



## ***Qorimayus*, a new genus of relictual, high-altitude harvestmen from western Argentina (Arachnida, Opiliones, Gonyleptidae) reveals trans-Andean phylogenetic links**

LUIS E. ACOSTA

*Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Cátedra de Diversidad Biológica II, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA), Av. Vélez Sarsfield 299, X5000JJC Córdoba, Argentina. E-mail: luis.acosta@unc.edu.ar*

### **Abstract**

A new genus of Gonyleptidae Pachylinae, *Qorimayus* **gen. nov.**, is described to place the high-altitude species originally named *Parabalta alticola* Ringuelet, endemic to Sierra de Famatina, western Argentina. While classical exomorphological features do not separate this new genus from *Parabalta* Roewer or *Pachyloides* Holmberg (to which the species was formerly combined), male genitalic features, especially the shape of the ventral process of stylus, differ clearly. In turn, penis morphology suggests the systematic relationship of *Qorimayus* **gen. nov.** with the Chilean genera *Metabalta* Roewer and *Nanophareus* Roewer. A cladistic analysis was performed to test the phylogenetic affinities of the new genus; 28 terminals were used, comprising selected species of *Parabalta*, *Pachyloides*, *Metabalta* and *Nanophareus*, as well as other Gonyleptidae to represent the ‘subtropical’ and the ‘Chilean’ opiliofaunistic elements; the most external outgroups included one cosmetid, one metasarcid and one nomoclastid. Results supported the recognition of *Qorimayus* as an independent genus, and its close relationship with the Chilean genera *Metabalta* and *Nanophareus*. A detailed redescription of *Qorimayus alticola* **comb. nov.**, along with some habitat notes are given. The presumed zoogeographical links of this endemic species with the central Chilean opiliofauna are briefly discussed.

**Key words:** Opiliones, Gonyleptidae, Neotropics, Argentina, Famatina, systematics, endemics

### **Introduction**

As generally agreed, arid environments represent a severe limitation for harvestmen distribution and diversity (Ringuelet 1957, 1959, Acosta 2002, Curtis & Machado 2007, Santos 2007). In contrast, humid and densely forested regions, like the tropical Atlantic forest in Brazil or the temperate Valdivian forest in southern Chile, harbor a high –sometimes impressive– degree of harvestmen diversity (Ringuelet 1959, Pinto-da-Rocha *et al.* 2005). In Argentina, the prevalence of arid and semi-arid environments is correlated with the comparatively low overall species richness of harvestmen (Acosta 2002). The whole western side of this country (east of the Andes, comprising the provinces Mendoza, San Juan, and a part of La Rioja and Catamarca) is an extensive area with marked xeric character. Together with the Patagonia, it forms a kind of broad ‘arid diagonal’, which separates the two main opilio-logical sectors in Argentina (central-northeast and Chilean), and was once accordingly thought to contain not even a single representative of the order (*i.e.*, it was considered a ‘negative’ region for Opiliones, Ringuelet 1957, 1959). The 400 mm annual isohyet was then presumed to be the physical boundary that determined presence or absence of harvestmen (Ringuelet 1957, 1959).

With time, several harvestmen populations were discovered in some favored locations, scattered over this rigorous area (Ringuelet 1962, Maury & Roig Alsina 1982, Maury 1986, Acosta 1995, 2002). All these populations proved to be isolated and restricted, and were assumed to represent a relictual condition. Relictual harvestmen from the provinces Catamarca, La Rioja, San Juan and northern Mendoza survive in reduced sites, either in high-altitude spots, often more humid than surrounding lowlands, or in protected valleys (Ringuelet 1962, Maury & Roig Alsina 1982, Acosta 1995). Those from southern Mendoza and Neuquén are associated to caves (Maury 1986, 1988). The

very first of these relictual harvestmen was found in Sierra de Famatina, La Rioja province, and was communicated and described by Ringuélet (1962) as *Parabalta alticola* Ringuélet, 1962 (Opiliones, Gonyleptidae, Pachylinae). When the definition of *Parabalta* Roewer, 1913 was revised and the genus became limited to the Chilean representatives (Acosta 1996a), *P. alticola* was provisionally reallocated to genus *Pachyloides* Holmberg, 1878. Further analysis revealed that this species represents a separate genus on its own, not related to either *Parabalta* or *Pachyloides*, which is described in this paper as *Qorimayus* **gen. nov.**

## Material and methods

**Cladistic analysis.** A cladistic analysis was performed to investigate the systematic affinities of *Qorimayus alticola* (Ringuélet, 1962) **comb. nov.** Considering that a prior  $\alpha$ -taxonomic inspection suggested a close relationship with the Chilean genera *Metabalta* Roewer, 1913, and *Nanophareus* Roewer, 1929 (as discussed below), the ingroup consisted of the focal species, *Q. alticola*, together with two species of *Metabalta* (*Metabalta efformata* Roewer, 1929; *Metabalta geniculata* Roewer, 1929) and all seven species currently assigned to *Nanophareus* (Hara 2016). Two previous cladistic analyses (Hara *et al.* 2012, Hara 2016) determined the monophyly of *Nanophareus*, although they were not conclusive regarding the genus position within Gonyleptidae. *Qorimayus alticola* was believed to represent a relictual species of ‘subtropical’ or ‘Brazilian’ origin (Ringuélet 1962, 1978, Maury 1986, Acosta 2002), but the aforementioned affinity with Chilean taxa seems to depict a trans-Andean link instead. Accordingly, terminals were selected to comprise a sample of both ‘subtropical’ and Chilean gonyleptid genera. For the subtropical elements, two species of *Eusarcus* Perty, 1833, *Discocyrtus testudineus* (Holmberg, 1876), *Acanthopachylus aculeatus* (Kirby, 1818) and three species of *Pachyloides* were included; members of the Chilean opiliofauna comprised two species of *Pachylus* Koch, 1839, two species of *Metagyndes* Roewer, 1913, two of *Parabalta*, *Neogonyleptes kaschii* (Sørensen, 1902) and *Tumbesia aculeata* Roewer, 1930. The addition of *Parabalta* and *Pachyloides* species in the analysis served, at the same time, to evaluate the affinities of *Qorimayus alticola* with two genera to which this species was formerly combined (Ringuélet 1962, Acosta 1996a, 2002). Outside the family, the most external outgroups included one cosmetid, *Gryne orensis* (Sørensen, 1879), one metasarcid, *Incasarcus diana* Kury & Maury, 1998, and one nomoclastid, *Quindina albomarginis* (Chamberlin, 1925), all sharing with Gonyleptidae their inclusion in the unranked clade Laminata (Kury & Villarreal 2015). *Quindina albomarginis* was selected to root the trees. It should be noted that the primary aim of this analysis was to investigate the relationships of *Qorimayus*, not to test the internal subdivisions of Gonyleptidae. In total, the study comprised 28 terminals; a taxon list, along with a detail of sources used for scoring the character states, is given in Table 1.

The analysis was made upon 76 morphological characters (Table 2): 7 refer to the carapace, 7 to the dorsal scutum, 1 to chelicerae, 13 to pedipalps, 4 to the venter, 2 to the tarsi, 1 to leg III, 21 to leg IV of male and 20 to penis morphology. The selection of characters was inspired in a small proportion in Kury & Villarreal (2015) and Hara (2016), but most were new or adapted to the special features of the terminals used (principally the focal genus *Qorimayus*, and its presumed relatives, *Metabalta* and *Nanophareus*). This is especially true for some meaningful features of pedipalps, chelicerae and penis, which were little exploited in the analysis of Hara (2016), and were here split into several characters for a more accurate description. Not all species of *Nanophareus* were available for direct inspection (Table 1), but the good descriptions and superb illustrations provided by Hara *et al.* (2012) and Hara (2016) enabled me to score them for most characters. The matrix was edited using Mesquite version 2.75 (freely available at <http://mesquiteproject.org>), then exported as Nona file (.ss) for analysis. The final list of characters and states is displayed in Table 2. Only eight characters were considered additive (Table 2) because they refer to meaningful structures (*e.g.*, pedipalps, chelicerae, penis) and were deemed to undoubtedly represent true transformation series across the states recognized. The matrix of 28 terminals x 76 characters is given in Table 3.

Tree search under parsimony was executed in the software TNT version 1.1 (Goloboff *et al.* 2008), with the ‘traditional search’ strategy (1000 replicates, 5 random seed, branch swapping with SPR). Memory setting was raised to 10000 trees. The parsimony analysis was made under implied weights (IW: Goloboff 1993), a method that assigns higher weight to the characters having less homoplasy, together with a run based on equal weights (EW, non-weighted) for comparison. IW analyses were performed for nine concavity (k) values (1, 3, 6, 9, 12, 15, 18, 30, 50). Lower values of k penalize more strictly the homoplastic characters; when values of k increase, the function tends to become similar to the linear function of EW. Trees obtained with TNT were then opened in Winclada 1.00.08 (Nixon

1999) to trace character changes (unambiguous optimization), and to calculate the tree length (L), the consistency index (Ci) and the retention index (Ri). Branch supports were assessed with TNT, by calculating three resampling-based measures: standard Bootstrap (sample with replacement), jackknifing (independent character removal, 36% removal probability) and symmetric resample (33% change probability). In all cases, support was calculated for each concavity value, upon 500 replicates using traditional search, with frequency difference (GC) as output, and a cut-off = 1 (branches below this value are collapsed).

**TABLE 1.** List of terminals used in the cladistic analysis, with a detail of voucher specimens and/or literature references employed to complete the scores.

Species	Source
NOMOCLASTIDAE	
1. <i>Quindina albomarginis</i> (Chamberlin, 1925)	Panamá: Barro Colorado island, viii-1985 (G. Mora), 1 ♂, 1 ♀ (LEA 000.419) + Kury & Villarreal (2015)
COSMETIDAE	
2. <i>Gryne orensensis</i> (Sørensen, 1879)	Argentina: Formosa, Herradura, Camping La Florencia, 3-xii-2011 (J. Vergara, R. González-Ittig, L. Vaschetto), 5 ♂♂, 4 ♀♀, 2 juv. (CDA 000.879)
METASARCIDAE	
3. <i>Incasarcus diana</i> Kury & Maury, 1998	Kury & Maury (1998)
GONYLEPTIDAE	
4. <i>Eusarcus hastatus</i> Sørensen, 1884	Argentina: Misiones, Comandante Andresito, 13-xii-2012 (L. Vaschetto, R. González Ittig, S. Poljak), 5 ♂♂, 1 ♀ (CDA 000.877) + Hara & Pinto-da-Rocha (2010)
5. <i>Eusarcus gemignanii</i> (Mello-Leitão, 1931)	Argentina: Córdoba, Pampayasta Sur (en hormiguero), 14-ii-2008 (L. Acosta, M. García, G. Rubio), 1 ♂, 2 ♀♀ (LEA 000.407) + Hara & Pinto-da-Rocha (2010)
6. <i>Discocyrtus testudineus</i> (Holmberg, 1876)	Argentina: Entre Ríos, Strobel, 24-iii-2006 (L. Acosta, M. García), 8 ♂♂, 19 ♀♀ (LEA 000.358)
7. <i>Pachyloides cochuna</i> Acosta, 1996a	Argentina: Tucumán, Río Cochuna, 10-i-1993 (L. Acosta, D. Hauser), 1 ♂, 1 ♀ paratypes (CDA 000.017) + Acosta (1996a)
8. <i>Pachyloides hades</i> Acosta, 1989	Argentina: Tucumán, El Infiernillo, 5-iv-1986 (L. Acosta), 1 ♂, 1 ♀ paratypes (CDA 000.014) + Acosta (1989)
9. <i>Pachyloides thorellii</i> Holmberg, 1878	Uruguay: Cerro Arequita (453 pies), 3-xii-1997 (L. Acosta) 3 ♂♂, 8 ♀♀ (LEA 000.151)
10. <i>Acanthopachylus aculeatus</i> (Kirby, 1818)	Uruguay: Cerro Arequita, 3-xii-1997 (L. Acosta), 3 ♂♂, 4 ♀♀ (LEA 000.150)
11. <i>Pachylus chilensis</i> (Gray, 1833)	Chile: Región V (Valparaíso), Prov. Valparaíso, Puente “Las Bayicas”, 24 km E de Algarrobo, 5-xi-1988 (E. Maury), 5 ♂♂, 6 ♀♀ (MACN-Ar 28824)
12. <i>Pachylus crassus</i> (Roewer, 1943)	Chile: Región VII (Maule), Prov. Curicó, Las Tablas, 27/29-ix-1983 (L. Peña), 3 ♂♂, 6 ♀♀ (MACN-Ar 28799)
13. <i>Metagyndes martensii</i> (Sørensen, 1902)	Chile: Prov. Aisén, Río Mañihuales, 30 km NE de Pto. Aisén, 9-xii-1986 (E. Maury), 16 ♂♂, 29 ♀♀, 4 juv. (MACN)
14. <i>Metagyndes pulchella</i> (Loman, 1899)	Argentina: Neuquén, Villa La Angostura, 15-i-2003 (S. Rizzuto), 1 ♂, 2 ♀ (LEA 000.391)
15. <i>Parabalta</i> sp.	Chile: Prov. Choapa, Quebrada Playa Agua Dulce, 46 km N Los Vilos, 5-6-xi-88 (E. Maury), 1 ♂, 1 ♀ (MACN)
16. <i>Parabalta cristobalia</i> (Roewer, 1943)	Chile: Prov. Petorca, entre Cachagua y La Laguna, 11-i-1984 (A. Roig), 1 ♂, 1 ♀ (MACN)
17. <i>Neogonyleptes karschii</i> (Sørensen, 1902)	Chile: Osorno, Camping “No me olvides”, 7 km E de Entrelagos, 30-i-1991 (E. Maury), 1 ♂, 1 ♀, 1 juv. (MACN)

.....continued on the next page

TABLE 1. (Continued)

Species	Source
18. <i>Tumbesia aculeata</i> Roewer, 1930	Chile: Malleco, Cordillera Nahuelbuta, 1200m, 22-xii-1985 (A. Roig A.) 12 ♂♂, 3 ♀♀ (MACN)
19. <i>Metabalta geniculata</i> Roewer, 1929	Chile: Valparaíso. Typus, 1 ♂, 1 ♀ (SMF RII 951/32)
20. <i>Metabalta efformata</i> Roewer, 1929	- Chile: Sierra de Chillón (Chillán). Typus, 2 ♂ (SMF RII 952/33). - Chile: Maule, W of Cauquenes, 350 m, 4-x-1983, 1 ♂ (AMNH) - Chile. VII Región (Maule), Prov. Linares, Bullileo, Parral, 5-8.xii.1990 (L.E. Peña), 4 ♂, 2 ♀ (AMNH)
21. <i>Qorimayus alticola</i> (Ringuelet, 1962)	This paper
22. <i>Nanophareus palpalis</i> Roewer, 1929	“Chile”, 1 ♂ lectotype, 1 ♂, 2 ♀ paralectotypes (designated by Hara <i>et al.</i> 2012; SMF 986/1) + Hara <i>et al.</i> (2012)
23. <i>Nanophareus bipartitus</i> Hara, Pinto-da-Rocha & Kury, 2012	Hara <i>et al.</i> (2012)
24. <i>Nanophareus bosqenublado</i> Hara, Pinto-da-Rocha & Kury, 2012	Chile: Aconcagua, Los Molles (elev. 2 m, under succulent rock cover along coast, 9-i-1985 (N.I. Platnick & O.F. Francke), 4 ♂♂ (AMNH) + Hara <i>et al.</i> (2012)
25. <i>Nanophareus bicornutus</i> Hara, 2016	- Chile: Region V (Valparaíso), Petorca, Quebrada Huaquén, Pichichuy (elev. 10 m), 2-x-1992 (N. Platnick, P. Goloboff & K. Catley), 2 ♂♂, 1 juv. (AMNH) - Chile: Aconcagua, Los Molles (elev. 2 m, under succulent rock cover along coast, 9-i-1985 (N.I. Platnick & O.F. Francke), 1 ♂ (AMNH) (same vial as <i>N. bosqenublado</i> ) + Hara (2016)
26. <i>Nanophareus araucanus</i> Hara, Pinto-da-Rocha & Kury, 2012	Hara <i>et al.</i> (2012)
27. <i>Nanophareus maipu</i> Hara, 2016	Hara (2016)
28. <i>Nanophareus polyhastatus</i> Hara, 2016	Hara (2016)

**Taxonomic methods.** Descriptions are based on all specimens available, rather than on a single one. To take into account the sexual dimorphism and to avoid repetitions, the exomorphological description is arranged in three parts: features referable to both male and female; then dimorphic features of males; finally, the same for females. Taxonomic terminology follows Acosta *et al.* (2007) regarding armature (an acute cuticular projection is a ‘spine’ if articulated in a socket, or an ‘apophysis’ when smoothly emerging from the tegument without a limit), topological terms in appendages (prolateral, retrolateral), and notation of the tarsal formula. For pedipalp spination, large spines are indicated as “I”, smaller ones as “i”, and the smallest spines (either bristle-like or with very small or no sockets) as dots (.); square brackets are used to denote contiguous spines sharing the same tegumentary elevation. Measurements are given in mm. Prosoma (carapace) length was measured from the front margin (median) to the angle formed in sulcus I by the two halves of area I. Since the ocular mound rises with no limit from the carapace, its height was taken from the inferior border of the eyes up to the apophysis tip, its width between the external borders of the eyes. Macrosetae patterns on the penis ventral plate (VP) were described according to Kury & Villarreal (2015).

Specimens were examined, measured and drawn using a Leica Wild M3C stereomicroscope with camera lucida. Male genitalia were studied and illustrated in temporary mounts in glycerol (Acosta *et al.* 2007) using a Nikon E200 microscope with camera lucida. Line drawings were digitized using the free software Inkscape 0.92 (<https://inkscape.org/>). The map was composed with the free, open source geographic information system software QGIS 2.4.0 - Chugiak (<https://qgis.org/>), using spatial data freely available at <http://www.diva-gis.org/Data>. Taxon names contained herein have been registered in ZooBank (Official Register of Zoological Nomenclature) (<http://zoobank.org/>), so that they have their respective LSID (Life Science Identifier). ZooBank LSIDs can be resolved and the associated information viewed through a web browser by appending the LSID to the prefix ‘<http://zoobank.org/>’.

Abbreviations of morphological terms: Pp: pedipalp, Cx: coxa, Troc: trochanter, Fe: femur, Pat: patella, Ti:

tibia, VP: ventral plate of penis; vps: ventral process of stylus. Abbreviations for clades: G: Gonyleptidae; MG: *Metabalta* group (*Qorimayus* + *Metabalta* + *Tumbesia* + *Neogonyleptes* + *Nanophareus*); M+Nan(+): *Metabalta* + (*Nanophareus*+NT); M: *Metabalta* spp.; Na(+): *Nanophareus*+NT; Na: *Nanophareus*; NT: *Neogonyleptes*, *Tumbesia*; PG: *Pachylus* group (*Metagyndes* spp. + *Acanthopachylus* + *Pachylus*); PsG: *Pachyloides* group (*Pachyloides* spp. + *Parabalta* spp.); e-s: eyes separated clade.

Acronyms of collections: AMNH: American Museum of Natural History, New York; CDA: Colección de Arácnidos, Cátedra de Diversidad Biológica II, FCEFYN, Universidad Nacional de Córdoba; LEA: Collection Luis E. Acosta, Córdoba (housed in CDA); MACN: Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires; SMF: Senckenberg Museum, Frankfurt.

**TABLE 2.** Characters, character states and coding, as applied in the cladistic analysis of the systematic affinities of *Qorimayus* **gen. nov.** Characters based on Hara (2016) are denoted with an ‘H’, followed by the corresponding character number. Additive characters are also indicated. For a definition of characters 30 and 31, see Figs. 3C–E.

Characters	states
1. Ocular mound – (H1)	0. divided, each eye placed on different elevations 1. single
2. Ocularium, armature	0. unarmed 1. with median unpaired armature 2. with paramedian paired armature
3. Ocularium, size of unpaired armature	0. rudimentary to low 1. well developed to very high
4. Ocularium, size of paired armature	0. rudimentary to low 1. well developed to very high
5. Carapace, frontal hump – (H7)	0. absent 1. present
6. Size of frontal hump, relative to ocular mound	0. equal sized as ocular mound 1. lower than ocular mound, or absent 2. taller than ocular mound
7. Armature on frontal hump – (modified H9)	0. unarmed 1. armed
8. Shape of dorsal scutum ♂ – (modified H11)	0. mesotergum slightly widened (type beta) 1. mesotergum widened in the middle (type alpha) 2. mesotergum widened more caudally (type gamma) 3. elongated gamma (coda extended, DS more oblong)
9. Granulation of dorsal scutum	0. granulous / tuberculate 1. smooth, at most paucigranulate
10. Scutal area III ♂, armature	0. unarmed 1. with paramedian pair of tubercles 2. with paramedian pair of spines 3. one median apophysis
11. Scutal areas III and IV, separation	0. areas III and IV separate, not fused 1. areas III and IV fused
12. Scutal area IV ♂, armature	0. unarmed 1. with paramedian pair of tubercles
13. Scutal area IV, division	0. single, undivided 1. divided in two halves
14. Scutal area V ♂, armature	0. unarmed 1. with paramedian pair of tubercles 2. one median apophysis 3. two large lateral apophyses
15. Basichelicerite, proportions - ADDITIVE	0. normal, with marked bulla 1. pedicel normal, bulla little marked 2. pedicel elongated, bulla attenuated

.....continued on the next page

**TABLE 2.** (Continued)

Characters	states
16. Pp coxa (dorsal view) - ADDITIVE	0. very short, hidden 1. short, not surpassing half of trochanter I 2. long, it equals trochanter I in length 3. very long and robust, it surpasses trochanter I
17. Pp femur, subapical prolateral spine - (H31)	0. absent 1. present
18. Pp femur, proportions	0. normal 1. slender, elongated
19. Pp femur, dorsal armature - ADDITIVE	0. smooth or finely rugulose 1. row of sparse rudimentary tubercles 2. row of well-defined tubercles
20. Pp femur, ventral armature	0. row of large apophyses 1. row of denticles 2. basal setigerous tubercle plus row of sparse small tubercles 3. basal setigerous tubercle, plus one isolated 4. only a basal tubercle, the rest smooth
21. Pp femur, size of ventrobasal setigerous tubercle	0. well developed 1. vestigial
22. Pp patella–tibia, dorsal surface	0. smooth or finely rugulose 1. tuberculate
23. Pp patella–tibia articulation - (H34)	0. posteriorly articulated 1. dorsally articulated 2. obliquely articulated
24. Pp tibia, shape	0. semi-cylindrical, without flap 1. strongly depressed and concave, with marginal flap
25. Pp tibia, ventro basal margin, lateral view – (H35)	0. oblique 1. curved at 90°
26. Pp tibia, retrolateral apical-subapical spines - ADDITIVE	0. On adjacent, but separate sockets 1. Sockets fused at the base (bifid) 2. One short stem, furcate at the tip 3. One long stem, furcate at the tip
27. Pp tibia–tarsus, relative dimensions	0. Ta comparable to Ti, or smaller 1. Ti shortened, Ta larger (it can be twice as large)
28. Pp tarsus, dorsal outline	0. gently convex 1. strongly convex, like a hump
29. Coxa II, shape and position (ventral view)	0. apical end diagonal 1. apical end curved
30. Coxa III, length relative to coxa II (ventral view) – ADDITIVE (Figs. 3C–E)	0. CxIII very short (not reaching X, to surpassing it very little) 1. CxIII moderately short (it reaches half way between X and Y) 2. CxIII long (fills more than half X–Y space, may almost fill it up) 3. CxIII very long (it surpasses Y)
31. Relative length of apical Cx II (projected onto Cx III width) (Fig. 3C–E)	0. free Cx II very short (less than half of Cx III width) 1. free Cx II moderate (projection about half of Cx III width) 2. free Cx II long (projection embraces or surpasses Cx III)
32. Stigmatic area, posterior border	0. gently concave (in a very slight arc) 1. deeply concave or as an undulated arc
33. Tarsus I, segmentation	0. with 5 tarsomeres 1. with 6 tarsomeres 2. more than 6 tarsomeres

.....continued on the next page

**TABLE 2.** (Continued)

Characters	states
34. Tarsal process (Roewerian 'pseudonychium'), legs III–IV	0. absent or vestigial 1. short 2. long
35. Ti III, sexual dimorphism	0. incrassate, armed ventrally in male 1. unarmed, either thickened or not
36. Cx IV, dorso-lateral surface - (modified H38)	0. granulous 1. paucigranulate or smooth
37. Cx IV ♂, proapical apophysis, orientation – ADDITIVE	0. sub-transverse (45° or more from body's axis) 1. diagonal (less than 45° from body's axis) 2. pointing backwards (does NOT leave a border of Cx IV visible) 3. internal-posterior (leaves a border of Cx IV visible)
38. Cx IV ♂, proapical apophysis, development	0. moderate 1. large
39. Cx IV ♂, proapical apophysis, branching pattern	0. single apophysis 1. ventral branch incipient, either basal or subdistal 2. ventral branch strong 3. apically bifid
40. Cx IV ♂, retroapical apophysis – (modified H44)	0. absent 1. small 2. large
41. Troc IV ♂, dimensions	0. short, subtrapezoidal 1. elongate
42. Troc IV ♂, prolateral submedian apophysis – (modified H45)	0. absent 1. small 2. large
43. Troc IV ♂, prodorsal apical apophysis – (modified H46)	0. absent 1. blunt 2. large
44. Troc IV ♂, retroapical apophysis – (modified H48)	0. absent 1. small 2. large
45. Fe IV ♂, relative length	0. shorter than scutum 1. same length as scutum 2. longer than scutum
46. Fe IV ♂, shape	0. sub-straight 1. curved in lateral view 2. slightly sigmoid 3. strongly sigmoid
47. Fe IV ♂, proventral basal apophysis	0. none 1. small 2. large
48. Fe IV ♂, dorsobasal apophysis	0. none 1. large
49. Fe IV ♂, proventral armature	0. unarmed 1. row of short apophyses distally larger 2. large subapical or apical apophysis
50. Fe IV ♂, retroventral armature	0. unarmed 1. row of short apophyses distally larger 2. 1–2 large apical apophyses 3. complete row of apophyses

.....continued on the next page

**TABLE 2.** (Continued)

Characters	states
51. Fe IV ♂, retrolateral armature	0. unarmed 1. several strong apophyses
52. Pat IV ♂, proventral apical armature	0. absent or just acute grains 1. large single apophysis 2. large bifid apophysis
53. Ti IV ♂, retrolateral armature	0. unarmed 1. large median apophyses
54. Ti IV ♂, pro- / retroventral armature	0. unarmed 1. larger acute granules distally 2. heavy apophyses distally 3. heavy apophyses all long
55. Ti IV ♂, shape in lateral view	0. straight 1. sigmoid
56. Ti IV ♂, degree of thickening	0. slender, similar width in all length 1. uniformly thickened in all length 2. slightly thickened distally 3. heavily thickened distally (normally associated to strong armature)
57. Ventral plate (VP), position in relation to truncus - ADDITIVE	0. distal truncus with ventral bulge, VP straight or gently inclined dorsad 1. truncus and VP in the same plan 2. distal end of truncus curved ventrad - then VP oriented distad 3. distal end of truncus curved ventrad + swollen - then VP distad 4. distal end of truncus curved ventrad + swollen + elongated - then VP distad
58. Latero-subdistal spiny sacs on truncus, presence	0. absent 1. present (Metasarcidae)
59. VP, overlapping with distal truncus	0. not overlapping 1. truncus reaching about half-length of VP 2. truncus overlapping very little, only at base
60. VP, microsetae cover	0. VP glabrous 1. VP with ventral and/or ventrolateral microsetae
61. VP, insertion in truncus	0. not sunken in truncus 1. sunken in truncus
62. Orientation of basal setae A–B	0. diagonal, pointing proximad 1. procumbent, pointing proximad 2. transverse, pointing to the sides
63. Insertion of basal group A–B	0. basally on VP 1. shifted apically on VP 2. lacking
64. Arrangement of basal setae A–B	0. forming a cluster 1. aligned longitudinally
65. Glans, lateral view	0. protrudes on apical ridge (amphora-like seen from above) 1. globose, protrudes in all extension 2. not protruding, transition to stylus smooth 3. protrusion restricted to a distal portion, anvil-like or round (oval from dorsal)
66. Dorsal process of glans – (H62)	0. absent 1. present
67. Ventral process of stylus (VPS) – (H63)	0. absent 1. present

.....continued on the next page



**TABLE 2.** (Continued)

Characters	states
68. VPS, apical end shape	0. peltate 1. spatulate 2. flabelliform 3. spiny tuft, single 4. unciform 5. bifid 6. spiny tuft, hemicircle
69. VPS, stalk orientation	0. dorsad, parallels the stylus 1. ventrad/anteriad, diverges from stylus 2. without stalk, sessile
70. VPS, apical end orientation	0. curved or bent dorsad 1. curved or bent ventrad 2. straight, diagonal pointing ventrad 3. curved or bent distad
71. VPS, subdistal spines on shaft	0. absent 1. present
72. Stylus, structure	0. cylindrical, with terminal opening 1. flattened and expanded as a serrate keel, with opening as a dorsal slit
73. Stylus, curvature	0. sigmoid 1. concave 2. straight 3. straight with flexure
74. Stylus, orientation - ADDITIVE	0. same as truncus axis 1. diagonal (45°) 2. sub-perpendicular to truncus axis
75. Stylus, apical narrowing	0. slightly narrowed 1. not narrowed
76. Stylus, armature	0. smooth, unarmed (at most vestigial) 1. spiny on ventral side 2. 1–2 spur-like ventral processes, and marginal membranes

## Results

### Cladistic analysis

Trees obtained with implied weights (IW) had overall a similar topology across the tested concavity span, in all cases resulting in a single most parsimonious tree (Table 4). The main discordance was the position of *Discocyrtus testudineus* and the cluster *Eusarcus gemignanii* + *Eusarcus hastatus* (Table 5): with  $k=1$  to  $k=6$ , *D. testudineus* occupies the basal-most position in Gonyleptidae (G), but is placed more internally from  $k=9$  onwards, as sister group of the clade PsG (*Pachyloides*-group), containing *Parabalta* and *Pachyloides*; conversely, the *Eusarcus* group is at the base of Gonyleptidae with  $k=9$  onwards, but between  $k=1$  and  $k=6$  it shifts internally, as sister clade of PG (*Pachylus*-group = *Metagyndes* + *Acanthopachylus* + *Pachylus*). The  $k$  value also affected the internal arrangement of genera *Metabalta* and *Nanophareus*, although their monophyly was constant in all treatments. It is noteworthy that *Nanophareus polyhastatus* always grouped together with *Metabalta* spp. (forming a clade here denoted as M), suggesting it should be moved from its original genus to *Metabalta*, to keep *Nanophareus* monophyletic. In the latter genus, from  $k=3$  to  $k=9$  a clade (*N. palpalis* Roewer, 1929 (*N. bosqenublado* Hara, Pinto-da-Rocha & Kury 2012 + *N. bipartitus* Hara, Pinto-da-Rocha & Kury 2012)) is formed, in which the remarkable state ‘eyes separated’ (char. 1, state 0) appears as an autapomorphy. Equal weights (EW) yielded 2 equally parsimonious trees (Table 4). Their strict consensus recovered most groups identified with IW, with some differences: in G, ‘*Eusarcus* spp. + PG + all



TABLE 3: Matrix of 76 characters x 28 terminals, employed in the cladistic analysis performed to assess the affinities of *Qorimayus* gen. nov.

	1	2	3	4	5	6	7
<i>Quindina albomarginis</i>	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Gryne orensis</i>	12-001-002	0000011012	1020000003	011211-001	0001200000	0000001000	021-200---
<i>Incasareus dianae</i>	10--01-012	00-0000021	?001--0012	002210-0-0	0000200000	0000002001	1011210---
<i>Eusareus hastatus</i>	10--110112	0010011000	0000000002	2020?1-0-0	00002000??	1100001101	1011200---
<i>Eusareus gemignanii</i>	12-101-203	0000011022	0020000000	2101000101	0201020011	0001021011	1001001110
<i>Discocyrtus testudineus</i>	12-001-200	0000011022	0020000000	2001000110	0200020010	0001031011	1201001110
<i>Pachyloides cochuna</i>	12-101-212	0010011004	0020000012	0111001112	1201030000	0001023021	1200201201
<i>Pachyloides hades</i>	12-1110201	0101011012	0020010010	1111113100	0221000011	0000023021	1201001501
<i>Pachyloides thorellii</i>	12-0100300	0000011012	0020010010	1111113101	1121010011	0000021021	1000001501
<i>Acanthopachylus aculeatus</i>	12-0100300	0000011012	0020110000	1111111100	0121000011	0000023021	1001001501
<i>Pachylus chilensis</i>	111-110210	0002010003	0020000001	0102011030	0100032013	0002030011	1201201322
<i>Pachylus crassus</i>	111-110200	0101010013	0020000001	0102111121	0201031011	2102030011	1201201322
<i>Metagyndes martensii</i>	111-110200	0101010013	0020010011	0102112111	0202022013	0002010011	1200201322
<i>Metagyndes pulchella</i>	110-110210	0000010003	1020010012	0101112100	1021010012	0103131011	1221201622
<i>Parabalta sp.</i>	110-110210	0000010003	1020010002	0101112110	1021010012	0102131011	1221201622
<i>Parabalta cristobalia</i>	12-1110210	0000011002	0020010000	1112111011	1120002010	2103123021	1001211001
<i>Neogonyleptes karschii</i>	12-1110210	0000011002	0020010000	1112111110	1222012021	0103133021	1001211001
<i>Tumbesia aculeata</i>	12-1100212	1--0020113	1110110102	1111101112	1021?20002	0012134021	120?301403
<i>Metabalta geniculata</i>	12-1101211	1--3020113	111010[01]102	0111101112	1122020011	2112134021	120030140[13]
<i>Metabalta efformata</i>	12-0110201	0111010012	0110111001	111000[01]011	1112032100	1002033021	1001001010
<i>Qorimayus alticola</i>	12-0110201	0111010012	0110111002	1110000111	1221032000	1002034021	1000001010
<i>Nanophareus palpatis</i>	12-0100210	0000011002	1020110002	1111111111	1112201011	0201024021	1200001010
<i>Nanophareus bipartitus</i>	00--1001?0	0000120102	1010121100	2000?01030	0101100000	0010014021	1200101110
<i>Nanophareus bosquenublado</i>	00--1001?0	0010230113	1110120100	20[01]0?01001	0100200000	000100?021	12001?1010
<i>Nanophareus bicornutus</i>	00--1211?2	0000230113	1010131100	2010003121	1121000012	0110013021	1100101110
<i>Nanophareus araucanus</i>	10--110201	0000230102	1000020100	2010100121	1122001010	2001024021	1100301110
<i>Nanophareus maipu</i>	111-1112?2	0000020113	1010131100	2010?01030	1111021010	200102?001	1100101110
<i>Nanophareus polyhasstatus</i>	110-110200	000012[01]112	0110131100	2010?01000	0111110011	0001003021	1101101110
	10--110201	0110020012	1110111002	111?000110	1212032102	1001023001	1200001010

**TABLE 4.** Summary results of the ten analyses (IW, k=1, 3, 6, 9, 12, 15, 18, 30, 50; equal weights, EW) performed on the matrix of Table 3. Preferred hypothesis (k=6) emphasized in bold.

Concavity (k)	Trees retained	Tree length	Ci	Ri	Best score (fit)
1	1	383	0.36	0.59	50.92302
3	1	379	0.36	0.60	34.71861
<b>6</b>	<b>1</b>	<b>376</b>	<b>0.37</b>	<b>0.60</b>	<b>23.91387</b>
9	1	376	0.37	0.60	18.35304
12	1	373	0.37	0.61	14.91950
15	1	372	0.37	0.61	12.57265
18	1	372	0.37	0.61	10.86635
30	1	372	0.37	0.61	7.05523
50	1	372	0.37	0.61	4.45887
None (EW)	2	372	0.37	0.61	n/a
consensus	-	380	0.36	0.60	n/a

Results of the resampling analyses (bootstrap, jackknifing and symmetrical resampling, performed for different concavities) resembled the most those obtained with IW, k=1 to k=6. Some nodes that appear resolved have, indeed, little support: they would collapse if a stricter cut-off rule is applied. *Discocyrtus testudineus* was always basal in G in all resampling analyses (Table 5), even for k=9 onwards. Again, in all cases the monophyly of *Nanophareus* is kept only with *N. polyhastatus* removed and transferred to M (this clade strongly supported). The internal arrangement of the redefined, well supported *Nanophareus* (Na) varied with treatments too; however, the basal-most terminal in this clade was always *N. bicornutus*, and the e-s clade is recognizable in most cases, though with little support (Table 5). Another well-supported clade is PG (*Pachylus* and allies), whereas its relationship with *Eusarcus* spp. is much weaker. *Parabalta* and *Pachyloides* have good support individually, but not the assemblage combining them (PsG).

The separation of *Qorimayus* from *Parabalta* or *Pachyloides* is supported by all analyses, showing a closer relationship to *Metabalta* and *Nanophareus*, as previously assumed (Fig. 1). The new genus was consistently placed at the base of a large clade (MG) containing *Metabalta* and *Nanophareus*, along with two other terminals (*Tumbesia*, *Neogonyleptes*), all but *Qorimayus* occurring in Chile. The recognition of *Qorimayus*, *Metabalta* and *Nanophareus* as independent genera is supported both by  $\alpha$ -taxonomic features (see below) and the constant topology of the major divisions of this clade; but as seen, species arrangement within *Metabalta* and *Nanophareus* may vary (Table 5).

## Taxonomy

### *Qorimayus* gen. nov.

urn:lsid:zoobank.org:act:21EFA2C1-F6F3-4395-84CD-F073E8944261

*Parabalta* (in part): Ringuet, 1962: 2; 1978: 258.

*Pachyloides* (in part): Acosta, 1996a: 8, 10; 2002: 79, 82; Kury 2003: 181.

**Type species:** *Parabalta alticola* Ringuet, 1962, here designated. Genus monotypic.

**Etymology:** The generic name combines two Quechua words (*qori* = gold, and *mayu* = river, stream), in reference to ‘Río Oro’, the valley in the Famatina range where all collecting sites are located; grammatical gender is masculine.

**Distribution:** Western Argentina, Sierra de Famatina, in the Río Oro valley between 2450 and 3080 m a.s.l.

**Diagnosis:** Medium- to large-sized, long-legged Gonyleptidae Pachylinae, of robust habitus. Ocular mound very low, practically unarmed or with very tiny paired grains. Frontal hump in lateral view as high as the ocular mound. Dorsal scutum flat, unarmed and almost smooth; sparse, tiny granules on areas I–IV. Area V with a row of granules. Free tergites I–III and dorsal anal plate unarmed; granulation on free tergites is similar to area V, with increasing size from free tergite I to III. Pedipalp femur armed with a moderate prolateral subapical spine. Leg IV

**TABLE 5.** Recovery and support of relevant clades, as obtained in different analytical treatments: implied weighting (IW), with different concavity (k) values; equal weights, strict consensus (EW-strict); resampling with bootstrap (B), jackknife (J) and symmetric resample (SR) for selected concavities. Recovered clades are indicated as ✓, not recovered as -. Values indicate branch support when ≥1 (=not collapsed), highest values (>60) in bold. Clades: **G**: Gonyleptidae; **MG**: *Metabalta*-group; **M+Na(+)**: *Metabalta* + *Nanophareus*, plus N+T; **M**: genus *Metabalta* (including *N. polyhastatus*); **Na(+)**: (*Nanophareus* (N+T)); **Na**: genus *Nanophareus*; **N+T**: *Neogonyleptes*+*Tumbesia*; **e-s clade**: eyes separated clade; **PG**: *Pachylus*-group; **PG+Eu**: *Pachylus*-group+*Eusarcus* spp.; **PsG**: *Pachyloides*-group. The column “Basal in G” identifies the basal group in the clade Gonyleptidae; either *Discocyrtus testudineus*, or *Eusarcus hastatus* + *E. gemignanii*. “Basal in M” and “Basal in Na” identify the basal-most terminal in those clades. Finally, “e-s clade” states whether or not the feature “eyes separated” (char. 1, state 0) supports a clade within Na.

	<b>G</b>	<b>Basal in G</b>	<b>MG</b>	<b>M+Na(+)</b>	<b>M</b>	<b>Basal in M</b>	<b>Na(+)</b>	<b>Na</b>	<b>Basal in Na</b>	<b>e-s clade</b>	<b>N+T</b>	<b>PG</b>	<b>PG+Eu</b>	<b>PsG</b>
IW - concavity	k 1	✓	<i>D. testudineus</i>	✓	✓	<i>M. efformata</i>	✓	✓	<i>N. araucanus</i>	-	✓	✓	✓	✓
	k 3	✓	<i>D. testudineus</i>	✓	✓	<i>M. efformata</i>	✓	✓	<i>N. bicornutus</i>	✓	✓	✓	✓	✓
	k 6	✓	<i>D. testudineus</i>	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	✓	✓	✓	✓	✓
	k 9	✓	<i>Eusarcus</i> spp.	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	✓	✓	✓	-	✓
	k 12	✓	<i>Eusarcus</i> spp.	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	-	✓	✓	-	✓
	k 15	✓	<i>Eusarcus</i> spp.	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	-	✓	✓	-	✓
	k 18	✓	<i>Eusarcus</i> spp.	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	-	✓	✓	-	✓
k 30	✓	<i>Eusarcus</i> spp.	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	-	✓	✓	-	✓	
resample k=3	B	<b>95</b>	<i>D. testudineus</i>	17	<b>96</b>	<i>N. polyhastatus</i>	10	<b>75</b>	<i>N. bicornutus</i>	-	<b>98</b>	<b>63</b>	7	9
	J	<b>97</b>	<i>D. testudineus</i>	21	<b>99</b>	<i>N. polyhastatus</i>	13	<b>86</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>68</b>	9	9
	SR	<b>98</b>	<i>D. testudineus</i>	22	<b>98</b>	<i>N. polyhastatus</i>	11	<b>82</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>73</b>	11	14
resample k=6	B	<b>95</b>	<i>D. testudineus</i>	21	<b>93</b>	<i>N. polyhastatus</i>	40	<b>89</b>	[polytomy]	6	<b>99</b>	<b>80</b>	10	6
	J	<b>99</b>	<i>D. testudineus</i>	26	<b>97</b>	<i>N. polyhastatus</i>	51	<b>96</b>	<i>N. bicornutus</i>	6	<b>99</b>	<b>88</b>	13	16
resample k=9	B	<b>96</b>	<i>D. testudineus</i>	20	<b>95</b>	<i>N. polyhastatus</i>	37	<b>88</b>	<i>N. bicornutus</i>	5	<b>99</b>	<b>77</b>	11	11
	J	<b>99</b>	<i>D. testudineus</i>	29	<b>98</b>	<i>N. polyhastatus</i>	50	<b>96</b>	<i>N. bicornutus</i>	10	<b>100</b>	<b>88</b>	14	18
resample k=12	B	<b>96</b>	<i>D. testudineus</i>	18	<b>95</b>	<i>N. polyhastatus</i>	30	<b>87</b>	<i>N. bicornutus</i>	6	<b>99</b>	<b>77</b>	9	11
	J	<b>99</b>	<i>D. testudineus</i>	29	<b>99</b>	<i>N. polyhastatus</i>	47	<b>96</b>	<i>N. bicornutus</i>	9	<b>100</b>	<b>86</b>	12	15
resample k=18	B	<b>97</b>	<i>D. testudineus</i>	19	<b>95</b>	<i>N. polyhastatus</i>	27	<b>87</b>	<i>N. bicornutus</i>	5	<b>99</b>	<b>72</b>	10	10
	J	<b>99</b>	<i>D. testudineus</i>	27	<b>99</b>	<i>N. polyhastatus</i>	39	<b>95</b>	<i>N. bicornutus</i>	2	<b>100</b>	<b>85</b>	12	14
resample k=30	B	<b>97</b>	<i>D. testudineus</i>	16	<b>96</b>	<i>N. polyhastatus</i>	24	<b>85</b>	<i>N. bicornutus</i>	2	<b>99</b>	<b>72</b>	9	8
	J	<b>99</b>	<i>D. testudineus</i>	22	<b>99</b>	<i>N. polyhastatus</i>	34	<b>96</b>	<i>N. bicornutus</i>	-	<b>100</b>	<b>84</b>	12	13
EW - strict (2 trees)	B	<b>98</b>	<i>D. testudineus</i>	24	<b>99</b>	<i>N. polyhastatus</i>	34	<b>95</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>85</b>	10	10
	J	<b>97</b>	[polytomy]	✓	✓	<i>N. polyhastatus</i>	✓	✓	<i>N. bicornutus</i>	-	✓	✓	-	✓
resample EW	B	<b>97</b>	<i>D. testudineus</i>	19	<b>95</b>	<i>N. polyhastatus</i>	19	<b>87</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>69</b>	4	6
	J	<b>98</b>	<i>D. testudineus</i>	27	<b>99</b>	<i>N. polyhastatus</i>	27	<b>93</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>79</b>	9	11
	SR	<b>99</b>	<i>D. testudineus</i>	24	<b>98</b>	<i>N. polyhastatus</i>	26	<b>95</b>	<i>N. bicornutus</i>	-	<b>99</b>	<b>81</b>	7	12

of males: a large diagonal apophysis on coxa; femur sub-straight, armed distally with a few short apophyses; patella with a distinctive forked proventral apophysis. Tarsal formula 6:(8±1):6:6. Penis: distal portion of trunk swollen and curved in lateral view (first dorsad, then ventrad). Stylus bearing heavy spines on its ventral side; it has a diverging vps, curved dorsad and flabellate-tipped, giving the apical end of the glans a forked appearance.

***Qorimayus alticola* (Ringuelet, 1962) comb. nov.**

Figs. 2, 3A,B, 4A, 5

*Parabalta* nov. sp. Ringuelet, 1961: 158.

*Parabalta alticola* Ringuelet, 1962: 2, figs. 1–5; 1978: 258; Maury 1986: 21; 1992: 2. urn:lsid:zoobank.org:act:EA3EF267-8B7C-4F7E-BE4E-0A42B23B2A61

*Pachyloides alticola*: Acosta, 1996a: 10; 2002: 79; Kury 2003: 181.

**Type series:** Holotype ♂ (MACN 7529), paratype (labelled as allotype) ♀ (MACN 7530), 3 paratypes ♂ (MACN 7531) and 3 paratypes ♀ (MACN 7532): ‘Mina El Oro, Chilecito, La Rioja, 3080 m snm, 6–8-ii-1956, [M.E.] Galiano’, examined. Remark: An additional vial with no accession number, stored in the same jar as the type series, contains 6 juveniles, not designated by Ringuelet (1962) as types.

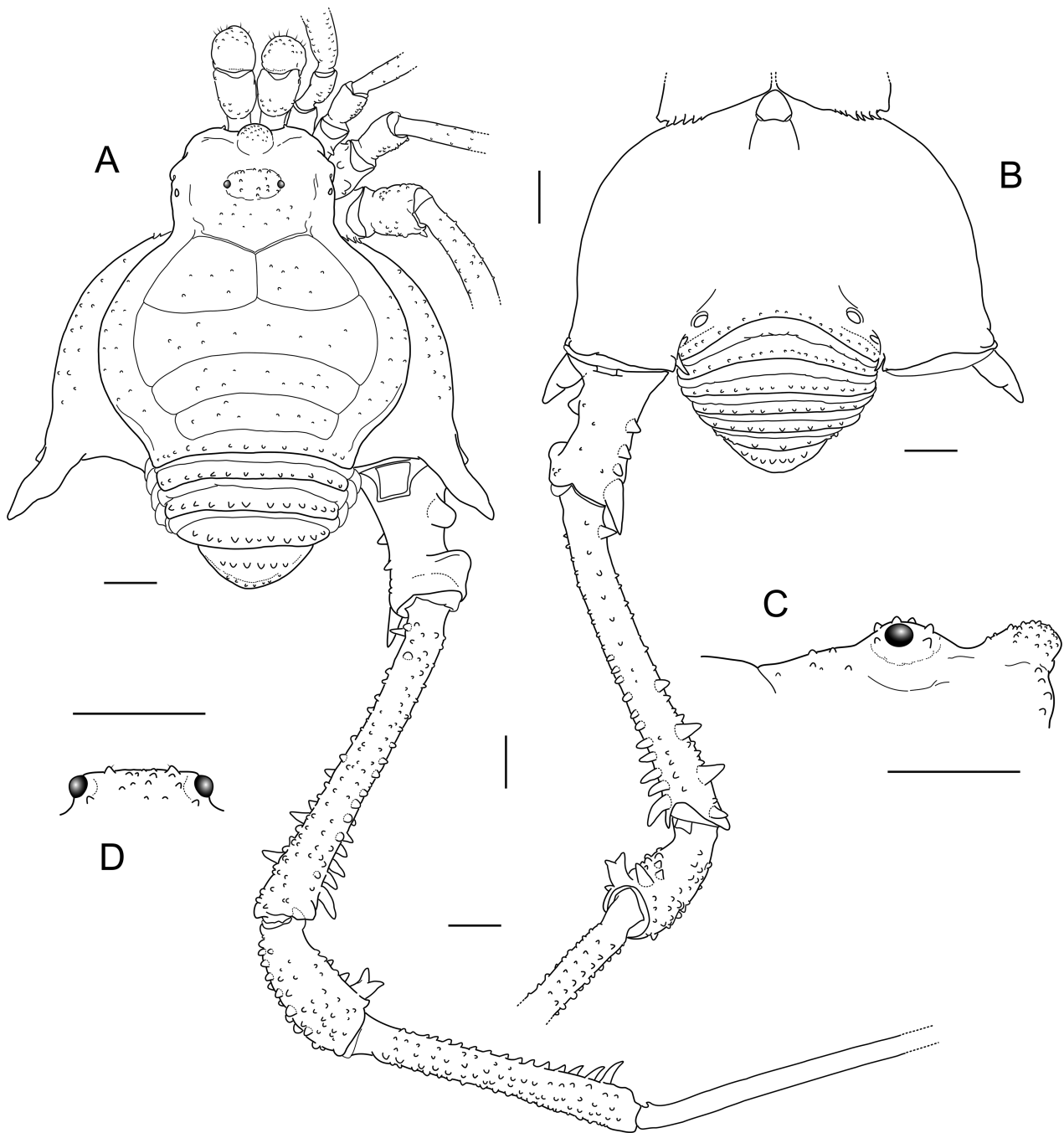
**Type locality:** Sierra de Famatina, Mina El Oro, canyon of Río Oro, 3080 m a.s.l. (ca. 29° 4’ 33.37”S 67° 44’ 9.61”W).

**New records:** ARGENTINA. *La Rioja Province*. Sierra de Famatina, road to Mina El Oro, Río Oro canyon, 6-xii-1998 (L. Acosta, M. Acosta, G. Repossi): site at 2550 m (ca. 29° 5’ 51.76”S 67° 41’ 53.39”O), shrubland, under stones (LEA 000.210), 7 ♂, 28 ♀, 4 juv.; site at 2450 m (29° 5’ 53.98” S 67° 41’ 51.92” W), U.V. light collection (LEA 000.212), 20 ♂, 10 ♀; same site, under stones (LEA 000.213), 1 ♂, 1 ♀, 1 juv.

**Redescription:** *Measurements*. Dorsal scutum length: males 5.11–6.58 (mean 6.06, n=32), females 5.66–6.40 (mean 6.06, n=43). Detailed measurements of holotype ♂ and allotype ♀: Table 6.

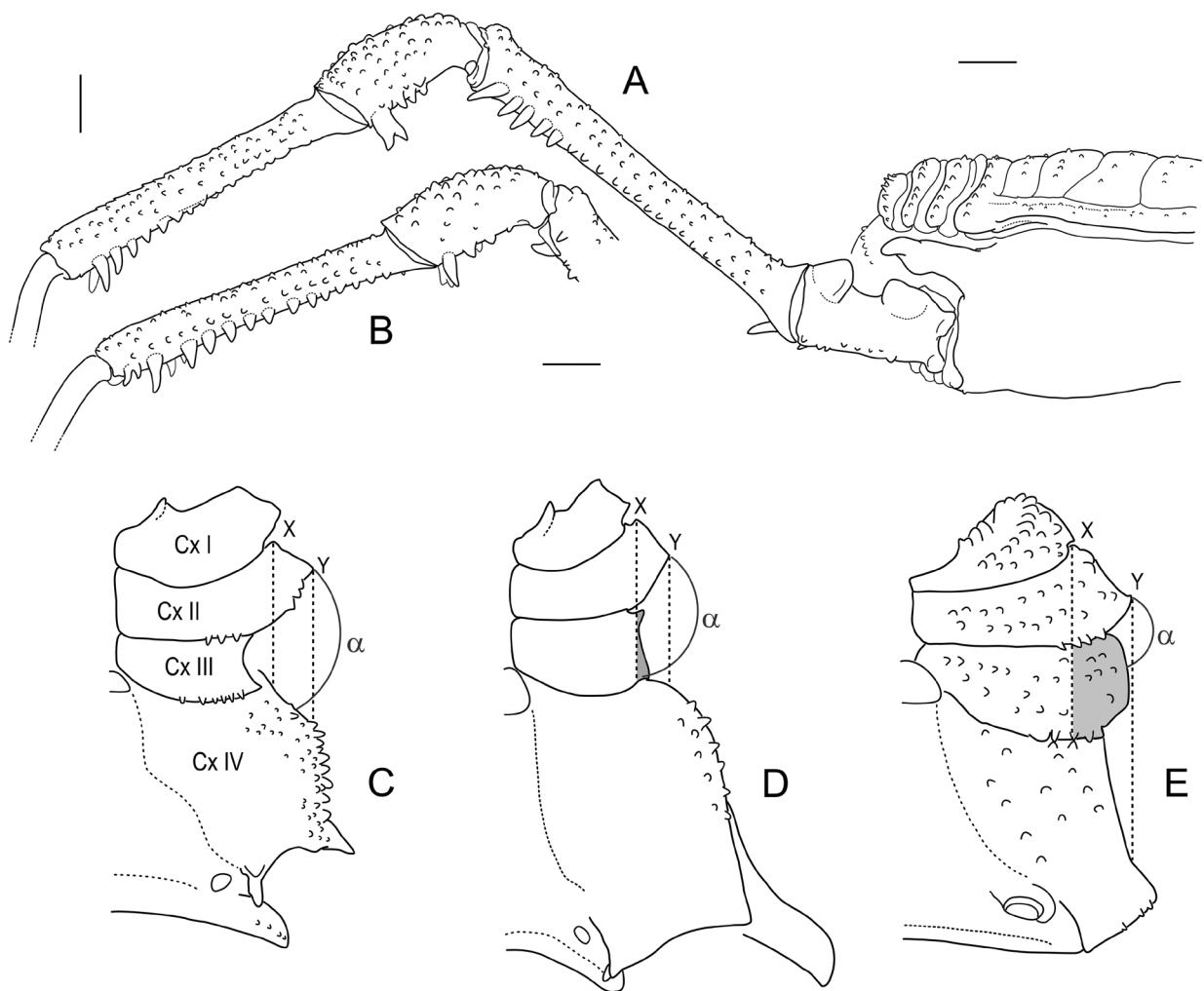
**TABLE 6.** Measurements (in mm) of the holotype ♂ (MACN 7529) and the allotype ♀ (MACN 7530) of *Qorimayus alticola* (Ringuelet, 1962) **comb. nov.**

	Holotype ♂	Allotype ♀
Total body length	8.6	8.8
Scutum, length / maximal width	6.1 / 5.6	5.9 / 5.2
Prosoma, length / width	2.2 / 3.0	2.2 / 2.9
Leg I, total length	13.5	12.1
trochanter I / femur I / patella I, length	0.7 / 3.4 / 1.2	0.7 / 3.1 / 1.1
tibia I / metatarsus I / tarsus I, length	2.5 / 3.4 / 2.3	2.3 / 3.0 / 1.9
Leg II, total length	22.9	20.1
trochanter II / femur II / patella II, length	0.8 / 5.7 / 1.7	0.8 / 5.3 / 1.5
tibia II / metatarsus II / tarsus II, length	4.6 / 5.2 / 4.9	3.8 / 4.4 / 4.3
Leg III, total length	19.5	16.9
trochanter III / femur III / patella III, length	0.9 / 5.8 / 1.7	0.8 / 4.9 / 1.5
tibia III / metatarsus III / tarsus III, length	3.5 / 5.4 / 2.2	3.1 / 4.6 / 2.0
Leg IV, total length	27.4	22.2
trochanter IV / femur IV / patella IV, length	2.2 / 7.0 / 2.8	1.2 / 6.0 / 2.1
tibia IV / metatarsus IV / tarsus IV, length	5.5 / 7.5 / 2.4	4.3 / 6.3 / 2.3
Pedipalp, total length	8.2	7.9
Pedipalp trochanter / femur / patella, length	0.6 / 2.1 / 1.0	0.7 / 2.0 / 0.9
Pedipalp tibia / tarsus / claw, length	1.4 / 1.6 / 1.5	1.4 / 1.5 / 1.4
Cheliceral hand, length / width	2.2 / 0.7	2.0 / 0.7
Ocular mound, width / height	1.1 / 0.3	1.1 / 0.2



**FIGURE 2.** *Qorimayus alticola* (Ringuelet, 1962) **comb. nov.**, holotype ♂ (MACN). A: Dorsal view (scutum, free tergites, chelicerae, base of right pedipalp and legs I–III, and right leg IV, from coxa to tibia). B: Ventral view (coxae IV, stigmatic segment, free sternites, right trochanter, femur and patella I). C–D: Ocular mound, C: right lateral view with front hump, D: posterior view. Scale bars: 1 mm.

*Color.* General color pale yellowish-straw; very faint pigment reticulation on prosoma (anterior and lateral borders, and both sides of the ocular mound), pedipalps (femur, tibia), legs I–III (femur, patella, tibia) and area V and free tergites; most scutum very pale, though in some specimens there are faint reticulate stripes on the scutal areas too. Leg IV of female of the general color. Leg IV of male darker (sclerotized appearance): coxa with same color as scutum except for the distal border and the prolateral apophysis, hazel-orangish; same color on trochanter, femur, patella and tibia, only distal end of femur and tibia slightly lighter; metatarsus and tarsus of the general color. Ventral surface of coxae quite uniform, slightly more hazel-orangish than the dorsum, with darker borders of coxa-trochanter articulation near stigmata. Color of smaller males tend to be more uniform than larger ones. Some females are exceptionally uniformly light hazel-orangish.



**FIGURE 3.** A–B: *Qorimayus alticola* (Ringuelet, 1962) **comb. nov.**, holotype ♂ (MACN), A: right leg IV (coxa to tibia), prolateral view. B: Left tibia and patella IV, retrolateral view. Scale bars: 1 mm. C–E: schematic representation (not at scale) of characters #30 (coxa III, length relative to coxa II) and #31 (relative length of apical Cx II projected onto Cx III width). Dashed vertical lines: projection of landmarks X and Y, as referred to in the characters list (Table 2), the portion of coxa III surpassing X is shaded. Arc ( $\alpha$ ): projection of the apical coxa II onto coxa III width. C: *Tricommatius brasiliensis* Roewer, 1912 (from Kury 2014), #30=0, #31=2; D: *Eusarcus hastatus* Sørensen, 1884, #30=0, #31=2; E: *Cynorta conspersa* (Perty, 1833) (from Kury *et al.* 2007), #30=2, #31=1.

*Exomorphology.* Prosoma and scutum sparsely set with very tiny granules. Frontal hump granulous, as tall as ocular mound; the latter is very low, covered by a few scattered conic granules. Scutum quite flat on male, with faint but complete sulci delimiting areas; area I divided. On areas I–IV granules are sparse, unordered and inconspicuous (especially in males). Lateral areas of scutum with tiny dispersed granules. Area V with a row of small grains. Free tergites with a row of grains each, becoming taller and more conical from I to III. Dorsal anal plate unarmed, granules of similar size as free tergites in a transverse row, plus additional unordered grains and a row of small ones on the posterior border; ventral anal plate with rows of minute granules on anterior and posterior margins.

Chelicerae and pedipalps developed as usual in the subfamily. Pedipalp femur with a medial subapical spine; patella articulates to tibia dorsally (Fig. 4A); two distal retroventral setae on tibia [Ii] on raised sockets that emerge from a common tegumentary elevation. Pedipalp spination (holotype): tibia I[Ii] (lateral), Ii.Ii (medial); tarsus IiI... (lateral and medial). Legs I–III unarmed. Femur I–III and patella-tibia III faintly granulous, the latter with taller grains on ventrodistal position; on male, retroapical border of femur III has a blunt grain. Trochanter III has a small but distinctive retroapical ventral conic granule both in male and female. Tegument of coxa IV smooth near the apophysis (male), to sparsely granulous on the sides, faintly rugulous ventrally (male and female). Number of tarsomeres: 6:7–9:6:6 (holotype ♂ and allotype ♀ with 6:8:6:6); variability on tarsus II: Table 7.



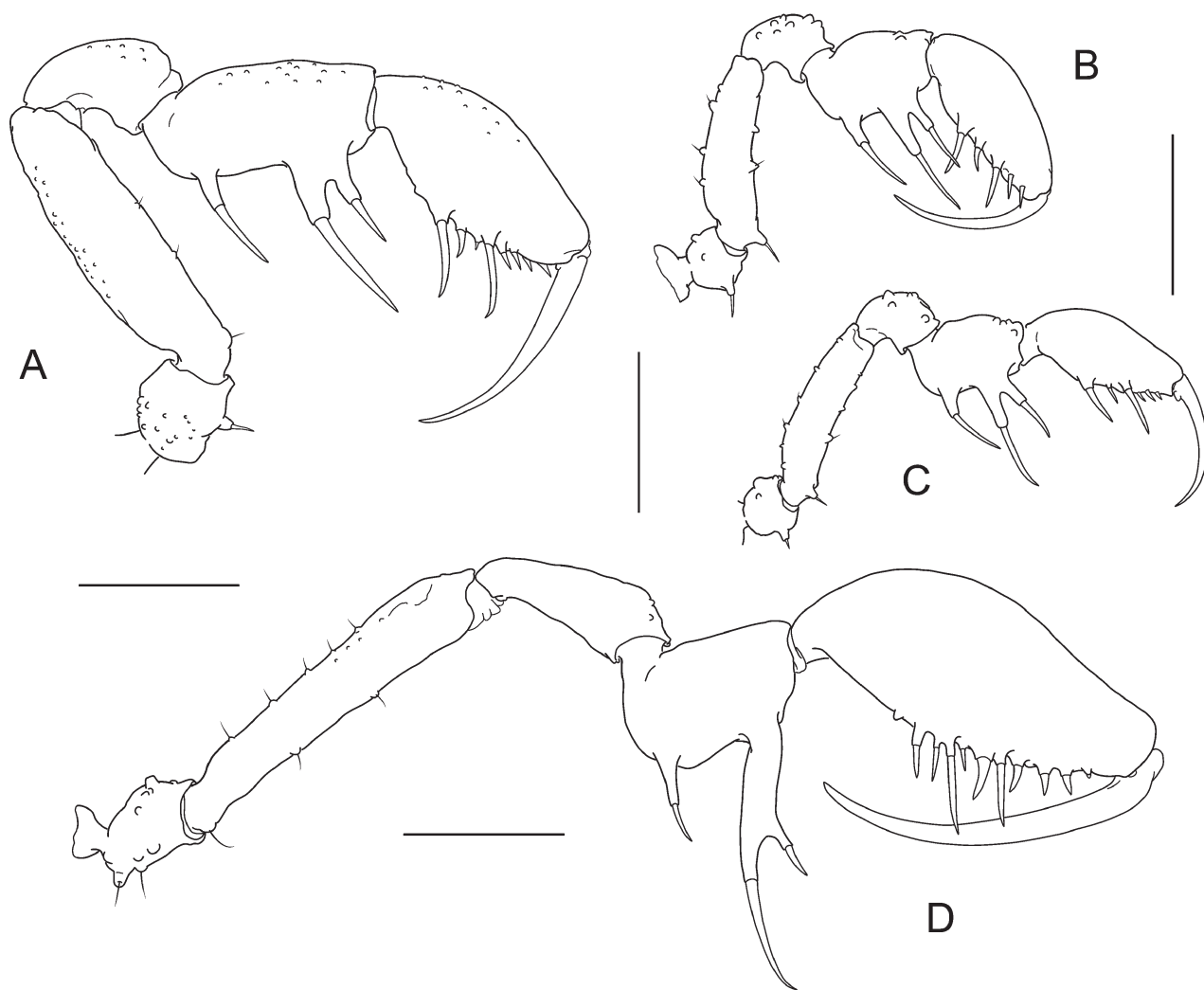
**TABLE 7.** Variability of the number of tarsomeres on leg II in the studied samples of *Qorimayus alticola* (Ringuelet, 1962) **comb. nov.**

Number of tarsal segments observed frequency	MALES				FEMALES			
	7	8	9	<i>n</i>	7	8	9	<i>n</i>
	15	39	4	<b>58</b>	35	44	3	<b>82</b>

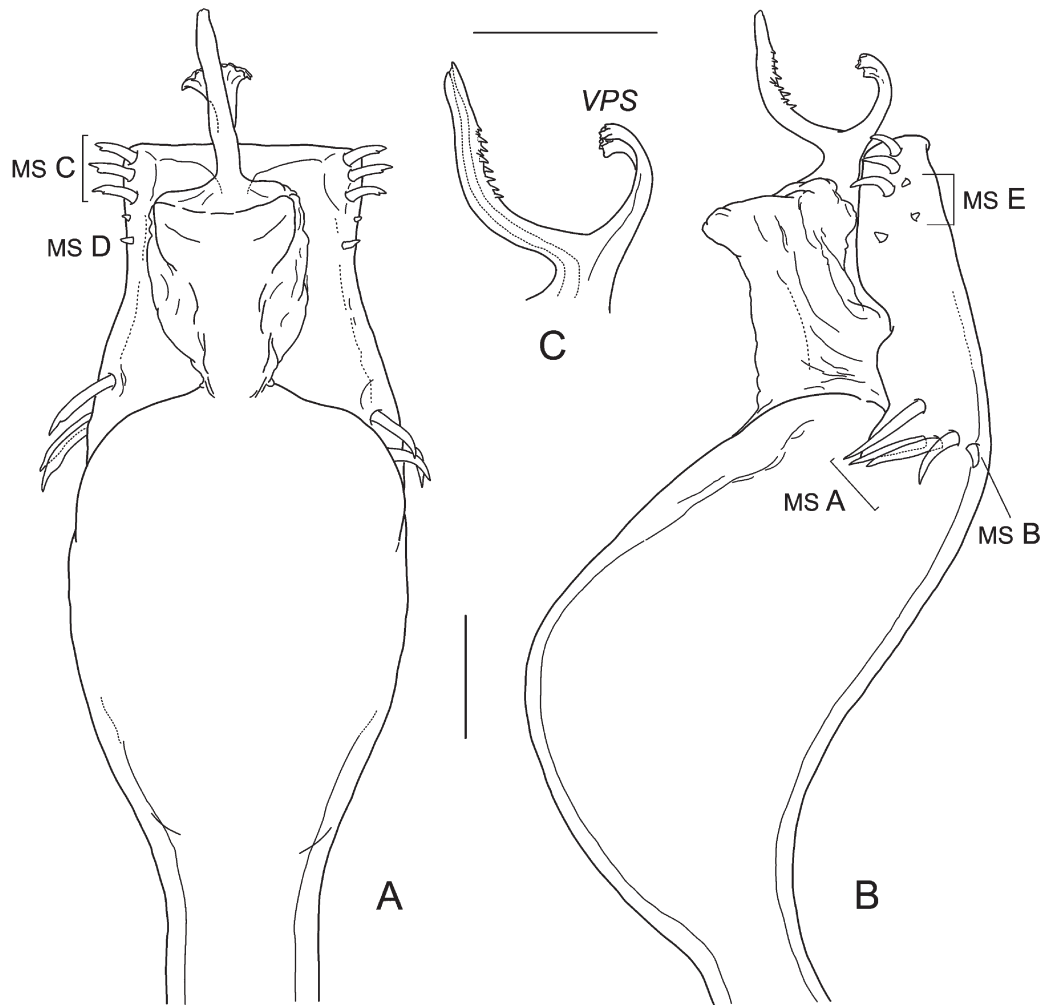
Leg IV (♂): Coxa IV with strong, diagonal prolateral apophysis, slightly dilated subterminally (insinuating an incipient bifid condition), its apical end slightly sigmoid in dorsal view; small acute retrolateral apophysis.

Trochanter IV elongated, armed with distinctive apophyses; one prodorsal sub-basal apophysis, ear-like and sclerotized; a marked prodorsal thickening of the apical border, from which a large, blunt prodorsal apophysis emerges, oriented upwards; a strong, acute retroventral apical apophysis, pointing caudad; in addition, 2–3 small conical apophyses (or acute grains in some specimens) on the retrolateral side.

Femur IV sub-straight, only weakly curved to the median line, gradually and slightly thickening towards the apical end; it is covered by longitudinal rows of conspicuous granules and a few distinct apophyses; retrolateral side with a sub-basal, small acute apophysis, and a row of 3–5 acute apophyses on distal half, with increasing size, ending in a large subapical one; proventral row of 4–5 smaller apophyses on the distal one third, ending in a large apical one; retroventral row insinuated by taller grains on the basal and distal portions, it ends in a rudimentary retroventral apical apophysis.



**FIGURE 4.** Right pedipalps, lateral view; all drawings at the same scale. A: *Qorimayus alticola* (Ringuelet, 1962) **comb. nov.**, holotype ♂ (MACN). B: *Metabalta efformata* Roewer, 1929, syntype ♂ (SMF). C: *Metabalta geniculata* Roewer, 1929, syntype ♂ (SMF) D: *Nanophareus bosquenublado* Hara *et al.*, 2012 (AMNH). Scale bars: 1 mm.



**FIGURE 5.** *Qorimayus alticola* (Ringuélet, 1962) **comb. nov.**, holotype ♂, distal end of penis. A: Dorsal view. B: Lateral view. C: Detail of stylus and ventral process of stylus (VPS). Macrosetae series are labelled as MS A, MS B, MS C, MS D and MS E, following the nomenclature of Kury & Villarreal (2015). Scales: 0.1 mm.

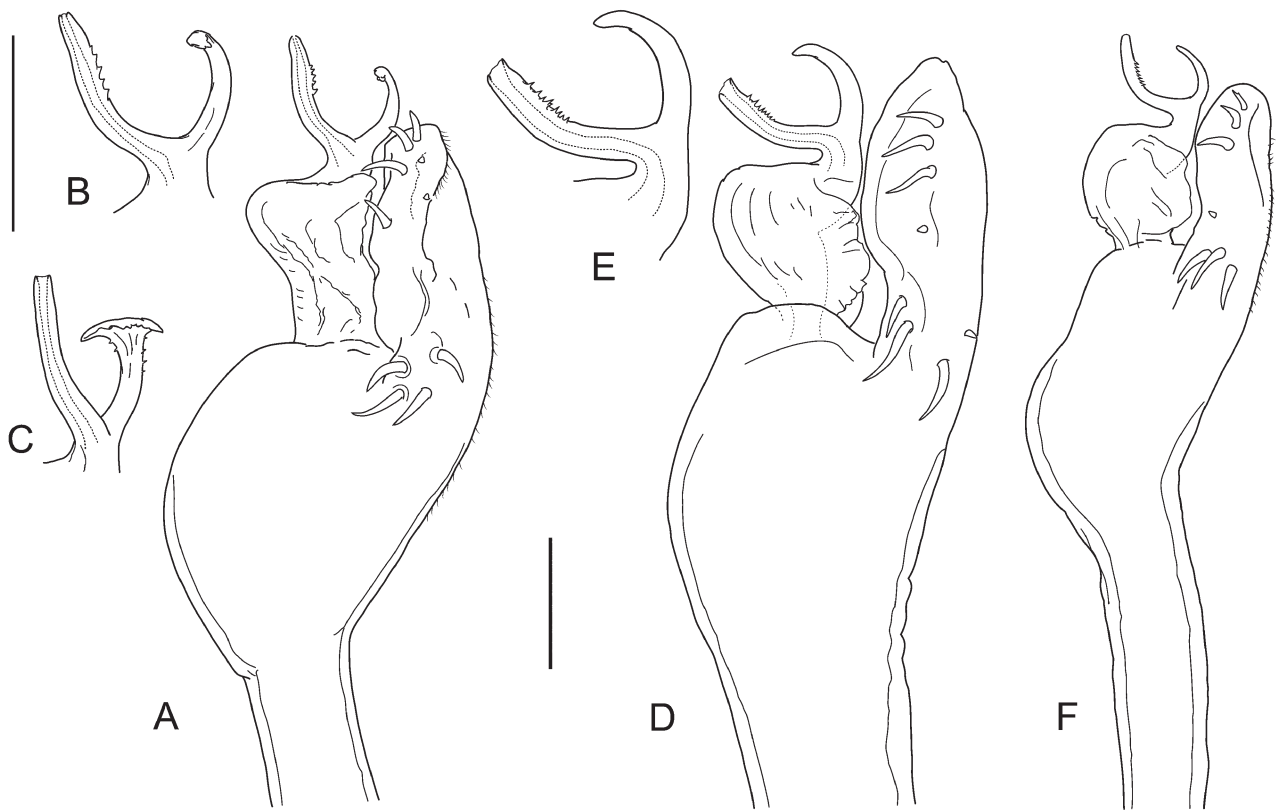
Patella IV: dorsal side densely covered by rounded grains; on the ventral side grains are taller and acute, ending in two large apical apophyses: a proventral, bifid one (seldom as two separate, close apophyses), and a retroventral apophysis.

Tibia IV: dorsal surface with granulation similar to patella; proventral and retroventral rows of acute projections, with increased size (grains at the base, tall apophyses distally); the proventral row ends subterminally but the retroventral row still has an apical rudimentary apophysis, often bifid or duplicated (Fig. 3B).

Leg IV (♀): Coxa with small acute prolateral apophysis and minute retrolateral apophysis (the latter sometimes hidden by tegumentary borders). Trochanter simple, with sparse granules; three small conic apophyses correspond to those of male: retroventral apical (the largest one), and two retrolateral. Femur, patella and tibia with rows of granules, with only a rudiment of the retrolateral sub-basal apophysis sometimes recognizable, otherwise unarmed.

**Male genitalia** (Fig. 5). Distal end of trunk markedly swollen and curved (first dorsad, then ventrad), so that the distal end is ventrally shifted from the trunk axis. VP subrectangular, slightly wider at the base; distal border straight; macrosetae forming two groups on each lateral: 3 apical C macrosetae, short and strong, transverse, and 3–4 longer basal macrosetae A, diagonally pointing proximad; a small macroseta D aligned to the C group, and two rudimentary macrosetae E, ventrally of the latter; the basal group has also one smaller ventral macroseta B. Ventrolateral surface of VP covered by two independent spiny fields in its whole extension, reaching the distal end of trunk. Subdistal portion of glans has a dorsad projected border. Stylus emerges in a single stem, then diverges from VPS; stylus smoothly bent dorsoapically, it bears heavy backward-pointing spination on its ventral border; VPS

curved, its flabellate tip (with irregularly scalloped margins) points dorsad, thus giving the apical end of the glans a forked appearance.



**FIGURE 6.** Distal end of penis, lateral views. A: *Metabalta efformata* Roewer, 1929, syntype ♂ (SMF), B–C: Detail of stylus and ventral process of stylus (vps); C is slightly rotated dorsolaterally to see the subapical spines on the vps shaft. D: *Nanophareus bosquenublado* Hara *et al.*, 2012 (AMNH), E: Detail of stylus and vps, F: *Nanophareus palpalis* Roewer, 1929, ♂ lectotype (SMF 986/1). Scales: 0.1 mm.

**Distribution and field observations.** *Qorimayus alticola* was collected in a reduced area (two localities separated by less than 5 km), on the eastern slope of Sierra de Famatina, La Rioja province, Argentina (Fig. 7). The Famatina range originated in the Ordovician—*i.e.*, it is older than the Andes—and behind the latter, is the second most elevated massif in South America (Ceï 1982). Its most outstanding feature, the ‘Nevado del Famatina’, covered by a permanent snow cap, has the highest peak in the non-Andean interior of Argentina (Cerro General Belgrano, 6097 m a.s.l.). The Sierra de Famatina has a remarkable biogeographical interest, because of its semi-insularity (surrounded by xeric basins), and its recognition as a relevant area of endemism. Agesen *et al.* (2012) listed 27 endemic vascular plants in this range, of which 21 exist above 1500 m a.s.l., the highest record at 4090 m a.s.l. Barboza *et al.* (2016) updated this number to 28 endemic entities (25 species, 3 varieties), out of 909 taxa (692 species, 34 subspecies, 137 varieties, and 5 forms) they counted in their checklist of Famatinan vascular plants. *Famatinanthus* (Asteraceae, monotypic) is the only endemic plant genus in this area (Barboza *et al.* 2016). Examples of endemic animals include two lizards, *Liolaemus famatinae* Ceï, 1980, and *Phymaturus mallimaccii* Ceï, 1980, captured between 3600 and 4200 m a.s.l. (Ceï 1980, 1982); a bothriurid scorpion, *Orobothriurus famatina* Acosta, in Acosta & Ochoa, 2001, with records at 2450–3060 m a.s.l. (Acosta & Ochoa 2001), as well as several high-Andean bird subspecies (Nores 1995).



**FIGURE 7.** Records of *Qorimayus alticola* (blue dots) in Sierra de Famatina, La Rioja Province, western Argentina, together with known localities of the Chilean genera *Nanophareus* (red dots) and *Metabalta* (yellow dots). Regional divisions in Chile: Coquimbo (COQ); Valparaíso (VAL); Región Metropolitana de Santiago (MET); Libertador General Bernardo O'Higgins (OHI); Maule (MAU); Ñuble (ÑUB); Bío-Bío (BIO). Inset: position of the represented area in South America; La Rioja Province indicated in gray.



**FIGURE 8.** Habitat of *Qorimayus alticola* in the Río Oro canyon (La Rioja Province, Argentina). A: General view of the valley at ca. 2400 m a.s.l. B: Scrubland bordering the track to Mina El Oro, at one collecting site (2450 m a.s.l.).

The general landscape is dominated by aridity, thereby making the presence of a gonyleptid completely unexpected when ascending the slopes. Up to 2400–2500 m, the lower parts of this mountain are covered by the xeric Monte shrubland (Ceï 1982). It is followed by an herbaceous / arbustive transition belt at 2400–3500 m a.s.l., above which the physiognomy changes into the high Andean vegetation, dominated by grasses and pulvinate plants. From 4500 m a.s.l. onwards vegetation is scarce and is replaced by periglacial rocky substrate (Ceï 1982). These altitudinal limits and the general conditions may vary dramatically, depending on the topography and the orientation. For example, on the road to Mina La Mejicana aridity reaches up to 3170 m a.s.l. (see Acosta & Ochoa 2001 for a map), so that all collecting efforts for harvestmen yielded negative results there. A different situation was met on the 4WD track to the type locality (Mina El Oro), which borders the Río Oro (also known as Río Amarillo). From approximately 2400 m a.s.l., the river canyon becomes narrower, and the vegetation (not more than grasses and shrubs, indeed) starts to look contrasting green (Fig. 8), slightly more humid than the xeric surroundings (Acosta & Ochoa 2001). I captured *Qorimayus alticola* between 2450 and 2550 m a.s.l. under rocks, in grassland and scrubland on the slopes. This species showed a weak bluish fluorescence under U.V. light, a feature known for a few other gonyleptids, like *Pachyloidellus goliath* Acosta, 1993 (fluorescence is yellowish in the latter; Acosta *et al.* 1995). U.V. sampling required much less effort than manual search, and enabled me to detect many specimens climbing at night on the vertical wall along the path cut on the hillside. A remarkable feature of those captures was the high proportion of ‘soft-bodied’ specimens, suggesting that in December (*i.e.*, the end of spring) the final molt to reach adulthood happened shortly before. In manual search (specimens sheltered under rocks) 60% of the individuals were soft-bodied, and the male-female ratio was 1:4. With U.V. light (specimens active at surface) the proportion of soft-bodied individuals decreased to less than 7%, and the male-female ratio turned to 2:1. When captured, *Q. alticola* rapidly elicited its defensive secretions, resembling the quick response of the well studied *Pachyloidellus goliath* (as described in Acosta *et al.* 1993); however, secretions themselves look different, consisting in *Q. alticola* of a dense white fluid with a curious smell recalling synthetic adhesives (no chemical analysis was available). No other gonyleptid was found in the area, but an undetermined *Ceratontia* (Triaenonychidae) was caught at 2550 m a.s.l., under stones.

### Comparisons: taxonomic affinities of *Qorimayus*

Classical features do not enable the separation of *Qorimayus* from other genera with similar ‘roewerian’ definitions: the combination of ocular mound with (incipient) paired armature, dorsal scute unarmed, palpal femur armed with a subapical medial spine and tarsal formula 6:n:6:6 would lead us to place *Q. alticola* in either *Parabalta* or *Pachyloides* as it formerly was. Those characters long proved to have little value in the genus-level systematics. On the contrary, male genital morphology of *Qorimayus* is clearly different from the mentioned genera, the best diagnostic feature referring to the apical end of glans: stylus + vps. These arise from a common stem in *Qorimayus*, then diverge in opposite directions; vps is gently curved, and is tipped by a small flabellate shape, pointing dorsad. The entire apical end of the glans, in lateral view, has a forked appearance (Fig. 5), and the ventral margin of the stylus is armed with several short, heavy spines. Such an orientation of vps is not observed in either *Parabalta* or *Pachyloides* (*cf.* figs. 2–9 in Acosta 1996a) nor in most Argentinean, Peruvian and Chilean ‘pachylines’. In these genera, the stalk of vps (whenever developed) is more or less inclined in the same direction as the stylus, and it is tipped with a projection pointing ventrad, not dorsad. A few Andean pachylines have the tip of vps oriented dorsad (*Junicus* Goodnight & Goodnight, 1947, *Tarmapachylus* Roewer, 1956, *Palcapachylus* Roewer, 1952, and *Biconisoma* Roewer, 1936), but even in those cases the stem of vps is not divergent from the stylus itself; in these genera the tip of vps is more or less ‘almond-like’, with no resemblance with *Qorimayus* (Acosta 2001, and unpubl. obs.).

*Qorimayus* has close similarities with two Chilean genera with forked stylus + vps: *Metabalta* and *Nanophareus*, the latter denoted as ‘Gonyleptidae *incertae sedis*’ by Kury (2003) and more recently confirmed in Pachylinae by Hara *et al.* (2012). I hereby propose to label this generic assemblage as the ‘*Metabalta* group’ (MG) within Pachylinae. According to the cladistic results, it should also preliminarily include other Chilean representatives, *Tumbesia* and *Neogonyleptes* (Fig. 1); but, as their genital shape does not match exactly the pattern shared by *Qorimayus*, *Metabalta* and *Nanophareus*, this presumed membership remains to be more thoroughly investigated (*e.g.*, by the inclusion of more terminals in the phylogenetic analysis).

The systematics of *Metabalta*, currently containing five small-sized Chilean nominal species (Kury 2003), is

poorly understood. The type material of the type species, *Metabalta tuberculata* Roewer, 1913, from Concepción (SMF RI/804, 809), is almost destroyed (Acosta 1996b), so that study of the penis morphology was impossible. Hence, *Metabalta efformata*, from ‘Ñuble, Sierra de Chillan’, and *Metabalta geniculata*, from ‘Valparaíso’ were examined, and it was assumed that the genital morphology of the studied species is representative of the genus (*Metabalta tuberculata* and *M. efformata*, separated by a trivial difference by Roewer 1929, might prove to be synonyms; pers. obs.). *Metabalta* was described as having an ocular mound with paired armature, and, like *Qorimayus*, to bear 6-n-6-6 tarsomeres. The external morphology of all species assigned to *Metabalta* is very distinct from *Qorimayus alticola* **comb. nov.**, especially with respect to leg IV of the male: in *Metabalta* the femur is shorter, consistently curved and heavily armed (Roewer 1913, 1929), while it is straight and little armed in *Qorimayus*; the coxa has a small retroapical apophysis in the latter, not seen in *Metabalta*. Moreover, the dorsal scutum in *Qorimayus* is flat and almost smooth, contrasting with the convex-swollen scutum of *Metabalta*, borne with paired median tubercles in scutal areas I–IV and free tergites I–III (Roewer 1913, 1929). Additional features referring to chelicerae, pedipalps, coxa IV and stylus + vps are compared in detail in Table 8. Penis similarities include the dilatation of the distal portion of trunk (Figs. 5, 6A–C): viewed laterally in *Qorimayus*, this part has a typical ‘dorsad, then ventrad’ curvature; and the same feature is a little attenuated but still recognizable in *M. efformata* (Fig. 6A), although not as accentuated in *M. geniculata*. vps is markedly flabellate in both studied species of *Metabalta*, in the case of *M. geniculata* showing a decided “Ginkgo-leaf” shape; the shaft of vps has minor subdistal bordering spines in *Metabalta* (Fig. 6C), not seen in *Qorimayus*. In both, the glans protrudes dorsally on its apical margin, which in dorsal view gives this structure an amphora-looking shape.

**TABLE 8.** Comparative overview of diagnostic features of genera *Qorimayus* **gen. nov.**, *Metabalta* Roewer and *Nanophareus* Roewer. Shared character states are indicated as (\*).

	<i>Qorimayus</i>	<i>Metabalta</i>	<i>Nanophareus</i>
a) Body size	large	small (*)	small (*)
b) Chelicera, basichelicerite	short, bulla inflated (*)	short, bulla inflated (*)	elongated, bulla little swollen
c) Pp coxa	short, not surpassing trochanter I (*)	short, not surpassing trochanter I (*)	long, it surpasses trochanter I
d) Pp femur, shape	normal (*)	normal (*)	elongated
e) Pp femur, subapical spine	yes	no (*)	no (except for one species) (*)
f) Pp patella-tibia joint	patella articulates tibia from above (*)	patella articulates tibia from above (*)	patella articulates tibia from above (*)
g) Pp tibia, shape	normal, retroposterior angle obtuse	short, retroposterior angle straight (*)	in most species: short, retroposterior angle straight (*)
h) Pp tibia, retrolateral apical-subapical spines	short, base bifid (*)	short, base bifid (*)	long, base furcate-tipped
i) Pp tarsus, dimensions	similar as tibia (*)	similar as tibia (*)	twice as large as tibia
j) Pp tarsus, dorsal outline	gently convex (*)	gently convex (*)	strongly convex
k) Cx II, length ventral view	moderate (*)	moderate (*)	long
l) Cx IV, retroapical apophysis	yes	no	varied
m) Border of stigmatic segment	intermediate	deeply concave	slightly concave
n) Glans, lateral view	protrudes on apical ridge (*)	protrudes on apical ridge (*)	globose, protrudes in all extension
o) Stylus, curvature	sigmoid (*)	sigmoid (*)	concave
p) Stylus, orientation	same as truncus axis (*)	same as truncus axis (*)	subperpendicular to truncus axis
q) Stylus, relative length	longer than vps (*)	longer than vps (*)	nearly as long as vps
r) Stylus, apical narrowing	narrowed (*)	narrowed (*)	not narrowed
s) vps, apical end	peltate (*)	peltate or flabelliform (*)	spatulate
t) vps, subapical spines on shaft	no (*)	yes	no (*)

As for *Nanophareus*, currently containing seven species (Hara *et al.* 2012; Hara 2016), penis similarities with *Qorimayus* include the general shape, the furcate stylus + vps, the ventral border of stylus armed with acute spines, and the distal part of trunk swollen. The vps tip of *Nanophareus* differs in being spatulate with smooth borders (Fig. 6D–F) instead of flabellate and with irregularly scalloped borders, as seen in *Metabalta* and *Qorimayus*. Aside from several subtle differences in the shape of the stylus (Table 8), in most species of *Nanophareus* it has a more truncated appearance than *Metabalta* and *Qorimayus*. The distal dilatation of trunk has some variation in the species examined, resembling *Qorimayus* the most in the case of *Nanophareus palpalis* (Fig. 6F), but in *N. bosquenublado* it is shorter and not as curved (Fig. 6D) (Hara *et al.* 2012, do not depict this portion of penis). The glans is dorsally protruding in *Nanophareus* too, but on its entire length, so that its outline is round both in lateral and dorsal views. In any case, these genital similarities were unexpected in the face of so many external peculiarities of *Nanophareus*. These are bizarre small-sized pachylines, with some species having many derived features, like the eyes separated, on a widened, very low ocular mound (Hara *et al.* 2012). Some pedipalp segments are remarkably hypertelic (Table 8): coxae are often enlarged, protruding anteriorly as large truncate pyramids; pedipalp femur is long and slender, completely unarmed; tibia and especially tarsus of *Nanophareus* are inflated; and two distal or subdistal spines on the ventrolateral row of palpal tibia fuse in a large apomorphic fork with a huge bifid socket (Fig. 4D; Roewer 1929; Hara *et al.* 2012). None of the mentioned palpal features exist in *Metabalta* or *Qorimayus* as such (Figs. 4A–C), albeit some diagnostic traits of *Nanophareus* (Hara *et al.* 2012) are present or insinuated in some way. The patella-tibia articulation of *Nanophareus*, for example, has been characterized as ‘dorsally articulated’, a condition also present in both *Metabalta* and *Qorimayus*. Even the tibial ‘fork’ in the pedipalps of *Nanophareus* can be matched to the small distal and large subdistal spines in *Metabalta* and *Qorimayus*, in both cases with sockets sharing a common tegumentary elevation (Figs. 4A–C). Overall, pedipalps of *Qorimayus* have rather ‘normal’ appearance and proportions, with femur armed. In *Metabalta* pedipalps are short, with femur unarmed but not elongated; tibia and tarsus are short and slightly globose, but not as accentuated as in *Nanophareus* (Table 8). Basichelicerite of *Nanophareus* is remarkably elongated at its base, with bulla slightly convex; *Metabalta* and *Qorimayus* bear normal chelicera, with short basichelicerite and well-developed bulla.

### ***Metabalta polyhastata* (Hara, 2016) comb. nov.**

*Nanophareus polyhastatus* Hara, 2016: 117; Pérez-Schultheiss *et al.*, 2019: 10. urn:lsid:zoobank.org:act:364BA304-56DD-4C73-9BF3-FA652B038A46

The results of the cladistic analysis (Fig. 1) demonstrated that *Nanophareus polyhastatus* Hara, 2016 forms a well-supported clade with species of *Metabalta*. This relationship is underpinned  $\alpha$ -taxonomically too, as evidenced by a close examination of the original description and illustrations of *N. polyhastatus*: the exomorphological and genital features of this species (Hara, 2016) best match the character states present in *Metabalta*, as defined in Table 8. For example, fig. 6A by Hara (2016) clearly displays pedipalp coxae with ‘normal’ appearance, *i.e.*, not elongated as in *Nanophareus*. In addition, *N. polyhastatus* has a ‘normal’ development of basichelicerite and pedipalp femur, and the retrolateral apical-subapical spines on tibia are placed in a bifid basal socket, not as large and furcate-tipped as in *Nanophareus* (Table 8, chars. b, d, h). Several genital characters support the transfer of *N. polyhastatus* into *Metabalta*, like the sigmoid curvature of stylus, its orientation and apical narrowing, and the apical end of vps (Table 8, chars. o, p, r, s); drawings of Hara (2016) are not detailed enough to see if also char. t (subapical spines on vps shaft) applies. Based on this evidence, I hereby formally propose the new combination *Metabalta polyhastata* (Hara, 2016) **comb. nov.** (the original spelling *polyhastatus* changed to *polyhastata* to ensure the agreement in grammatical gender with the genus name *Metabalta*).

Aside, Pérez-Schultheiss *et al.* (2019) suggested that *N. polyhastatus* and *Metabalta albipes* Mello-Leitão, 1931 might prove to be the same. Although the latter species has no original figure available for a comparison, that of *Metabalta porteri* Mello-Leitão, 1936 (currently under synonymy of *M. albipes*, after Ringuélet 1959) looks identical to *M. polyhastata*, as described and drawn by Hara (2016); key similarities refer to the general apophysis pattern on femur IV, and the shape (and thickness) of apophysis of coxa IV. Until the relevant types are studied I prefer not to formalize this presumed specific synonymy. It should be noted that *M. polyhastata* was included by Hara (2016) in his cladistic analysis of *Nanophareus*, but resulted in an internal position in the genus.

**Additional material examined.** *Metabalta efformata*: Chile: Sierra de Chillán, 2 ♂ syntypes (SMF RII 952);



*Metabalta geniculata*: Chile: Valparaíso, 1 ♂, 1 ♀ syntypes (SMF RII 951); *Nanophareus palpalis*: ‘Chile’, 1 ♂ lectotype, 1 ♂, 2 ♀ paralectotypes (designated by Hara *et al.* 2012; SMF 986/1); *Nanophareus bosqenublado*: Chile: Los Molles, elev. 2 m, under succulent rock cover along coast, 9 Jan. 1985, N.I. Platnick & O.F. Francke (AMNH).

## Discussion

Relictual harvestmen dwelling in the middle of an extensive hostile region open meaningful questions on the historical origin of such isolated populations (Maury 1986, Acosta 2002). It seems clear that those relicts might represent the remnants of a wider ancestral range, which was affected by isolation and further differentiation. Therefore, in order to learn more about the ancestral distribution, we must first identify their closest relatives. Until now, the dominating belief was that relictual harvestmen of western Argentina (among them *Qorimayus alticola*) were related to a ‘subtropical’ ancestry (Maury 1986, Acosta 2002). The meaning of the term ‘subtropical’, in this context, is based on Ringuélet (1961, 1978). This author recognized three main zoogeographic domains for Argentina: the ‘Brazilian’ or ‘subtropical’ component, whose current distribution would reach up to the sub-Andean and Pampean sierras; the ‘Araucanian’ or ‘austral’ component, in the temperate humid forests of southern Chile; and the ‘Andean-Patagonian’ fauna, spread over the xeric diagonal separating the two former. Ringuélet himself (1961) explicitly stressed that *Q. alticola* ‘derived from the subtropical generic ensemble’. In the original paper, Ringuélet (1962) provides a thorough speculation on evolutionary relationships, hypothesizing three lineages that might have derived from a ‘basal *Neopucroliella* stock’ with long-tarsal process. One of these lineages would be represented by the Argentinean species of ‘*Parabalta*’ (currently in *Pachyloides*; Acosta 1996a), with *Q. alticola* representing a supposed further evolutionary step. However, Ringuélet’s (1962) discussion was actually based on some incorrect assumptions, like the polarity of the tarsal process (the long tarsal process was demonstrated to be apomorphic in this group; Acosta 1990) and the inclusion of *Q. alticola* in this assemblage.

Just for the sake of simplicity, in this discussion the opiliofauna of central Chile together with the Valdivian one (‘Araucanian’) will be collectively referred to as ‘Chilean’. This use is intended to emphasize its separation and differentiation from the subtropical gonyleptid fauna, a vicariant event derived from the rise of the Andes (start at the end of the Cretaceous, main uplift in the Miocene-Pliocene). These major tectonic events led to a progressive aridity in western Argentina, which would have determined the northward-eastward withdrawal of subtropical elements (Maury 1986, Ringuélet 1978). It should be noted that for Ringuélet (1961, 1978), the whole Chilean gonyleptid fauna was to be regarded as having ‘Brazilian’ (subtropical) origins, as a remnant of a formerly continuous family range. Despite being true, this assertion might be too general and of little use in the chronological and spatial scales needed to understand the relictual condition of *Qorimayus*. Setting aside some suspect taxonomic inaccuracies (like an alleged Chilean ‘*Discocyrtus*’ or a Brazilian ‘*Sadocus*’; Soares & Soares 1954: 249, 271, Kury 2003: 163, 191), all Chilean gonyleptid genera seem well defined (pers. obs.), constituting an opiliofaunistic component not hitherto known beyond the Andean watershed (for central Chile) or the Valdivian forests boundaries (for the Araucanian portion). If a ‘subtropical’ ancestry was assumed for *Qorimayus* and the other relictual harvestmen in western Argentina, the main implication would be that the separation of the Chilean opiliofauna must have preceded the events deemed to have isolated the referred relicts (likely, the withdrawal of subtropical elements due to increased aridity). The former generic placement of *Q. alticola*, first assigned to ‘*Parabalta*’ (regarded as a ‘Chacoan’ taxon by Ringuélet 1978), then to *Pachyloides*, implicitly invoked this simplest scenario: a retracting subtropical fauna that left isolates (Ringuélet 1978). However, as shown in this study, affinities of *Qorimayus* reveal no direct subtropical ancestry, but (ancient) trans-Andean links with two Chilean genera instead (Fig. 7). In this scenario, an ancestral range ‘*Metabalta* + *Nanophareus* + *Qorimayus*’ must have preceded the formation of the Andes and became split by the rise of the orographic barrier. Subsistence of *Qorimayus* might have been possible by microclimatic conditions in a protected valley, at higher elevation. Trans-Andean links for gonyleptids are indeed rare, but still supported by the central Chilean genus *Pachylus*, and its presumed Argentinean-Uruguayan relatives, *Pachyloidellus* Müller, 1918, and *Acanthopachylus* Roewer, 1913 (Föttinger *et al.* 2010).

## Acknowledgements

The author wishes to recognize Dr Miguel Archangelsky, Marcos Acosta and Gastón Repossi for their kind help with the collection of specimens; special thanks are due to the former, for driving his 4WD in harsh roads and tracks in the Sierra de Famatina to find suitable collecting sites. For enabling me to study relevant materials from their collections, I also acknowledge Peter Jäger and Julia Altmann (SMF), and Cristina Scioscia (MACN). TNT software was made available with the sponsorship of the Willi Hennig Society. Many comments and suggestions made by an anonymous reviewer and by the Subject Editor, Abel Pérez-González, improved greatly the final manuscript. L.E.A. is a researcher of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This research received financial support by CONICET (P.E.I. N° 0406/97) and SECyT-UNC.

## References

- Aagesen, L., Bena, M.J., Nomdedeu, S., Panizza, A., López, R.P. & Zuloaga, F.O. (2012) Areas of endemism in the southern Central Andes. *Darwiniana*, 50 (2), 218–251.
- Acosta, L.E. (1989) *Pachyloides hades*, nueva especie de opilión de la Argentina (Opiliones, Gonyleptidae, Pachylinae). *Journal of Arachnology*, 17 (1), 137–142.
- Acosta, L.E. (1990) Redescrición de *Neopucroliella mesembrina* Ringuelet, 1961 nov. stat. (Opiliones, Gonyleptidae, Pachylinae). *Revista de la Sociedad Entomológica Argentina*, 48 (1–4), 97–105.
- Acosta, L.E. (1993) El género *Pachyloidellus* Müller, 1918 (Opiliones, Gonyleptidae, Pachylinae). *Bonner zoologische Beiträge*, 44 (1–2), 1–18.
- Acosta, L.E. (1995) A remarkable finding of *Pachyloides sicarius* (Opiliones, Gonyleptidae, Pachylinae) in the Province of Catamarca, Northwestern Argentina. *Biogeographica*, 71 (1), 33–36.
- Acosta, L.E. (1996a) An emendation of the generic concept of *Pachyloides*, with the description of a new species (Opiliones, Gonyleptidae, Pachylinae). *Revue Suisse de Zoologie, Memoirs of the XIIIth International Congress of Arachnology, Genève*, Hors Série, 1, 5–14.
- Acosta, L.E. (1996b) Die Typus-Exemplare der von Carl-Friedrich Roewer beschriebenen Pachylinae (Arachnida: Opiliones: Gonyleptidae). *Senckenbergiana biologica*, 76 (1–2), 209–225.
- Acosta, L.E. (2001) The identity of *Acrographinotus erectispina*, with a review of the generic diagnosis, and the description of a new species (Opiliones, Gonyleptidae, Pachylinae). *Bulletin of the British Arachnological Society*, 12 (2), 58–66.
- Acosta, L.E. (2002) Patrones zoogeográficos de los Opiliones argentinos (Arachnida: Opiliones). *Revista Ibérica de Aracnología*, 6, 69–84.
- Acosta, L.E. & Ochoa, J.A. (2001) Two new species of *Orobothriurus* Maury, 1976 from Argentina and Peru, with comments on the systematics of the genus (Scorpiones: Bothriuridae). In: Fet, V. & Selden, P.A. (Eds.), *Scorpions 2001. In Memoriam Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, pp. 203–214.
- Acosta, L.E., Poretti, T.I. & Mascarelli, P.E. (1993) The defensive secretions of *Pachyloidellus goliath* (Opiliones, Gonyleptidae, Pachylinae). *Bonner zoologische Beiträge*, 44 (1–2), 19–31.
- Acosta, L.E., Pereyra, F.E. & Pizzi, R.A. (1995) Field observations on *Pachyloidellus goliath* (Opiliones, Gonyleptidae) in Pampa de Achala, province of Córdoba, Argentina. *Bulletin of the British Arachnological Society*, 10 (1), 23–28.
- Acosta, L.E., Pérez González, A. & Tourinho, A.L. (2007) Methods for taxonomic study. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, Massachusetts, pp. 494–505.
- Barboza, G.E., Cantero, J.J., Chiarini, F.E., Chiapella, J., Freire, S., Nuñez, C.O., Palchetti, V. & Ariza Espinar, L. (2016) Vascular plants of Sierra de Famatina (La Rioja, Argentina): an analysis of its biodiversity. *Phytotaxa*, 248 (1), 1–123. <https://doi.org/10.11646/phytotaxa.248.1.1>
- Cei, J.M. (1980) New endemic iguanid lizards from the Famatina mountains of Western Argentina. *Journal of Herpetology*, 14 (1), 57–64. <https://doi.org/10.2307/1563876>
- Cei, J.M. (1982) Aspetti geo-biogeografici inediti della Sierra di Famatina, il più elevato massiccio d'America del Sud dopo le cordigliere andine (Argentina centro-occidentale). *L'Universo*, 62 (4), 643–672.
- Chamberlin, R.V. (1925) Diagnoses of new American Arachnida. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 67 (4), 211–248.
- Curtis, D.J. & Machado, G. (2007) Ecology. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, pp. 280–308.
- Föttinger, P., Acosta, L.E., Leis, H.J. & Rasputnig, G. (2010) Benzoquinone-rich exudates from the harvestman *Pachylus paessleri* (Opiliones: Gonyleptidae: Pachylinae). *Journal of Arachnology*, 38, 584–587. <https://doi.org/10.1636/B09-110SC.1>
- Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–91.

- <https://doi.org/10.1111/j.1096-0031.1993.tb00209.x>
- Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.  
<https://doi.org/10.1111/j.1096-0031.2008.00217.x>
- Goodnight, C.J. & Goodnight, M.L. (1947) Phalangida from Tropical America. *Fieldiana, Zoology*, 32 (1), 1–58.
- Gray, G.R. (1833) *Gonoleptes spinipes*, *Gonoleptes chilensis*. In: Cuvier, G., Griffith, E. & Pidgeon, E. (Eds.), *The Animal Kingdom arranged in conformity with its organization. Vol. 13. Annelida, Crustacea, and Arachnida*. Whittaker, Treacher and Co., London, pp. 1–539, pl. 20, figs. 1–2.
- Hara, M.R. (2016) Cladistic analysis and description of three new species of the Chilean genus *Nanophareus* (Opiliones: Gonyleptidae: Pachylinae). *Zootaxa*, 4105 (2), 101–123.  
<https://doi.org/10.11646/zootaxa.4105.2.1>
- Hara, M.R. & Pinto-da-Rocha, R. (2010) Systematic review and cladistic analysis of the genus *Eusarcus* Perty 1833 (Arachnida, Opiliones, Gonyleptidae). *Zootaxa*, 2698 (1), 1–136.  
<https://doi.org/10.11646/zootaxa.2698.1.1>
- Hara, M.R., Pinto-da-Rocha, R. & Kury, A.B. (2012) Revision of *Nanophareus*, a mysterious harvestman genus from Chile, with descriptions of three new species (Opiliones: Laniatores: Gonyleptidae). *Zootaxa*, 3579 (1), 37–66.  
<https://doi.org/10.11646/zootaxa.3579.1.2>
- Holmberg, E.L. (1876) Arácnidos argentinos. *Anales de Agricultura de la República Argentina*, 4, 1–30. [separatum]
- Holmberg, E.L. (1878) Notas arcnológicas. Sobre los Solpúgidos argentinos. *El naturalista argentino*, 1 (1), 69–74.
- Kirby, W. (1818) A century of insects, including several new genera described from his cabinet. *Transactions of the Linnean Society of London*, 12 (Part II), 375–453, pls. 21–22.  
<https://doi.org/10.1111/j.1095-8339.1817.tb00239.x>
- Koch, C.L. (1839) *Übersicht des Arachnidensystems*. C.H. Zeh’schen Buchhandlung, Nürnberg, 38 pp.
- Kury, A.B. (2003) Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). *Revista Ibérica de Aracnología*, Volumen Especial Monográfico, 1, 5–337.
- Kury, A.B. (2014) Why does the Tricommatinae position bounce so much within Laniatores? A cladistic analysis, with description of a new family of Gonyleptoidea (Opiliones, Laniatores). *Zoological Journal of the Linnean Society*, 172, 1–48.  
<https://doi.org/10.1111/zoj.12165>
- Kury, A.B. & Maury, E.A. (1998) A new genus and five new species of Metasarcinae from Peru (Arachnida, Opiliones, Gonyleptidae). *Zoological Journal of the Linnean Society*, 123, 143–162.  
<https://doi.org/10.1111/j.1096-3642.1998.tb01297.x>
- Kury, A.B. & Villarreal, M.O. (2015) The prickly blade mapped: establishing homologies and a chaetotaxy for macrosetae of penis ventral plate in Gonyleptoidea (Arachnida, Opiliones, Laniatores). *Zoological Journal of the Linnean Society*, 174, 1–46.  
<https://doi.org/10.1111/zoj.12225>
- Kury, A.B., Villarreal Manzanilla, O. & Sampaio, C. (2007) Redescription of the type species of *Cynorta* (Arachnida, Opiliones, Cosmetidae). *Journal of Arachnology*, 35, 325–333.  
<https://doi.org/10.1636/H06-35.1>
- Loman, J.C.C. (1899) Die Opilioniden der Sammlung Plate. *Zoologische Jahrbücher*, Supplement 4 (Fauna Chilensis), 2, 1–14., pl. I.
- Maury, E.A. (1986) Hallazgo arcnológico en cavernas del oeste argentino. *Salamanca*, 2 (2), 20–24.
- Maury, E.A. (1988) Triaenonychidae sudamericanos. V. Un nuevo género de Opiliones cavernícolas de la Patagonia (Opiliones, Laniatores). *Mémoires de Biospéologie*, 15, 117–131.
- Maury, E.A. (1992) Lista de los ejemplares típicos de “Arachnida” (Opiliones, Scorpiones y Solifugae) depositados en el Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Suplemento I. *Aracnología*, 6 (Suplemento), 1–10. [Montevideo]
- Maury, E.A. & Roig Alsina, A.H. (1982) Sobre la presencia de Opiliones en las provincias argentinas de Mendoza y San Juan (Arachnida, Opiliones). *Neotropica*, 28 (79), 39–40.
- Mello-Leitão, C. de (1931) Notas sobre arcnídeos argentinos. *Annaes da Academia Brasileira de Ciencias*, 3 (2), 83–97.
- Mello-Leitão, C. de (1936) Étude sur les arcnides de Papudo et Constitution (Chili), recueillis par le Prof. Dr. Carlos E. Porter. *Revista Chilena de Historia Natural*, 40, 112–129.
- Müller, A. (1918) Einige neue Gonyleptiden. *Zoologischer Anzeiger*, 49 (3–4), 89–94.
- Nixon, K.C. (1999) *Winclada. Version 1.00.08*. Published by the author, Ithaca, New York. [program]
- Nores, M. (1995) Insular biogeography of birds on mountain-tops in north western Argentina. *Journal of Biogeography*, 22, 61–70.  
<https://doi.org/10.2307/2846073>
- Pérez-Schultheiss, J., Urra, F. & Otárola, A. (2019) Opiliones Laniatores (Arachnida) de la Cordillera de Nahuelbuta: un desconocido hotspot de diversidad. *Boletín Nahuelbuta Natural*, 4, 1–24.
- Perty, M. (1833) *Delectus animalium articulorum*. Impensis Editoris, Munich, 205 pp.
- Pinto-da-Rocha, R., da Silva, M.B. & Bragagnolo, C. (2005) Faunistic similarity and historic biogeography of the harvestmen of southern and southeastern Atlantic Rain Forest of Brazil. *Journal of Arachnology*, 33, 290–299.  
<https://doi.org/10.1636/04-114.1>

- Ringuelet, R.A. (1957) Biogeografía de los arácnidos argentinos del Orden Opiliones. *Contribuciones Científicas, Serie Zología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires*, 1 (1), 1–33.
- Ringuelet, R.A. (1959) Los arácnidos argentinos del Orden Opiliones. *Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoológicas*, 5 (2), 127–439, pls. I–XX.
- Ringuelet, R.A. (1961) Rasgos fundamentales de la Zoogeografía de la Argentina. *Physis*, 22 (63), 151–170.
- Ringuelet, R.A. (1962) Un nuevo opilión de fauna de altura y observaciones sobre vinculaciones evolutivas en algunos Pachylinae (Arachnida). *Revista de la Sociedad Entomológica Argentina*, 23, 1–6, figs. 1–5. [1960]
- Ringuelet, R.A. (1978) Dinamismo histórico de la fauna brasílica en la Argentina. *Ameghiniana*, 15 (1–2), 255–262.
- Roewer, C.F. (1912) Die Familien der Assamiden und Phalangodiden der Opiliones-Laniatores (=Assamiden, Dampetriden, Phalangodiden, Epedaniden, Biantiden, Zalmoxiden, Samoiden, Palpipediden anderer Autoren). *Archiv für Naturgeschichte*, 78A (3), 1–242.
- Roewer, C.F. (1913) Die Familie der Gonyleptiden der Opiliones-Laniatores. *Archiv für Naturgeschichte*, 79A (4), 1–256.
- Roewer, C.F. (1929) Weitere Weberknechte III. III. Ergänzung der: „Weberknechte der Erde“, 1923. *Abhandlungen vom naturwissenschaftlichen Verein zu Bremen*, 27 (2), 179–284.
- Roewer, C.F. (1930) Weitere Weberknechte IV. IV. Ergänzung der: „Weberknechte der Erde“, 1923. *Abhandlungen vom naturwissenschaftlichen Verein zu Bremen*, 27 (3), 341–452.
- Roewer, C.F. (1936) Zwei sonderbare Pachylinen aus Peru. *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen*, 1 (3), 341–343, pl. 14.
- Roewer, C.F. (1943) Über Gonyleptiden. Weitere Weberknechte (Arachn., Opil.), XI. *Senckenbergiana*, 26 (1–3), 12–68.
- Roewer, C.F. (1952) Neotropische Arachnida Arthrogastra, zumeist aus Peru. *Senckenbergiana*, 33 (1–3), 37–58.
- Roewer, C.F. (1956) Arachnida Arthrogastra aus Peru, II. *Senckenbergiana biologica*, 37 (5–6), 429–445.
- Santos, F.H. (2007) Ecophysiology. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, pp. 473–488.
- Soares, B.A.M. & Soares, H.E.M. (1954) Monografía dos gêneros de opiliões neotrópicos. *Arquivos de Zoologia do Estado de São Paulo*, 8 (9), 225–302.
- Sørensen, W. (1879) Om bygningen af Gonyleptiderne, en Type af Arachnidernes Classe. *Naturhistorisk Tidsskrift*, Series 3, 12, 97–222, pls. I–II.
- Sørensen, W. (1884) Opiliones Laniatores (Gonyleptides W.S. olim) Musei Hauniensis. *Naturhistorisk Tidsskrift*, Series 3, 14, 555–646.
- Sørensen, W. (1902) Gonyleptiden (Opiliones, Laniatores). *Ergebnisse der Hamburger Magalhaensischen Sammelreise*, 2, 1–36.