seven; (1) eight; (2) nine

(*19*) *Antennal club, number of antennomeres*: (0) three; (1) four

(*20*) *Antennal club, insertion of funicle*: (0) basal (Fig. 6*C*); (1) sub-basal, displaced from base (Fig. 4*B*)

Pronotum

(*21*) *Pronotal posterior angle*: (0) angulose; (1) rounded

(*22*) *Pronotal surface*: (0) entirely rugopunctate; (1) entirely sparsely punctate; (2) entirely densely punctate; (3) entirely densely punctate, except in middle where it is smooth; (4) entirely smooth

(*23*) *Pronotal margins*: (0) all margins beaded; (1) beaded, except apical margin in middle; (2) beaded, except apical and basal margin in middle

Elytra

(*24*) *Elytral striae*: (0) striae evident, well defined; (1) striae not evident or defined, surface rugose

(*25*) *Elytral sutural carina*: (0) absent; (1) present, tapered at elytral apex; (2) present, not tapered at elytral apex

Pygidium–Propygidium

(*26*) *Pygidial shape*: (0) circular (Fig. 18*E*); (1) triangular (Fig. 4*D*)

(*27*) *Pygidial surface*: (0) glabrous; (1) densely setose

(*28*) *Propygidium*: (0) glabrous; (1) densely setose

Legs

(*29*) *Protibial shape*: (0) robust (Fig. 11*C*); (1) slender (Fig. 10*C*)

(*30*) *Protibia, number of teeth*: (0) two; (1) three

(*31*) *Protibial basal tooth*: (0) well developed (Fig. 5*C*); (1) poorly developed (Fig. 5*D*); (2) absent

(*32*) *Protibial spur*: (0) well developed (Fig. 9*C*); (1) poorly developed (Fig. 13*C*)

(*33*) *Protarsomeres 2–4*: (0) not flattened dorsoventrally; (1) dorsoventrally flattened

(*34*) *First metatarsomere, outer surface*: (0) mostly glabrous; (1) setose, with long slender setae

(*35*) *Tarsal claws*: (0) toothed; (1) simple; (2) split at apex. On Rutelinae both claws of the same leg are usually different, most of times one of them is simple and the other may be simple (but different in size), toothed or split at apex. When Rutelinae species were coded for the matrix, only the latter claw was considered

(*36*) *Mesotarsal claws*: (0) symmetric; (1) asymmetric. Mesotarsal claws were chosen for this character to avoid sexual dimorphism more common on protarsal and metatarsal claws

(*37*) *Protibial setae*: (0) with no setae, or dorsal setae not forming a defined fringe; (1) with one dorsal fringe of setae; (2) with two dorsal fringes of setae

(*38*) *Protarsomere 5, length*: (0) longer than 3 and 4 combined; (1) equal or shorter than 3 and 4 combined

(*39*) *Metatibial transversal carinae*: (0) one; (1) two

(*40*) *Mesotibial tranversal carinae*: (0) one; (1) two

(*41*) *Mesotibial apical area (in apical view)*: (0) with two lobe-shaped areas of glabrous surface (Fig. 18*A*, *G*); (1) with one lobe-shaped area of glabrous surface (Fig. 4*G*); (2) with no glabrous surface, surface covered by setae (Fig. 4*E*); (3) no surface developed, narrow apex (Fig. 18*K*)

(*continued next page*)

Table 2. (*continued*)

(*42*) *Metatibial apex, shape in cross section*: (0) ovoid (Fig. 18*A*, *G*); (1) laterally compressed (kidney-shaped) (Fig. 4*F*); (2) semicircular (Fig. 4*H*)
(*43*) *Metatibial spurs*: (0) absent (Fig. 18*L*); (1) with two spurs developed (Fig. 4*F*); (2) with one spur highly reduced (outer spur visible only at 40× or higher magnification) (Fig. 4*H*). The common state on Scarabaeoidea is having two well-developed spurs on metatibial apex
(*44*) *Metatibial apical process*: (0) absent (Fig. 9*D*); (1) present, poorly developed (Fig. 7*D*); (2) present, well developed (Fig. 6*E*). This character was coded as ordered assuming the progressive growth of the structure
(*45*) *Metatibial 'brush'*: (0) absent (Fig. 8*D*); (1) present with small, soft setae reaching medial carina (Fig. 9*D*); (2) present with large, hard setae, not reaching medial carina (Fig. 13*D*). The common state for this character in Scarabaeoidea is the absence of 'brushes' on metatiabiae. The character was coded as ordered considering the progressive development of this structure in *Neogutierrezia*
(*46*) *Metatibial spurs, position*: (0) medial (Fig. 18*H*); (1) ventral (Fig. 4*F*, *H*); (2) absent (Fig. 18*L*)
(*47*) *Metatibial spurs, tibial insertion*: (0) subcontiguous (Fig. 18*H*); (1) contiguous (Fig. 4*H*); (2) – (Fig. 18*L*)

Aedeagus
(*48*) *Male genitalia, structure*: (0) parameres not fused (Fig. 18*D*); (1) parameres fused (Figs 5–14*D*)
(*49*) *Parameres shape*: (0) short (≤2.5× as long as wide) (Fig. 8*E*); (1) long (>3.0× as long as wide) (Fig. 9*E*)
(*50*) *Aedeagus base (ventral)*: (0) lacking tooth (Fig. 18*D*); (1) with well-developed tooth (Figs 11*F*, 13*F*); (2) with poorly-developed tooth (Fig. 12*F*)
(*51*) *Spiculum gastrale*: (0) slender (Fig. 4*I*); (1) robust (Fig. 18*D*). Most Palearctic Pachydemini (Sanmartín 2003) present a robust spiculum gastrale, whereas a slender spiculum gastrale is common for Rutelinae, Dynastinae and some Melolonthinae (Jameson 1998)

Ventrites and abdominal spiracles
(*52*) *Ventrites 1–5*: (0) strongly narrowed in middle (Fig. 4*D*); (1) not narrowed in middle (Fig. 18*E*)
(*53*) *Last abdominal spiracle, position*: (0) dorsal (or pleural suture obsolete); (1) on pleural suture; (2) ventral to pleural suture

The following standards were used for characters:

Body length. Measured from the apex of the clypeus to the apex of the elytra.

Puncture density. Defined as dense if punctures are nearly confluent to less than two puncture diameters apart, moderately dense if punctures are between two to six puncture diameters apart and sparse if punctures are separated by more than six puncture diameters.

Length of setae. Defined as minute if less than 0.2 mm, short if 0.2–0.5 mm, moderately long if 0.5–1.0 mm and long if more than 1.0 mm.

Type of setae. Defined as 'hair-like' if slender and erect, 'thickened' if slightly thick and erect or partially decumbent and 'spine-like' if broad and thick. Setae are subject to wear and may be abraded.

Setae density. Setae were defined as 'sparse' if there were few setae, 'moderately dense' if the surface was visible but with many setae and 'dense' if the surface was not visible through the setae.

Colour. Described based on specimens that are viewed with magnification and illumination.

Material examined

The results of this study were based on specimens from the following institutions and collections.

CMNC: Canadian Museum of Nature, Ottawa, Canada (R. S. Anderson, F. Génier).
HAHC: Henry and Anne Howden Collection, Ottawa, Canada (at CMNC, R. S. Anderson, F. Génier).
IAZA: Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (F. C. Ocampo [Scarabaeoidea]).
IMLA: Fundación e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (M. V. Colomo).
MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (A. Roig).
MLPA: Museo de La Plata, La Plata, Argentina (A. Lanteri).
UNSM: University of Nebraska State Museum, Lincoln, Nebraska, U.S.A. (B. C. Ratcliffe).

Biogeographic analysis

Historical biogeography of *Neogutierrezia* was inferred from the result of the phylogenetic analysis. Area relationships were reconstructed by replacing terminal taxa by their area of occurrence. To define the areas we followed the biogeographic scheme proposed by Morrone (1999), Roig-Juñent *et al*. (2001, 2008), Rundel *et al*. (2007) and Roig *et al*. (2009), according to which the Monte Biogeographic province is delimited from North-eastern Salta province in Argentina (starting as a narrow strip of land) down to Eastern Chubut province (including Península Valdés and Eastern Neuquén province). Other schemes, proposed by the same or different authors, differ with the preferred one in that they do not include North-eastern Chubut and Eastern Neuquén as part of the Monte (Morrone 2001, 2006). The reason for this inconsistency is, in part, because the southern limit of the Monte is not well defined (i.e. by a geographic barrier), there being a gradual transition between Monte and Patagonia. Based on evidence from insect fauna, we consider that the selected scheme better represents the historical biogeography and ecology of the region (see Roig-Juñent *et al*. 2001, 2008).

Predictive models of species distribution

Species distribution models (SDMs) can be used to predict the potential distribution of a species, which, in turn, are useful to test biogeographical, ecological and evolutionary hypotheses (Graham *et al*. 2004). Predictive distributions are obtained by relating known collection localities of a species to a set of environmental variables that, presumably, reflect the ecological niche of the species (Guisan and Thuillier 2005).

Georeferenced localities for each *Neogutierrezia* morphospecies were obtained directly from specimens' labels

or locality data were georeferenced using the BioGeomancer workbench application (http://www.biogeomancer.org/index.html, verified 7 April 2010). These data were mapped to model species distribution using predictive methods based on 21 bioclimatic variables (Hijmans *et al*. 2005), soil type (categorical) and elevation. The resolution of the environmental layers was ~4.6 × 4.6 km. Data were analysed using MaxEnt (Phillips *et al*. 2006).

Results and discussion

Molecular evidence and the systematic placement of the genus Neogutierrezia

Structural alignment and models

A multiple sequence alignment of the expansion segments D2 and D3 of 28S rRNA was generated across 23 scarabaeoid taxa. The comparative aproach undertaken in this study yielded the first annotated structural alignment of 28S D2–D3 that spans all major scarab subfamilies. It will be useful as homology template for future phylogenetic studies of scarabaeoids and related beetles. The complete annotated structural alignment is posted as supplementary material for this article on line and also at the jRNA website (http://hymenoptera.tamu.edu/rna/models.php, verified 7 April 2010). Appendix 2 shows the areas, named as in the alignment, that contain the synapomorphies that support the proposed systematic placement of *Neogutierrezia.*

Phylogenetic placement of the genus Neogutierrezia

The final alignment consisted of 676 characters, of which 167 were parsimony-informative. Maximum parsimony analysis of the aligned 28S rDNA sequences resulted in one tree of length 801 (Fig. 1) (Consistency index [CI] = 0.5506; Homoplasy index [HI] = 0.4494; CI excluding uninformative characters = 0.4667; HI excluding uninformative characters = 0.5333). The results provide strong support (bootstrap = 100) that *Neogutierrezia* is sister to Rutelinae + Dynastinae. Additionally, the results provide evidence that the subfamily Melolonthinae is a grade made up of at least two lineages (represented by *Melolontha* + *Phyllophaga* [Melolonthini] in one clade and *Acylochilus* + *Puelchesia* [Pachydemini] in another clade). The *Neogutierrezia* + Rutelinae + Dynastinae clade is separated from the Pachydemini clade by the Cetoniinae. Thus, the genus *Neogutierrezia* is more closely related to members of the Rutelinae + Dynastinae than to South American Pachydemini or Melolonthini. Both the D2 and D3 28S rDNA regions (characters 1–419 and 420–676, respectively, in the analysed data file) contribute unambiguous synapomorphies supporting the clade *Neogutierrezia* + Rutelinae + Dynastinae (see also Appendix 2): eight are from D2 (two are unique changes) and four are from D3 (two are unique changes).

Other clades supported by molecular evidence in the cladogram are: Aphodiinae + Scarabaeinae, Hybosoridae + Ochodaeidae (both widely accepted as monophyletic groups); and a clade Orphninae + Allidiostomatinae, for which morphological evidence has just been discovered (Ocampo and Colby, unpubl. data).

Phylogeny of the genus *Neogutierrezia* based on morphology

The parsimony analysis yielded one most parsimonious tree (Length: 133, CI: 0.63, RI: 0.078 and RC: 0.45) (Fig. 2). Forty-eight characters were parsimony-informative, whereas five were parsimony-uninformative.

Our results of the phylogenetic analysis provide evidence that *Neogutierrezia* is a monophyletic lineage. The monophyly of the genus is supported by 11 unambiguous synapomorphies (Fig. 2, node a): Frons surface rugose (character 2, state 2); frontoclypeal suture complete, convex towards apex (character 3, state 3); mandibles margin angulose (character 9, state 1); 1/3 of eye diameter visible in dorsal view (character 15, state 0); protarsomeres 2–4 dorsoventrally flattened (character 33, state 1); mesotibial apex (in apical view) with one lobe-shaped area and glabrous surface (character 41, state 1); aedeagal base with well-developed ventral tooth (character 50, state 1).

Within the *Neogutierrezia* lineage, three clades are distinguished: (*N. chelii* (*N. payuniensis* + *N. bicolor*)), (*N. mirabilis* (*N. araucana* + *N. affinis*)) and (*N. lagosae* (*N. galileoi* (*N. variabilis* + *N. scutata*))) (Fig. 2, nodes b, c, d, respectively). Within each of these clades, species are distributed in a grade (Fig. 2). The *N. lagosae* + *N. scutata* clade corresponds to a 'Central Monte' lineage with species distributed in central and northern Mendoza province, whereas the other two clades (*N. mirabilis* + *N. affinis* and *N. chelii* + *N. bicolor*) correspond to the 'Southern Monte' (also see biogeography section below).

Systematic placement of the genus Neogutierrezia

According to D'Hotman and Scholtz (1990), two conditions of the male genitalia help to define (although not solely) the scarab subfamily Rutelinae (also found in Dynastinae): (*1*) male genitalia with parameres completely fused and (*2*) spiculum gastrale 'Y' shaped and with apical setae (Figs 5*E* and 4*I* respectively). These two conditions are present in *Neogutierrezia* species as well as the globose shape of the phallobase, also considered as a ruteline characteristic (D'Hotman and Scholtz 1990). A third characteristic of ruteline male genitalia is the presence of ventral plate (D'Hotman and Scholtz 1990; Jameson 1996), which is absent in *Neogutierrezia* species. Based on our morphological analysis, the *Neogutierrezia* + Rutelinae + Dynastinae clade is supported by the following unambiguous synapomorphies: Labrum kidney-shaped (character 12, state 1); eye canthus small, thumb-like (character 16, state 1); metatibia with two transverse carinae (character 39, state 1); *spiculum gastrale* slender (character 51, state 0).

Preliminary molecular and morphological phylogenetic analyses provide evidence that the tribe Pachydemini is polyphyletic (Ruiz-Manzanos and Ocampo, unpubl. data; Smith *et al*. unpubl. data). Similar to those found by Evans (1988) for African pachydemines, our results on Neotropical pachydemines suggest that the Neotropical genera do not constitute a natural group. The tribe, as defined today, includes genera whose species have independently evolved and adapted to xeric conditions, resulting in a high degree of convergent morphologies. Reduced mouth-parts, brachypterous females,

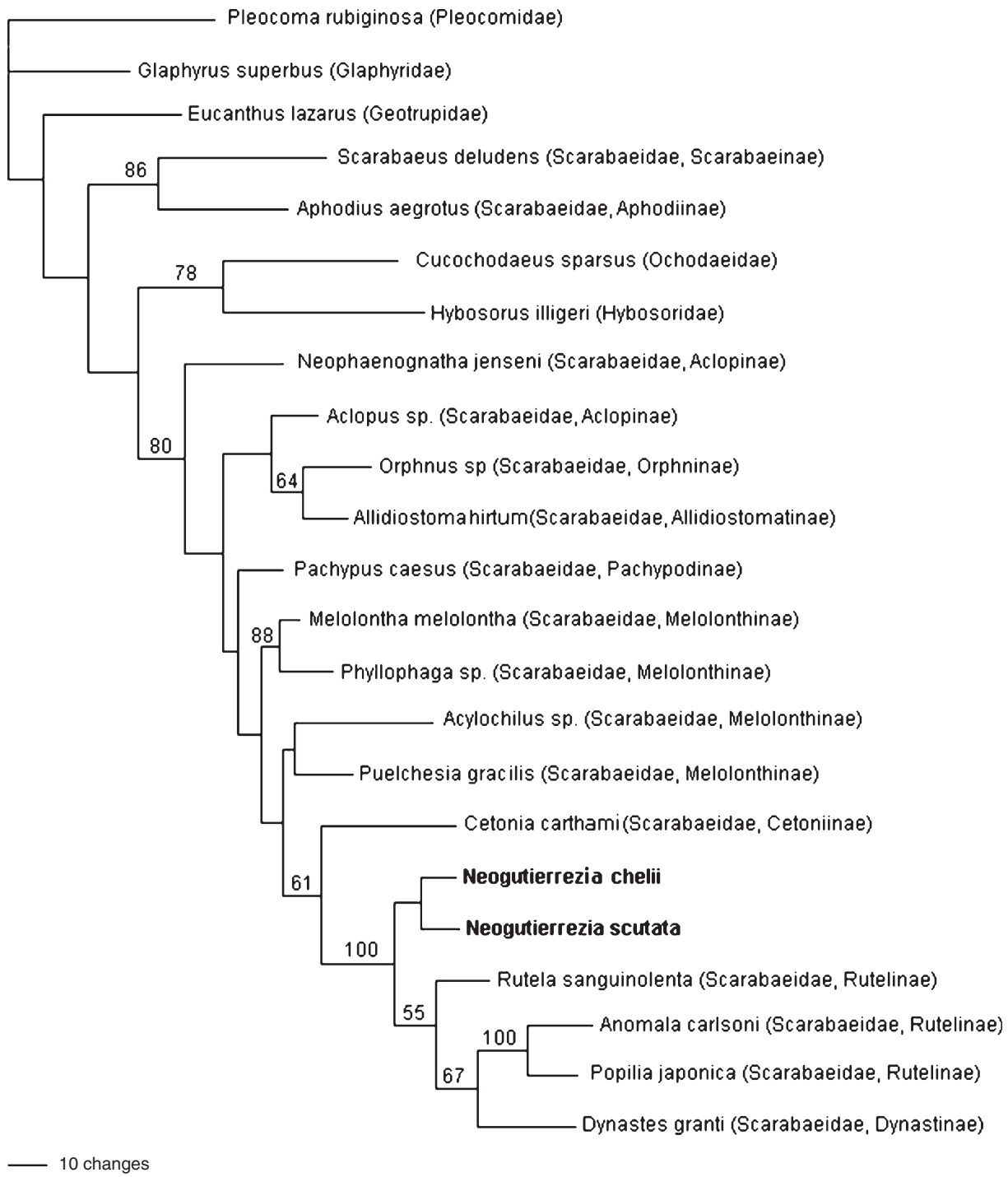

Fig. 1. Single most parsimonious tree based on molecular data from 28S D2–D3 regions showing the phylogenetic relationships of the genus *Neogutierrezia*. Maximum parsimony bootstrap values are indicated above nodes.

densely setose abdomen and pronotum, slender and elongate tarsi, males with abdominal ventrites strongly narrowed in middle, are morphological traits present in taxa currently considered Neotropical Pachydemini. These traits (all or some) are also relatively common in other Neotropical scarabs adapted to arid environments such as Aclopinae, Rutelinae (i.e. *Pseudogeniates* Ohaus) and in many Nearctic and Afrotropical (mainly African Subsaharan) genera currently placed in the Pachydemini. Our evidence indicates that most of the characters used to place *Neogutierrezia* in Melolonthinae are homoplasies that resulted from adaptation to arid conditions.

According to recent phylogenetic analysis (Smith *et al*. 2006), Rutelinae is paraphyletic with respect to Dynastinae and they (combined) constitute a well supported monophyletic group of Scarabaeidae. Our molecular evidence strongly supports the hypothesis that *Neogutierrezia* is closely related to the Ruteline–Dynastinae clade. Accordingly, morphological evidence, particularly that provided by male genitalia (see above), supports the hypothesis of relationship of *Neogutierrezia* with rutelines. Based on both data sources (morphologial and molecular), we are confident to transfer *Neogutierrezia* from Melolonthinae : Pachydemini to Rutelinae (*incertae sedis*), new placement.

Certainly, *Neogutierrezia* is one of the most intriguing scarab genera in the Neotropics. A comprehensive phylogenetic study based on morphological and molecular evidence, and including as many ruteline taxa as possible, is necessary to know the relationships of *Neogutierrezia* within Rutelinae, as well as to clearly delimit the subfamily. Such a study will finally help to understand many aspects of the morphological evolution as well as ecological adaptations of these scarabs.

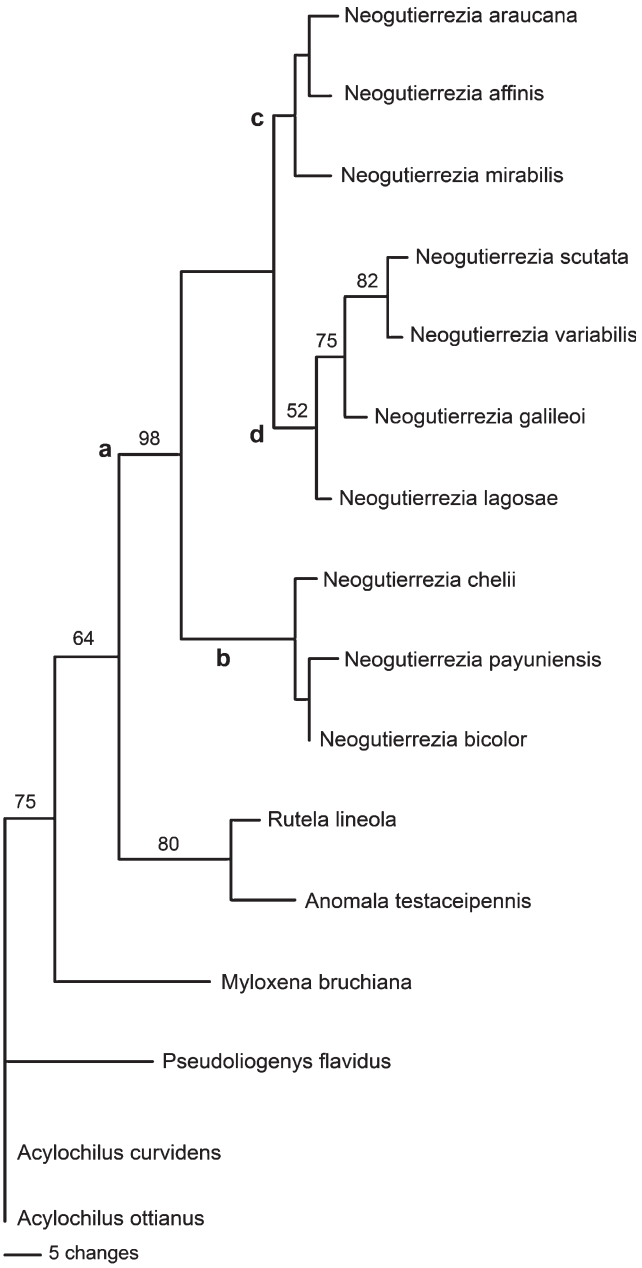

Fig. 2. Single most parsimonious tree based on adult morphological data of *Neogutierrezia* and outgroups. Maximum parsimony bootstrap values are indicated above nodes. Major clades (see text) are labelled within the tree.

Taxonomy

Order COLEOPTERA

Family SCARABAEIDAE

Subfamily RUTELINAE

Genus *Neogutierrezia* Martínez

(Figs 3–14, 16–18)

Neogutierrezia Martínez, 1953: 2. – Martínez 1958: 102 (citation), Martínez 1973: 27 (redescription and new species), 1975: 229 (key to genera and catalogue); Evans, 2003: 220 (catalog); Lacroix, 2007: 376 (catalog).

Type species: *Neogutierrezia mirabilis* Martínez, 1953 by original designation.

Diagnosis

The genus *Neogutierrezia* can be recognised from other Argentinean scarabs by the following combination of characters: antennal club with three or four antennomeres, club longer than funicle; labrum kidney-shaped; mandibles with

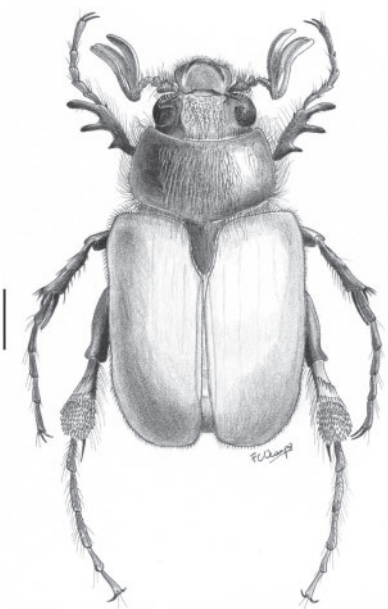

Fig. 3. *Neogutierrezia scutata*, habitus drawing.

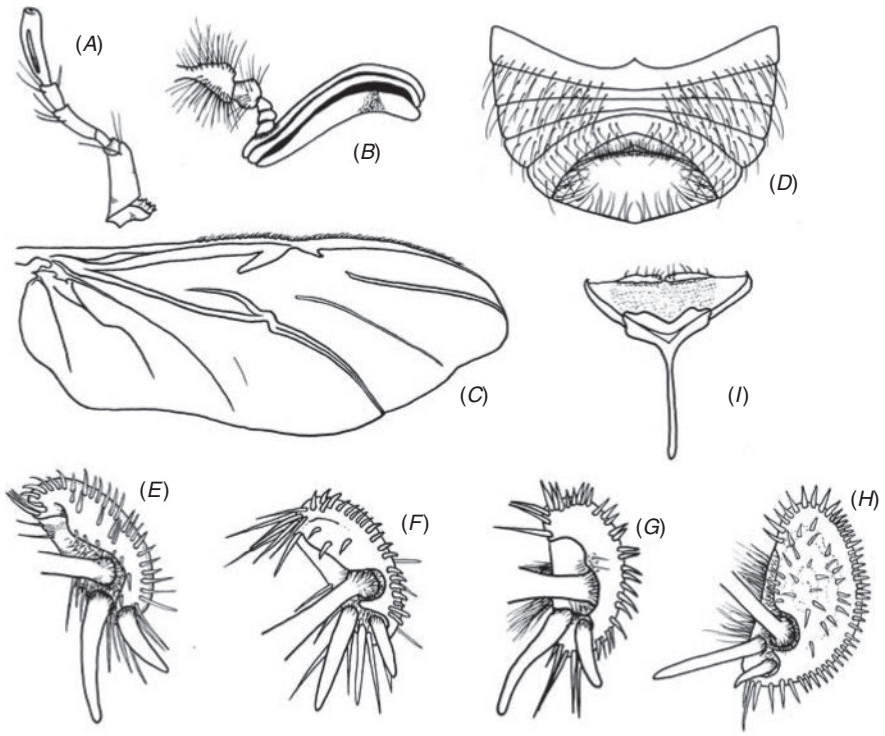

Fig. 4. *Neogutierrezia variabilis. A*, Maxilla. *N. scutata*: *B*, antenna; *N. lagosae: C* metathoracic wing; *D*, abdomen; *F*, metatibial apex; *I*, spiculum gastrale. *N. galileoi*: *E*, mesotibial apex; *H*, metatibial apex. *N. bicolor*: *G*, metatibial apex.

external margin angulose, visible on dorsal view; pygidial apex strongly recumbent towards metacoxae (males); tarsal claws simple; parameres fused; *spiculum gastrale* Y-shaped, slender.

Description

Male

Colour. Head, pronotum, scutellum, venter, pygidium and legs dark brown; elytra yellowish brown.

Head (Figs 3, 4, 5*A, B*, 6*A, B*, 7*A, B*, 8*A, B*, 9*A, B*, 10*A, B*, 11*A, B*, 12*A, B*, 13*A, B*, 14*A, B*). Frons convex on basal half, flat on apical half; apical half rugose, glabrous or sparsely setose, setae moderately long. Frontoclypeal suture evident; developed as transverse carina or not, complete or obsolete in middle. Clypeal shape variable, surface smooth to sparsely punctate. Clypeal margins strongly or slightly reflexed. Labrum rectangular, setose and setae thick and moderately long. Mandibles with external margin angulose, setose, flattened at apex; molar area poorly-developed, weakly sclerotised. Maxillae poorly developed, fused with labium; palp with four palpomeres, palpomeres cylindrical, palpomere 4 as long as palpomeres 2 and 3 combined, apex truncate, sensory area groove-like, on dorsolateral surface (Fig. 4*A*). Labium narrow, densely setose, setae long; labial palp with three cylindrical palpomeres; palpomere 3 longer than 1 and 2 combined. Antennae with seven, eight or nine antennomeres (Figs 4*B*, 6*C*); antennal club with three or four antennomeres, club longer than funicle, glabrous, with microscopic (visible at >40×) punctures, punctures dense. Eyes well developed, ventrally globose. Eye canthus flattened, thumb-like, with thick setae on anterior margin and apex.

Pronotum. Convex, transverse; margins densely setose, setae long, slender. Margins beaded except anterior margin at middle. Anterior angles obtuse, posterior margins broadly rounded. Anterior margin convex, posterior margin sinuous.

Scutellum. Setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate or striate, sutural striae well developed from base to elytral apex, discal striae poorly defined. Metathoracic wing fully developed, with fringe of minute setae on dorsal margin, anal anterior$_{1+2}$ (AA_{1+2}) reduced to a sinus, media posterior$_4$ (MP_4) vestigial, radius anterior$_4$ (RA_4) free, radius posterior$_1$ (RP_1) absent (Fig. 4*C*).

Propygidium. Surface setose; setae long, slender. Last abdominal spiracle on tergo–ventral suture.

Pygidium. Exposed, not covered by elytra (although not visible on dorsal view), wider than long; surface setose, setae long, slender; pygidial apex strongly recumbent towards metacoxae (males).

Venter (Fig. 4*D*). Surface rugose to punctate, moderately to densely setose, setae long, slender. Metasternum large, wider than long. Sternites 1–4 strongly narrowed in middle, 5 as long as 2–4 combined, 5–6 separated by a membrane; last abdominal sternite as long as 1–5, emarginated at middle.

Legs (Figs 3, 4*E, H*, 5*C, D*, 6*D, E*, 7*C, D*, 8*C, D*, 9*C, D*, 10*C, D*, 11*C, D*, 12*C, D*, 13*C, D*, 14*C, D*). Procoxa as long as femur; procoxal and femoral surfaces setose, setae long,

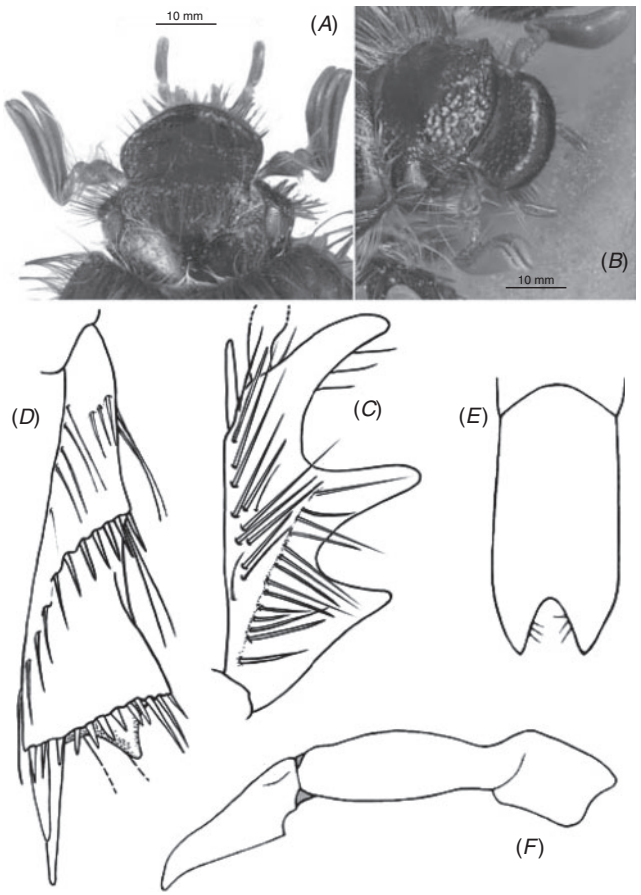

Fig. 5. *Neogutierrezia affinis*. *A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

slender. Protibia tridentate (basal tooth occasionally reduced), apical tooth with dorsobasal notch; protibial spur nearly straight, slender. Protarsomere 5 longer than 3 and 4 combined. Tarsal claws simple, slender, curved on apical 1/3. Meso- and metatibiae with two well-developed, transverse carinae; carinae setose, setae thick. Meso- and metatibial outer edge with fringe of long setae; inner edge nearly straight. Meso- and metatibial apex with thick, short setae. Mesotibial inner spur longer than tarsomere 1, outer spur shorter than tarsomere 1, spurs slightly curved. Meso- and metatarsi with tarsomeres 1–4 decreasing in length, tarsomere 5 longer than 4. Metatibial tarsal insertion with ventral notch. Meso- and metatibial spurs contiguous, on tibial notch; metatarsus folds dorsally to metatibial spurs.

Genitalia (Figs 5*E*, *F*, 6*F*, *G*, 7*E*, *F*, 8*E*, *F*, 9*E*, *F*, 10*E*, *F*, 11*E*, *F*, 12*E*, *F*, 13*E*, *F*, 14*E*, *F*). Phallobase longer than parameres, globose at base. Parameres dorsally fused, longer than wide, nearly straight, slightly curved downwards at apex.

Spiculum gastrale (Fig. 4*I*). Y-shaped, slender, vestigial sternite partially-developed.

Remarks

The genus is feminine in gender.

Neogutierrezia consists of 10 known species.

Distribution

ARGENTINA: Mendoza, Río Negro, Neuquén, Chubut.

Neogutierrezia affinis Martínez, new status

(Fig. 5*A–F*)

Neogutierrezia mirabilis affinis Martínez, 1973: 35. – Martínez 1975: 248 (catalog); Evans, 2003: 221 (catalog); Lacroix, 2007: 377 (catalog).

Material examined

Holotype. ♂, Argentina: Río Negro, S. Antonio Oeste, Las Grutas, Martínez, i.1966 (MACN).

Paratypes. **ARGENTINA:** 7♂ (1♂ at IMLA, others at CMNC), Río Negro, S. Antonio Oeste, Las Grutas, Martínez, i.1966.

Other material examined. **ARGENTINA:** 1♂ (CMNC), Río Negro, S. A. Oeste, P. Las Grutas, Bordon, xii.1973; 4♂ (CMNC), Río Negro, S. A. Oeste, Las Grutas, Martínez, xii.1992.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus rounded, sparsely punctated; clypeal margins strongly reflexed; frontoclypeal suture evident, developed as transverse carina; labrum not visible in dorsal view; antenna with nine antennomeres, funicle–club joint placed on base of club; scutellum with apex rounded or sligthly pointed; protibial spur as long as or slightly shorter than protarsomere 1; protarsomere 5 as long as or slightly shorter than 3 and 4 combined; metatibial carinae well developed; metatibial apex with well-developed process.

Description

Holotype male

Length. 8.75 mm; maximum width 4.38 mm.

Colour. Head, pronotum, scutellum, elytra, venter, pygidium and legs reddish-brown; head and pronotum darker than elytra.

Head (Fig. 5*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, glabrous or sparsely setose, setae moderately long. Frontoclypeal suture evident, curved, developed as a transverse carina. Clypeus broadly rounded, surface smooth to sparsely punctate. Margins strongly reflexed. Labrum not visible in dorsal view, concealed by clypeus, setose; setae thick, moderately long. Antennae with eight or nine antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–6 combined, glabrous, with microscopic (visible at >40×) punctures; punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc; setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate or striate, with short, sparse setae; sutural striae well developed from base to elytral apex; discal striae (if present) poorly defined.

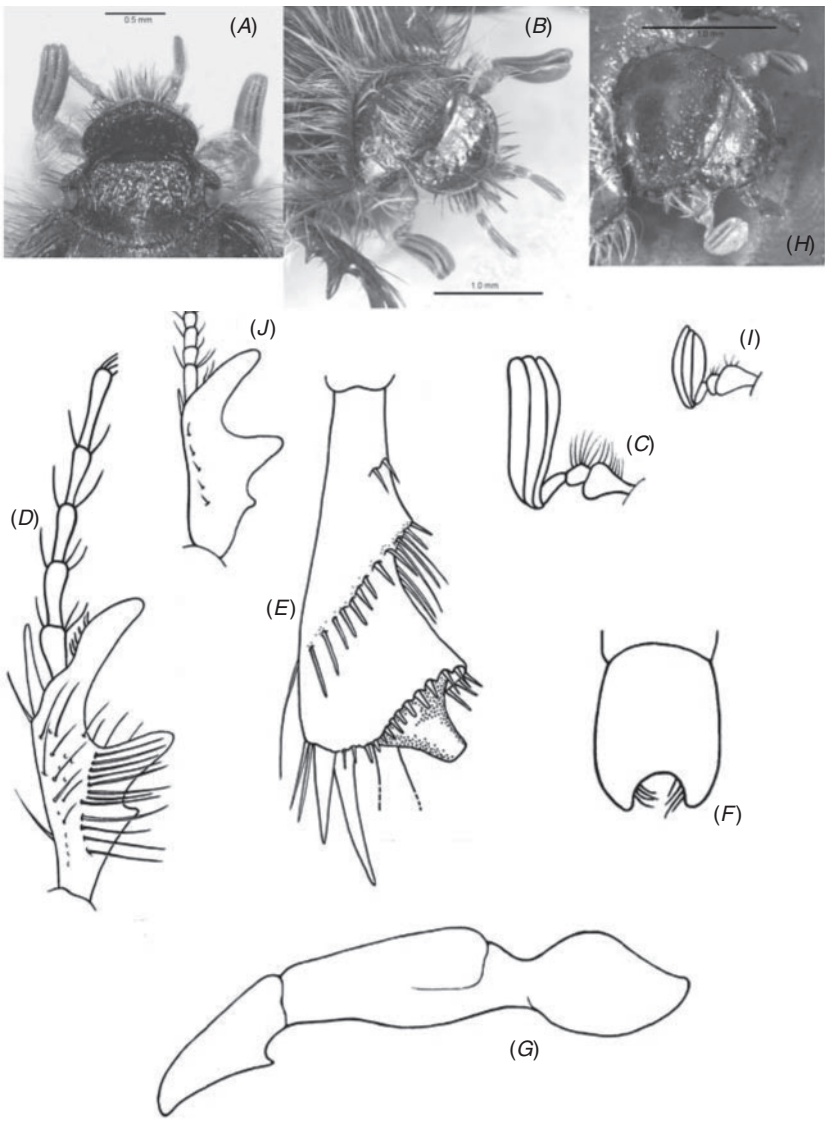

Fig. 6. *Neogutierrezia araucana*. *A–G*, Male: *A*, *B*, head; *C*, antenna; *D*, protibia; *E*, metatibia; *F, G*, genitalia. *H–J*, Female: *H*, head; *I*, antenna; *J*, protibia.

Pygidium. 1.67× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose, setae long, slender, hair-like. Metasternum large, 2× wider than long.

Legs (Fig. 5*C*, *D*). Protibia tridentate, basal tooth well developed, base of medial tooth 2/3 as wide as tibia in middle; protibial spur as long as or slightly shorter than protarsomere 1, nearly straight, slender. Protarsomere 5 as long as or sligthly shorter than tarsomeres 3 and 4 combined. Meso- and metatibiae laterally flattened, with two well-developed transverse carinae; carinae setose, setae thick. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with well-developed process.

Genitalia (Fig. 5*E*, *F*). Phallobase 1.63× longer than parameres. Parameres dorsally fused, 2× longer than wide.

Female

Unknown.

Variation

Length: 7.00–8.75 mm; width: 3.50–4.38 mm. Specimens of *N. affinis* possess eight or nine antennomeres (when eight, 3–4 fused, club with three antennomeres). Colour of elytra testaceous to dark brown, pronotum light to dark brown.

Distribution

ARGENTINA. Río Negro: San Antonio Oeste, Las Grutas [40°48′05.86″S, 65°05′03.08″W] (14).

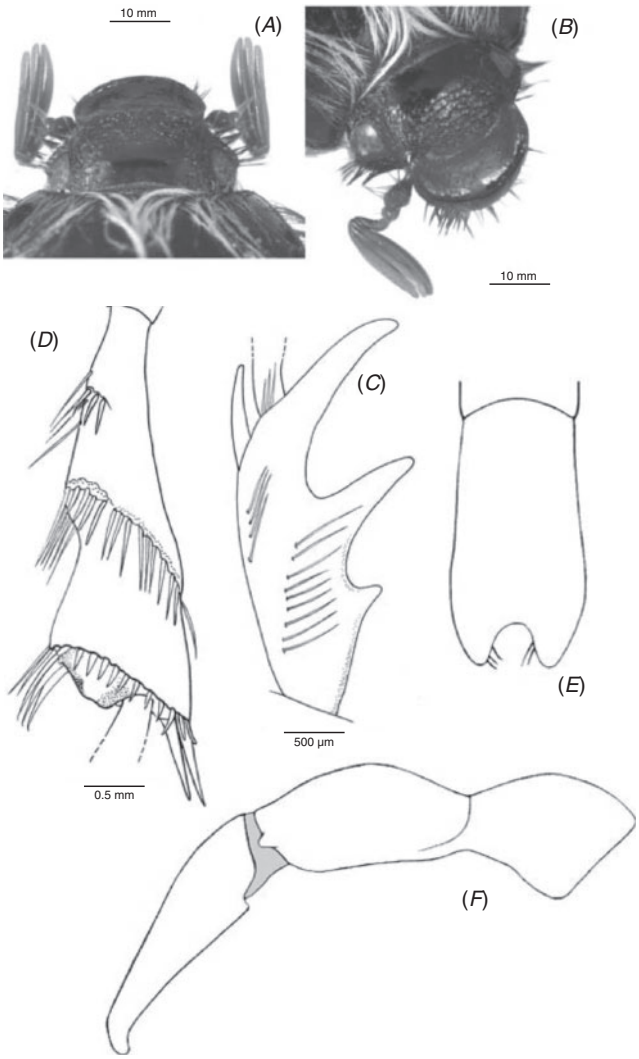

Fig. 7. *Neogutierrezia bicolor. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

Temporal distribution

January (8), December (6)

Biology

Specimens of *N. affinis* were collected at the light of a kerosene lamp early at night in a sandy area near the sea shore (Martínez 1973).

Neogutierrezia araucana Martínez

(Fig. 6*A–J*)

Neogutierrezia araucana Martínez, 1973: 36. – Martínez 1975: 248 (catalog); Evans, 2003: 220 (catalog); Lacroix, 2007: 377 (catalog).

Material examined

Holotype. ♂, Argentina: Neuquén, A° Picún Leufú y Ruta 5, Martínez, i.1965 (MACN).

Allotype. ♀, **ARGENTINA:** Neuquén, A° Picún Leufú y Ruta 5, Martínez, i.1965 (MACN).

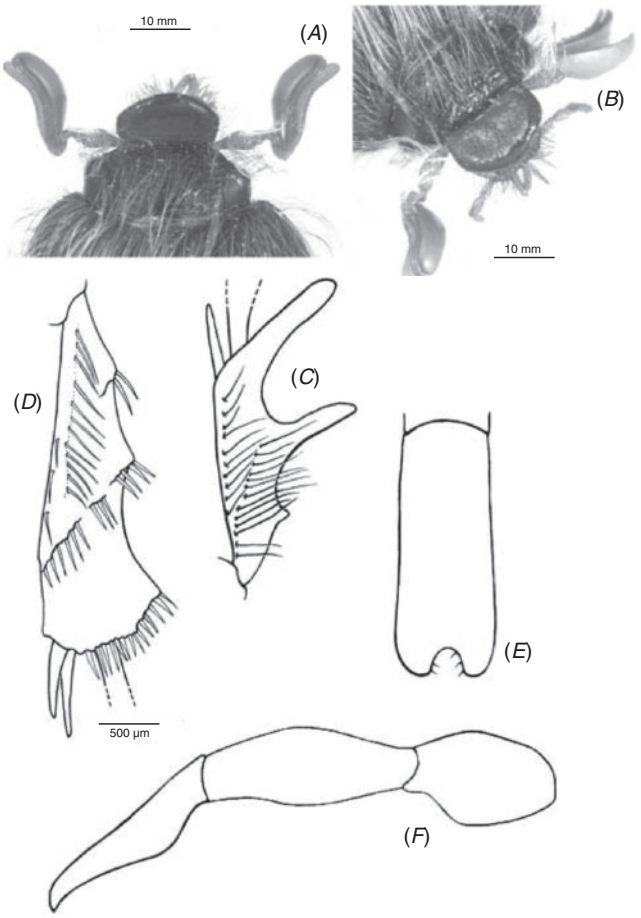

Fig. 8. *Neogutierrezia chelii. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

Paratypes. **ARGENTINA:** 7♂, 1 ♀ (1♂ at IMLA, 6 at CMNC, ♀ at CMNC), Neuquén, A° Picún Leufú y Ruta 5, Martínez, i.1965; 3♂, Neuquén, A° Picún Leufú y Ruta a S.M.A., Martínez, i.1965 (CMNC).

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus rounded, sligthly pointed at middle; clypeal margins strongly reflexed; frontoclypeal suture evident, developed as transverse carina; labrum not visible in dorsal view; antenna with eight antennomeres, funicle–club joint basal; scutellum with apex rounded, slightly truncated; protibial basal tooth poorly developed, medial tooth base 2/3 as wide as tibia in middle; protibial spur as long as or slightly shorter than protarsomere 1; protarsomere 5 shorter than 3 and 4 combined; metatibial carinae well developed; metatibial apex with well-developed process.

Description

Holotype male

Length. 8.00 mm, maximum width: 4.37 mm.

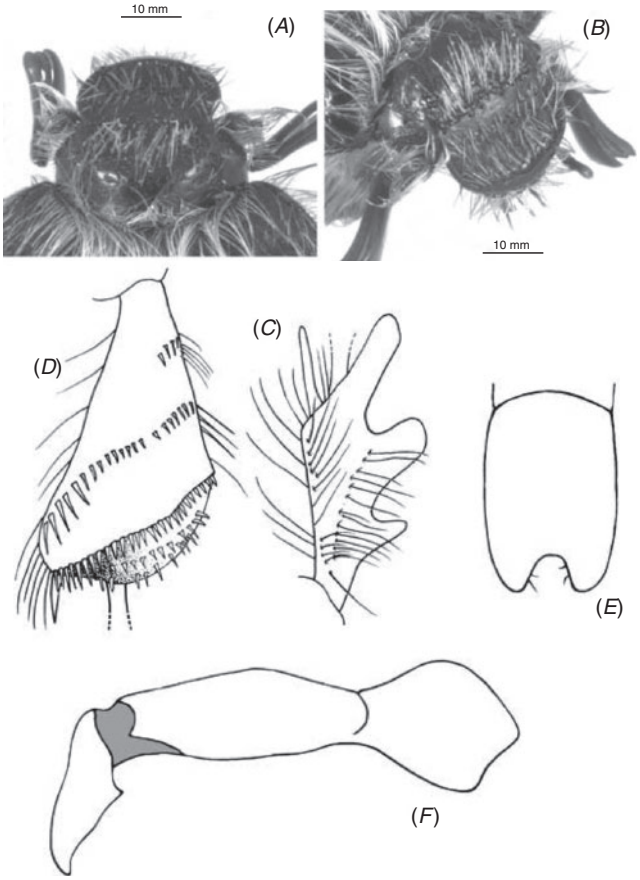

Fig. 9. *Neogutierrezia galileoi. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

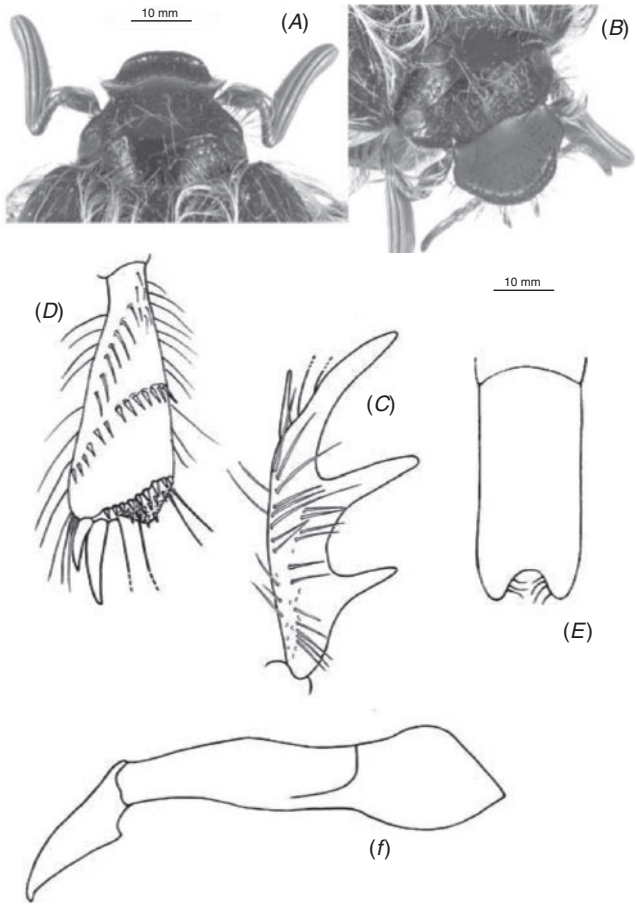

Fig. 10. *Neogutierrezia lagosae. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

Colour. Head, pronotum, scutellum, elytra, venter, pygidium and legs reddish-brown.

Head (Fig. 6*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, setose; setae moderately dense, moderately long. Frontoclypeal suture evident, curved, developed as a transverse carina. Clypeus broadly rounded, slightly pointed at middle; surface smooth at base becoming punctate towards margins. Apical and lateral margins strongly reflexed. Labrum not visible in dorsal view, concealed by clypeus, setose; setae thick, moderately long. Antennae with eight antennomeres (Fig. 6*C*); antennal club with three antennomeres, club longer than antennomeres 1–5 combined, glabrous, with microscopic (visible at >40×) punctures, punctures dense. Eyes developed, 1/3 of diameter visible on dorsal view.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc, setae long, slender.

Scutellum. Densely setose, apex rounded or slightly truncate, with few punctures.

Elytron. Convex, surface rugopunctate or striate, with short, sparse setae; sutural striae well developed from base to elytral apex; discal striae (if present) poorly defined.

Pygidium. 1.34× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 2.56× wider than long.

Legs (Fig. 6*D*, *E*). Protibia tridentate, basal tooth poorly developed, base of medial tooth 2/3 as wide as tibia in middle; protibial spur as long as or slighly shorter than protarsomere 1, nearly straight, slender. Protarsomere 5 shorter than tarsomeres 3 and 4 combined. Meso- and metatibiae laterally flattened, with two well-developed transverse carinae, carinae setose, setae thick, spine-like. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with well-developed process.

Genitalia (Fig. 6*F*, *G*). Phallobase 2.62× longer than parameres. Parameres dorsally fused, 1.31× longer than wide.

Allotype female

Length. 6 mm; maximum width 3.1 mm.

Colour. Testaceous.

Head (Fig. 6*H*). Frons convex on basal half, flat on apical half, frons rugose. Frontoclypeal suture evident, slightly curved, developed as transverse carina. Clypeus broadly rounded,

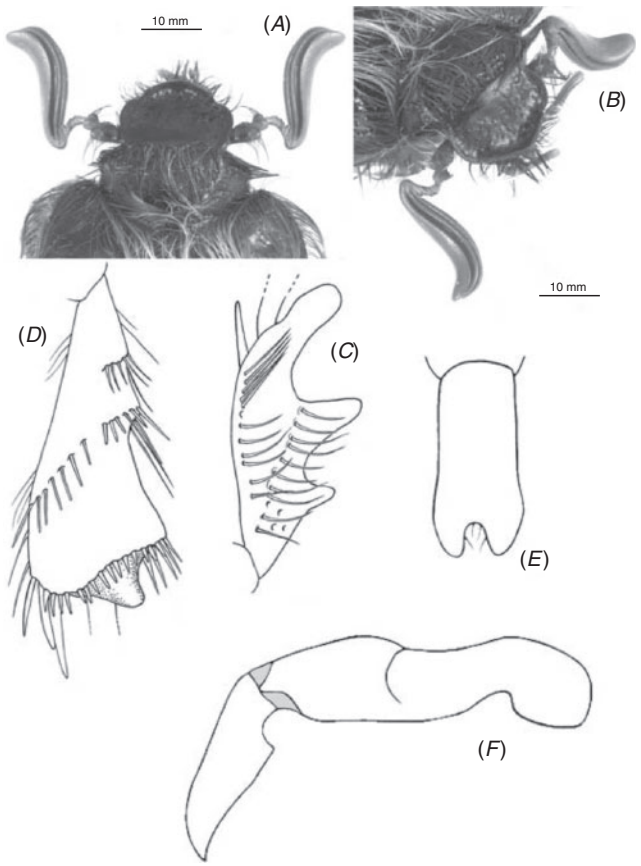

Fig. 11. *Neogutierrezia mirabilis*. *A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

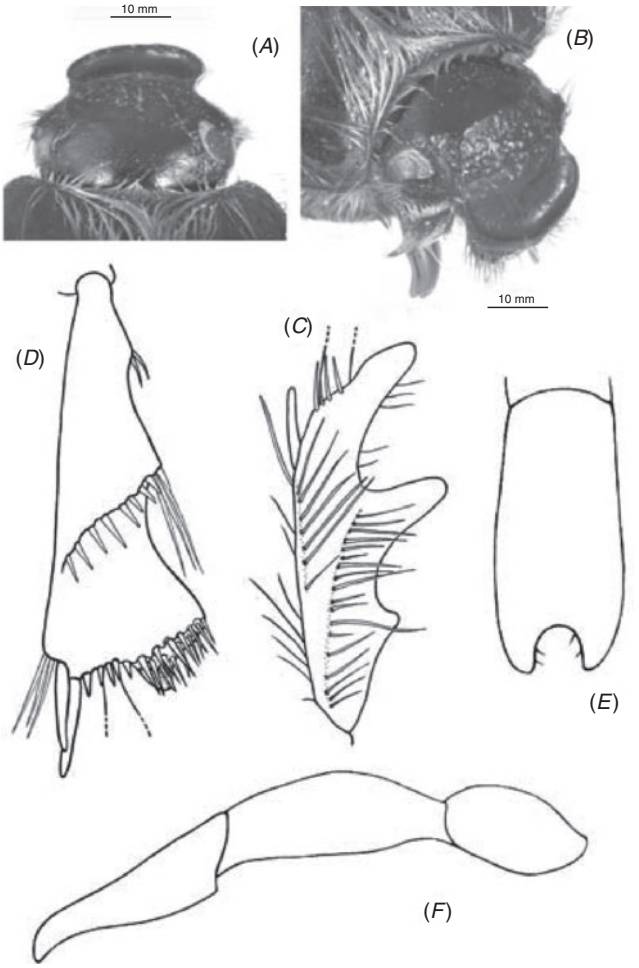

Fig. 12. *Neogutierrezia payuniensis*. *A*, *B*, head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

surface smooth. Apical margin slightly reflexed, lateral margins reflexed at apex, less reflexed towards base. Labrum not visible in dorsal view, concealed by clypeus. Mandibles external margin angulose, setose, flattened at apex; molar area poorly developed, weakly sclerotised. Maxillae poorly developed, fused with labium; palp with four palpomeres, palpomeres cylindrical, palpomere 4 as long as 2 and 3 combined, apex acute, sensory area groove-like, dorsolateral. Labium narrow, densely setose, setae long; labial palp with three cylindrical palpomeres. Antennae with six antennomeres (Fig. 6*I*); antennal club with three antennomeres, club shorter than antennomeres 1–3 combined, glabrous. Eyes small, slightly visible on dorsal view, ventrally globose. Eye canthus well developed, flattened, wide, with thin setae.

Pronotum. Convex, transverse, surface smooth on disc, slightly punctate on basal margin, slightly setose at apical 1/3, setae long, slender. Margins beaded. Anterior angles obtuse, posterior margins broadly rounded. Anterior margin concave, posterior margin sinuous; margins densely setose, setae long, slender.

Scutellum. Sparsely setose on margins, setae short, surface smooth, apex rounded.

Elytron. Convex, surface rugopunctate or striated, striae poorly developed.

Propygidium. Surface setose, setae short to long, slender; last abdominal spiracle on tergo–ventral suture.

Pygidium. 1.5× wider than long, exposed, not covered by elytra, surface setose, setae short to long, slender; pygidial apex rounded.

Venter. Surface rugose to punctate, moderately to densely setose, setae long, slender, hair-like. Metasternum large, 1.85× wider than long. Sternites not narrowed in middle, sternite 5 as long as 1–4 combined, 6th slightly longer than 5th; sternites 5 and 6 separated by a membrane; last abdominal sternite emarginated at middle.

Legs (Fig. 6*J*). Procoxa as long as femur, procoxal and femoral surface setose, setae long, slender. Protibia tridentate, basal tooth short, medial tooth base 3/4 as wide as tibia in middle; protibial spur as long as protarsomere 1, straight, slender. Protarsomere 5 shorter than tarsomeres 3 and 4 combined. Tarsi with one tarsal claw, claw small, simple, slender. Meso- and metatibiae laterally flattened, with two transverse carinae, carinae setose, setae thick; basal carina weak, medial carinae well developed. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight, tarsal insertion with notch. Meso- and

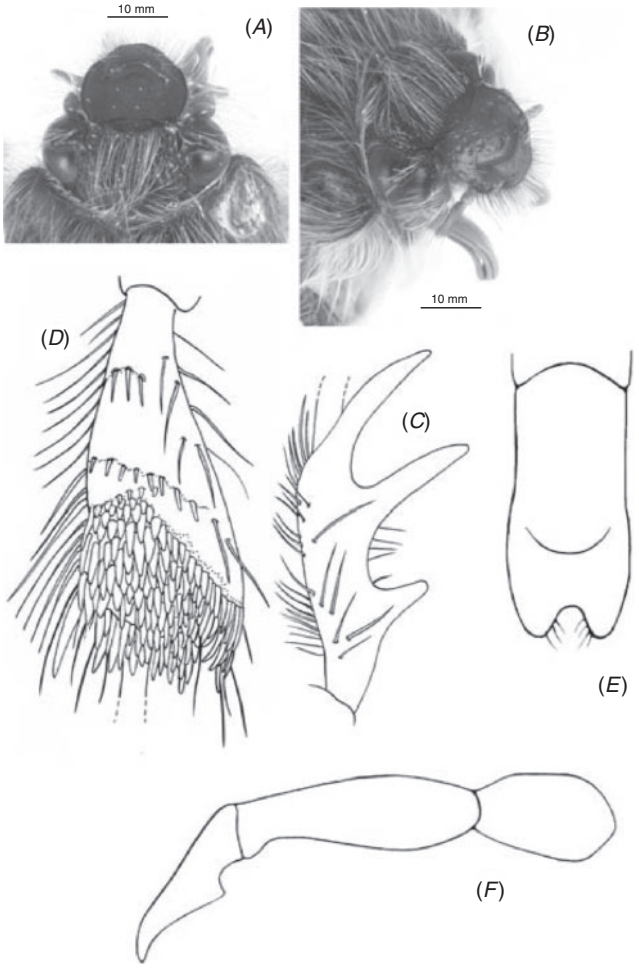

Fig. 13. *Neogutierrezia scutata. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

metatibial spurs contiguous, on tarsal notch, tarsal insertion dorsal to spurs. Mesotibial inner spur longer than tarsomere 1, outer spur shorter than tarsomere 1, spurs slightly curved. Meso-and metatarsi with tarsomeres 1–4 decreasing in length, tarsomere 5 longer than 4. Metatibial apex with well-developed process.

Variation

Males

Length. 6.5–8.25 mm; width: 4–4.63 mm. Specimens of *N. araucana* show either seven or eight antennomeres (when seven, 3–4 fused, antennal club always presents three antennomeres). Colour of elytra testaceous to dark brown, pronotum light brown to reddish-black.

Females

Length. 6.00–6.38 mm; width 3.10–3.19 mm. The single female paratype does not differ significantly from allotype.

Distribution

ARGENTINA. Neuquén: Arroyo Picún Leufú and RN 40 [39°01′33.29″S, 70°03′45.24″W] (13).

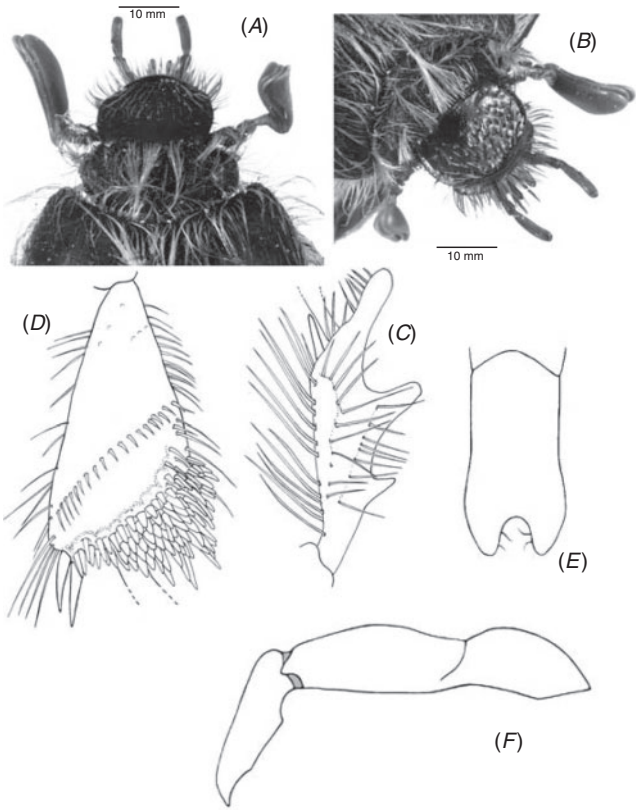

Fig. 14. *Neogutierrezia variabilis. A*, *B*, Head; *C*, protibia; *D*, metatibia; *E*, *F*, male genitalia.

Temporal distribution

January (13).

Biology

Males of *N. araucana* were found flying early in the morning in a sandy area. Males actively fly close to ground surface seeking for females, females are flightless and presumably they spend their live underground and only come to surface to mate (Martínez 1973). Feeding habits and larvae are unknown.

Neogutierrezia bicolor Ocampo and Ruiz-Manzanos sp. nov.

(Fig. 7*A–F*)

Material examined

Holotype. 1♂ (IAZA), Argentina: Neuquén, Sierra Cuchillo Curá, 975 m, M. Gentili, 15.xii.1974.

Paratype. **ARGENTINA:** 1♂ (IAZA), Neuquén, Sierra Cuchillo Curá, 975 m, M. Gentili, 15.xii.1974.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: colour, head, pronotum, scutellum, venter, pygidium and legs

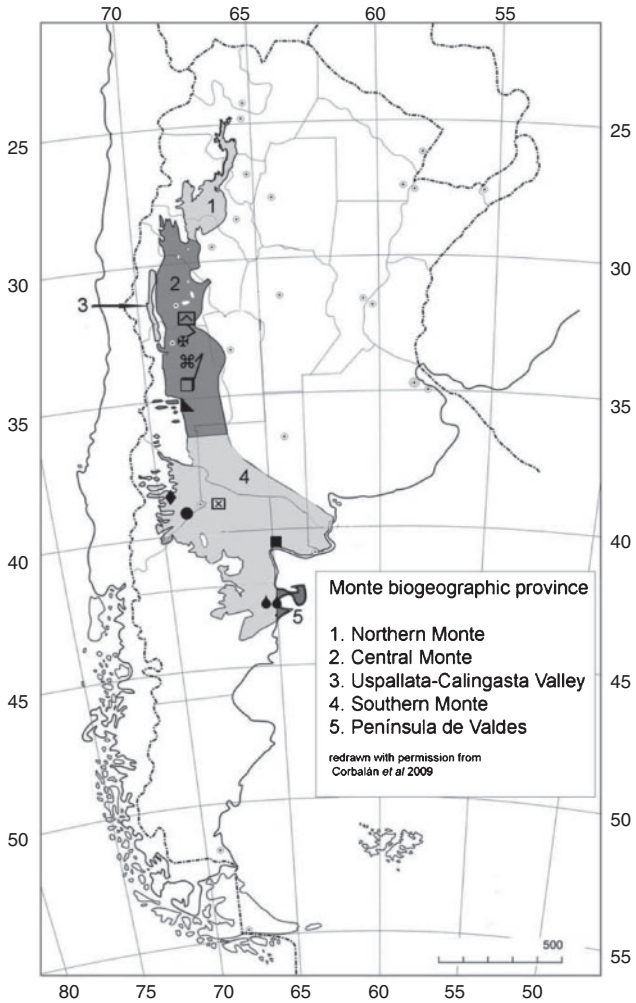

Fig. 15. Distribution map of *Neogutierrezia* species. Black square, *N. affinis*; circle, *N. araucana*; diamond, *N. bicolor*; black drops, *N. chelii*; open square, *N. galileoi*; pound, *N. lagosae*; rectangle with ×, *N. mirabilis*; triangle, *N. payuniensis*; cross, *N. scutata*; rectangle with inverted v, *N. variabilis*.

dark brown, elytra brown; clypeus rounded; clypeal apical margin strongly reflexed, lateral margins poorly reflexed; frontoclypeal suture obsolete; labrum not visible in dorsal view; antenna with nine antennomeres, funicle–club joint on base of club; eyes 1/3 of ventral diameter visible in dorsal view; pronotum smooth; scutellum with apex rounded; protibial basal tooth poorly developed, medial tooth base 2/3 as wide as tibia in middle; protibial spur longer than protarsomere 1; protarsomere 5 shorter than 3 and 4 combined; metatibial carinae well developed; metatibial spurs well developed; metatibial apex with poorly-developed process.

Description

Holotype male

Length. 8.75 mm; maximum width 4.88 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs dark brown, elytra brown.

Fig. 16. Collecting site showing the habitat of *Neogutierrezia scutata* in Reserva Provincial Telteca, Mendoza province, Argentina.

Fig. 17. Map of predictive distribution of *Neogutierrezia* species based on 21 bioclimatic variables, soil type (categorical), and elevation. Lighter colours indicate higher probabilities of occurrence.

Head (Fig. 7*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, sparsely setose, setae short. Frontoclypeal suture obsolete. Clypeal shape broadly rounded,

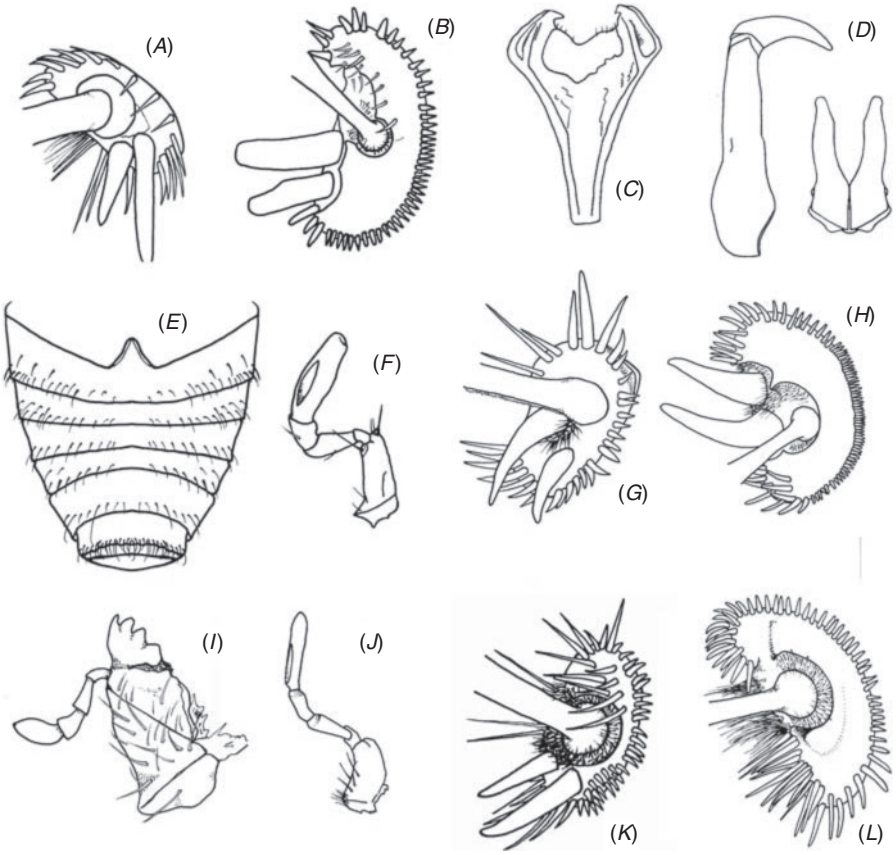

Fig. 18. *A*, *B*, *E*, *F*, *Pseudoliogenys flavidus*: *A*, mesotibial apex; *B*, metatibial apex; *E*, pygidium; *F*, mandible.*C*, *D*, *Acylochilus curvidens*: *C*, spiculum gastrale; *D*, male genitalia. *G, H, J*, *Acylochilus ottianus*: *G*, mesotibial apex; *H*, metatibial apex; *J*, mandible. *I, K, L*, *Myloxena bruchiana*: *I*, mandible; *K*, mesotibial apex; *L*, metatibial apex.

surface smooth. Clypeal anterior margin strongly reflexed, lateral margin poorly reflexed. Labrum not visible in dorsal view, concealed by clypeus, setose; setae thick, moderately long. Antennae with nine antennomeres; antennal club with three antenomeres, club as long as antennomeres 1–6 combined, glabrous, with microscopic (visible at >40×) punctures, punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface smooth.

Scutellum. Densely setose, apex rounded, with few punctures.

Elytron. Convex, surface rugopunctate, glabrous. Sutural striae well developed from base to elytral apex.

Pygidium. 1.38× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 2.27× wider than long.

Legs (Fig. 7*C*, *D*). Protibia tridentate, basal tooth poorly developed, medial tooth base 2/3 as wide as tibia in middle; protibial spur nearly straight, slender, longer than protarsomere 1 (protarsi missing except left tarsomere 1). Meso- and metatibiae laterally flattened, with two well-developed transverse carinae, carinae setose, setae thick, spine-like. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with poorly-developed process.

Genitalia (Fig. 7*E*, *F*). Phallobase 1.41× longer than parameres. Parameres dorsally fused, 2.56× longer than wide.

Female

Unknown.

Variation

Length 8.63–8.75 mm; width 4.75–4.87 mm. Protarsomere 5 is shorter than protarsomeres 3–4 combined in the single paratype.

Etymology

From the Latin '*bicolor*', indicating the notorious colour pattern of this species.

Distribution

ARGENTINA. Neuquén: Sierra Cuchillo Curá [38°40′44.51″S, 70°22′59.99″W] (2).

Temporal distribution

December (2).

Biology

Nothing is known about the biology of *N. bicolor*.

Neogutierrezia chelii Ocampo & Ruiz-Manzanos sp. nov.

(Fig. 8*A–F*)

Material examined

Holotype. ♂ (IAZA), Argentina: Chubut, Puerto Madryn, CENPAT, G. Cheli, 2.xii.2003.

Paratypes. **ARGENTINA:** 2♂ (IAZA), Chubut, Puerto Madryn, CENPAT, G. Cheli, 2.xii.2003; 1♂ (IAZA), Chubut, Telsen, G. Cheli, 22.xi.2003.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus pentagonal; clypeal margins strongly reflexed; frontoclypeal suture evident, developed as transverse carina; labrum visible in dorsal view; antenna with nine antennomeres, antennal club with four antennomeres, funicle–club joint basal; eyes 1/3 of ventral diameter visible in dorsal view; pronotum densely punctated; scutellum with apex rounded, slightly pointed; protibial basal tooth poorly developed, medial tooth base as wide as tibia in middle; protibial spur as long as protarsomere 1; protarsomere 5 as long as 3 and 4 combined; metatibial carinae well defined; metatibial spurs well developed; metatibial apex with poorly-developed process.

Description

Holotype male

Length. 7.38 mm; maximum width 4.00 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs brown; elytra yellowish brown.

Head (Fig. 8*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, glabrous or sparsely setose, setae moderately long. Frontoclypeal suture evident developed as a transverse carina. Clypeal shape pentagonal, surface smooth to sparsely punctate. Clypeal margins strongly reflexed. Labrum visible in dorsal view, rectangular, setose, setae thick, moderately long. Antennae with nine antennomeres (Fig. 8*A*); antennal club with four antennomeres, club longer than antennomeres 1–5 combined, glabrous, with microscopic (visible at >40×) puncture; punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface densely punctate, setose; setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate or striate, sparsely setose, setae minute, sutural striae well developed from base to elytral apex, discal striae poorly defined.

Pygidium. 1.03× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 1.35× wider than long.

Legs (Fig. 8*C*, *D*). Protibia tridentate, basal tooth poorly developed, medial tooth base as wide as tibia in middle;; protibial spur nearly straight as long as tarsomere 1, slender. Protarsomere 5 as long as 3 and 4 combined. Meso- and metatibiae laterally flattened, with two well-developed transverse carinae, carinae setose, setae thick, spine-like. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with process poorly developed (Fig. 8*D*).

Genitalia (Fig. 8*E*, *F*). Phallobase 1.69× longer than parameres. Parameres dorsally fused, 2.91× longer than wide.

Female

Unknown.

Variation

Length 6.38–7.38 mm; width 3.25–4.00 mm. The rest of the type series does not differ significantly from the holotype.

Etymology

We take great pleasure in naming this species after our colleague and enthusiastic entomologist Germán Cheli (Centro Nacional Patagónico [CENPAT]) who has contributed to our knowledge of *Neogutierrezia* by collecting the specimens of this new species.

Distribution

ARGENTINA. Chubut: Pto. Madryn [42°46′59.99″S, 65°30′06.0″W] (3), Telsen [42°26′15.70″S, 66°56′34.27″W] (1)

Temporal distribution

November (1), December (3).

Biology

Specimens of *N. chelii* were collected with unbaited pitfall traps on sandy areas near the seashore (Puerto Madryn) and inland (Telsen).

Neogutierrezia galileoi Ocampo & Ruiz-Manzanos sp. nov.

(Fig. 9*A–F*)

Material examined

Holotype. ♂ (IAZA), Argentina: Mendoza, Santa Rosa, Ñacuñán, S. Lagos, 18.vii–16.viii.1998.

Paratype. **ARGENTINA:** 1 ♂ (IAZA), Mendoza, Ñacuñán, A. Roig, ii.1974

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus rounded; clypeal lateral margins slightly reflexed, apical margin reflexed; frons not reflexed near frontoclypeal suture; frontoclypeal suture evident, obsolete in middle; labrum slightly visible in dorsal view; funicle–club joint basal; eyes 1/3 of ventral diameter visible in dorsal view; scutellum with apex rounded, slightly pointed; protibial basal tooth well developed, medial tooth base narrower than tibia in middle; protibial spur longer than protarsomere 1; protarsomere 5 longer than 3–4 combined; metatibial carinae well defined; metatibial apex outer surface with short, dark, spine-like setae; metatibial outer spur poorly developed; metatibial apex lacking process.

Description

Holotype male

Length. 9.00 mm; maximum width 4.75 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs black; elytra brown, with darker suture.

Head (Fig. 9*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, not reflexed near frontoclypeal suture, setose, setae long. Frontoclypeal suture evident, curved, obsolete in middle. Clypeus broadly rounded, surface smooth. Clypeal lateral margins slightly reflexed; anterior margin reflexed. Labrum slightly visible in dorsal view, mostly concealed by clypeus, setose; setae thick, moderately long. Antennae with eight antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–5 combined, glabrous, with microscopic (visible at >40×) punctures, punctures dense; funicle–club joint on base of club. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Convex, transverse; surface densely punctate on disc except small longitudinal area in middle, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc, setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate, glabrous; sutural striae well developed from base to elytral apex, discal striae poorly defined.

Pygidium. 1.42× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 1.98× wider than long.

Legs (Fig. 9*C*, *D*). Protibia tridentate, basal tooth well developed, medial tooth base narrower than tibia in middle; protibial spur slender, longer than protarsomere 1. Protarsomeres dorsoventrally flattened, tarsomere 5 longer than 3 and 4 combined. Meso- and metatibiae laterally flattened, with two transverse carinae, carinae setose, setae thick, spine-like. Mesotibial outer edge with fringe of long spine-like setae, inner edge nearly straight. Metatibial apex rounded, with thick, short, spine-like setae. Metatibial apex with outer surface with short, spine-like, dark setae. Metatibial outer spur highly reduced. Metatibial apex lacking process. Metatarsomere 1 outer surface mostly glabrous (metatarsomeres 2–5 missing).

Genitalia (Fig. 9*E*, *F*). Phallobase 2.41× longer than parameres. Parameres dorsally fused, 1.71× longer than wide.

Female

Unknown.

Variation

Length 8.75–9 mm; width 4.5–4.75 mm. Some specimens possess antennna with seven antennomeres.

Etymology

We name this species in honour to Galileo Galilei. It has been 400 years since he invented the telescope, a major step for our knowledge of the Universe and a symbol of discovery.

Distribution

ARGENTINA. Mendoza: Reserva de la Biosfera Ñacuñán [34°02′40.92″S, 67°54′33.84″W] (2).

Temporal distribution

February (1), July–August (1).

Biology

Nothing is known about the biology of *N. galileoi*.

Neogutierrezia lagosae Ocampo & Ruiz-Manzanos sp. nov.

(Fig. 10*A–F*)

Material examined

Holotype. ♂ (IAZA), Argentina: Mendoza, Ñacuñan, A. Roig, ii.1974.

Paratypes. **ARGENTINA:** 3♂ (IAZA), Mendoza, Ñacuñan, A. Roig, ii.1974; 5♂ (IAZA), Mendoza, Dto. Santa Rosa, Ñacuñan, S. Lagos, 20.x–22.xi.1997; 1♂ (IAZA), Mendoza, Sta Rosa, Ñacuñán, S. Lagos, 29.xii.1997–07.ii.1998; 1♂ (IAZA), Mendoza, Sta Rosa, Ñacuñan, S. Lagos, 22.xi.1997; 1♂ (IAZA), Mendoza, Reserva de la Biósfera Ñacuñán, E. Ruiz-Manzanos, 05–06.ii.05.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus pentagonal; clypeal lateral margins not reflexed, apical margin strongly reflexed; frons slightly reflexed on apex, before suture; frontoclypeal suture evident, obsolete in middle; labrum slightly visible in dorsal view; funicle–club joint basal; eyes 1/3 of ventral diameter visible in dorsal view; scutellum with apex rounded, slightly pointed; protibial basal tooth well developed, medial tooth as wide as tibia in middle; protibial spur as long as protarsomere 1; protarsomere 5 shorter than 3 and 4 combined; metatibial carinae well developed; metatibial spurs well developed; metatibial apex with poorly-developed process.

Description

Male

Length. 7.75 mm; maximum width 4.25 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs reddish-brown; elytra brown.

Head (Fig. 10*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, glabrous or sparsely setose; setae moderately long; frons slightly reflexed on apex, before suture. Frontoclypeal suture evident, curved, not developed as transverse carina, obsolete in middle. Clypeal shape pentagonal, surface smooth to sparsely punctate. Lateral margins not reflexed, apical margin strongly reflexed. Labrum slightly visible in dorsal view, mostly concealed by clypeus, setose; setae thick, moderately long. Antennae with nine antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–6 combined, glabrous, with microscopic (visible at >40×) punctures, punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc; setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate or striate, with short, sparse setae; sutural striae well developed from base to elytral apex, discal striae (if present) poorly defined.

Pygidium. 1.11× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 1.36× wider than long.

Legs (Fig. 10*C*, *D*). Protibia tridentate, basal tooth well developed, base of medial tooth as wide as tibia in middle; protibial spur nearly straight as long as tarsomere 1, slender. Protarsomere 5 shorter than tarsomeres 3 and 4 combined. Meso- and metatibiae laterally flattened, with two well-developed transverse carinae, carinae setose, setae thick, spine-like. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spur at apex. Metatibial apex with process poorly developed (Fig. 10*D*).

Genitalia (Fig. 10*E*, *F*). Phallobase 2.33× longer than parameres. Parameres dorsally fused, 2.14× longer than wide.

Female

Unknown.

Variation

Length 6.13–7.75 mm; width 3.38–4.25 mm. Some specimens present antennae with eight antennomeres.

Etymology

We take great pleasure in naming this species after our friend and colleague Dr Susana Lagos (Instituto Argentino de Investigaciones de las Zonas Aridas), who has contributed to our knowledge of *Neogutierrezia* and collected most of the specimens of this new species.

Distribution

ARGENTINA. Mendoza: Dpto. Santa Rosa: Reserva de la Biosfera de Ñacuñan [34°02′40.92″S, 67°54′33.84″W] (11).

Temporal distribution

October–November (5), November (1), December–February (1), February (4).

Biology

Nothing is known about the biology of *N. lagosae*. Specimens were collected with un-baited pitfall traps located beneath *Prosopis* trees (Leguminosae).

Neogutierrezia mirabilis Martínez

(Fig. 11*A*–*F*)

Neogutierrezia mirabilis Martínez, 1953: 2. – Martínez 1973: 31 (redescription).

Neogutierrezia mirabilis mirabilis Martínez. – Martínez, 1975: 249 (catalog); Lacroix, 2007: 377 (catalog).

Neogutierrezia mirablis mirablis Martínez. – Evans, 2003: 220 (incorrect spelling; catalog).

Material examined

Holotype. ♂, Argentina: Río Negro, Cnel. Gómez, J. Grasso, xi.1946 (MACN).

Paratype. **ARGENTINA:** 1♂, Río Negro, Cnel. Gómez, J. Grasso, xi.1946 (CMNC).

Other material examined. 1♂, **ARGENTINA:** Río Negro, Cervantes, G. Zurbarán, 7.i.2006 (IAZA).

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus rounded, slighly punctate towards apex; frontoclypeal suture evident, developed as transverse carina; labrum not visible in dorsal view; antenna with nine antennomeres, funicle–club joint on base of club; scutellum with apex rounded; protibial basal tooth poorly developed, medial tooth base 2/3 as wide as tibia in middle; protibial spur as long as protarsomere 1; protarsomere 5 as long as 3 and 4 combined; Meso- and metatibial basal carinae weak, medial carinae well developed; metatibial apex with well-developed process.

Description

Male

Length. 8.13 mm; maximum width 4.38 mm.

Colour. Head, pronotum and scutellum dark brown; elytra brown with dark-brown margins; venter, pygidium and legs dark brown.

Head (Fig. 11*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, setose; setae moderately dense, moderately long. Frontoclypeal suture evident, curved, developed as a transverse carina. Clypeus broadly rounded, surface smooth at base becoming punctate towards apex. Apical margin slightly reflexed, lateral margins slightly reflexed at apex, less reflexed towards base. Labrum not

visible in dorsal view, concealed by clypeus, setose; setae thick, moderately long. Antennae with nine antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–6 combined, glabrous, with microscopic (visible at >40×) punctures, punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3, setae long, slender.

Scutellum. Densely setose, apex rounded, with few punctures.

Elytron. Convex, surface rugopunctate; sutural striae well developed from base to elytral apex.

Pygidium. 1.16× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 2.22× wider than long.

Legs (Fig. 11*C*, *D*), Protibia tridentate, basal tooth short, base of medial tooth 2/3 as wide as tibia in middle; protibial spur as long as protarsomere 1, nearly straight, slender. Protarsomere 5 as long as 3 and 4 combined. Meso- and metatibiae laterally flattened, with two transverse carinae, carinae setose; setae spine-like, thick; basal carina weak, medial carina well developed. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with well-developed process.

Genitalia (Fig. 11*E*, *F*). Phallobase 2.07× longer than parameres. Parameres 2.14× longer than wide.

Female

Unknown.

Variation

Length 7.75–9 mm; width 4.15–5.01 mm. The rest of the type series does not differ significantly from the holotype.

Distribution

ARGENTINA. Río Negro: Coronel Gómez [39°01′59.99″S, 67°38′59.99″W] (2), Cervantes [39°02′59.99″S, 67°23′00″W] (1).

Temporal distribution

January (1), November (2).

Biology

Adults of this species were collected at light (Martínez 1953).

Neogutierrezia payuniensis Ocampo & Ruiz-Mazanos sp. nov.

(Fig. 12*A*, *F*)

Material examined

Holotype. ♂ (IAZA), Argentina: Mendoza, Dto. Malargüe, Reserva la Payunia, F. Ocampo, A.B.T. Smith, S. Roig-Juñent, G. Flores, 6.i.03.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: clypeus rounded; clypeal margins strongly reflexed; labrum slightly visible in dorsal view; antenna with eight antennomeres, funicle–club joint on base of club; eyes 1/3 of ventral diameter visible in dorsal view; pronotum smooth; scutellum with apex rounded; protibial basal tooth poorly developed, medial tooth base as wide as tibia in middle; protibial spur as long as protarsomere 1; protarsomere 5 as long as 3 and 4 combined; Meso- and metatibial basal carina weak, medial carinae well developed; metatibial spurs well developed; metatibial apex with well-developed process.

Description

Male

Length. 7.37 mm; maximum width 4 mm.

Colour. Head, pronotum, scutellum, venter, pygidium, elytra and legs brown.

Head (Fig. 12*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, sparsely setose, setae moderately long. Frontoclypeal suture evident. Clypeal shape broadly rounded, surface smooth. Clypeal margins strongly reflexed. Labrum slightly visible in dorsal view, concealed by clypeus, setose; setae thick, moderately long. Antennae with eight antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–5 combined, glabrous, with microscopic (visible at >40×) punctures; punctures dense. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface smooth, setose at apical 1/3 on middle, setae long, slender.

Scutellum. Densely setose, apex rounded, with few punctures.

Elytron. Convex, surface rugopunctate, sparsely setose, setae minute; sutural striae well developed from base to elytral apex.

Pygidium. 1.03× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose, setae long, slender, hair-like. Metasternum large, 2.13× wider than long.

Legs (Fig. 12*C*, *D*). Protibia tridentate, basal tooth poorly developed, base of medial tooth as wide as tibia in middle; protibial spur nearly straight, slender, as long as protarsomere 1 (protarsi missing except left tarsomere 1). Meso- and metatibiae laterally flattened, with two transverse carinae, carina setose, setae thick, spine-like; basal carina weak, medial carina well developed. Meso- and metatibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Meso- and metatibial apex rounded, with thick, short, spine-like setae. Metatibia with two well-developed spurs at apex. Metatibial apex with well-developed process.

Genitalia (Fig. 12*E*, *F*). Phallobase 1.39× longer than parameres. Parameres dorsally fused, 2.71× longer than wide.

Female

Unknown.

Etymology

We name this species 'payuniensis' from the Type locality in Reserva Provincial La Payunia.

Distribution

ARGENTINA. Mendoza: Reserva Provincial la Payunia, Puesto Los Relinchos [36°07′01′S, 68°48′01′W] (1).

Temporal distribution

January (1).

Biology

The only known specimen of *N. payuniensis* was collected at a mercury vapor light in a sandy area.

Neogutierrezia scutata Ocampo & Ruiz-Manzanos, sp. nov.

(Figs 3, 13*A–F*)

Material examined

Holotype. ♂ (IAZA), Argentina: Mendoza, 1 km N Reserva Telteca, 540 m, 32°18′40′S 67°54′08′W, F.C.Ocampo, A.B.T.Smith, 4.i.2003.

Paratypes. **ARGENTINA:** 15 ♂ (11 IAZA, 4 CMNC), Mendoza, 1 Km N Reserva Telteca, 540 m, 32°18′40′S 67°54′08′W, F.C.Ocampo, A.B.T.Smith, 4.i.2003 (8 paratypes preserved in 95% etanol); 2 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, 9.xii.2002.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: Clypeus rounded, anterior half with well-developed shield-like dorsal projection; clypeal margins not reflexed; frons slightly reflexed near frontoclypeal suture; frontoclypeal suture evident, obsolete in middle; labrum slightly visible in dorsal view; antenna with 8 antennomeres; funicle–club joint on1/3 of first club antennomere; eyes 1/2 of ventral diameter visible in dorsal view; scutellum with apex rounded, slightly pointed; medial tooth base 2/3 as wide as tibia in middle; protibial spur highly reduced; protarsomere 5 shorter than 3–4 combined; metatibial carinae poorly defined; metatibial apex outer surface densely covered with short, yellowish, spine-like setae; metatibial outer spur highly reduced; metatibial apex lacking process.

Description

Male holotype

Length: 6.00 mm; Maximum width: 3.00 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs brown; elytra light yellow.

Head (Figs 3, 13*A, B*). Frons convex on basal half, flat on apical half, apical half rugose slightly reflexed near frontoclypeal suture, setose; setae long. Frontoclypeal suture evident, curved, obsolete in middle. Clypeus broadly rounded, surface smooth. Clypeal margins not reflexed; anterior half with well-developed shield-like dorsal projection. Labrum slightly visible in dorsal view, mostly concealed by clypeus, setose, setae thick, moderately long. Antennae with 8 antennomeres; antennal club with 3 antennomeres, club longer than antennomeres 1–5 combined, glabrous, with microscopic (visible at >40× magnification) punctures; punctures dense; funicle–club joint on 1/3 of first club antennomere. Eyes developed, 1/2 of ventral diameter visible on dorsal view, ventrally globose.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc; setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate, with short, sparse setae, sutural striae well developed from base to elytral apex, discal striae poorly defined.

Pygidium. 1.07× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose, setae long, slender, hair-like. Metasternum large, 1.47× wider than long.

Legs (Fig. 13*C, D*). Protibia tridentate, basal tooth well developed, base of medial tooth 2/3 as wide as tibia in middle; protibial spur highly reduced. Protarsomeres dorsoventrally flattened; tarsomere 5 shorter than 3–4 combined. Meso- and metatibiae laterally flattened, with two transverse carinae, carinae setose, metatibial carinae poorly defined, setae thick. Mesotibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Metatibial apex rounded, with thick, short, spine-like setae. Metatibial apex with outer surface densely covered with short, spine-like, yellowish setae. Metatarsomere 1 outer surface setose; setae moderately dense. Metatibial outer spur highly reduced. Metatibial apex lacking process.

Genitalia (Fig. 13*E, F*). Phallobase 2.17× longer than parameres. Parameres dorsally fused, 2.40× longer than wide.

Female

Unknown.

Variation

Length 6–8.63 mm; Width 3–3.75 mm. Some specimens of *N. scutata* possess elytra yellowish to testaceous in colour. The rest of the type series does not differ significantly from the holotype.

Etymology

The specific name is derived from the Latin *scutatus* (*fem scutata*), meaning shield-shaped, in reference to the shield-like projection on the clypeus of this species, which makes it easily distinguishable from all other in the genus.

Distribution

ARGENTINA. Mendoza: Reserva Provincial Telteca [32°18′40′S, 67°54′08′W] (5).

Temporal distribution

January (3), December (2).

Biology

Specimens of *N. scutata* were collected at light (UV) on sand dunes.

Neogutierrezia variabilis Ocampo & Ruiz-Manzanos, sp. nov.

(Fig. 14*A–F*)

Material examined

Holotype. 1 ♂ (IAZA), Argentina: Mendoza, Lavalle, Telteca, G. Flores, S. Roig, 2.xi–1.xii.1994.

Paratypes. **ARGENTINA:** 4 ♂ (IAZA), Mendoza, Telteca, 32°23′06′S 68°02′99′W, G. Flores, S. Roig, 25.ix–25.xi.1996; 2 ♂ (IAZA), Mendoza, Telteca, 32°23′06′S 68°02′99′W, G. Flores, S. Roig, 17.viii–24.ix.1996; 2 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, S. Roig, 24.xi.1995–15.ii.1996; 1 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, S. Roig, 24.xii.1995–15.ii.1996; 1 ♂ (IAZA), Mendoza, Telteca, 32°23′06′S 68°02′99′W, G. Flores, S. Roig, 25.ix–05.xii.1995; 1 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, S. Roig, 06.xi–03.xii.1996; 1 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, 03.ii–14.iii.1995; 1 ♂ (IAZA), Mendoza, Lavalle, Telteca, G. Flores, S. Roig, 03.xii.1996–06.i.1997.

Diagnosis

This species is distinguished from all other species in the genus *Neogutierrezia* by the following combination of characters: Clypeus rounded; clypeal lateral margins not reflexed, anterior margin reflexed; frons slightly reflexed near frontoclypeal suture; frontoclypeal suture evident, obsolete in middle; labrum slightly visible in dorsal view; antenna with nine antennomeres; funicle–club joint on 1/3 of first club antennomere; eyes 1/3 of ventral diameter visible in dorsal view; scutellum with apex rounded, slightly pointed; protibial medial tooth base 2/3 as wide as tibia in middle; protibial spur as long as protarsomere 1; protarsomere 5 shorter than 3 and 4 combined; metatibial carinae poorly defined; metatibial apex outer surface densely covered with short, yellowish, spine-like setae; metatibial spurs well developed; metatibial apex lacking process.

Description

Male

Length. 7.75 mm; maximum width 3.63 mm.

Colour. Head, pronotum, scutellum, venter, pygidium and legs brown; elytra yellowish-brown.

Head (Fig. 14*A*, *B*). Frons convex on basal half, flat on apical half, apical half rugose, slightly reflexed near frontoclypeal suture, setose; setae long. Frontoclypeal suture evident, curved, obsolete in middle. Clypeus broadly rounded, surface smooth. Clypeal lateral margins not reflexed; anterior margin reflexed. Labrum slightly visible in dorsal view, mostly concealed by clypeus, setose; setae thick, moderately long. Antennae with nine antennomeres; antennal club with three antennomeres, club longer than antennomeres 1–6 combined, glabrous, with microscopic (visible at >40×) punctures; punctures dense; funicle–club joint basal. Eyes developed, 1/3 of ventral diameter visible on dorsal view.

Pronotum. Surface densely punctate on disc, sparsely punctate on sides, setose at apical 1/3 and centre of pronotal disc, setae long, slender.

Scutellum. Densely setose, apex rounded or slightly pointed, with few punctures.

Elytron. Convex, surface rugopunctate, glabrous, sutural striae well developed from base to elytral apex, discal striae poorly defined.

Pygidium. 1.14× wider than long.

Venter. Surface rugose to punctate, moderately to densely setose; setae long, slender, hair-like. Metasternum large, 2.33× wider than long.

Legs (Fig. 14*C*, *D*). Protibia tridentate, basal tooth well developed, medial tooth base 2/3 as wide as tibia in middle; protibial spur slender, shorter than or as long as protarsomere 1. Protarsomeres dorsoventrally flattened, tarsomere 5 shorter than 3 and 4 combined. Meso- and metatibiae laterally flattened, with 2 transverse carinae; carinae setose, metatibial carinae poorly defined, setae thick. Mesotibial outer edge with fringe of long, spine-like setae, inner edge nearly straight. Metatibial apex rounded, with thick, spine-like, short setae. Metatibial apex with outer surface densely covered with short, spine-like, yellowish setae. Metatibia with two spurs well developed. Metatarsomere 1 outer surface setose; setae moderately dense. Metatibial apex lacking process.

Genitalia (Fig. 14*E*, *F*). Phallobase 2.06× longer than parameres. Parameres dorsally fused, 2.07× longer than wide.

Female

Unknown.

Variation

Length 6.50–8.63 mm; width 3.50–4.38 mm. Colour of elytra yellowish to dark brown. Some specimen with protibial basal tooth of poorly developed.

Etymology

From the Latin ‘*variabilis*’ meaning different or changeable, referring to the different colour and sizes observed in the type series of this species.

Distribution

ARGENTINA. Mendoza: Reserva Natural Telteca [32°18′40′S, 67°54′08′W] (14).

Temporal distribution

August–September	(2),	September–November	(4),
September–December	(1),	November–December	(2),
December–January	(1),	December–February	(3),
February–March	(1).		

Biology

Nothing is known about the biology of *N. variabilis*. Specimens were collected with un-baited pitfall traps located beneath *Prosopis flexuosa* D.C. (Leguminosae).

Key to *Neogutierrezia* species

1. Metatibial apex covered with small spine-like setae (brush-like) (Figs 3, 9*C*, 13*C*, 14*C*) 2
   Metatibial apex not covered with setae (Figs 5*C*, 6*C*, 7*C*, 8*C*, 10*C*, 11*C*, 12*C*) 4
2. Metatibia with outer apical spur reduced, visible only at high magnification (40×) (Figs 9*C*, 13*C*) 3
   Metatibia with outer apical spur developed, visible at low magnification (10–20×) (Fig. 14*C*) ..... *N. variabilis* Ocampo & Ruiz-Manzanos, sp. nov.
3. Metatibia with apical transverse carina partially covered by setae, carina poorly defined; protibial spur poorly developed, nearly obsolete (Fig. 13*D*) ..... *N. scutata* Ocampo & Ruiz-Manzanos, sp. nov.
   Metatibia with apical transverse carina not covered with setae, transverse carina well defined and with fringe of setae (Fig. 9*C*); protibial spur reduced but clearly visible, at least twice as long as wide ..... *N. galileoi* Ocampo & Ruiz-Manzanos, sp. nov.
4. Clypeus with anterior and lateral margins strongly reflexed and complete 5
   Clypeus with anterior margin strongly reflexed, developed as dorsal process, lateral margin reflexed or not, if reflexed, not continuous with anterior process 6
5. Metatibia with apical process poorly developed (Fig. 10*C*) ..... *N. lagosae* Ocampo & Ruiz-Manzanos, sp. nov.
   Metatibia with apical process well developed (Fig. 11*C*) ..... *Neogutierrezia mirabilis* Martínez
6. Frons and clypeus placed in different horizontal plane, frontoclypeal surface interrupted by a transversal ridge (Figs 5*A*, *B*, 8*A*, *B*) 7
   Frons and clypeus placed on same horizontal plane (although surface convex), frontoclypeal surface continuous, not interrupted by a transversal ridge (Figs 6*A*, *B*, 7*A*, *B*, 12*A*, *B*) 8
7. Antennal club with four antennomeres. Foretibiae with basal tooth poorly developed (Fig. 8*D*) ..... *N. chelii* Ocampo & Ruiz-Manzanos, sp. nov.
   Antennal club with three antenommeres. Foretibiae with basal tooth well developed (Fig. 5*D*) ..... *Neogutierrezia affinis* Martínez
8. Pronotal disc glabrous, surface smooth. Clypeus not pointed at apex 9
   Pronotal disc setose at basal 1/2 on each side, surface punctate. Clypeus slightly pointed at apex ..... *Neogutierrezia araucana* Martínez
9. Labrum distinctively visible on dorsal view; antenna with eight antennomeres; body colour uniform, dark brown ..... *N. payuniensis* Ocampo & Ruiz-Manzanos, sp. nov.
   Labrum not visible in dorsal view or slightly visible beneath clypeus; antenna with nine antennomeres; body bicolored, head and pronotum black, elytra brown ..... *N. bicolor* Ocampo & Ruiz-Manzanos, sp. nov.

Biogeography

Distributional data of species in the genus indicate that *Neogutierrezia* is endemic to the Monte Biogeographic province in Argentina (Figs 15, 16). Annual rainfall in this region ranges from 80 to 250 mm and the annual mean temperature ranges from 11 to 17°C. The area is a mosaic of two types of vegetation: shrubby steppes (dominant) and open woodlands of *Prosopis* spp. trees that occur in places where ground water is available (particularly in Northern and Central Monte). The distribution of *Neogutierrezia* species coincides with the distribution of *Larrea* spp., *Bulnesia* spp. and *Plectocarpha* spp. (all Zygophyllaceae). The range of other plants of the shrub steppes is also determined by edaphic factors, and these species are adapted to azonal conditions with saline, sandy or waterlogged soils.

Biogeographically, the Monte is an interesting region forming an extensive transitional zone between Neotropical and Andean assemblages (Morrone 2006; Rundel *et al*. 2007). South American deserts constitute very old habitats as elucidated from the presence of many endemic suprageneric and generic taxa well-adapted to arid conditions (Roig Juñent *et al*. 2001; Ocampo and Hawks 2006*b*). In the Monte, endemic, relictual taxa coexist with other endemic taxa that would have rapidly speciated in the area but with sister groups in neighbouring non-desert regions (ex. Eucraniini distributed in Monte, Phanaeini (distributed mostly in tropical South and Central America [Scarabaeinae]). Thus, the Monte biota has multiple origins with most genera being from Neotropical origin followed by groups with Patagonian affinities.

The Monte, according to Roig-Juñent *et al*. (2001), has five natural areas. Each area in the Monte is recognised based on species assemblages of reptilian, anuran, insects and plants (Roig-Juñent and Flores 2001; Ocampo 2004; Rundel *et al*. 2007): Northern Monte, Central Monte, Uspallata–Calingasta valley, Southern Monte and Península Valdés. Species of *Neogutierrezia* are distributed in two natural areas of the Monte (Fig. 15). The *N. lagosae–N. scutata* clade has species distributed in Central Monte, the *N. araucana–N. mirabilis* clade has species distributed in Southern Monte and the *N. chelii–N. bicolor* clade also occurs in the Southern Monte, although closer to the transitional zone with the Patagonian region. The historical biogeographic reconstruction of *Neogutierrezia* provides support that there is a sister-region relationship between the Central and Southern Monte.

The Central Monte extends from La Rioja province to southern Mendoza. It contacts widely with the Chaco in the north-east and with the Espinal in the east. This area has several elements that belong to the Neotropical and Patagonian biotas (Roig-Juñent *et al*. 2001). The Central Monte and Southern Monte are connected as a gradual transition without a clear biogeographical barrier in a long fringe ~300 km wide, and with elements from both the Southern and the Central Monte. The Southern Monte continues in eastern Neuquén, Río Negro and the southern tip of Buenos Aires province. Southern Monte constitutes the largest natural area within the Monte and is rich in endemic species.

The Monte is also characterised by the presence of sand dune communities. Sand dunes occupy large discontinuous extensions and have their own endemic insect fauna (Fig. 16). All known species of *Neogutierrezia* are associated with sand dune habitats and the available data indicate a high level of endemicity. Although female specimens are only known for one species of *Neogutierrezia*, we infer that brachyptery might be an attribute of most, if not all, females in the genus and a condition that contributes to the high endemicity owing to the low dispersal ability of the species.

Morphological divergence of *Neogutierrezia*, known geographic distribution and predictive distribution (Fig. 17) suggest that the genus constitutes an endemic taxon in Central and Southern Monte. Our hypothesis suggests that *Neogutierrezia* is a relictual ruteline genus and has evolved *in situ* and adapted to the extreme arid conditions of the desert sand dunes. Other scarab genera that corroborate this

hypothesis are *Neophaenognatha* (Aclopinae) and *Eucranium* (Scarabaeinae).

The relationship between species and their overall environment can cause different distribution patterns. In general, isolated distributions observed over a small area are likely to result from a patchy distribution of resources driven by micro-topographic variation or habitat fragmentation (Guisan and Thuillier 2005). On the other hand, extended and gradual distributions are likely to be controlled by climatic variables (Guisan and Thuillier 2005). Results of SDM suggest that the distribution and biogeography of species of *Neogutierrezia* fit within the first pattern. According to the SDM, four variables contribute to 94.6% of the prediction in the Maxent model: soil (51.4%), seasonality (33.6%), precipitation of the warmest quarter (6%) and annual precipitation (3.6%). According to our results, soil type has a crucial influence on the distribution of species of *Neogutierrezia*. This variable, along with seasonality, has the most influence in the predictive model. Three kinds of soils: arenosols, calcisols and fluviosols, contribute to species distribution patterns in the genus *Neogutierrezia*. Second in importance for predicting the distribution of *Neogutierrezia* species is seasonality, which might be relevant to the survivorship of this species on a scenario of climate change.

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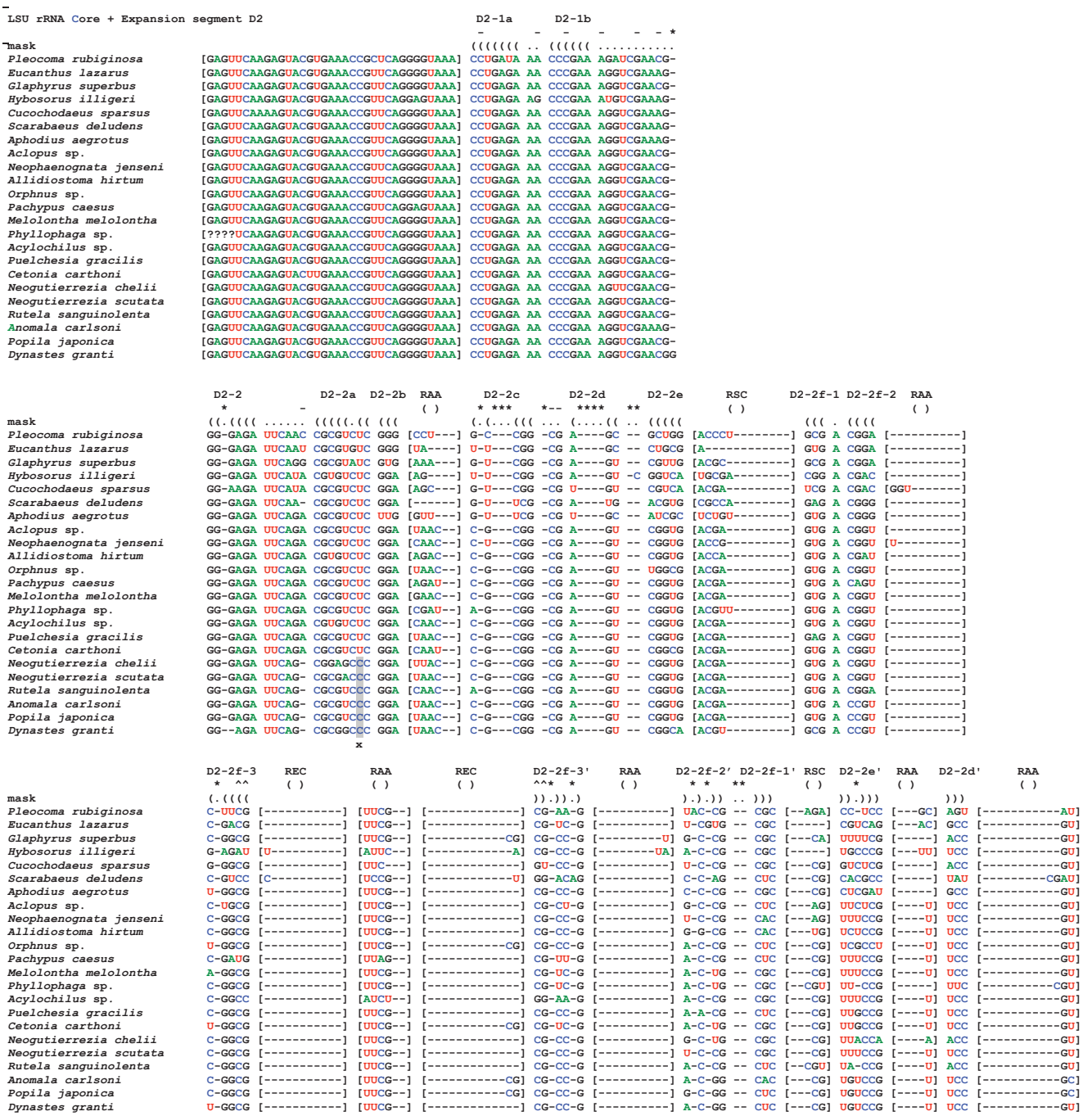
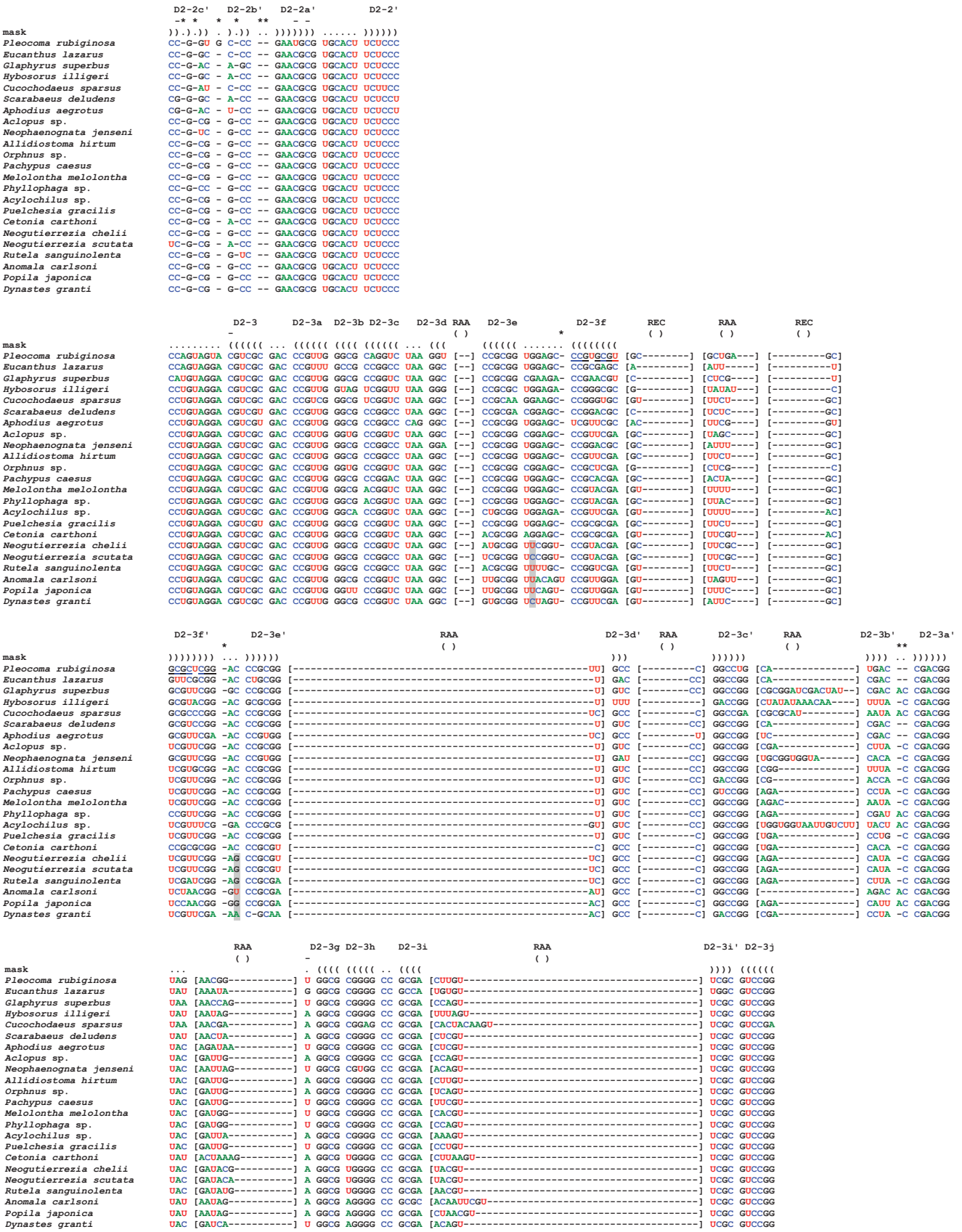
Appendix 1. Morphological data matrix
Polymorphisms: A = 1&2, B = 0&1

Taxa	Characters					
	0000000001	1111111112	2222222223	3333333334	4444444445	555
	1234567890	1234567890	1234567890	1234567890	1234567890	123
Neogutierrezia araucana	A211BB0010	1111011B00	1311211101	1010102111	1112011101	001
Neogutierrezia mirabilis	1211010110	1111011200	1211211101	0010102011	1112011101	001
Neogutierrezia affinis	1212000010	1111011A?0	1311211101	0010102111	1112011101	001
Neogutierrezia scutata	1221120211	1111111101	1311211111	0111102111	2220211101	001
Neogutierrezia variabilis	12A112021B	1111011200	1211211111	BB11102A11	2210211101	001
Neogutierrezia galileoi	1210010011	1111011100	1211211111	0010102011	2220111101	001
Neogutierrezia lagosae	12A0120111	1111011A00	1211211111	0010102111	1111011101	001
Neogutierrezia chelii	2212000012	1111011210	1211211111	1010102111	1111011111	001
Neogutierrezia payuniensis	2210000011	1111011100	1411211101	1010102111	1112011112	001
Neogutierrezia bicolor	2210000010	1111011200	1411211101	1010102111	1111011111	001
Acylochilus ottianus	2130000000	0001000100	1001111101	0000001001	0011000000	101
Acylochilus curvidens	2130000000	0001000100	1001111101	0000001001	0011000000	101
Pseudoliogenys flavidus	2100211001	0010100A00	0101000001	0000000100	0010001000	110
Myloxena bruchiana	0000010002	1022101200	1210111110	2001001100	3100022000	112
Rutela lineola	3040220000	1101111200	0121210011	0000110011	3110011100	011
Anomala testaceipennis	3000320000	1122111200	010011001B	A100212011	3110011000	010

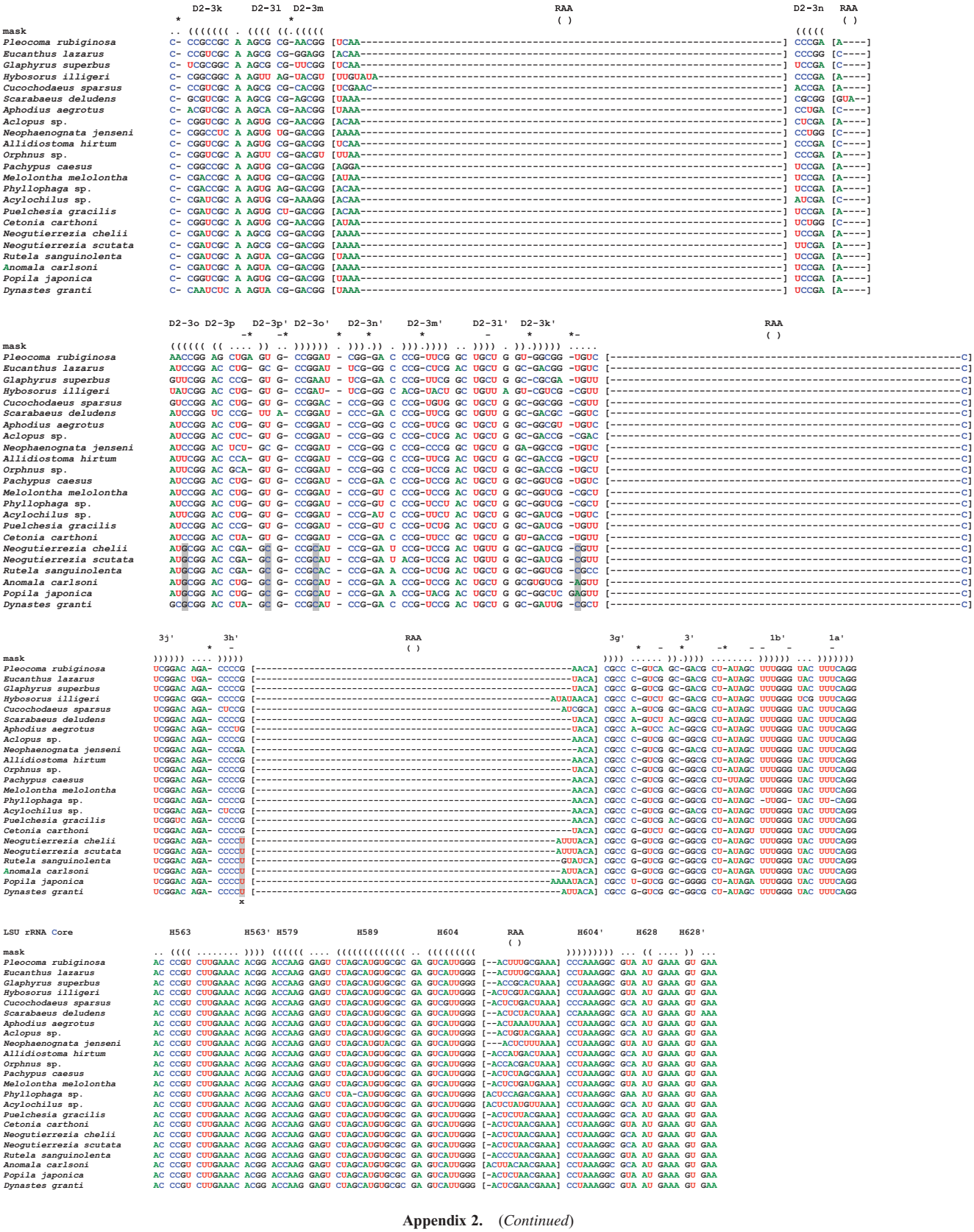
Appendix 2. Structural alignment of the expansion segments D2 and D3 of the 28S rRNA gene region from 23 scarabaeoid species

Notation above the sequences: Complementary strands are indicated with a prime (e. g. strand X hydrogen bonds with strand X′ to form helix X); regions of alignment ambiguity (RAA), slipped-strand compensation (RSC) and expansion and contraction (REC) are placed within square brackets; nucleotide positions within helices involved in hydrogen-bonding are depicted by parentheses in the mask; single insertions (*) and deletions (–) are noted as in Kjer *et al*. (2001). Note: the D2 alignment has not been amended for these 23 taxa but from the alignment of 103 beetle sequences by Marvaldi *et al*. (2009), and thus gaps and insertions may correspond to taxa not presented in this figure. Unambiguous synapomorphies of the '*Neogutierrezia* clade' are shaded; those marked with an 'x' are unique changes

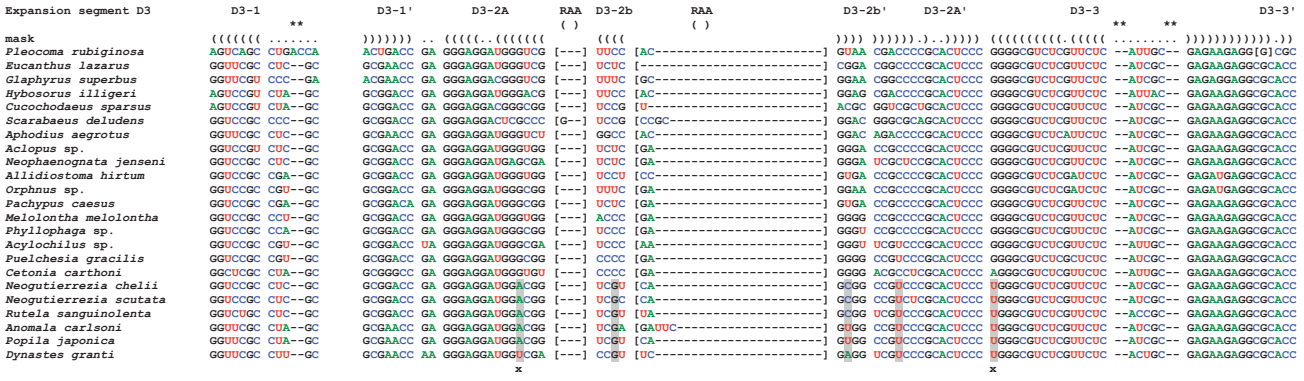


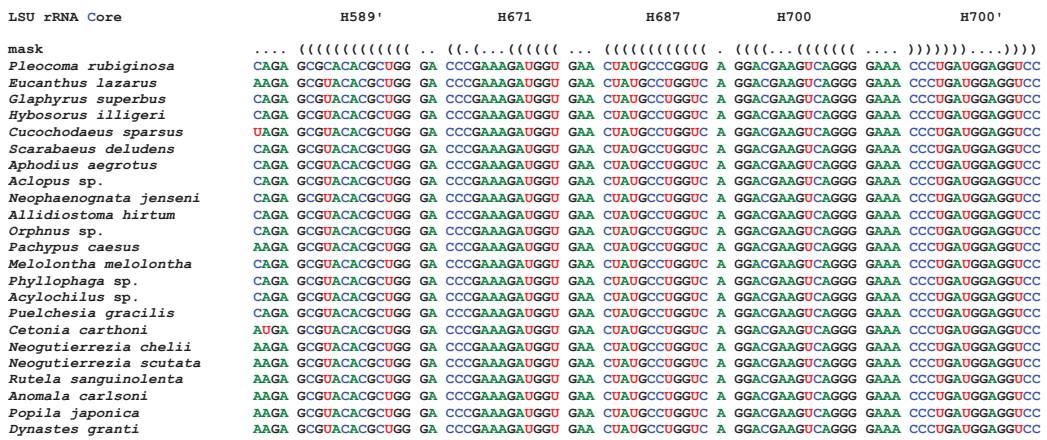


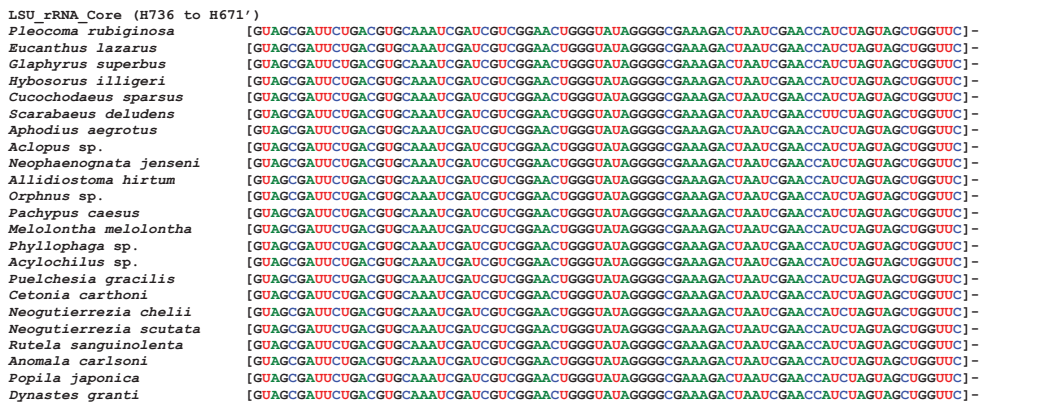
Appendix 2. (*Continued*)



Appendix 2. (*Continued*)







Appendix 2. (*Continued*)