
Phylogenetic revision of the spider genus *Negayan* (Araneae, Anyphaenidae, Amaurobioidinae)

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A taxonomic revision and phylogenetic analysis of the spider genus *Negayan* Ramírez, 2003 (Anyphaenidae, Amaurobioidinae, Amaurobioidini) is presented. All 12 known species of *Negayan* plus representatives of each of the other nine amaurobioidini genera (25 taxa in total) were scored for 134 morphological characters. The cladistic analysis of this matrix results in a single most parsimonious tree (LE = 382; CI = 0.42; CI for informative characters = 0.36; RI = 0.49). The monophyly of *Negayan* is corroborated, although with low support values. My results correspond to those of a previous study, with *N. paduana* as the basal species of the genus and *Selknamia* as the sister-group of *Negayan*. *Negayan* is diagnosed by the genitalic morphology in both sexes. Males of *Negayan* have a characteristic retrolateral tibial apophysis on palps that is long, thick and sinuous at the tip. Females of *Negayan* have a characteristic genitalic pattern with coiled copulatory ducts and contiguous spermathecae. New diagnostic characters are proposed. The genus *Negayan* comprises 12 species, four of them known only from females. It is known from Argentina, Chile and Peru. Eight new species are described here: *N. puno* sp. nov., *N. cerronegro* sp. nov., *N. tata* sp. nov., *N. ancha* sp. nov., *N. enrollada* sp. nov., *N. tucuman* sp. nov., *N. tarapaca* sp. nov., and *N. argentina* sp. nov. New morphological data are added to the descriptions of *N. tridentata* (Simon), *N. paduana* (Karsch) and *N. coccinea* (Mello-Leitão). The male of *N. excepta* (Tullgren) is described for the first time and the female is redescribed. *Negayan tridentata* is a senior synonym of *Gayenna exigua* (Mello-Leitão); and *N. paduana* is a senior synonym of *Tomopisthes lebruni* (Simon).

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Introduction

The anyphaenid spider genus *Negayan* Ramírez 2003 comprises twelve species. It occurs in Argentina, Chile and Peru. Most species live under stones or in leaf litter, while some are found under stones at shores of streams or lakes (Ramírez 2003). *Negayan* (formerly known as the ‘*Gayenna strigosa*’ group; Ramírez 1997) was recently erected to include those amaurobioidines with a characteristic shape of the male palp retrolateral tibial apophysis (Ramírez 2003).

Within the context of a cladistic analysis of the anyphaenid subfamily Amaurobioidinae Hickman 1949 (see Ramírez 1995a for the subfamilies of Anyphaenidae), Ramírez (2003) subdivided this subfamily into two tribes, Amaurobioidini and Gayennini. The genus *Josa* Keyserling 1891 was proposed as the sister group of Gayennini. Within Amaurobioidini, the monophyly of the genus *Negayan* was relatively well supported, although only three species were considered in the analysis: *N. tridentata* (Simon 1886) (type species), *N. paduana*

(Karsch 1880) and *N. coccinea* (Mello-Leitão 1943). *Selknamia* Ramírez 2003 was proposed as the sister group.

The diagnosis of *Negayan* was based on the morphology of the retrolateral tibial apophysis of the male palp, which is long, thick, and sinuous at the tip. The female genitalia, although characteristic, seem similar to those of the amaurobioidini *Ferrieria echinata* Tullgren 1901 and *Acanthoceto pichi* Ramírez 1997; hence, no distinctive and diagnostic features were proposed for then females of *Negayan* (Ramírez 2003). This study provides a taxonomic revision and a species-level cladistic analysis of the genus.

Materials and methods

Specimens

The following institutions and curators made available the specimens examined in this study: American Museum of Natural History, New York (AMNH, Norman Platnick);

The Natural History Museum, London (BMNH, Paul Hilliard); California Academy of Sciences, San Francisco (CAS, Charles Griswold); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN, Léon Baert); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires (MACN-Ar, Cristina Scioscia); Muséum National d'Histoire Naturelle, Paris (MNHN, Christine Rollard); Museo Nacional de Historia Natural, Santiago de Chile (MHNS, Ariel Camousseight); Museo de La Plata, Argentina (MLP, Luis Pereira); Naturhistoriska Riksmuseet, Stockholm (NR, Torbjörn Kronestedt); Universidad de Concepción, Chile (UC, Viviane Jerez); Universidad de San Luis, Argentina (USL, Adriana V. de Simonati); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM, Jonathan Coddington); Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB, Jason A. Dunlop); Zoologisk Museum, University of Copenhagen (ZMUC, Nikolaj Scharff).

Methods of study

Specimens were studied in 80% ethanol using a Leitz stereomicroscope. All measurements are in millimeters. 'Short tibia' on male palp refers to a length that is equal to or less than the width, while 'long tibia' refers to a length greater than the width. All drawings were made with a camera lucida attached to the stereomicroscope. After dissection, epigyna were cleared in clove oil. Species descriptions, spination notation, and measurements follow Ramírez (2003). Spination pattern is described in order from leg I to IV, and within each leg from proximal to distal segments (i.e. from femur to tarsus). Within each segment the spines are listed from each of the four surfaces, in the following order: dorsal (d), prolateral (p), retrolateral (r), and ventral (v). Only legs, segments, and surfaces with spines are listed.

Although there seems to be a conservative basic spination pattern within amaurobioidines, spination can vary intraspecifically, even within the same specimen. The spine positions of both sides of the spider are coded as right and left side values, in this order, separated by a slash. The same notation is also used for cheliceral teeth. If pairing between two rows of spines on the same segment surface is not regular, it is indicated in parentheses after the notation.

When a spine is located apically or basally in the side of a segment, it carries the suffix 'ap' or 'bas', respectively. For example 'd 1ap' describes one spine located in the middle line on the dorsal surface of a segment, in apical position. This is equivalent to 'd 0-0-0-1'. For basal spines, 'd 1bas' is equivalent to 'd 1-0-0-0'. In some segments an 'apical comb' (several apical spines on the same surface) is often present. In such cases, it is noted as 'comb' at the end of the spine notation for that surface, keeping in mind that it is referring to apical spines.

When spines are paired, I have indicated whether they are placed on a particular side of a surface. For example, p 2-d1-1 indicates four spines on the prolateral surface (two basal, one median dorsally displaced, and one apical on the median line). When two spines are not strictly paired (usually one located on the middle line, the other on the side of a surface), but are close to each other, they are associated in parentheses. For example, 0-d1-(1-d1) is equivalent to 0-0-0-0-d1-0-0-0-1-d1.

Although there is some intraspecific variation in the spination patterns in some *Negayan* species as well as other amaurobioidine spiders, the characters related to spines proposed by Ramírez (2003: chars. 129–199, see Appendix 1) are mainly for patterns that are relatively constant in all species and therefore reliable for phylogenetic information. Distal spines on the dorsal femoral surface in legs are shorter than median ones. Basal spines on the same surface can present three different lengths: 'normal' (as long as distal spines), 'long' (longer than distal spines, but equal to median spines), and 'very long' (longer than distal and median spines) (see char. 212, Appendix 2).

Leg formula refers to the relative length of legs. For example, leg formula 4123 means that the leg IV is longer than leg I, leg I longer than II, and leg II longer than III. If two legs are of equal length they are coded with '=' between them; for example, 41=23 means that leg IV is the longest, legs I and II are of equal length, and leg III is the shortest. The distance between tracheal spiracle and spinnerets is measured from the posterior margin of the spiracle up to the posterior margin of the abdominal cuticle (Ramírez 2003). Because different physiological conditions or conditions of specimen preservation can lead to different measurements, this measurement is only intended to give an idea of the size and aspect of the specimen.

Genital morphology

The terminology proposed by Sierwald (1989) for female genitalia appears to work for many spider groups. While it also seems to do so for Amaurobioidinae, Ramírez (2003) has proposed several changes, which I follow. Here, Spermatheca (S) means 'the ample chamber immediately connected to the Fertilization Duct (FD), Copulatory Duct (CD) the tube running from Copulatory Opening (CO) to Spermatheca, and Accessory Bulb (AB) the blind sac bearing conspicuous pores, connected to the copulatory duct by a tube of variable length' (Ramírez 2003).

Cladistic analysis

Taxon sample. In total, 25 taxa were scored for this analysis. The ingroup consists of all 12 *Negayan* species: *N. tridentata* (Simon 1886), *N. ancha* sp. nov., *N. argentina* sp. nov., *N. cerronegro* sp. nov., *N. coccinea* (Mello-Leitão 1943),

N. enrollada sp. nov., *N. excepta* (Tullgren 1901), *N. paduana* (Karsch 1880), *N. puno* sp. nov., *N. tarapaca* sp. nov., *N. tata* sp. nov., and *N. tucuman* sp. nov. Outgroup selection was based on the phylogenetic hypothesis of Ramírez (2003). Outgroup taxa were represented by the type species of all the other nine genera within Amaurobioidini, plus *Josa*.

To account for generic diversity, basal species (i.e. those species sister to the remaining species within a genus) were included only when a genus was represented by more than four representatives in Ramírez' analysis, or when the type species was known by only one gender. Basal species were added for *Josa*, *Acanthoceto*, and *Aysenia*. The outgroup comprises the following species: *Josa lutea* (Keyserling 1878), *Josa nigrifrons* (Simon 1896), *Acanthoceto acupicta* (Nicolet 1849), *Acanthoceto pichi* Ramírez 1997, *Amaurobioides maritima* O.P.-Cambridge 1883, *Axyracrus elegans* Simon 1884, *Aysenia elongata* Tullgren 1902, *Aysenia cylindrica* Ramírez 2003, *Aysenoides terricola* Ramírez 2003, *Coptoprepes flavopilosus* Simon 1884, *Ferrieria echinata* Tullgren 1901, *Gamakia hirsuta* Ramírez 2003, and *Selknamia minima* Ramírez 2003.

Characters. Taxa were coded for all 200 characters included in Ramírez' (2003) matrix. Because the taxon sample in this study is much smaller than that of Ramírez, 115 characters became phylogenetically uninformative. Those characters with only one of their states coded in all 25 taxa (82 out of 115, excluding the uninformative characters with autapomorphies) were not taken into account in this study.

The 118 characters from Ramírez' analysis included in the present analysis are listed below (numbering corresponds to his original): 0, 1, 6, 7, 9–12, 15–21, 23, 26, 28, 33, 35, 36, 41–44, 48, 50, 53, 54, 57, 59, 61, 62, 64, 65, 67–69, 73, 75–79, 84, 92, 95–98, 100, 102, 111–113, 115–118, 123–128, 132–134, 136, 138, 140–142, 146–148, 150–154, 156, 158, 160, 162–182, 184, 186, 188, and 190–199 (see Appendix 1). Throughout the text, chars. 0–199 are from Ramírez (2003; see also Appendix 1), and chars. 200–215 are new characters proposed in this study (see Appendix 2). Five of the new characters are related to female genitalia, five to male genitalia and six to somatic morphology. The genitalic homologies of amaurobioidines are relatively well understood (Ramírez 1993, 1995a,b, 1997, 1999, 2003; Ramírez & Kochalka 1993).

Six of Ramírez' (2003) characters were modified from their original description. Chars. 20 and 23 were both coded separately for females and males (see chars. 214 and 215, Appendix 2) because within *Negayan*, these characters showed sexual dimorphism. In char. 64, the median apophysis in *Aysenia cylindrica* was considered 'reduced' instead of 'present' (as in Ramírez 2003), because it was smaller than that of *Negayan paduana*, which itself has a 'reduced' median apophysis.

The state 'reduced' throughout this paper refers to a structure that is smaller in size than the fully developed 'present'

structure, and it does not indicate assumptions of reduction of the structure in an evolutionary context. The two states of char. 65 were split into four, in order to better represent the morphological variation of the median apophysis, and the character was treated as unordered. State 1 of char. 75 was absent from the taxon sample, and thus it was deleted (see Appendix 1). Finally, the state 'reduced' was proposed for char. 77, because in some species of *Negayan*, the prolateral process on the primary conductor is smaller. The total number of characters employed is 134.

All new multistate characters proposed here (chars. 65, 77 from Ramírez 2003, and 200–203, 207, 209, 211, 213–215) were treated as unordered (non additive). Originally ordered multistate characters in Ramírez (2003) — chars. 11, 15, 16, 64, 75, and 138 — were also treated as unordered, although the original treatment was explored and the same results were obtained in the analysis.

The original coding of Ramírez (2003) was not altered. The rationale of his coding scheme was to try to maximize the binary coding of the characters when they are not ordered, because the homoplasy downweighting during the implied weighting procedure is affected and not performed similarly in multistate characters (Goloboff 1993). This way, Ramírez coded the absences and presences in one character, and then the shapes independently in another. For ordered characters he just combined the states altogether in one character. Because the data matrix is analysed using implied weights (Goloboff 1993), his binary coding is preserved, as well as his 'ordered' characters as originally coded, in order to make the analyses with ordered/unordered characters comparable.

The dataset is summarized in Table 1, and a detailed description and brief comment on the evolution of each new character are summarized in Appendix 2.

Evaluation of cladistic hypotheses — search for most parsimonious trees. The dataset was analysed performing heuristic searches with parsimony under implied weights using TNT (Goloboff 1993; Goloboff *et al.* 2003). A phylogenetic analysis under equal weights was also performed. Shortest trees were found by submitting 100 different addition sequences to the tree bisection-reconnection branch-swapping method (TBR), retaining 100 trees per replication. Internal branches were considered unsupported and collapsed during searches if any possible states were shared between ancestor and descendant nodes (i.e. the minimum length was zero; see Coddington & Scharff 1994). State transformations are considered synapomorphies for a given node only if they are unambiguous, and if they are shared by all dichotomous most parsimonious trees. Unambiguous character state optimizations, and matrix and tree editing were done using Winclada (Nixon 1999a).

Choice of concavity. The weighting scheme proposed in the implied weighting procedure assigns higher weight to those characters with less homoplasy, while downweighting those with higher degree of homoplasy. Instead of minimizing the length of a cladogram while searching for most parsimonious trees, the value to be maximized under the implied weighting procedure is the *Fit*. The *Fit* is defined as the sum of the *fit* of each individual character in a given tree. It is determined by a decreasing concave function that takes into account the homoplasy (i.e. extra steps) of a character *i* in the tree under evaluation, and a constant, *K*, that defines the concavity of the function (Goloboff 1993).

The higher the degree of homoplasy, the lower the *fit* of a character to a given tree. *K* is usually an integer that varies between 1 and 100 (as implemented in TNT). The concavity of the function is steeper at lower values of *K*, therefore penalizing more strictly the homoplastic characters. At higher values of *K*, the function becomes asymptotically similar to the linear function of equal weights. So far, the decision concerning on how strongly to weight against homoplasy, that is the choice of a *K*-value, has been subjective.

Ramírez (2003) proposed a more objective scheme for choosing among different concavities when performing phylogenetic analyses under implied weights. The idea behind this resampling scheme is to choose among those concavity values that present higher predictive power. Higher predictive power is defined in this case as recovering the higher number of clades from the ‘correct tree’ (the one defined by the complete dataset) when part of the data has been eliminated.

Succinctly, if *T* is the number of clades in the consensus from the complete datasets, \mathcal{J} the number of clades in the consensus from the pseudoreplicate (jackknifed) dataset, and \mathcal{J}_T the number of clades recovered in the pseudoreplicate (the number of ‘correct’ clades); then we can calculate $PC = \mathcal{J}_T/T$, the proportion of correct clades recovered in the pseudoreplicate. The higher the *PC*, the higher the predictive power, although, as mentioned by Ramírez (2003), greater resolution of the resulting cladograms can also increase *PC*. An error $E = \mathcal{J} - \mathcal{J}_T$, defined as the number of incorrect clades in the consensus from the pseudoreplicate, was also calculated. A normalized error, $PE = (\mathcal{J} - \mathcal{J}_T)/\mathcal{J}$, reflects the proportion of wrong clades from the pseudoreplicate.

One thousand pseudoreplicate jackknifed datasets were generated (probability of character elimination = 0.36), and analysed under 20 different concavity values ($K = 1-20$) and also under equal weights. One hundred iterations of 50 random addition sequences followed by TBR branch swapping were submitted to parsimony ratchet (Nixon 1999b), keeping 20 trees on each iteration (commands **ratchet: iter 100; mult: tbr ratchet replic 50 hold 20**). This was executed for each pseudoreplicate under each concavity constant.

Support values. Three different support indices were calculated in TNT (Goloboff *et al.* 2003) — Jackknifing frequencies, Bremer support, and Relative Bremer support — in order to explore clade support: Jackknifing frequencies (Farris *et al.* 1996) generate matrices (pseudoreplicates) randomly discarding subsets of the characters (probability of elimination: 0.36), reanalysing the modified data, and evaluating which groups still remain after the manipulation. A thousand pseudoreplicates were computed, performing heuristic searches with the same commands as above. Supported groups show jackknifing frequencies larger than 50%.

Bremer Support (BS) was also calculated (Bremer 1988, 1994; Källersjö *et al.* 1992). The BS of a clade represents the number of extra steps a most parsimonious tree requires to collapse the monophyly of that clade. BS was calculated heuristically searching trees suboptimal by 0.001, 0.0025, 0.005, ..., until 0.025, and by 0.03, 0.04, ..., until 0.17 units of *Fit*, performing 1000 random addition sequences followed by TBR branch swapping, retaining from 2000 to 44 000 trees. Lowest values of Bremer support for all these searches are reported.

The third support measure calculated was Relative Bremer support (RBS, Relative Fit Difference; Goloboff & Farris 2001), that takes into account the relative amounts of evidence contradictory to, and favourable to, a group. The RBS was calculated in the same manner as for the calculation of the BS. This measure may suffer from some biases, and the rationale of using only those trees suboptimal in a number of steps no greater than the BS for a group was proposed (as explained in Goloboff & Farris 2001: S32). RBS was calculated under this approach, although all but one clades showed highest support (reported as ‘100?’ in TNT; all clades except the clade containing all amaurobioidines, with RBS = 23%) and it is not clear what the meaning of this value is (Pablo Goloboff, pers. comm.). RBS as originally proposed by Goloboff & Farris (2001) — i.e. taking into account all suboptimal trees — was then calculated. Support measures are illustrated in Fig. 1.

Results

Results from the analyses of the choice of concavities are shown in Fig. 3 and Table 2. In every analysis (under implied and equal weights), *Negayan* is monophyletic. Equal weights produced four most parsimonious cladograms (MPC) of 383 steps (CI = 0.420, RI = 0.493), the strict consensus is shown in Fig. 2. The analysis under implied weights produced one MPC for each *K*, and three different cladograms were produced in total. Under $K = 10-20$, one MPC resulted, which is one of the four MPC under equal weights (same tree description, Fig. 1). Under $K = 2-9$, only one MPC was produced, although it was slightly different from that produced by higher *K*-values (length: 385). $K = 1$ produced a different MPC of 387 steps.

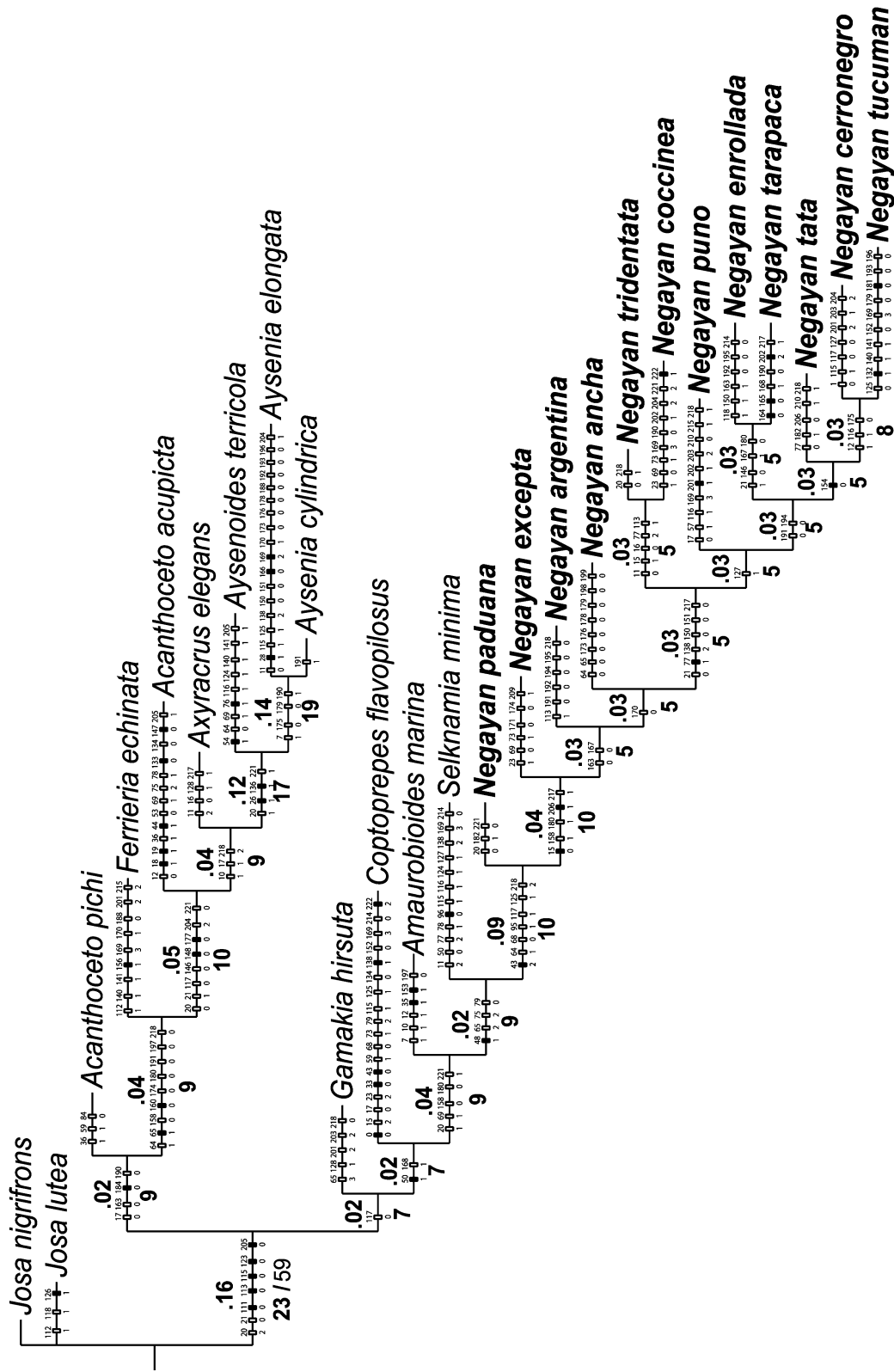


Fig. 1 The single most parsimonious tree resulted under implied weights with concavity values $K = 10-20$. Tree statistics: length = 383; CI = 0.420; RI = 0.493. Unambiguous character optimizations are shown for every node. Bold numbers above each node indicate Bremer Support values in terms of *Fit*. Below each node (separated by a slash), they indicate Relative Bremer Support values, while plain (regular) numbers indicate Jackknife frequencies. Empty and filled hashmarks represent homoplasious and nonhomoplasious transformations, respectively.

Table 2 Summary of the mean values \pm SD for 1000 pseudoreplicates for the analyses under each concavities and equal weights. E = error, number of incorrect groups in the consensus from pseudoreplicates; EW = equal weights; J = number of groups in the consensus from the pseudoreplicate; J_T = number of groups common to consensus from complete dataset and jackknifed pseudoreplicate; K = concavity under implied weights; PC = proportion of correct groups recovered by the pseudoreplicate; PE = proportion of wrong groups from the jackknifed pseudoreplicate; T = number of groups in consensus from complete dataset.

K	T	J	J_T	PC	E	PE
EW	44	36.499 \pm 6.725	30.634 \pm 3.041	0.6962 \pm 0.0691	5.865 \pm 5.365	0.1421 \pm 0.1164
1	47	46.911 \pm 1.657	30.960 \pm 3.141	0.6587 \pm 0.0668	15.951 \pm 3.677	0.3389 \pm 0.0742
2	47	46.870 \pm 1.566	30.739 \pm 3.668	0.6540 \pm 0.0780	16.131 \pm 4.034	0.3433 \pm 0.0826
3	47	46.896 \pm 1.648	31.330 \pm 4.125	0.6666 \pm 0.0878	15.566 \pm 4.446	0.3310 \pm 0.0916
4	47	46.845 \pm 1.624	32.007 \pm 4.106	0.6810 \pm 0.0874	14.838 \pm 4.451	0.3158 \pm 0.0922
5	47	46.888 \pm 1.597	32.323 \pm 4.200	0.6877 \pm 0.0894	14.565 \pm 4.538	0.3097 \pm 0.0941
6	47	46.921 \pm 1.546	32.184 \pm 4.105	0.6848 \pm 0.0873	14.737 \pm 4.368	0.3133 \pm 0.0909
7	47	46.930 \pm 1.335	32.358 \pm 3.990	0.6885 \pm 0.0849	14.572 \pm 4.245	0.3098 \pm 0.0883
8	47	46.922 \pm 1.637	32.362 \pm 4.083	0.6886 \pm 0.0869	14.560 \pm 4.440	0.3093 \pm 0.0920
9	47	46.834 \pm 1.484	32.362 \pm 4.099	0.6886 \pm 0.0872	14.472 \pm 4.425	0.3081 \pm 0.0917
10	48	46.856 \pm 1.505	33.138 \pm 4.089	0.6904 \pm 0.0852	13.718 \pm 4.216	0.2923 \pm 0.0882
11	48	46.830 \pm 1.727	33.277 \pm 4.047	0.6933 \pm 0.0843	13.553 \pm 4.290	0.2886 \pm 0.0890
12	48	46.846 \pm 1.625	33.133 \pm 3.933	0.6903 \pm 0.0819	13.713 \pm 4.175	0.2919 \pm 0.0870
13	48	46.799 \pm 1.769	33.032 \pm 3.923	0.6882 \pm 0.0817	13.767 \pm 4.101	0.2935 \pm 0.0853
14	48	46.935 \pm 1.520	33.149 \pm 3.909	0.6906 \pm 0.0814	13.786 \pm 4.079	0.2931 \pm 0.0850
15	48	46.787 \pm 1.779	33.349 \pm 4.030	0.6948 \pm 0.0840	13.438 \pm 4.275	0.2863 \pm 0.0888
16	48	46.900 \pm 1.540	33.309 \pm 4.175	0.6939 \pm 0.0870	13.591 \pm 4.302	0.2892 \pm 0.0901
17	48	46.846 \pm 1.610	33.283 \pm 3.925	0.6934 \pm 0.0818	13.563 \pm 4.164	0.2887 \pm 0.0867
18	48	46.848 \pm 1.570	33.440 \pm 3.976	0.6967 \pm 0.0828	13.408 \pm 4.165	0.2855 \pm 0.0867
19	48	46.861 \pm 1.696	33.308 \pm 3.896	0.6939 \pm 0.0812	13.553 \pm 4.157	0.2884 \pm 0.0864
20	48	46.816 \pm 1.639	33.161 \pm 3.767	0.6909 \pm 0.0785	13.655 \pm 4.009	0.2909 \pm 0.0833

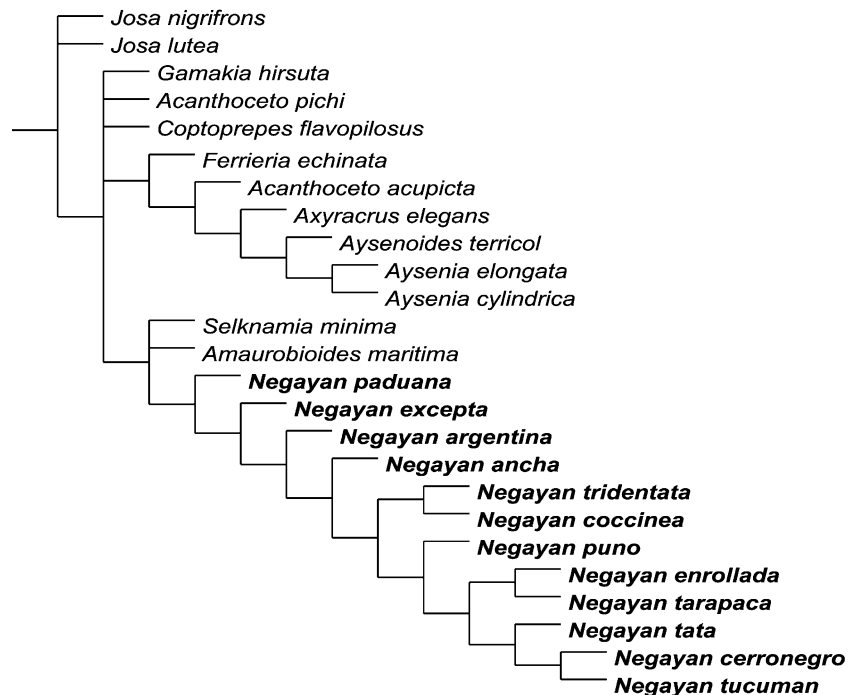


Fig. 2 Strict consensus of the four most parsimonious cladograms resulted under equal weights. Tree statistics: length = 383; CI = 0.420; RI = 0.493.

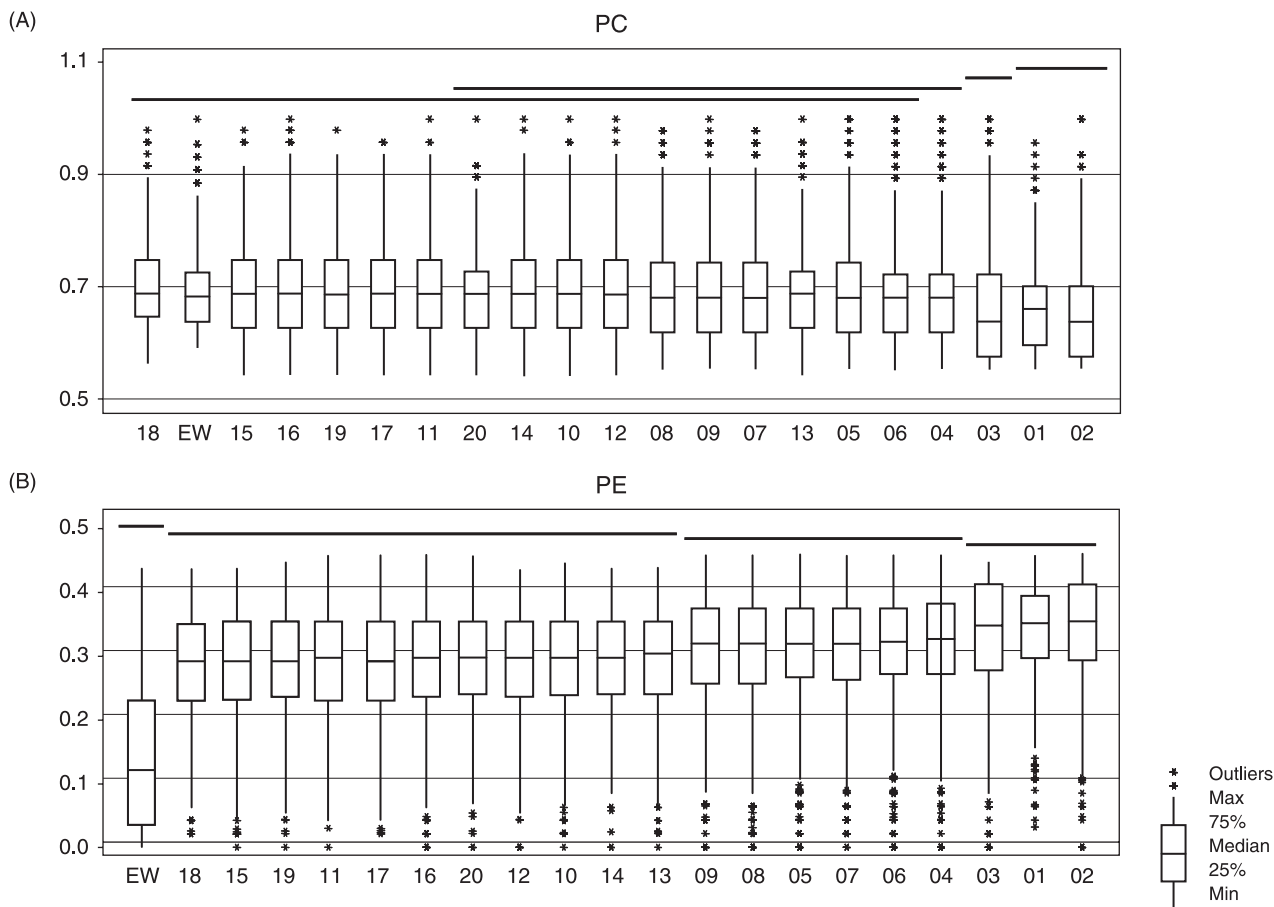


Fig. 3 A, B. Box and whisker plot of the pseudoreplicates of the different implied weighting concavities (EW = equal weights). Concavity values below horizontal solid bars do not have significantly different means. A posteriori multiple contrasts to find differences among means were performed with a Student–Newman–Keuls Test (SNK; Zar 1999) ($\alpha = 0.05$) with the statistical program SAS (SAS Institute 1989). —A. PC: proportion of correct groups recovered by the pseudoreplicate. —B. PE: proportion of incorrect groups from the jackknifed pseudoreplicate.

The proportion of clades recovered by the pseudoreplicates (*PC*) is higher under $K = 18$, although it is not significantly different from most concavity values and equal weights (Fig. 3A). The proportion of contradicted clades in the consensus of the pseudoreplicates (*PE*) is significantly lower under equal weights (Fig. 3B). This might be an artifact produced by the lower resolution, and it is expected as the equal weights analysis was the only analysis producing more than one MPC. Because the consensus of the optimal cladograms and that of the pseudoreplicates were taken into account in the choice of concavities, fewer contradicted clades might be expected than in a fully resolved cladogram.

The second group with significantly lower *PE* values includes all K -values between 10 and 20, the same values that produced a similar MPC shown in Fig. 1. The tree in Fig. 1 was produced by a group of concavity values with higher *PC* and lower *PE* (especially $K = 18$). Also, among the four trees included in Fig. 2, it is the MPC with a slightly higher fit

value (91.56 compared to 91.53–91.54). Therefore, the results from the concavity constant value $K = 18$ are preferred as the working hypothesis. Unambiguous character transformations for each node and terminal are optimized in Fig. 1, and there is a brief description of character evolution in Appendices 1 and 2.

The analysis supports the monophyly of *Negayan*, places *N. paduana* as the basal species of the genus, and *Selknamia* as the sister-group of *Negayan*. These results agree with the conclusions of Ramírez (2003). The relationships among *Negayan* species resulted in an almost completely pectinated pattern; hence, no grouping within the genus can be proposed without a proliferation of taxonomic ranks.

As previously proposed by Ramírez (1997, 2003), *Negayan* is diagnosed by the shape of the retrolateral tibial apophysis (char. 43). The states of other characters, although homoplastic, have arisen at the *Negayan* node and are shared by almost all *Negayan* species. These include the median apophysis

reduced or absent and a long embolus in male palps (chars. 64 and 95, respectively), copulatory ducts coiled and spermathecae contiguous in female epigyna (chars. 117 and 125), and very long dorsobasal spines in male legs (char. 212). Eyes minute (char. 15) and a sloped retrolateral tibial apophysis (char. 205) are synapomorphic for all *Negayan* species excluding its basal species. Group support values are low in general: BS = 0.09 (RBS = 10%) in *Negayan* node and BS = 0.02 (RBS = 9%) in (*Negayan* + *Selknamia*) (Fig. 1), Jackknifing frequencies are below 50% in every *Negayan* and amaurobioidine node, except for the node grouping all amaurobioidines (59%).

Abbreviations in text and figures

AB	accessory bulb
ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
AME	anterior median eyes
ap	apical
bas	basal
C	primary conductor
CD	copulatory duct
CO	copulatory opening
comb	apical comb of spines
CyC	cymbial conductor
d	dorsal
E	embolus
FD	fertilization duct
LF	lateral lobes of fields
MA	median apophysis
MF	median lobe or field
p	prolateral
PLE	posterior lateral eyes
PMA	paramedian apophysis
PS	posterior spinnerets
r	retrolateral
RTA	retrolateral tibial apophysis
S	spermathecae
T	tegulum
v	ventral

Taxonomy

Family Anyphaenidae Bertkau, 1878
 Subfamily Amaurobioidinae Hickman, 1949
 Tribe Amaurobioidini Hickman, 1949

Genus *Negayan* Ramírez, 2003

'*Gayenna strigosa*' group: Ramírez, 1997: 179.
Negayan Ramírez, 2003: 96.

Type species. *Gayenna tridentata* Simon, 1886 by original designation.

Diagnosis. In *Negayan* males can be distinguished from other members of the tribe Amaurobioidini by the characteristic shape of the retrolateral tibial apophysis (long, thick, sinuous at the tip; Ramírez 1997, 2003) (e.g. Fig. 9E,F), a reduced or absent median apophysis, long embolus, and very long dorsal-basal spines in legs; females by the coiled copulatory ducts and contiguous spermathecae.

Description. Somatic morphology more or less uniform across species (Fig. 6A,B), except for the size, and sometimes the abdominal coloration pattern. Carapace narrowed in front, ocular area not projecting. Chelicerae unmodified, slightly smaller in males (Ramírez 2003) except in *N. pumo*, promargin with three or four teeth on females (rarely five) and three teeth on males (rarely four), retromargin with two to five teeth on females, and two to four on males (rarely one or five). Legs 4123 or 41=23. AME minute and contiguous to ipsilateral ALE. Dorsal basal femoral spines usually longer than distals and medians.

Epigyna. General epigynum morphology in *Negayan* characterized by a central area or median field (MF), and two lateral lobes or fields (LF) on both sides (e.g. Figs 7A and 9A,B). The fold between lobes is the epigynal fold, where the copulatory openings arise (Sierwald 1989). MF in general elevated, a posterior pouch can occur (as in *N. pumo* and *N. cerronegro*, Figs 10B, 11B, respectively). In some cases, the lobes are fused or strongly modified from their original condition and they cannot be recognized or even homologized (as in *N. cerronegro*, *N. tucuman* and *N. tarapaca*, Figs 11A, 15A, and 16A, respectively).

Ducts. The internal organization of female genitalia varies little (compare cleared epigyna in Figs 7C, 9C, 12C, 13C, and 17C). In general, CO located relatively close to epigastrium (except in *N. pumo* and *N. tridentata*). AB located on external sides of the epigynum, and dorsally to S (except in *N. cerronegro* and *N. coccinea*). Junction point between ducts of AB and CD quite close to the beginning of the latter, both ducts running a very short trajectory before joining. From there, CD usually coiled 360° (along the longitudinal axis) before ending in the S. Degree of coiling can vary from absent (*N. cerronegro*, Fig. 11C) to around four times 360° (*N. enrollada*, Fig. 14B). Spermathecae contiguous, small or large relative to the epigynum size as a whole, and lobated or irregular.

Male palp. Retrolateral tibial apophysis (RTA) with characteristic shape: long, sinuous and with a curved tip. Cymbium wide and short, with prolateral apical notch where the tip of the primary conductor (C) fits. The cymbium also has a conductor ('cymbial conductor' Ramírez 2003) (CyC) related to the C and the embolus (Figs 11E and 12E).

Copulatory bulb. The arrangement of palpal sclerites is rather uniform across *Negayan* species. C is massive and well developed, prolateral in the bulb, with a prolateral ridge where the embolus fits. The tip of the conductor is dorsal to the embolus and can be single (Figs 9I and 12I) or bifid (Fig. 7B). The secondary conductor is absent. The median apophysis (MA) is small ('reduced') relative to other amaurobioidines, and can be absent (Fig. 10G). It varies from thick (Fig. 13H) to conical (Fig. 7B), to hook-shaped (Figs 9G and 12G) and can have a membranous lobe in its base (Fig. 12H).

The paramedian apophysis (PMA) is a short cusp, located ventrally to the median apophysis, near the tegular edge. Sometimes the PMA is related to a ventral-prolateral membranous fold (arrows in Figs 10H, 12I and 13G, H; slightly sclerotized in some cases). There is some controversy regarding this term. It was first coined by Comstock (1910) for araneid spiders, and subsequently used to refer to tegular sclerites other than median apophysis and conductor within Araneidae and other families.

To avoid the dubious statement of homology of the PMA, some authors had added a taxon reference to the term (e.g. 'theridiid tegular apophysis'; Coddington 1990; 'amaurobioidine paramedian apophysis'; Ramírez 1995a), and this has been done for other palp sclerites (e.g. Griswold *et al.* 1998). This has caused a proliferation of names for every sclerite of dubious homology. The PMA has been described as nonhomologous within Araneidae (Scharff & Coddington 1997), and it possibly is nonhomologous to the PMA of amaurobioidines. Scharff & Coddington (1997) suggested that this term should be restricted to the original usage in a few araneid genera.

According to its location within the male palp, the term PMA appears to be appropriate in terms of its descriptiveness. Because the same terminology has been used for more than 10 years in both araneids and amaurobioidines, and in order to avoid the proliferation of names for sclerites of dubious homology, I prefer to be consistent with amaurobioidine nomenclature, keeping the term for *Negayan* species. See Ramírez (2003) for a discussion on palpal sclerite homologies in amaurobioidines.

Natural history. Most specimens have been collected on the ground, under stones, or in leaf litter. Some species are common under stones on beaches of lakes, or on the banks of mountain streams (Ramírez 2003).

Composition. Twelve species, from Argentina, Chile, and Peru.

Negayan tridentata (Simon 1886) (Figs 4A and 7A–D)

Gayenna tridentata Simon, 1886: 570 (lectotype female and one paralectotype juvenile designated by Ramírez 2003: 97, from Argentina, Santa Cruz, in MNHN, N2189); Simon 1897: 91 (*tridentens*, lapsus).

Gayenna tridentens Simon, 1897: 91 (lapsus calami).

Gayenna exigua Mello-Leitão, 1940: 58 (holotype male from Argentina, Río Negro, in MLP, N.14404, examined); Ramírez 2003: 97 (as *Negayan exigua*). **syn. nov.**

Negayan tridentata: Ramírez, 2003: 97, fig. 48.

Described specimens. One female and one male from ARGENTINA: TIERRA DEL FUEGO: Lago Roca, bosque de *Notbofagus antarctica*, 27.I.1971, J. Vellard, 2♂ 3♀ 4 juvs. (MACN-Ar 9820).

New records. ARGENTINA: CHUBUT: Epuyén, 12.VI.1962, A. Kovacs, 3♂ 1♀ (AMNH); RÍO NEGRO: El Bolsón, alt. 1500 m, 6.III.1962, A. Kovacs, 1♂ (AMNH); 3♀ 2♂ (AMNH); Los Repollos, 5.V.1962, A. Kovacs, 8♀ 6♂ (AMNH); Ñorquinco, 3.VII.1966, A. Kovacs, 1♀ (AMNH).

Diagnosis. Females can be distinguished from other *Negayan* species by having the posterior margins of epigynal lateral lobes relatively close to each other (Fig. 7A,C), converging over the median field (Ramírez 2003). Both sexes commonly have three teeth on the cheliceral pro- and retromargin. Males can be distinguished by the characteristic conical MA (Fig. 7B) (Ramírez 2003: fig. 48G,H).

New morphological data

Female. Legs 4123. Chelicerae with three promarginal teeth. Anterior sternal margin straight. **Colour:** carapace yellowish orange, with two brown longitudinal stripes. Ocular area darker than carapace colour. Lateral margins of carapace very dark. Legs yellowish with brown dots, mostly on spine bases. Chelicerae orange, slightly darker basally. Sternum yellowish, slightly darker on margins. Dorsal abdomen brown with yellow W-shaped stripes and two anterior yellow dots. Ventral abdomen yellow with light brown spots. **Eyes:** posterior eye row procurved. **Epigynum** (Fig. 7A): median lobe ventrally elevated, and triangle-shaped, the triangle base is anterior, lateral lobes converging posteriorly. **Ducts** (Fig. 7C,D): it is not clear where the AB ducts join the CD. CD coiled 360°. Spermathecae small, lobated and located posteriorly in the central area of the MF. AB dorsolateral.

Male. Chelicerae with three promarginal teeth. Anterior sternal margin as in female. **Eyes:** posterior eye row dorsal and slightly procurved. AME not contiguous to their ipsilateral ALE. **Palp:** tibia short. RTA length reaches MA base in ventral view. RTA tip is rounded and sloped toward the bulb (see Ramírez 2003: fig. 48G). **Copulatory bulb** (Fig. 7B): MA conical. PMA tip slightly rounded. PMA with a prolateral fold slightly sclerotized, which has also a small retrolateral apophysis.

Distribution. Patagonian forests in Argentina, from Río Negro to Tierra del Fuego (Fig. 4A).

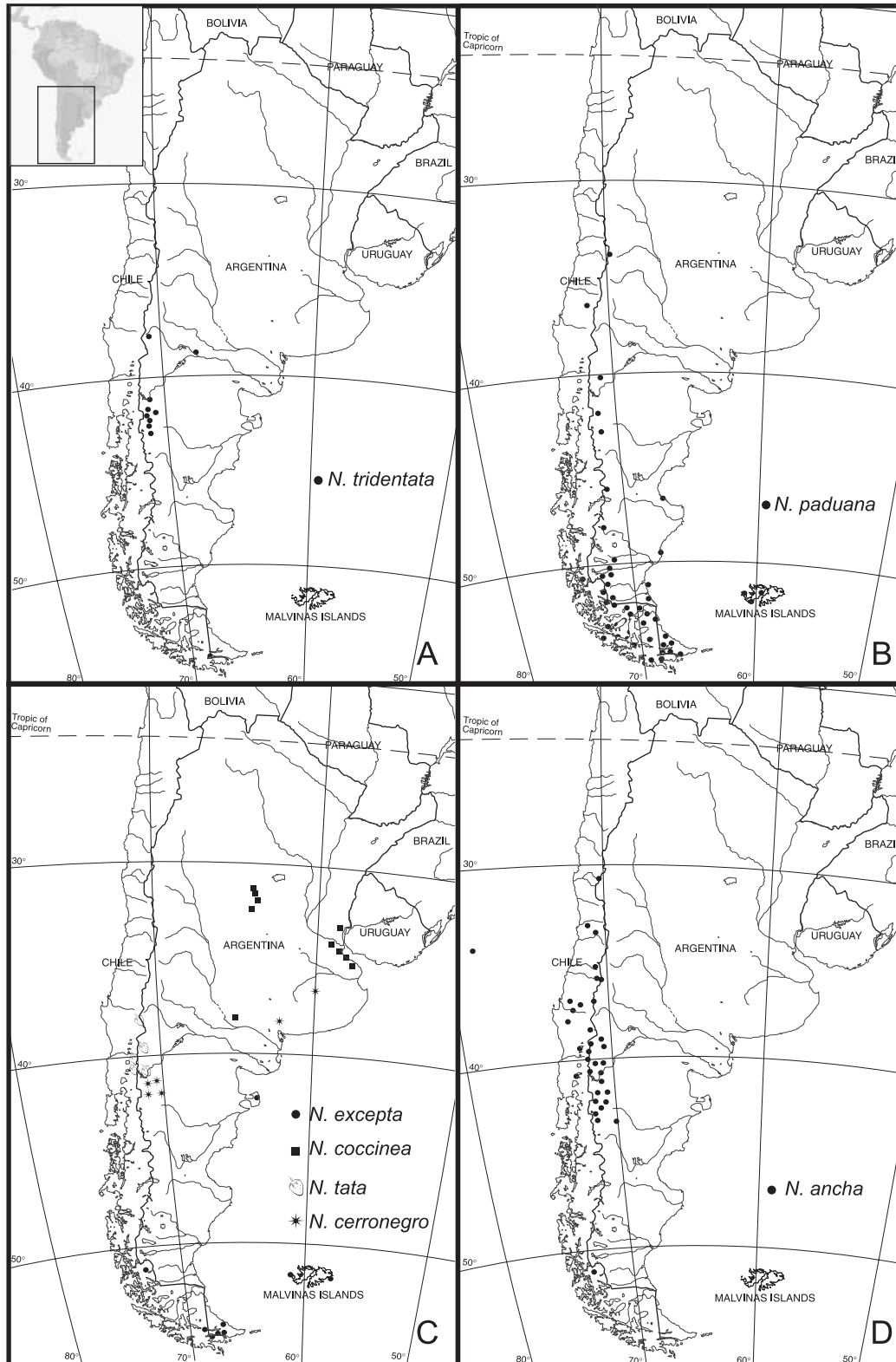


Fig. 4 A–D. Maps showing the geographical distribution of *Negayan* species. —A. *N. tridentata*. —B. *N. paduana*. —C. *N. excepta*, *N. coccinea*, *N. tata* and *N. cerronegro*. —D. *N. ancha*.

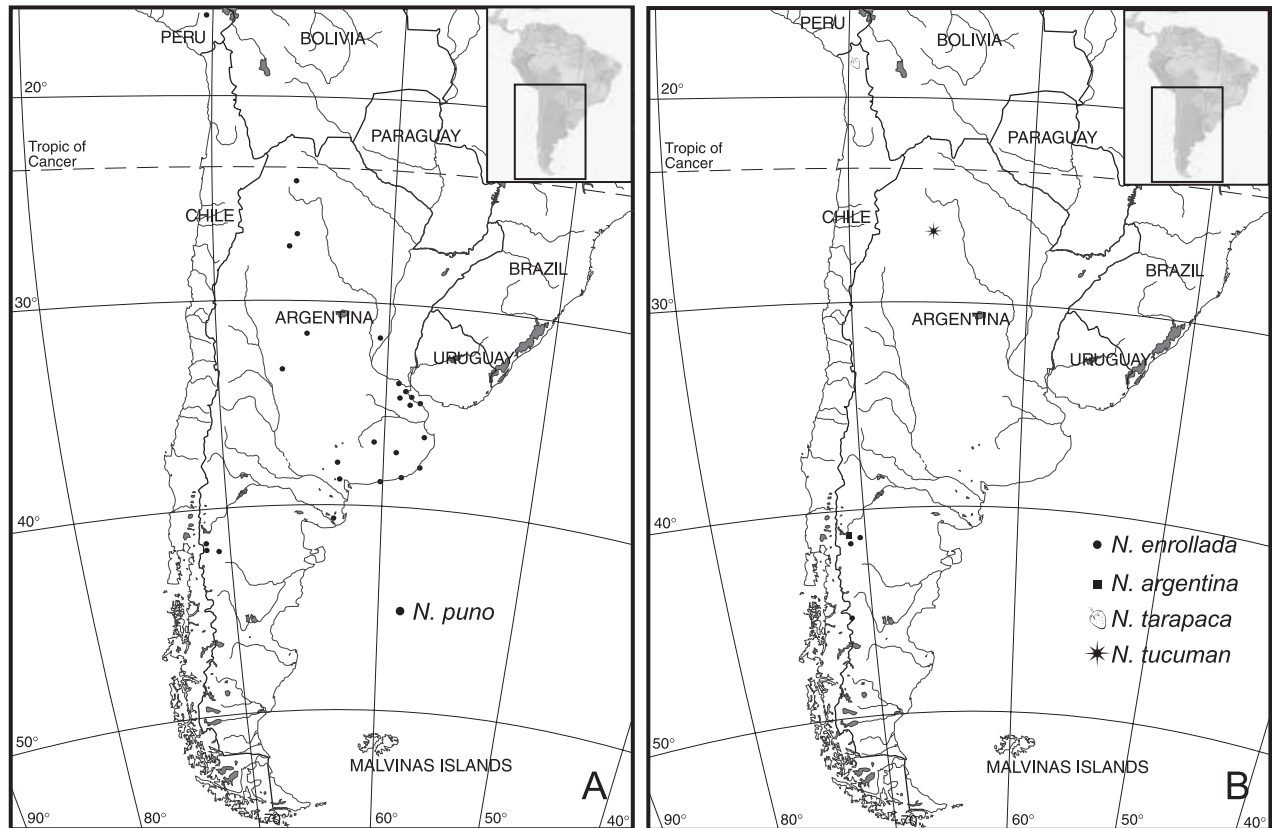


Fig. 5 A, B. Maps showing the geographical distribution of *Negayan* species. —A. *N. puno*. —B. *N. enrollada*, *N. argentina*, *N. tarapaca* and *N. tucuman*.

***Negayan paduana* (Karsch 1880) (Fig. 4B)**

Clubiona paduana Karsch, 1880: 379 (female holotype from Chile, Punta Arenas, Estrecho de Magallanes, Exp. ‘Gazelle’, in ZMB no. 2622, revised and redescribed by Ramírez 2003: 100, figs 49A–E and 50A–D).

Tomopisthes lebruni Simon, 1886: 570 (two females syntypes in MNHN no. 7733, not examined); Mello-Leitão 1940: 61; Ramírez 2003: 97 (as *Negayan lebruni*). **syn. nov.**

Tomopisthes magellanicus Simon, 1887: 32 (female holotype from Chile, Punta Arenas, in MNHN no. 6685); 1895: 168; 1896: 142; 1897: 91; 1902: 32; Ramírez 2003: 100 (syn.).

Gayenna strigosa Tullgren, 1901: 237, 259 (male lectotype and several female paralectotypes; one female of *Sanogasta maculosa*, and one juvenile cf. Amaurobiidae, paralectotypes, designated by Platnick 1977: 196, in NR, revised and synonymized by Ramírez 2003: 100). Schiapelli & Gerschman de Pikelin, 1974: 91; Ramírez, 1997: 178; 2003: 100 (syn.).

Tomopisthes strigosus: Simon, 1902: 34.

Philisca colulata Hogg, 1911: 42 (female holotype from Islas Malvinas, in BMNH). Synonymized with *G. strigosa* by Platnick 1977: 196.

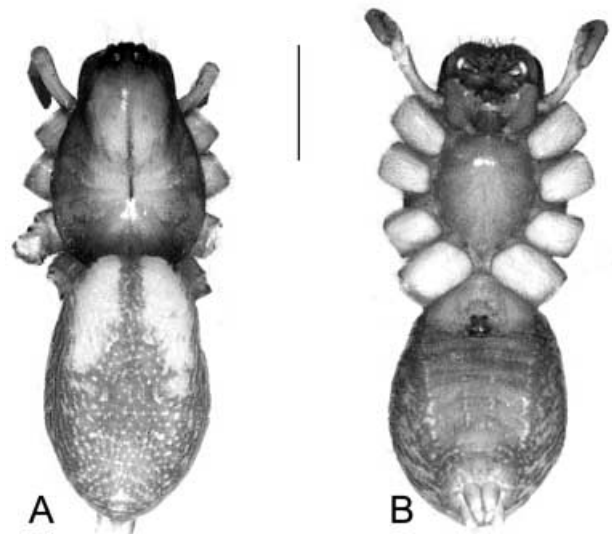


Fig. 6 A, B. *Negayan tata* sp. nov. Habitus. Female (Antillanca): dorsal (left) and ventral (right) views. Scale bar = 1 mm.

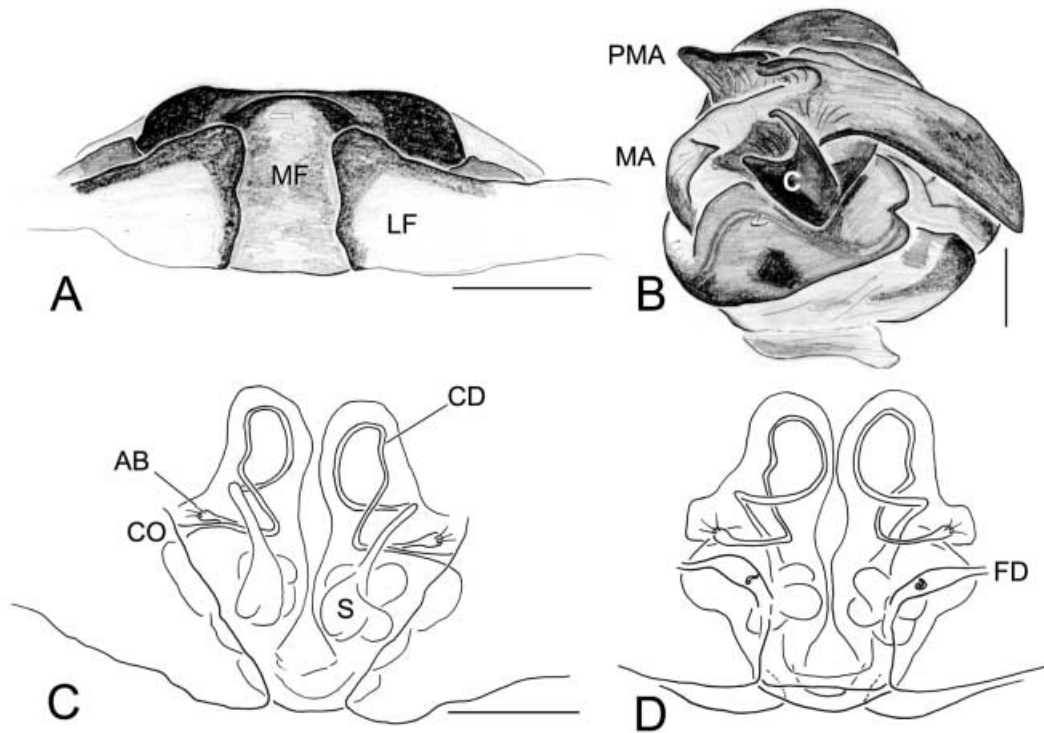


Fig. 7 A–D. *Negayan tridentata* (Simon). A, C, D: female (Lago Roca); B: male (Cholila). —A. Epigyne, posterior view. —B. Copulatory bulb, apical view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. Scale bars = 0.1 mm.

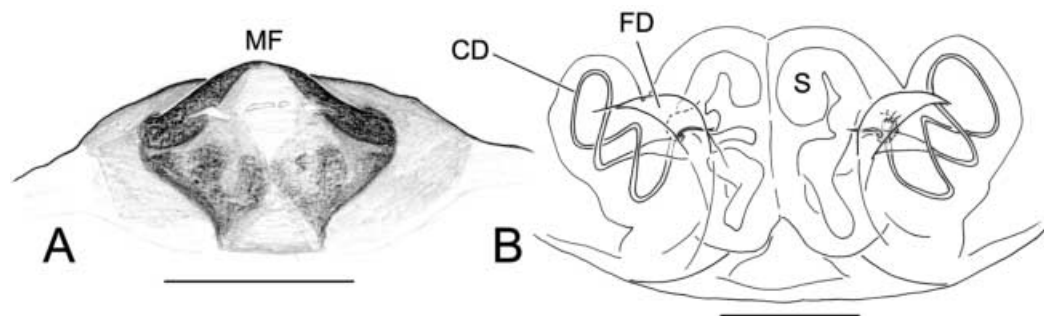


Fig. 8 A, B. *Negayan coccinea* (Mello-Leitão), female (Cabana). —A. Epigyne, posterior view. —B. Cleared epigyne, dorsal view. Scale bars = 0.1 mm.

Gayenna magellanica: Merian, 1913: 13.

Negayan paduana: Ramírez, 2003: 100, figs 49, 50.

Described specimens. One male from ARGENTINA: Tierra del Fuego: Río Grande, 3.II.1965, 3♂ (MLP); and one female from ARGENTINA: Islas Malvinas, New Island, I.1972, Rumboll, 1♀ (MACN-Ar).

New records. ARGENTINA: SANTA CRUZ: Las Cruces, Tres Lagos, 9.III.1948, Birabén, 1♂ 1♀ (MLP); TIERRA DEL FUEGO: without specific locality, 1♂ (MACN-Ar); Bahía Tethys, 2.II.1951, B. A. Torres, 1♂ (MLP); Laguna Negra, Lalegia,

XII.1989, 3♀ 2 juvs. (MLP); Río Grande, 14.II.1951, Torres, 2♀ (MLP); 7♀ 4♂ (MLP); Ushuaia, 1♀ (MACN-Ar); 25.II.1951, Torres, 8♀ 2♂ (MLP); III.1951, J. Boero, 1♀ (MLP); XII.1967, Bachmann, 6♀ 1 juv (MACN-Ar). CHILE: REGION METROPOLITANA: Farellones, 2400–2700 m, Cat-736, III.1983, M. Elgueta, 2♀ 2♂ 1 juv (MHNS); REGION XII (MAGALLANES AND ANTÁRTICA): MAGALLANES: Cueva del Milodón, 28.I.1976, T. Cekalovic, 4♀ 1 juv (UC); Canal Fitz Roy, Punta Turn, 31.I.1976, T. Cekalovic, 7♀ 5♂ (AMNH); Monte Alto (Laguna Korber), 17.II.1971, T. Cekalovic, 1♀ (AMNH); ÚLTIMA ESPERANZA: Cerro Castillo (pie), Cat:151, 10.II.1957, 1♀ (MHNS). Without locality, 1♀, 1♀, 1♂ (MACN-Ar).

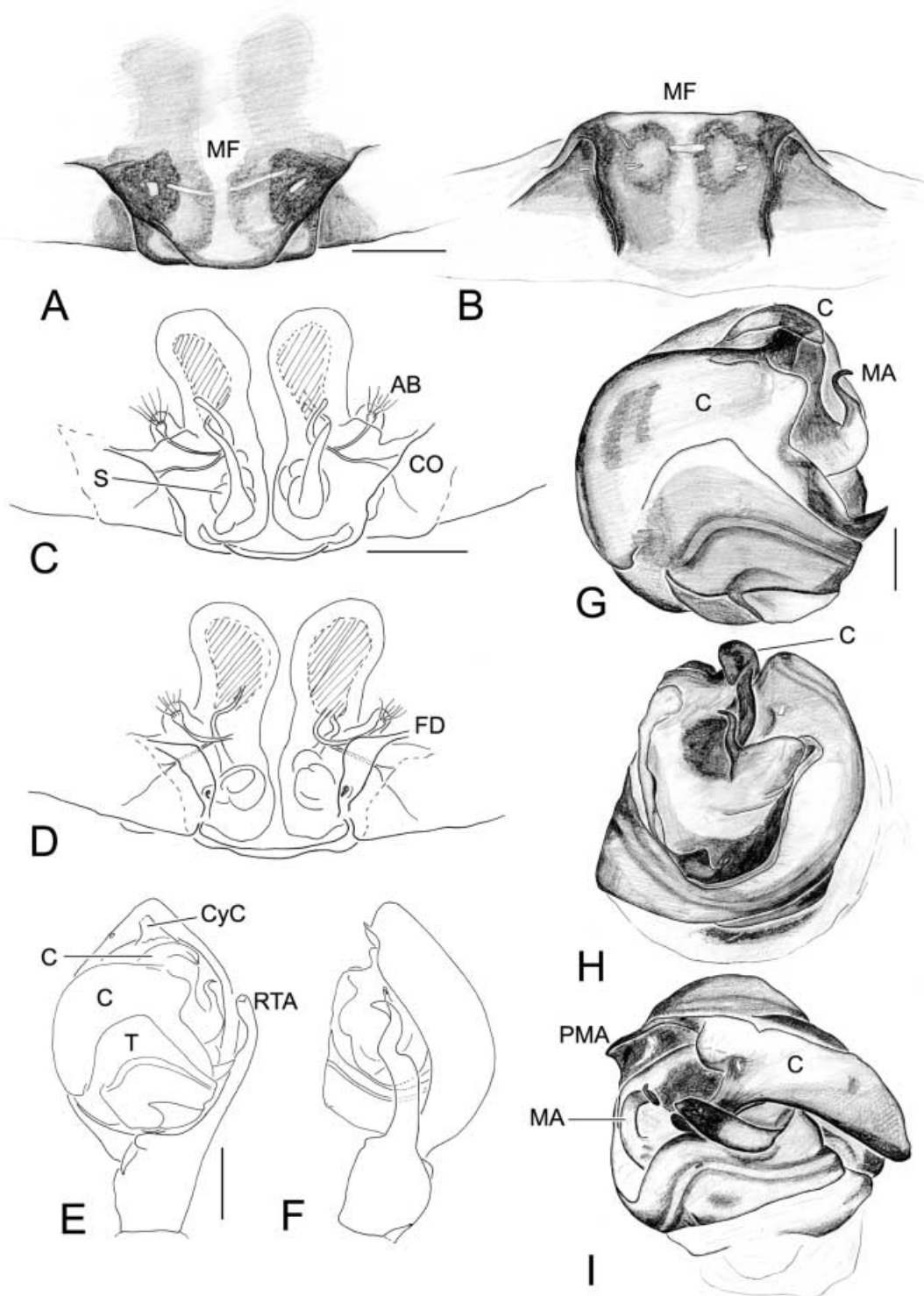


Fig. 9 A–I. *Negayan excepta* (Tullgren). A–D: female (Ushuaia); E–I: male (Rio Ewan). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. —E. Palp, ventral view. —F. Same, retrolateral view. —G. Copulatory bulb, ventral view. —H. Same, retrolateral view. —I. Same, apical view. Scale bars: A–D, G–I = 0.1 mm; E, F = 0.2 mm.

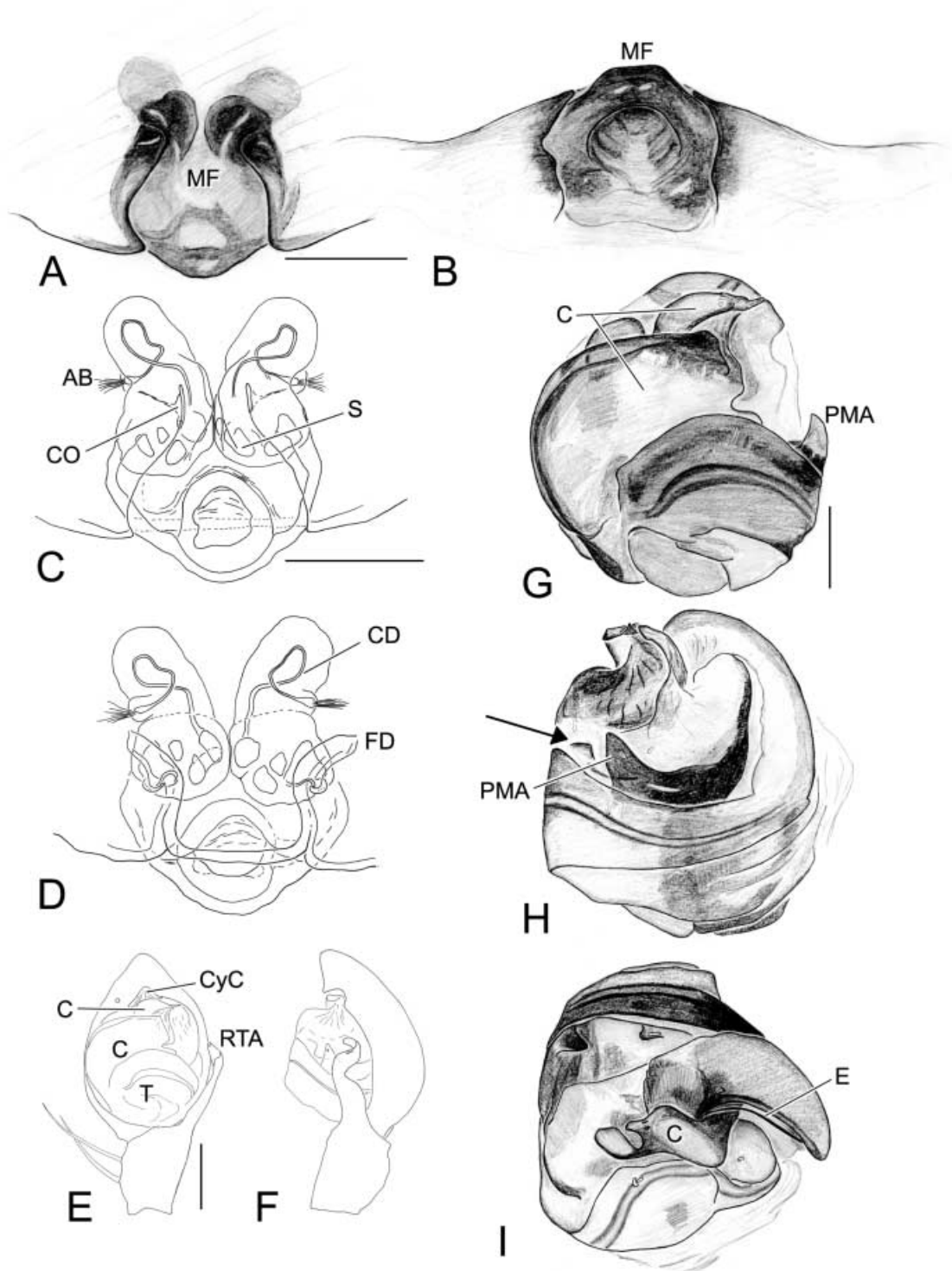


Fig. 10 A–I. *Negayan puno* sp. nov. A–D: female (paratype); E–I: male (paratype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. —E. Palp, ventral view. —F. Same, retrolateral view. —G. Copulatory bulb, ventral view. —H. Same, retrolateral view. Arrow to prolateral cusp of PMA. —I. Same, apical view. Scale bars: A–D, G–I = 0.1 mm; E, F = 0.2 mm.

Diagnosis. Males can be distinguished by the shape of the retrolateral tibial apophysis without slope toward the bulb, the narrowing of the spermatid duct before reaching the embolus, and the median apophysis hook-shaped (Ramírez 2003: fig. 50B). Females are distinguished by having the posterior elevations of epigynal lateral lobes just below the median field (Ramírez 2003: fig. 49C,F). Both sexes commonly have two teeth on the cheliceral retromargin and three teeth on promargin.

New morphological data

Female. Legs 4123. Chelicerae with three promarginal teeth. Anterior sternal margin convex. *Spines:* legs **III** and **IV**, metatarsus v 2-2-2-comb. *Eyes:* posterior eye row straight. *Epigynum* (Ramírez 2003: fig. 49D): CO arise at the anterior margin of epigynal fold, far from each other and from the epigastrium. *Ducts* (Ramírez 2003: fig. 49D,E): CD coiled 360°. S small and irregular, and located in the posterior central area of the median lobe. AB far from each other and dorsolateral to the S.

Male. Legs 4123. Chelicerae with three promarginal and 2/1 retromarginal ones. *Spines:* Legs **III** and **IV**, metatarsus v 2-2-2-comb. Dorsal basal femoral spines very long. *Colour:* sternum brown. Abdomen orange ventrally with a large lilaceous spot above the tracheal spiracle, and above epigastrium. Carapace as in female. Dorsal abdomen lilaceous, with two anterior yellow dots running toward the posterior margin, showing W-shaped stripes. Chelicerae brown as sternum, distally yellowish. *Eyes:* as in female. *Palp* (Ramírez 2003: fig. 50A–C): tibia long. RTA long, its length reaches the MA tip in ventral view, without slope toward the bulb, just straight. RTA tip slightly triangular and pointed.

Distribution. Argentina and Chile, from Neuquen and Aisén Provinces (respectively) to Tierra del Fuego and Islas Malvinas (Fig. 4B).

***Negayan coccinea* (Mello-Leitão 1943) (Figs 4C and 8A,B)**

Axyracrus coccineus Mello-Leitão, 1943: 115 (female holotype from Argentina, Córdoba, Bajo Grande, I.1940, M. Birabén, in MLP no. 15800, examined, revised by Ramírez 2003: 103). *Negayan coccinea*; Ramírez 2003: 103, figs 47, 51.

Described specimens. One female and one male from ARGENTINA: CÓRDOBA: Cabana, II.1950, M. Birabén (MLP).

New records. ARGENTINA: BUENOS AIRES: Atucha, I.XI.1981, Zanetic, Goloboff & Ramírez, 1 ♀ (MACN-Ar); VIII.1987, Goloboff, 1 ♂ (MACN-Ar). Without locality, 1 ♂ (MLP).

Diagnosis. Females of this small species within *Negayan* can be distinguished by the copulatory ducts wrapped on oblique axes, accessory bulbs ventral, spermathecae located all along

the epigynum, and having the copulatory openings in the epigastric furrow (Fig. 8B); males by the absence of median apophysis, and conductor with a globose lobe (Ramírez 2003: fig. 51A). Males have four promarginal and five retromarginal cheliceral teeth.

New morphological data

Female. Legs 4123. Anterior sternal margin straight. *Eyes:* posterior eye row straight. *Epigynum* (Fig. 8A): median lobe triangular, triangle base posterior. CO difficult to observe, probably positioned posteriorly in the folds, near epigastrium. *Ducts* (Fig. 8B): CD coiled 360°. S large, irregular, placed all along the epigynum. AB ventral and slightly lateral.

Male. Legs 4123. Chelicerae with four promarginal teeth. Anterior sternal margin as in female. Dorsal basal femoral spines very long. *Eyes:* posterior eye row straight. *Palp:* tibia short. RTA long, its length slightly higher than the C lobe's base in ventral view. RTA tip sloped toward the bulb, and it is rounded (see Ramírez 2003: fig. 51A,B).

Distribution. Central Argentina (Fig. 4C).

***Negayan excepta* (Tullgren 1901) (Figs 4C and 9A–I)**

Gayenna excepta. Tullgren, 1901: 234, 259 (female holotype from Chile: Región XII, Magallanes, Sierra del Toro, Mars. 1899, Nög Shog, S. Nordenskiöld, in NR, transferred to *Negayan* by Ramírez 2003); Petrunkevich 1911: 484; Merian 1913: 13; Mello-Leitão 1933: 55.

Negayan excepta; Ramírez 2003: 97.

Described specimens. One male from ARGENTINA: TIERRA DEL FUEGO: Río Ewan, II.1975, Rumboll, 1 ♂ (MACN-Ar); and one female from ARGENTINA: TIERRA DEL FUEGO: Ushuaia, 1–14.XII.1952, Exc. Castellanos-Gómez 1 ♀ (MACN-Ar).

Material examined. ARGENTINA: CHUBUT: Punta Delgada 1956, Vellard, 1 ♂ (MACN-Ar); TIERRA DEL FUEGO: 33: Lago Fagnano, Kaiken, 100 m, 18–19.I.1979, Misión Científica Danesa, 1 ♀ (ZMUC-IRSN); Lago Fagnano-XXV, bosque de *Notofagus antarctica* (Ñire), 26.II.1959, Vellard, 2 ♀ (MACN-Ar); -XXVII, 2 ♀ 3 juvs. (MACN-Ar); Ushuaia, 25.II.1951, B. Torres, 1 ♂ (MLP); ISLAS MALVINAS: New Island, I.1972, Rumboll, 1 ♂ (MACN-Ar 6671); Puerto Stanley, XI.1971, Rumboll, 2 ♀ (MACN-Ar ex-6670); CHILE: REGIÓN XII (MAGALLANES AND ANTÁRTICA): MAGALLANES: Rusffin #18, 8.III.1957, J. Vellard, 1 ♀ (MACN-Ar).

Diagnosis. Males can be distinguished from those of other *Negayan* species by the pointed tip of the retrolateral tibial apophysis, median apophysis hook-shaped, a membranous

lobe in the median apophysis base, and a retrolateral hyaline lobe on the conductor (see Fig. 9E–I); females with an elevated triangular area on the median lobe of the epigynum (Fig. 9A,B).

Female. Total length 6.22. Carapace length 2.40, width 1.70. Legs 41=23. Length of tibia/metatarsus: **I** 1.18/1.06; **II** 1.14/1.06; **III** 1.02/1.26; **IV** 1.56/1.72. Palp tarsus length 0.64. Chelicerae with four promarginal (the most apical one reduced), and three retromarginal teeth. Sternum length 1.28, width 0.98. Anterior sternal margin convex. Abdomen length 4.20, width 2.44. Tracheal spiracle to spinnerets 0.48; tracheal spiracle to epigastrium 1.14. **Spines:** legs **I**, femur d 1-1-1, p d1ap; tibia v 2-2-2; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v r1-2-2; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p 0-d1-d1, r 0-d1-d1; patella r 1; tibia d r1bas, p 1-d1-1, r 0-d1-1, v p1-2-2; metatarsus d 2-p1-2, p 0-d1-1, r 0-d1-1, v 2-2-2/2-p1-2. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v p1-2-2; metatarsus d 2-p1-2, p 0-d1-1(or 0-1-1), r 0-d1-1(or 0-1-1), v 2-2-2. **Colour:** carapace and legs orange, darker on ocular area and the chelicerae. Margin of carapace covered with white setae. Ventral abdomen yellowish. Dorsal abdomen light brown with two anterior yellow dots running toward the posterior abdominal end. **Eyes:** posterior eye row procurved. **Epigynum** (Fig. 9A,B): median lobe with a central blunt triangular elevated area, triangle base anterior. CO arise in the anterior one-third of the folds in ventral view. **Ducts** (Fig. 9C,D): the CD seem to be coiled at least 360° although it is difficult to observe. S small and lobated, located posteriorly. AB dorsolateral.

Male. Total length 4.12. Carapace length 1.98, width 1.40. Legs 41=23. Length of tibia/metatarsus: **I** 1.52/1.46; **II** 1.42/1.30; **III** 1.14/1.34; **IV** 1.56/1.94. Chelicerae with three promarginal, and 3/2 retromarginal teeth (can be 3/3). Sternum length 1.06, width 0.80. Abdomen length 2.14, width 1.22. ALS more sclerotized than PS. Tracheal spiracle to spinnerets 0.18; tracheal spiracle to epigastrium 1.08. **Spines:** legs **I**, femur d 1-1-1, p (1-d1)ap; tibia p 1 ba/0, v 2-2-2; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-2; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p 0-d1-d1, r 0-d1-d1; patella r 1; tibia d 1 ba, p 1-d1-1, r 0-d1-1, v p1-2-2; metatarsus d 2-1-2, p 0-1-1, r 0-1-1, v 2-p1-2/2-2-2. **IV**, femur d 1-1-1, p 0-d1-d1, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v 2-2-2 (irregularly paired); metatarsus d1, p d1-1-1, r d1-1-1, v 2-2-2. Dorsal basal femoral spines very long. **Colour:** carapace orange. Ocular area slightly darker. Sternum and legs yellow, legs darker from middle tibia to the distal end. Chelicerae orange. Dorsal abdomen brown, with two anterior yellow dots running toward the posterior abdominal end. Ventral abdomen orange. **Eyes:** as in female.

Palp (Fig. 9E,F): tibia long. RTA wide, suddenly narrowing in the middle. RTA tip sloped toward bulb. RTA length reaches half MA height in ventral view. RTA tip pointed. **Copulatory bulb** (Fig. 9G–I): MA hook-shaped, with an incipient membranous lobe at its base. PMA with prolateral membranous fold, related to C. C single, with a retrolateral hyaline lobe.

Natural history. Unknown.

Distribution. In southern regions in Argentina and Chile (Fig. 4C).

***Negayan puno sp. nov.* (Figs 5A and 10A–I)**

Holotype. 1♀, ARGENTINA: Tucumán province: Río Cochuna, Laguna del Tesoro (2000 m), IX.1973, Maio, in MACN-Ar 10254.

Paratypes. 1♀, ARGENTINA: Córdoba province: Pampa de Achala, El Cóndor, 20.XI.1983, Galiano, in MACN-Ar 10255; 1♂ ARGENTINA: Jujuy province: Lag. de Yala, V.1983, Goloboff, in MACN-Ar 10256.

Other material examined. ARGENTINA: BUENOS AIRES: (no specific locality) III.1940, Schiapelli, 1♂ (MACN-Ar); B. Daguerre, no. 31344, 1♀ (MACN-Ar); Atucha, 16.VI.1985, P. Goloboff, C. Scioscia, 1♀ (MACN-Ar); 23.VI.1985, P. Goloboff & M. Ramírez, 1♂ (MACN-Ar); Burzaco, I.193?, Ibarra Grasso, 1♀ (MACN-Ar); Capital Federal, II.1959, V. Lugano, 1♂ (MACN-Ar); Carmen de Patagones, XI.1971, Aguilera, 1♀ (MACN-Ar); Claromecó, I.1954, H. Rossi, 1♂ (MACN-Ar); El Tordillo, XI.1969, S. Maury, 2♀ (MACN-Ar); Ezeiza, 14.VI.1981, Ramírez, 1♀ (MACN-Ar); Felipe Solá, XII.1951, Martínez, 1♂ (MLP); La Plata, 1942, 1♂ (MLP); Los Médanos, Energía, 8.IV.65, J. M. Gallardo & S. Maury, 1♀ (MACN-Ar); Mar del Plata, Costa Brava, XII.1946, Birabén, 1♂ (MLP); Quequén, 7–12.VI.1931, J. M. Daguerre, 1♂ (MACN-Ar 28871); Río Luján, 10 km aguas arriba de Luján, X.1982, Goloboff, Roig Alsina, Ramírez, 1♀ (MACN-Ar); Sierra de La China, 25 km O de Olavarría, 20.III.1983, S. Maury, 1♀ (MACN-Ar); Tandil, IV.1963, Ogueta, 1♂ 5 juvs. (MACN-Ar); Zelaya, no date, Pereira, no. 30176, 1♀ (MACN-Ar); CHUBUT: El Hoyo, 10.IX.1961, A. Kovács, 1♂ (AMNH); 26.V.1962, 15♂; 12♂; 7♂; 15♀; 25♀; 20♀; 1♀ (AMNH); VI.1962, 1♀ 1♂ (AMNH); VII.1962, 4♀ 7♂ (AMNH); VIII.1962, 7♀ 2♂ (AMNH); Fo-fo Cahuel, 8.X.1966, A. Kovacs, 1♂ (AMNH); CÓRDOBA: Pampa de Achala, El Cóndor, 20.XI.1983, M. S. Galiano, 1♀ (MACN-Ar); ENTRE RÍOS: Distrito Antonio Tomas, Depto. Paraná, bajo una piedra a orillas del Río Paraná, 13.VII.1916, A. G. Frers, 1♂ (MACN-Ar); SAN LUIS: II.1993, Diez 1♂ (USL); RÍO NEGRO: El Bolsón, 13.VIII.1961,

A. Kovacs, 1 ♂ (AMNH); 20–27.V.1962, 1 ♂ (AMNH); 25.VI.1962, 1 ♂; 1 ♀; 1 ♀ (AMNH); 19.VIII.1962, 1 ♀ (AMNH); X.1963, Birabén, 2 ♂ (MACN-Ar); TUCUMÁN: ruta 307, 10 km NO de El Indio, 24.XI.1994. M. Ramírez & P. Goloboff, 1 ♀ (MACN-Ar). PERÚ: PUNO: Mañazo, 15.X.1983, S. Maury, 1 juv (MACN-Ar).

Etymology. The species epithet is a noun in apposition taken from the locality of the only specimen collected in Peru.

Diagnosis. Males are distinguished by having larger chelicerae than females, median apophysis absent, a flat retrolateral salience in the conductor (Fig. 10I), and the retrolateral tibial apophysis short (Fig. 10E,F). Females have a posterior pouch in the epigynum (Fig. 10B), copulatory openings close to each other, and copulatory ducts coiled 180° in oblique axes (Fig. 10C).

Female (holotype). Total length 4.48. Carapace length 1.98, width 1.40. Legs 4123. Length of tibia/metatarsus: **I** 1.16/0.92; **II** 1.00/0.86; **III** 0.84/0.92; **IV** 1.26/1.46. Palp tarsus length 0.54. Chelicerae with three promarginal, and four retromarginal teeth. Sternum length 1.06, width 0.82. Anterior sternal margin straight. Abdomen length 2.56, width 1.40. ALS more sclerotized than PS. Tracheal spiracle to spinnerets 0.22; tracheal spiracle to epigastrium 1.30. *Spines:* Legs **I**, femur d 1-1-1, p d1ap/(1-d1)ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-0; metatarsus p d1-0, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 0-1/0-1-1-0, v p1-p1-2/p1-2-2; metatarsus d 0-p1-2, p d1-1-1, r d1-1-1, v 2-p1-0-comb/2 ba-comb. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v p1-2-2; metatarsus d 0-p1-2, p d1-1-1, r d1-1-1, v 2-2-0-comb. *Colour:* carapace orange-brown with some lateral darker radii. Legs orange, darker distally, with brown dots. Chelicerae and sternum orange-brown. Dorsal abdomen brown with two anterior yellow dots posteriorly extended one-third of abdomen, and tiny yellow dots in a W-shaped pattern. Ventral abdomen light brown with four thin longitudinal yellow stripes. *Eyes:* posterior eye row straight. *Epigynum* (Fig. 10A,B): MF wide, anteriorly narrower and more sclerotized, and with a posterior pouch. CO far from the epigastrium near the anterior fold edge. *Ducts* (Fig. 10C,D): First section of CD is difficult to recognize. CD coiled 180°. AB dorsolateral. S located where the MF narrows.

Male (paratype). Total length 4.08. Carapace length 1.90, width 1.30. Legs 1423. Length of tibia/metatarsus: **I** 2.08/1.88; **II** 1.46/1.40; **III** 1.13/1.22; **IV** 1.64/1.92. Chelicerae with three promarginal, and 3/4 retromarginal teeth. Sternum length 1.02, width 0.86. Abdomen length 2.16, width

1.14. Tracheal spiracle to spinnerets: 0.22; tracheal spiracle to epigastrium: 1.02. *Spines:* legs **I**, femur d 1-1-1, p [(1)d1]ap; tibia v 2-2-0; metatarsus p 1, v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-0; metatarsus p 1-0, v 2 ba. **III** femur d 1-1-1, p d1ap, r d1ap; tibia p d1-1/0-1, r d1-1, v p1-2-0; metatarsus d 0-p1-2, p 0-d1-1-0-1, r 0-d1-1-0-1, v 2 ba. **IV**, femur d 1-1-1, p d1ap, r d1ap; tibia d r1bas, p d1-1, r d1-1, v p1-2-0/2-2-0; metatarsus d 0-p1-2, p d1-1-1, r d1-1-1, v 2-2-0/2-p1-0. Dorsal basal femoral spines long. *Colour:* carapace orange, two longitudinal brown stripes with darker radii. Ocular area dark. Legs yellowish, with many darker dots and stripes. Sternum light brown, with some darker radii. Dorsal abdomen dark brown with two orange dots extended to the middle abdomen, and a big orange posterior dot. Ventral abdomen dark brown with four yellow longitudinal stripes. *Eyes:* posterior eye row straight. *Palp* (Fig. 10E,F): tibia long. RTA short and thick. RTA tip thick and rounded, and sloped to the bulb. *Copulatory bulb* (Fig. 10G–I): MA absent. PMA without ventral membranous fold, but with a little cusp in the area (arrow in Fig. 10H). C single, but with two processes: a ventral lobe-shaped bulge, and a less sclerotized retrolateral laminar process.

Natural history. In Atucha and Río Luján, collected in leaf litter and in grasses (Ramírez, pers. comm.), in Entre Ríos collected under stones in river bank.

Distribution. All over Argentina, and in Puno, Perú (Fig. 5A).

Negayan cerronegro sp. nov. (Figs 4C and 11A–I)

Negayan tridentata. Ramírez, 2003: 100 (misidentification, see ‘Note’ below).

Holotype. 1 ♀, ARGENTINA: Buenos Aires province: Sierra de la Ventana, Cerro Negro 29.IX–2.X., 1972, Galiano in MACN-Ar 10257.

Paratypes. 1 ♀ 2 ♂, ARGENTINA: Chubut province: Epuyén, 12.VI.1962, A. Kovacs in AMNH.

Other material examined. ARGENTINA: BUENOS AIRES: Argerich, Villarino, VI–VII.1958, H. Hepper, 1 ♀ (MACN-Ar), Sierra de la Ventana, Cerro Negro 29.IX–2.X.1972, Galiano, 1 ♂ (with Holotype); CHUBUT: Cholila, 25.VIII.1962, A. Kovács, 1 ♀ (AMNH); Epuyén, 12.VI.1962, A. Kovacs, 6 ♀ 2 ♂ (AMNH); 1.IX.1965, 1 ♀ (AMNH); 5.VIII.1966, 3 ♀ 2 ♂ (AMNH); RÍO NEGRO: El Bolsón, 20.VII.1962, A. Kovacs, 1 ♀ (AMNH); Ñorquinco, 3.VII.1966, A. Kovacs, 1 ♂ (AMNH); 1 ♀ (AMNH).

Etymology. The species epithet is a noun in apposition taken from the type locality.

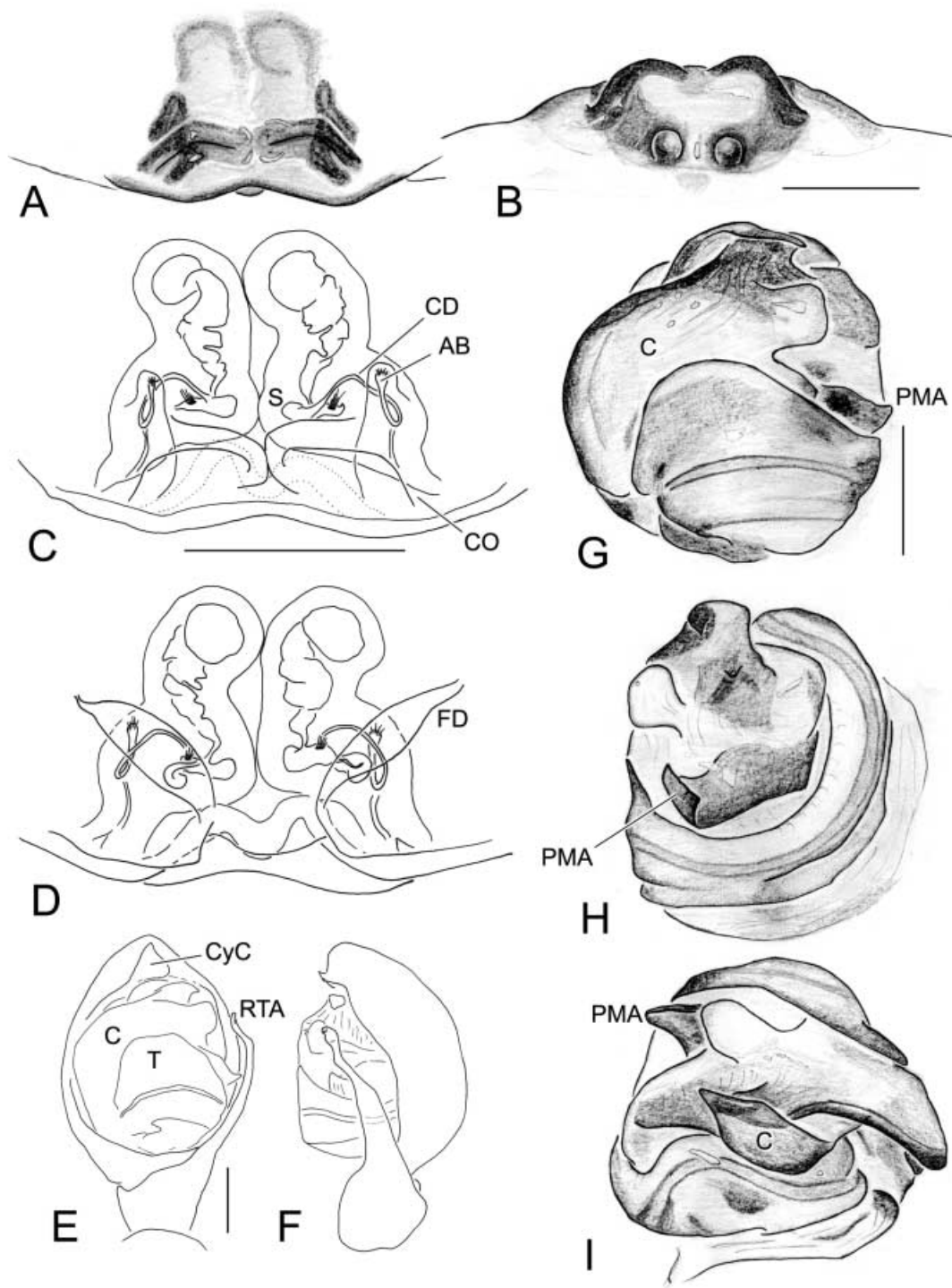


Fig. 11 A–I. *Negayan cerronegro* sp. nov. A–D: female (holotype); E–I: male (paratype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. —E. Palp, ventral view. —F. Same, retrolateral view. —G. Copulatory bulb, ventral view. —H. Same, retrolateral view. —I. Same, apical view. Scale bars = 0.1 mm.

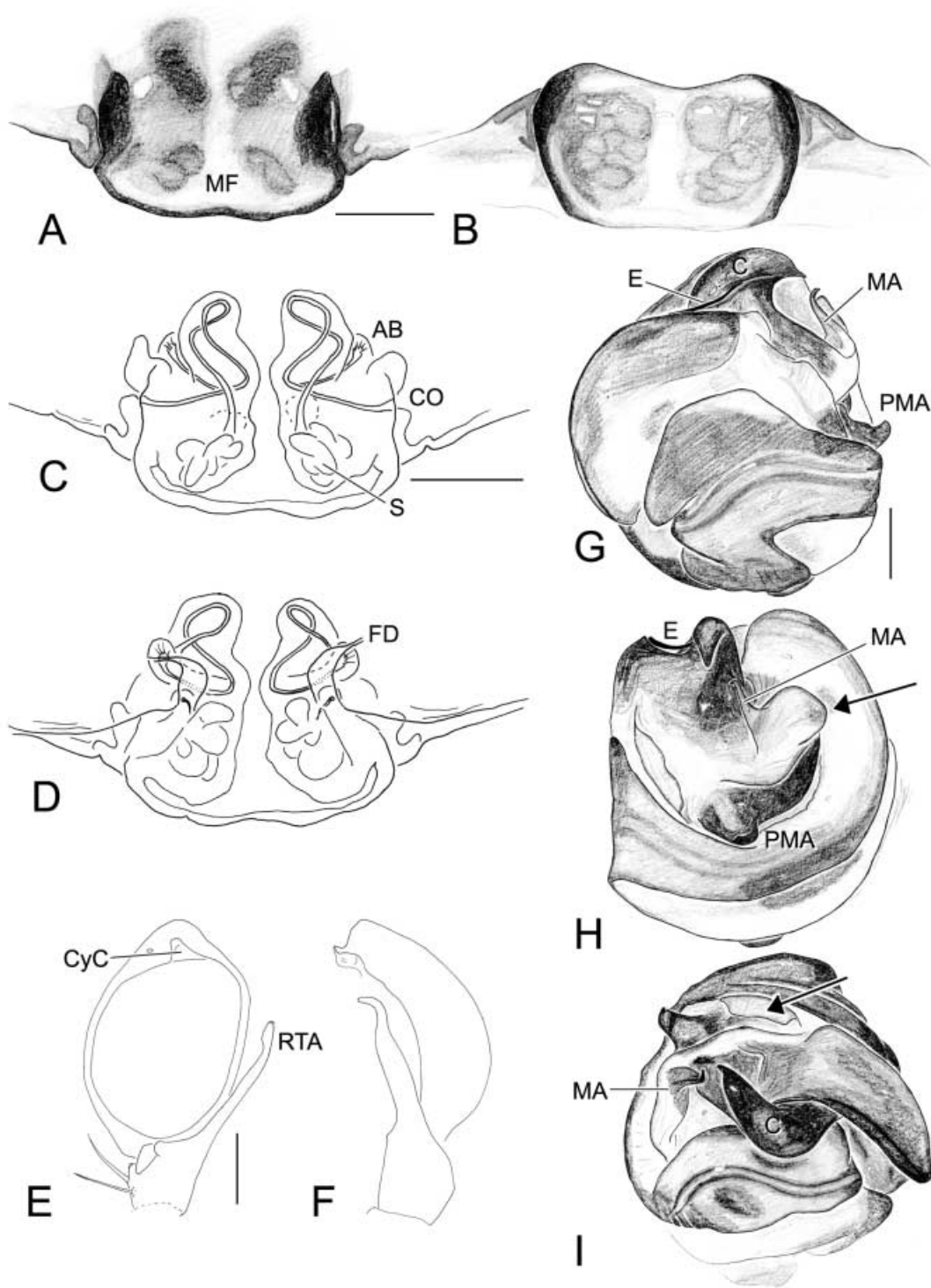


Fig. 12 A–I. *Negayan tata* sp. nov. A–D: female (holotype); E–I: male (paratype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. —E. Palp, ventral view. —F. Same, retrolateral view. —G. Copulatory bulb, ventral view. —H. Same, retrolateral view. Arrow to membranous lobe at base of MA. —I. Same, apical view. Arrow to prolateral membranous fold of PMA. Scale bars: A–D, G–I = 0.1 mm; E, F = 0.2 mm.

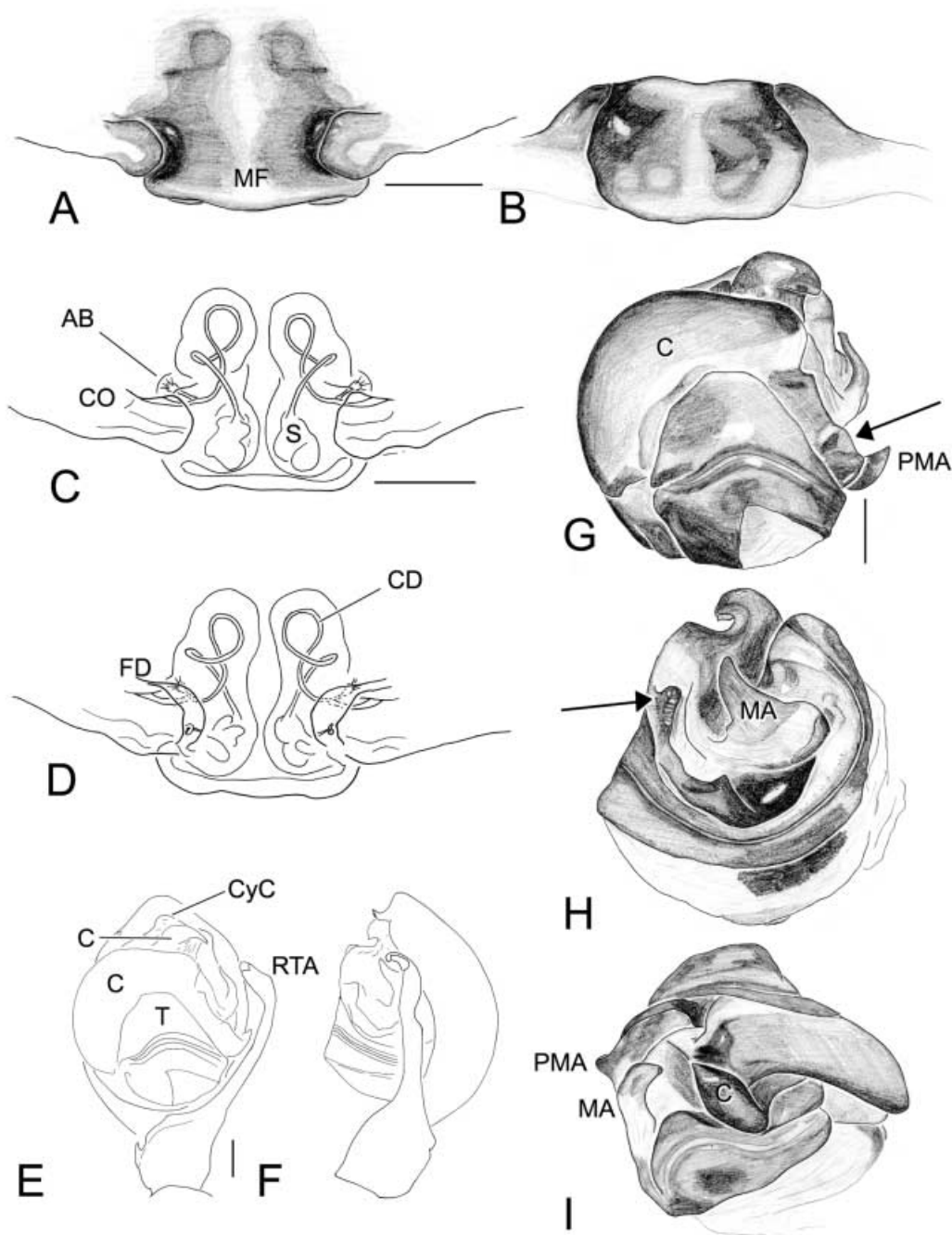


Fig. 13 A–I. *Negayan ancha* sp. nov. A–D: female (holotype); E–I: male (paratype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. —E. Palp, ventral view. —F. Same, retrolateral view. —G. Copulatory bulb, ventral view. Arrow to prolateral membranous fold of PMA. —H. Same, retrolateral view. Arrow to prolateral membranous fold of PMA. —I. Same, apical view. Scale bars = 0.1 mm.

Note. One of the eight females from Argentina, Chubut Province: Cholila, 25.VIII.1962, A. Kovács (AMNH), and the three females and two males from Chubut province: Epuýén, 5.VIII.1966, A. Kovacs (AMNH) determined as *N. tridentata* in Ramírez (2003) were misidentified.

Diagnosis. Males of this small species are distinguished by absence of median apophysis, globose lobe on conductor (Fig. 11G), and the retrolateral tibial apophysis sinuous and thin (Fig. 11F). Females have two posterior pouches in epigynum (Fig. 11B), and a particular morphology of the vulva (Fig. 11C,D).

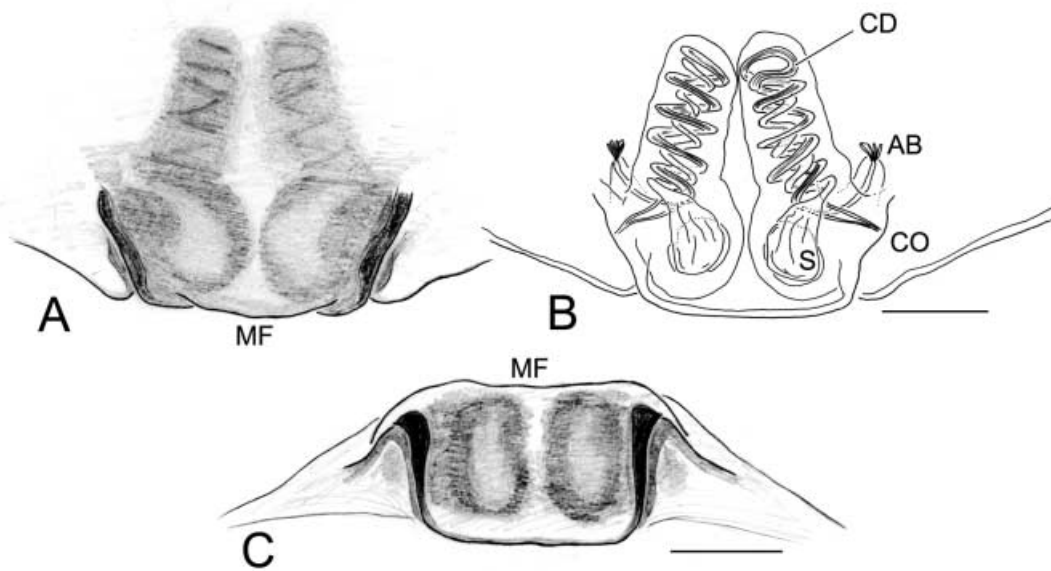


Fig. 14 A–C. *Negayan enrollada* sp. nov. Female (holotype). —A. Epigyne, ventral view. —B. Cleared epigyne, ventral view. —C. Epigyne, posterior view. Scale bars = 0.1 mm.

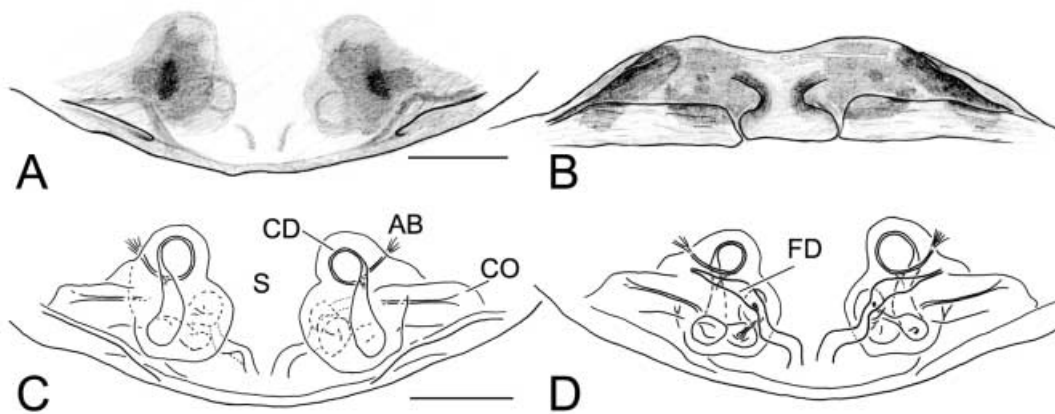


Fig. 15 A–D. *Negayan tucuman* sp. nov. Female (holotype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. Scale bars = 0.1 mm.

Female (paratype). Total length 3.36. Carapace length 1.28, width 0.84. Legs 41=23. Length of tibia/metatarsus: **I** 0.68/0.56; **II** 0.64/0.56; **III** 0.52/0.60; **IV** 0.88/0.96. Palp tarsus length 0.34. Chelicerae with four promarginal, and four retromarginal teeth. Sternum length 0.72, width 0.57. Abdomen length 1.87, width 1.08. Tracheal spiracle to spinnerets 0.16; tracheal spiracle to epigastrium 0.92. *Spines*: legs **I**, femur d 1-1-1, p d1ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-0; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; tibia d r1bas, p 1-d1-1, r d1-1, v p1-p1-2; metatarsus d 0-r1-2, p 0-d1-1, r 0-d1-1, v 2-0-p1-comb. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p d1-d1-1, r d1-1, v p1-2-2;

metatarsus d 0-p1-2, p 0-d1-1, r 0-d1-1, v 2-2-2. *Colour*: carapace orange, lateral margins black. Ocular area darker than carapace colour. Legs yellow with brown dots. Chelicerae orange. Sternum yellowish orange, darker on posterior margins. Dorsal abdomen brown with three anterior yellow dots resembling a triangle with anterior base, posteriorly with yellow W-shaped stripes. *Eyes*: posterior eye row slightly recurved. *Epigynum* (Fig. 11A,B): difficult to recognize and homologize location of lobes. On sides of the folds, the epigynum is more sclerotized, as are all the posterior edges. CO on distal folds ends. Two circular pouches in posterior view. *Ducts* (Fig. 11C,D): CD with no loops. S small, located on central area, and seem to have an

extended anterior reservoir in their bases. AB ventral and lateral.

Male (paratype). Total length 2.88. Carapace length 1.22, width 0.84. Legs 4123. Length of tibia/metatarsus: **I** 0.74/0.62; **II** 0.66/0.58; **III** 0.56/0.64; **IV** 0.86/0.98. Chelicerae with three promarginal, and 3/4 retromarginal teeth. Sternum length 0.66, width 0.56. Abdomen length 1.46, width 0.80. Tracheal spiracle to spinnerets 0.18; tracheal spiracle to epigastrium 0.74. *Spines*: legs **I**, femur d 1-1-1, p d1ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-0; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; tibia d r1bas, p 1-d1-1, r 1-d1-1, v p1-p1-2; metatarsus d 0-p1-2, p d1-1-1, r 0-d1-1, v 2-0-p1-comb. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-1, v p1-2-2; metatarsus d 0-r1-2, p d1-1-1, r d1-1-1, v 2-2-2. Dorsal basal femoral spines very long. *Colour*: as in female, but lighter. *Eyes*: as in female. *Palp* (Fig. 11E,F): tibia short. RTA sinuous, its length reaches the height of the C lobe in ventral view. RTA tip thin and rounded, sloped to the bulb. *Copulatory bulb* (Fig. 11G–I): MA absent. PMA with a prolateral sclerotized fold which joins the C lobe. C with a retrolateral hyaline lobe. Retrolateral and dorsally, the C have a minute apophysis hidden behind the hyaline lobe in ventral view.

Natural history. Unknown.

Distribution. In Argentina, in Buenos Aires, Chubut and Río Negro Provinces (Fig. 4C).

***Negayan tata sp. nov.* (Figs 4C, 6A,B and 12A–D)**

Holotype. 1♀, ARGENTINA: Río Negro province: S. C. de Bariloche, Colonia Suiza, 800 m, 5–7.I.1982, Nielsen & Karsholt, in ZMUC.

Paratypes. 1♀, ARGENTINA: Neuquén province: Parque Nacional Lanín, Puerto Canoas y Lago Curilaufquen, 8.I.1985, Ramírez, in MACN-Ar 10258; 1♂, CHILE: Región X (Los Lagos): Osorno province: Parque Nac. Puyehue, Volcán Casa Blanca, 1130–1180 m, 20–25.XII.1982, A. Newton & M. Thayer, in AMNH.

Other material examined. CHILE: REGIÓN IX (ARAUCANIA): MALLECO: Malalcahuello, 9–15.XII.1985, L. Peña, 1♀ (AMNH); REGIÓN X (LOS LAGOS): OSORNO: Parque Nac. Puyehue, Antillanca, 40°46'30"S, 72°11'30"W, 1050–1350 m, 1.XII.2000–2.I.2001, alpine meadow, Miller, Agnarsson, Alvarez, Codrington & Hormiga, 3♀ (USNM).

Etymology. The species epithet is a noun in apposition, after my grandmother Aldona 'Tata' Tamosiunas.

Diagnosis. Males can be recognized by the straight retrolateral tibial apophysis, its apical narrowness (Fig. 12E,F), and the median apophysis hook-shaped (Fig. 12G). Female epigynum is similar to that of *N. paduana*, but the median field narrows slightly at the posterior margins of the lateral fields (Fig. 12A).

Female (holotype). Total length 4.76. Carapace length 1.70, width 1.20. Legs 4123. Length of tibia/metatarsus: **I** 0.94/0.72; **II** 0.86/0.70; **III** 0.74/0.78; **IV** 1.16/1.30. Palp tarsus length 0.48. Chelicerae with 4/3 promarginal (if 4, the second basal one larger), 5/4 retromarginal teeth. Sternum length 0.88, width 0.72. Abdomen length 1.44, width 0.88. Tracheal spiracle to spinnerets 0.40; tracheal spiracle to epigastrium 1.72. *Spines*: legs **I**, femur d 1-1-1, p (1-d1)ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-0/2-2-p1; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 0-d1-1, v p1-p1-2; metatarsus d p1, p d1-1-2, r d1-1-2, v 2-1-0. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v 2-2-2; metatarsus d 1, p d1-1-2, r d1-1-2, v 2-2-p1 (irregularly paired). *Colour*: carapace orange with two longitudinal and diffuse darker stripes, and neat blackish radii. Ocular area slightly dark. Chelicerae dark orange, same colour as longitudinal stripes on carapace. Legs yellowish orange at base, orange from tibia to distal end. Legs with orange-brown dots on spine bases. Sternum reddish-brown. Abdomen orange-brown, with two dorsal anterior yellow dots and several tiny yellowish ventral dots conforming two longitudinal yellow stripes. *Eyes*: posterior eye row straight. *Epigynum* (Fig. 12A,B): median lobe wide, highly sclerotized on the lateral margins. LF with a concave sclerotization on anterior margins. *Ducts* (Fig. 12C,D): CD coiled 360°. AB dorsolateral. S lobated, ventral and posterior.

Male (paratype). Total length 3.96. Carapace length 1.84, width 1.34. Legs 4123. Length of tibia/metatarsus: **I** 1.36/1.20; **II** 1.24/1.08; **III** 1.00/1.16; **IV** 1.42/1.64. Chelicerae with three promarginal (the basal bigger), 3/4 retromarginal teeth. Sternum length 1.00, width 0.80. Anterior sternal margin straight or slightly convex. Abdomen length 2.06, width 1.06. Tracheal spiracle to spinnerets approximately 0.16; tracheal spiracle to epigastrium 1.12. *Spines*: legs **I**, femur d 1-1-1, p(1-d1)ap; tibia v 2-2-p1/p1-r1-p1; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v r1-2-p1; metatarsus p 1-0, v 2 ba. **III**, femur d 1-1-1, p 0-d1-d1, r d1ap; tibia d r1bas, p 1-d1-1, r d1-1, v p1-2-2; metatarsus d 2-p1-r1-2ap, p 0-1-1, r 0-1-1, v 2-p1-2. **IV**, femur d 1-1-1, p d1ap, r d1ap; tibia d 1 ba, p d1-1, r 1-d1-1, v 2-2-2/2-2-0; metatarsus d 2-2-2 (middle pair irregularly paired), p 0-1-1, r 0-1-1, v 2-2-2. Dorsal basal femoral spines long. *Colour*: carapace orange, with some darker radii from a longitudinal darker stripe

anterior to the fovea. One tuft of white hairs posteriorly between PME-PLE on each side. Sternum dark orange. Dorsal abdomen yellowish-brown, with two anterior yellow dots extending posteriorly to half the abdomen. Ventral abdomen yellow. *Eyes*: as in female. *Palp* (Fig. 12E,F): tibia short. RTA thick and straight in ventral view, tip rounded. Length of RTA to MA base in ventral view. COPULATORY BULB (Fig. 12G-I): tegulum slightly projected ventrally. MA hook-shaped, with membranous lobe at base (arrow in Fig. 12H). PMA with a retrolateral membranous fold (arrow in Fig. 12I). Apical cusp of C suddenly narrowed and pointed.

Natural history. Unknown.

Distribution. In Neuquén and Río Negro provinces (Argentina), and Osorno and Malleco provinces (Chile) (Fig. 4C).

***Negayan ancha* sp. nov. (Figs 4D and 13A-I)**

Negayan tridentata. Ramírez, 2003: 100 (misidentification, see 'Note' below).

Holotype. 1 ♀, CHILE: Región X (Los Lagos): Osorno province, P.N. Puyehue, Los Derrumbes, 18.I.1989, Ramírez, in MHNS.

Paratypes. Same data as holotype, 8 ♀ in MACN-Ar 10259; 1 ♂, CHILE: Región IX (Araucanía): Cautín province: Pucón 15.XI–2.XII., 1989, lakeshore pan, S. A. Marshall, in AMNH; 1 ♂, CHILE: Región VII (Maule): Talca province: Gil de Vilches, 7.I.1989, Ramírez, in MACN-Ar 10260.

Other material examined. ARGENTINA: CHUBUT: Cholila, 25.VIII.1962, A. Kovács, 1 ♂ (AMNH); El Hoyo, 3.IX.1961, A. Kovács, 2 ♀ (AMNH); 1 ♀ (AMNH); 10.IX.1961, 6 ♀ 4 ♂ 5 juvs. (AMNH); 15.V.1962, 1 ♀ 3 ♂ 1 juv (AMNH); 26.V.1962, 28 ♀; 1 ♀; 29 ♀ 1 juv; 38 ♀ 82 juvs; 16 ♂; 30 ♂; 4 ♂; 16 ♂ (AMNH); VI.1962, 6 ♀ 9 ♂ 16 juvs. (AMNH); VII.1962, 17 ♀ 8 ♂ (AMNH); VIII.1962, 6 ♀ 5 ♂ (AMNH); 15.IX.1962, 8 ♀ 7 ♂ 6 juvs. (AMNH); 2.X.1962, 10 ♀ 3 ♂ 15 juvs. (AMNH); Epuyén, 42°15'S, 71°23'W, 18.XI.1962, A. Kovács, 1 ♂ (AMNH); Epuyén, 1.IX.1965, A. Kovacs, 1 ♀ 1 ♂ (AMNH); 17.X.1966, 1 ♂ (AMNH); Lago Puelo, 42°S, 71°W, 13.I.1964, A. Kovacs, 1 ♂ (AMNH); Languiñeo, Estancia Manantiales, 6–10.XI.1985, L. Peña, 1 ♂ (AMNH); Los Cipreses, XI.1982, Ramírez, no. 42, 2 ♂ (MACN-Ar); Parque Nacional Los Alerces: Chucaco, XI.1982, Ramírez, 1 ♀ (MACN-Ar); NEUQUÉN: Isla Victoria, IV.1945, Havrylenko, 1 ♂ (MLP); P. Nac. Lanín: Lago Aluminé, II.1974, E. Maury, 2 ♀ (MACN-Ar); Quillén, II.1968, E. Maury y Müller, 1 ♀ (MACN-Ar); Río Pucará, S shore, Lago Lácar, 8 km E Hua Hum, 655 m, *Notbofagus* for. w/*Mirceogenella* trunks, bamboo, 13.I.1986, N. I. Platnick, P. A. Goloboff, R. T. Schuh, 8 ♀ (AMNH); San

Martín de los Andes, 640 m, 2.XI.1981, Nielsen y Karsholt, 1 ♂ 1 juv (ZMUC); San Martín de los Andes, Gentili property, app. 900 m, FIT nr.pond 23.XI–1.XII., 1989, S. A. Marshall, 1 ♂ (AMNH); Río NEGRO: El Bolsón, from trees, 1.II.1961, A. Kovacs, 10 ♀ (AMNH); under stones, 28.II.1961, 1 ♀ (AMNH); El Bolsón, 7.VII.1961, 1 ♀ 1 ♂ (AMNH); 8.VII.1961, 5 ♀ 1 ♂ 15 juvs. (AMNH); 13.VIII.1961, 3 ♀ 13 juvs. (AMNH); 9.IX.1961, 2 ♀ 3 ♂ (AMNH); 28.X.1961, 1 ♀ (AMNH); 29.IV.1962, 2 ♀ 4 ♂ (AMNH); 12.V.1962, 20 ♀ 12 ♂ 2 juvs. (AMNH); 20–27.V.1962, 24 ♀ 18 ♂ 6 juvs. (AMNH); 3.VI.1962, 4 ♀ 8 ♂ 9 juvs. (AMNH); 25.VI.1962, 9 ♀ 11 ♂ (AMNH); 19.VIII.1962, 2 ♀ 2 ♂ 2 juvs. (AMNH); 6.IX.1962, 5 ♀ 2 ♂ 2 juvs. (AMNH); 24.XI.1962, Birabén, 1 ♀ (MACN-Ar); Los Repollos, 5.V.1962, A. Kovács, 4 ♀ 2 ♂ 1 juv (AMNH); S. C. de Bariloche, Colonia Suiza, 800 m, 7.XII.1981, Nielsen y Karsholt, 1 ♂ (ZMUC); 21–22.XII.1981, 1 ♂ (ZMUC); Ternero, 8.VII.1962, A. Kovacs, 3 ♀ 1 ♂ (AMNH); CHILE: REGIÓN IV (COQUIMBO): Coquimbo: 6 km SW Hurtado, 1040 m, Puente Morrillos, 30°16'S, 70°40'W, 28.X.1994, R. Leschen & C. Carlton, #021 (ex: along stream), 1 ♀ 1 ♂ (AMNH); #022 (ex: sifting litter), 1 ♀ 1 ♂ subad 4 juvs. (AMNH); REGIÓN V (VALPARAÍSO): VALPARAÍSO: Juan Fernández Islands, Masatierra Portazuelo, 500 m, 7.IV.1962, B. Malkin, 1 ♂ (AMNH); Quintero, 9.I.?, 1 ♂ (MACN-Ar); Santiago, IV.1970, Fritz, 1 ♀ (MACN-Ar); REGIÓN VII (MAULE): ARAUCO: Los Morongos, E. Los Niches, Curicó, 600 m, 17–20.XI.1994, L. Peña, 2 ♂ (AMNH); TALCA: Gil de Vilches, 7.I.1989, M. Ramírez, 3 ♀ (MACN-Ar); 47.3 km E. San Clemente, 400 m, 35°46'S, 70°59'W, 6.XI.1994, R. Leschen & C. Carlton, #053 (ex: washing moss), 1 ♀ (AMNH); 55.08 km E. San Clemente, 510 m, 35°48'S, 70°58'W, 6.XI.1994, R. Leschen & C. Carlton, #061 (ex: flood debris), 1 ♀ 1 ♂ (AMNH); REGIÓN VIII (BÍO-BÍO): BÍO-BÍO: Lago Lanalhue, 12.I.1989, M. Ramírez, 9 ♀ (MACN-Ar); CONCEPCIÓN: Cabrero, 12.XI.1989, T. Cekalovic, 1 ♀ (AMNH); Concepción, Lomas de San Andrés, 24.XII.1988, T. Cekalovic, 1 ♀ (AMNH); Escuadrón, 29.VII.1990, T. Cekalovic, 1 ♀ (AMNH); 17.IX.1989, TC-239, 1 ♂ (AMNH); ÑUBLE: 72 km S.E. Chillán, Termas road, elev. 1175 m, 36°55'S, 71°30'W, 16.XI.1993, Platnick, Catley, Ramírez & Allen, 1 ♀ 1 ♂ (AMNH); REGIÓN IX (ARAUCANÍA): CAUTÍN: N.E. Caburgua, 5.II.1979, Quezada, 1 ♀ 1 juv (UC); Los Pinos, nr. Loncoche, 20.XII.1985, L. Peña, 3 ♀ 1 ♂ (AMNH) Pucón, Volcán Villarrica, FIT in 'tundra', 8.XI–3.XII.1989, S. A. Marshall, 1 ♂ (AMNH); MALLECO: Curacautín, 16.XII.1985, L. E. Peña, 1 ♀ (AMNH); REGIÓN X (LOS LAGOS): OSORNO: Lago Rupanco, 23.I.1984, Ruiz, 1 ♀ (UC); VALDIVIA: Coñaripe, 18.II.1977, T. Cekalovic, 1 ♀ (AMNH); E. side Volcán Coshueno (nr Neltume), 23.XI.1988, V. & B. Roth, 1 ♂ (CAS); REGIÓN XII (MAGALLANES Y ANTÁRTICA): MAGALLANES: Parque Nacional Torres del Paine, 150 m, scrub, 10-II-1985, N. I. Platnick & O. F. Francke, 1 ♀ (AMNH);

Río Chico, 1956, J. Vellard, 2 ♀ (MACN-Ar). NO SPECIFIC LOCALITY 1 ♀ 1 ♂ (MACN-Ar); 1 ♂ (UC).

Etymology. The species epithet is a Spanish adjective that means 'wide', referring to the shape of the median apophysis.

Note. One of the three males from Argentina: Chubut Province: Cholila, 25.VIII.1962, A. Kovács (AMNH), determined as *N. tridentata* in Ramírez (2003) was misidentified.

Diagnosis. Males can be recognized by the wide and flat median apophysis (Fig. 13G,H) and a prolateral apophysis in the prolateral fold of the paramedian apophysis (Fig. 13G–I, arrowed). Females have the lateral margins on the median lobe significantly narrowed posteriorly (Fig. 13A).

Female (holotype). Total length 4.24. Carapace length 1.90, width 1.38. Legs 4123. Length of tibia/metatarsus: **I** 0.94/0.84; **II** 0.90/0.80; **III** 0.80/0.90; **IV** 1.18/1.36. Palp tarsus length 0.50. Chelicerae with three promarginal, four retromarginal (apical bigger) teeth. Sternum length 0.94, width 0.82. Anterior sternal margin convex. Abdomen length 2.52, width 1.40. ALS more sclerotized than PS. Tracheal spiracle to spinnerets 0.26; tracheal spiracle to epigastrium 1.12. *Spines:* legs **I**, femur d 1-1-1, p (d1-d1)ap; tibia v 2-2-2; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-2; metatarsus p 1, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 0-d1-1, v p1-p1-2; metatarsus d p1, p 1-1-2, r 1-0-2/1-1-2, v 2-0-2. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v p1-2-2 (regular/irregularly paired); metatarsus d p1, p d1-1-2, r d1-1-2, v 2-2-2/2-1-2. *Colour:* carapace yellowish with two orange-brown longitudinal stripes, ocular area darker. Sternum dark brown. Chelicerae dark orange, as the ocular area. Legs yellowish. Dorsal abdomen brown, with two anterior yellow dots. Ventral abdomen yellowish, with three longitudinal brown stripes. *Eyes:* posterior eye row straight or slightly procurved. *Epigynum* (Fig. 13A,B): median lobe wide and slightly protruded posteriorly, highly sclerotized on lateral margins. CO on anterior end of epigynal fold. *Ducts* (Fig. 13C,D): CD coiled 360°. AB dorsolateral. S small and lobate, posterior.

Male (paratype, Chile: Pucón). Total length 3.80. Carapace length 1.78, width 1.36. Legs 4123. Length of tibia/metatarsus: **I** 1.42/1.32; **II** 1.38/1.24; **III** 1.08/1.16; **IV** 1.44/1.60. Chelicerae with three promarginal, three retromarginal (distal one bigger) teeth. Sternum length 0.94, width 0.76. Abdomen length 2.12, width 1.04. Tracheal spiracle to spinnerets 0.20; tracheal spiracle to epigastrium 1.10. *Spines:* legs **I**, femur d 1-1-1, p (1-d1)ap; tibia p 0-0-1/1-0-1, v 2-2-2; metatarsus p 0/1, v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 1-d1-

1, v 2-2-2; metatarsus p 1, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 0-d1-1, v p1-2-2; metatarsus d 1, p d1-1-2, r d1-1-2, v 2-0-2. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d 1-0-1, p 1-d1-1, r 1-d1-1, v p1-2-2; metatarsus d 1, p d1-1-1, r d1-1-1, v 2-2-2. Dorsal basal femoral spines very long. *Colour:* body dark orange, abdomen lighter, with two dorsal anterior yellow dots. Ventral abdomen as in female. Carapace with two darker stripes. Chelicerae orange. *Eyes:* as in female. *Palp* (Fig. 13E,F): tibia short. RTA long and thin, slightly higher than MA apex in ventral view, and with a slope towards the bulb. *Copulatory bulb* (Fig. 13G–I): MA wide and flat. PMA with a prolateral sclerotized fold and a prolateral second apophysis, connected to C (arrows in Fig. 13G,H). Apical C thick.

Natural history. The holotype was collected on the shore of a lake.

Distribution. Central and southern Chile, and in Chubut, Neuquén and Río Negro provinces of Argentina (Fig. 4D).

***Negayan enrollada* sp. nov. (Figs 5B and 14A–C)**

Holotype. 1 ♀, ARGENTINA: Chubut province: El Hoyo, VIII.1964, Birabén in MACN-Ar 10261.

Paratype. 1 ♀, CHILE: Región XI (Ibáñez del Campo): Aisén province: Balmaceda, 17–22.I.1961, L. Peña in IRSN IG 23.077.

Other material examined. ARGENTINA: CHUBUT: El Maitén, IX.1961, A. Kovacs, 1 ♀ (MLP).

Etymology. The species epithet is a Spanish adjective that means 'coiled', referring to the extremely coiled copulatory ducts of this species.

Note. As the holotype was faded, colour description is based on the paratype.

Diagnosis. Females have extremely coiled copulatory ducts, with 4–5 loops of 360° (Fig. 14B).

Female (holotype). Total length 5.17. Carapace length 1.82, width 1.38. Legs 4123. Length of tibia/metatarsus: **I** 1.04/0.82; **II** 0.92/0.82; **III** 0.84/0.96; **IV** 1.28/1.42. Palp tarsus length 0.52. Chelicerae with three promarginal, three retromarginal (basal one bigger) teeth. Sternum length 1.12, width 0.86. Anterior sternal margin convex. Abdomen length 3.32, width 1.60. Tracheal spiracle to spinnerets 0.32; tracheal spiracle to epigastrium 1.94. *Spines:* legs **I**, femur d 1-1-1, p (1-d1)ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v r1-2-p1; metatarsus p 1-0, v 2 ba. **III**,

femur d 1-1-1, p 0-d1-d1, r d1ap; tibia p 1-d1-1, r 0-d1-1, v p1-2-2; metatarsus d 0-p1-2, p d1-1-1, r d1-1-1, v 2-p1-2. **IV**, femur d 1-1-1, p d1ap, r d1ap; tibia p 1-d1-1, r 1-d1-1, v p1-2-2; metatarsus d 2-2-2 (irregularly paired), p 0-d1-1, r 0-d1-1, v 2-2-2. Basal spines on femur **IV** as long as the median ones. *Colour*: (paratype) Carapace orange with some darker diffuse spots. Legs yellowish orange at base, orange from tibia to distal end. Abdomen dark brown, with a large dorsal anterior yellow dot. Chelicerae orange. Sternum yellowish orange. *Eyes*: posterior eye row procurved. *Epigynum* (Fig. 14A,C): similar to that of *N. paduana*. Median lobe wide, highly sclerotized on the lateral margins. Lateral lobes weakly sclerotized. *Ducts* (Fig. 14B): CD extremely coiled, 4–5 loops of 360°. S irregular, close to the posterior margin of median lobe. AB dorsolateral.

Male. Unknown.

Variability. Spines: leg **II**, metatarsus p 1. **III**, tibia v p1-p1-2; metatarsus v 2-2-2. **IV**, tibia r 1-d1-d1-1, v 2-p1-2-2.

Natural history. Unknown.

Distribution. Argentina (Chubut province), and Chile (Aisén province) (Fig. 5B).

***Negayan tucuman sp. nov.* (Figs 5B and 15A–D)**

Holotype. 1 ♀, ARGENTINA: Tucumán province: Cochuna, 2.VII.1995, Ramírez & Goloboff, in MACN-Ar 10262.

Other material examined. None.

Etymology. The species epithet is a noun in apposition taken from the province where the holotype was collected.

Diagnosis. Females of this small species have five promarginal teeth on chelicerae, epigynal folds distant and parallel to the posterior margin of epigynum (Fig. 15A), spermathecae not contiguous, copulatory ducts coiled 180° (Fig. 15C,D).

Female (holotype). Total length 3.18. Carapace length 1.42, width 1.08. Legs 4123. Length of tibia/metatarsus: **I** 0.90/0.68; **II** 0.80/0.68; **III** 0.66/0.76; **IV** 1.08/1.18. Palp tarsus length 0.38. Chelicerae with 5 promarginal, four retromarginal teeth. Sternum length 0.88, width 0.66. Anterior margin of sternum straight. Abdomen length 1.82, width 1.06. Tracheal spiracle to spinnerets 0.10; tracheal spiracle to epigastrium 0.80. ALS more sclerotized than PS. *Spines*: Legs **I**, femur d 1-1-1, p d1ap; tibia v 2-2-2-0; metatarsus v 2-2-0. **II**, femur d 1-1-1, p d1ap; tibia v 2-2-2-0; metatarsus v 2-2-0. **III**, femur d 1-1-1, p d1ap, r d1ap; tibia d 1 ba, p d1-1, r d1-1, v p1-p1-2;

metatarsus d 2, p 0-d1-1, r 0-d1-1, v 2 ba-comb. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d p1bas, p d1-1, r d1-1, v 0-2-2; metatarsus d 2-0-2, p 0-1-0-1, r 0-1-0-1, v 2-2-0. Basal spines on femur **IV** longer than the median ones. Strong ventral spines on tibia and metatarsus **I** and **II**. *Colour*: carapace yellowish with two darker longitudinal stripes and dark, neat radii. Legs and palps yellowish with several brown dots. Chelicerae dark brown at base, yellowish distally. Sternum dark brown. Dorsal abdomen brown with orange W-shaped stripes and two anterior yellow dots. Ventral abdomen orange with three brown longitudinal stripes converging towards the spinnerets. *Eyes*: posterior eye row recurved. *Epigynum* (Fig. 15A,B): epigynum wide. As in *N. cerronegro*, it is difficult to recognize and homologize the location of the lobes. *Ducts* (Fig. 15C,D): CD coiled 180°. S small, long and lobated, lateral and near the posterior margin of the epigynum. AB dorsolateral.

Male. Unknown

Natural history. Holotype collected in moss on trees (Martín J. Ramírez, pers. comm.).

Distribution. Only known from the type locality (Fig. 5B).

***Negayan tarapaca sp. nov.* (Figs 5B and 16A–D)**

Holotype. 1 ♀, CHILE: Región I (Tarapacá): Parinacota, 24 km S. Zapahuira, elev 3640 m, 18°25'S, 69°31'W, 4.II.1994, N. Platnick, K. Catley, R. Calderón, R. T. Allen, in AMNH.

Other material examined. None.

Etymology. The species epithet is a noun in apposition taken from the type locality.

Diagnosis. Females of this small species have epigynal folds contiguous and parallel to the posterior margin of epigynum (Fig. 16A), and copulatory ducts coiled 180° (Fig. 16C).

Female (holotype). Total length 3.56. Carapace length 1.36, width 0.92. Legs 4123. Length of tibia/metatarsus: **I** 0.66/0.52; **II** 0.60/0.50; **III** 0.50/0.56; **IV** 0.86/0.98. Palp tarsus length 0.36. Chelicerae with three promarginal, 3/4 retromarginal teeth. Sternum length 0.80, width 0.60. Anterior margin of sternum straight. Abdomen length 2.34, width 1.30. Tracheal spiracle to spinnerets 0.16; tracheal spiracle to epigastrium 1.34. ALS more sclerotized than PS. *Spines*: legs **I**, femur d 1-1-1, p d1ap; tibia v 2-2-0; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v r1-r1-0/r1-2-0; metatarsus p 1, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; tibia d r1bas, p d1-1, r d1-1, v p1-p1-0; metatarsus d 0-p1-2, p d1-1-1, r d1-1-1, v 2-2-0. **IV**, femur d 1-1-1, p d1ap, r d1a; tibia d r1bas, p d1-1, r d1-1, v p1-p1-2/p1-2-2; metatarsus d 2-p1-2, p 0-1-1, r 0-1-1, v 2-p1-2.

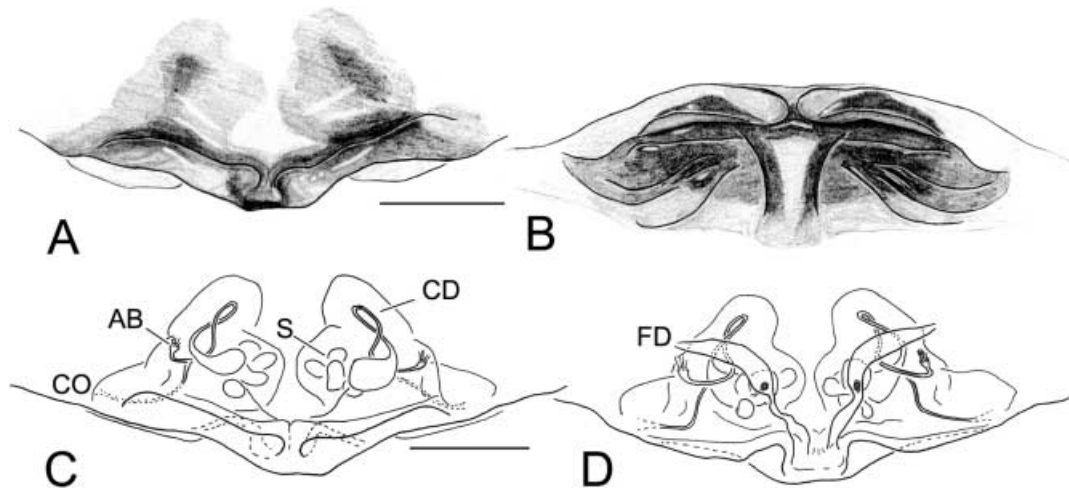


Fig. 16 A–D. *Negayan tarapaca* sp. nov. Female (holotype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. Scale bars = 0.1 mm.

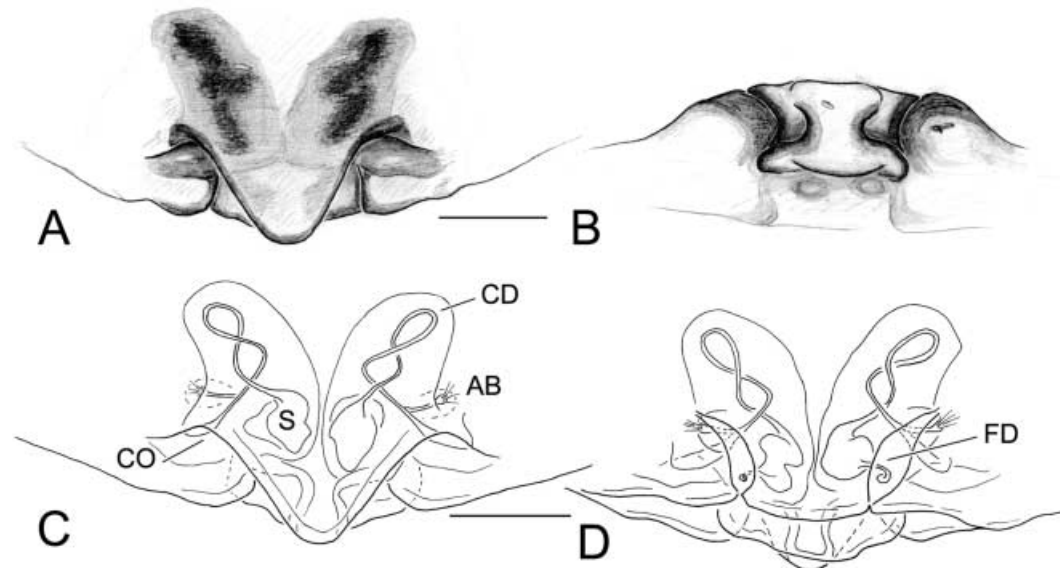


Fig. 17 A–D. *Negayan argentina* sp. nov. Female (holotype). —A. Epigyne, ventral view. —B. Same, posterior view. —C. Cleared epigyne, ventral view. —D. Same, dorsal view. Scale bars = 0.1 mm.

Basal spines on femur **IV** longer than the median ones. *Colour*: carapace orange with two longitudinal darker stripes and brown, neat radii from a brown spot anterior to the fovea. Legs yellowish basally, orange from tibia to distal end, with several dark brown dots. Chelicerae orange. Sternum orange anteriorly, posteriorly brown. Dorsal abdomen dark brown with yellowish W-shaped stripes and two anterior yellow dots. Ventral abdomen brown with several yellow tiny dots, and two yellow longitudinal stripes. *Eyes*: posterior eye row straight. *Epigynum* (Fig. 16A,B): Epigynum wide. As in *N. cerronegro* and *N. tucuman*, it is difficult to recognize and homologize the position of the

lobes. Epigynal folds contiguous and running parallel to the posterior margin of the epigynum. Anterior central margin of the folds more sclerotized. *Ducts* (Fig. 16C,D): CD coiled c. 360°. S lobated and contiguous. AB dorsolateral.

Male. Unknown.

Natural history. Unknown.

Distribution. Only known from the type locality in northern Chile (Fig. 5B).

Negayan argentina sp. nov. (Figs 5B and 17A–D)

Holotype. 1 ♀, ARGENTINA: Río Negro province: El Bolsón, 12.V.1962, A. Kovacs, in AMNH.

Other material examined. None.

Etymology. The species epithet is a noun in apposition taken from the country where the holotype was collected.

Diagnosis. Females can be distinguished by a triangular and pointed elevation on the median lobe which projects posteriorly (Fig. 17A).

Female (holotype). Total length 4.44. Carapace length 1.82, width 1.36. Legs 41=23. Length of tibia/metatarsus: **I** 1.02/0.84; **II** 0.98/0.86; **III** 0.86/0.96; **IV** 1.28/1.44. Palp tarsus length 0.52. Chelicerae with 3/2 promarginal, 4/3 retromarginal teeth. Sternum length 1.02, width 0.82. Anterior margin of sternum straight. Abdomen length 2.84, width 1.68. Tracheal spiracle to spinnerets 0.22; tracheal spiracle to epigastrium 1.46. ALS more sclerotized than PS. *Spines*: legs **I**, femur d 1-1-1, p (1-d1)ap; tibia v 2-2-2; metatarsus v 2 ba. **II**, femur d 1-1-1, p d1ap; tibia p 0-1, v 2-2-2; metatarsus p 1, v 2 ba. **III**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia p 1-d1, r 1-d1, v p1-p1-2; metatarsus d 0-p1-2, p d1-1-1-, r d1-1-1, v 2-0-2-comb. **IV**, femur d 1-1-1, p d1ap, r d1ap; patella r 1; tibia d r1bas, p 1-d1-1, r 1-d1-1, v p1-2-2; metatarsus d 0-p1-2, p 0-d1-1, r 0-d1-1, v 2-2-2-comb. Basal spines on femur **IV** as long as the median ones. *Colour*: carapace orange with two darker longitudinal stripes and darker radii. Ocular area darker. Each PME with a dark posterior dot converging in the anterior fovea. Legs yellowish at base, orange from median tibia to distal end of leg. Chelicerae orange-brown. Sternum brown. Dorsal abdomen brown with two anterior yellow dots extending posteriorly to half the abdomen. Ventral abdomen yellowish with three longitudinal brown stripes converging posteriorly. *Eyes*: posterior eye row procurved. *Epigynum* (Fig. 17A,B): triangular elevation on median lobe. *Ducts* (Fig. 17C,D): CD coiled 360°. AB dorsolateral. S lobated.

Male. Unknown.

Natural history. Unknown.

Distribution. Only known from the type locality in southern Argentina (Fig. 5B).

Discussion

The monophyly of *Negayan* is corroborated, although with relatively low support values. It is beyond the scope of this study to perform a generic phylogenetic analysis of Amaurobioidini, or to test the monophyly of the genera included or

even the tribe itself. In this analysis, as well as in Ramírez (2003), *Selknamia* remains the sister-group of *Negayan*, and *N. paduana* is the basal species of the genus.

Negayan is monophyletic and includes 12 species. Males and females of *N. excepta*, *N. pumo*, *N. tata* and *N. ancha* are tentatively paired, as both sexes were not collected together, but their geographical distributions partially overlap. Few new characters define groups within *Negayan*, and even though the number of characters and taxa from the original analysis were decreased, this did not simplify the analysis, because under the present taxon sample, many characters which defined groups in Ramírez' (2003) analysis became homoplastic or only autapomorphic, so a large amount of information was lost. Factors decreasing the values of group support include the absence of males in four species, the great amount of conflictive informative characters (Table 1), and also the number of polymorphic terminals.

Furthermore, one problem found in the taxonomy of *Negayan* is the remarkable intraspecific and even intrasexual variation. Some characters were not included in the analysis because of their high level of variation between and within sexes of the same species, hence not providing reliable grouping information. The weak clade support of *Negayan* and its internal nodes suggests that our knowledge is still incomplete, and that more data are needed, such as male data in those species for which only females are known, or perhaps molecular data.

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Appendix 1.**List of informative and autapomorphic (i.e. uninformative characters with apomorphies) characters from Ramírez (2003)**

The states of the 118 informative or autapomorphic characters from Ramírez (2003) used in this analysis are listed below. Length (le) and consistency (ci) and retention (ri) indices are reported for each character. A brief summary of the evolution of characters is given only when their transformations concern *Negayan* species; these are optimized on the tree in Fig. 1. For description, justification, and detailed and complete synopsis of the evolution of all the characters see Ramírez (2003). All multistate characters are unordered. Character numbering follows Ramírez (2003). Except where noted (0) indicates absent and (1) present.

Colour and body pattern

0. Body pattern: (0) colour uniform; (1) with contrasting patches, spots or dots. Autapomorphic.

1. Ventral longitudinal dark stripe on abdomen. The absence of a dark stripe is plesiomorphic in *Negayan*, and the optimization is ambiguous within it, as it is gained and lost many times. le = 6; ci = 0.16; ri = 0.28.

Carapace

6. Carapace narrowness: (0) normal; (1) narrow (see Ramírez 2003: 15, for statistical explanation). le = 1; ci = 1; ri = 1.

7. Carapace and chelicerae *Amaurobioides*-like (the carapace is wide in front, the chelicerae are very strong, and the ocular area is relatively small, see Ramírez 2003: 15). le = 2; ci = 0.5; ri = 0.5.

Eyes

9. Ocular area black. Autapomorphic.

10. Ocular area protruded. le = 2; ci = 0.5; ri = 0.75.

11. Anterior eye row: (0) procurved; (1) straight; (2) recurved. Straight anterior eye row is the plesiomorphic state in *Negayan*, becomes procurved in (*N. coccinea* + *N. tridentata*). le = 7; ci = 0.28; ri = 0.28.

12. Posterior eye row: (0) procurved or straight; (1) recurved. Posterior eye row becomes recurved in (*N. cerronegro* + *N. tucuman*). le = 5; ci = 0.2; ri = 0.55.

15. Ratio anterior median eye/anterior lateral eye (AME/ALE): (0) AME minute; (1) AME < ALE; (2) AME = ALE; (3) AME > ALE. AME minute is a synapomorphy of *Negayan* (excluding *N. paduana*). Reverts to AME < ALE in (*N. coccinea* + *N. tridentata*). le = 6; ci = 0.33; ri = 0.63.

16. Ratio posterior median eye/posterior lateral eye (PME/PLE): (0) PME < PLE; (1) PME = PLE; (2) PME > PLE. Equal eyes is a potential synapomorphy of *Negayan* (excluding *N. paduana*). Reverts to PME < PLE in (*N. coccinea* + *N. tridentata*). le = 6; ci = 0.16; ri = 0.16.

Chelicerae and endites

17. Male chelicerae: (0) strong, as in female or larger; (1) smaller than in female. Reverts to strong chelicerae in *N. pumo*. le = 4; ci = 0.25; ri = 0.25.

18. Male retromarginal distal tooth: (0) similar to the basal; (1) much larger than the basal (see Ramírez 1997, 2003). Autapomorphic.

19. Male distal pro- and retromarginal teeth: (0) separate; (1) contiguous, on a common protuberance (see Ramírez 1997, 2003). Autapomorphic.

20. Number of retromarginal cheliceral teeth in female: (0) one; (1) two; (2) three; (3) four or more. This character (as char. 23) was coded separately for females and males because within *Negayan*, the number of cheliceral teeth seems to be sexually dimorphic. Char. 20 refers to female retromarginal teeth, but see char. 214 for males. Only three of the four original states for these two characters were represented by the taxon sample of this dataset (Table 1). One retromarginal tooth is not present in all taxa here examined, thus states in both char. 20 and 214 are: (0) two; (1) three; (2) four or more. le = 8; ci = 0.25; ri = 0.45.

21. Size of retromarginal teeth: (0) small denticles; (1) regular teeth. Regular teeth are a potential synapomorphy of *Negayan*, with a reversal and secondary gain within it. le = 6; ci = 0.16; ri = 0.44.

23. Number of promarginal cheliceral teeth in female: (0) three; (1) four; (2) five or more. Same as in char. 20, coded only for females, but see char. 215 for males. Same states as in the original character. Four teeth arise in *N. excepta*, *N. coccinea* and ambiguously in *N. cerronegro*. Five teeth arise independently in *N. tucuman*. le = 5; ci = 0.4; ri = 0.

Female legs and palp

26. Leg III orientation: (0) backward; (1) forward. le = 1; ci = 1; ri = 1.

28. Shape of tibia I: (0) straight; (1) slightly sinuous. Autapomorphic.

Claw-tufts and scopulae

33. Scopulae on anterior tibiae. Autapomorphic.

Abdomen

35. PMS with many aciniform gland spigots. Autapomorphic.

36. Male abdomen projecting over anal tubercle (Ramírez 1997: fig. 16). le = 2; ci = 0.5; ri = 0.

Male palp

41. Femoral apophysis. Autapomorphic.

42. Retrolateral tibial apophysis (RTA). Autapomorphic.

43. Shape of RTA: (0) thick or spatulate; (1) thin, narrow, spine-shaped; (2) *Negayan* type: elongate and distally hooked. State (2) is a synapomorphy of *Negayan*. le = 2; ci = 1; ri = 1.

44. *RTA extremely thin* (Ramírez 1997). Autapomorphic.
 48. *Cymbial conductor position*: (0) apical; (1) subapical. Cymbial conductor subapical is a synapomorphy of (*Selknamia* + *Negayan*). le = 1; ci = 1; ri = 1.
 50. *Retrolateral apical notch on cymbium*. le = 2; ci = 0.5; ri = 0.87.

Copulatory bulb

53. *Apical loop of the sperm duct (SD), dorsal to secondary conductor*. le = 2; ci = 0.5; ri = 0.
 54. *Loop of the SD dorsal to median apophysis*. Autapomorphic.
 57. *Sperm duct suddenly narrowed before reaching the embolus*. Present in *N. puno*, and arises ambiguously in *N. paduana* and *N. excepta*. le = 4; ci = 0.25; ri = 0.
 59. *Tegulum displaced basally*. le = 2; ci = 0.5; ri = 0.5.
 61. *Basal notch of tegulum displaced prolaterally*. Autapomorphic.
 62. *Ventral cusp on tegulum*. Ambiguous. Potential synapomorphy of node containing *N. ancha* and its sister group, independently lost in *N. cerronegro*. le = 2; ci = 0.5; ri = 0.75.
 64. *Median apophysis (MA)*: (0) present; (1) reduced; (2) absent. The median apophysis in *Aysenia cylindrica* was considered 'reduced' instead of 'present' (Ramírez 2003), because it was smaller than that of *N. paduana*, which itself has a reduced MA. Median apophysis reduced is a synapomorphy of *Negayan*, with a reversal to present in *N. ancha*, and completely absent in *N. coccinea*, *N. puno* and *N. cerronegro*, although optimization is ambiguous. le = 7; ci = 0.28; ri = 0.44.
 65. *Shape of median apophysis*: (0) thick; (1) slender; (2) conical; (3) S-shaped. The two original states in this character (thick and conical) were split in four, in order to better represent the variation found in the current taxon sample. The character became highly homoplastic, but by limiting it to only two states a great amount of information is lost. le = 8; ci = 0.37; ri = 0.37.
 67. *Paramedian apophysis (PMA)*. Autapomorphic.
 68. *Shape of PMA*: (0) one short cusp; (1) two or more short cusps; (2) thick, simple and elongate, type *Philisca*; (3) slender, type *Monapia* or *Sanogasta*; (4) bifid. Only the first two states were scored for the selected taxa. One short cusp is present in *N. puno*, and ambiguously present in *N. tata* and *N. cerronegro*. le = 3; ci = 0.33; ri = 0.33.
 69. *One cusp of the PMA on the primary conductor (C)*. Same distribution as char. 68 in *Negayan*. le = 5; ci = 0.2; ri = 0.33.
 73. *Globose lobe on C, at the origin of PMA*. Independently gained in *N. coccinea*, *N. excepta*, *N. cerronegro* and *Coptoprepes*. le = 4; ci = 0.25; ri = 0.
 75. *Primary conductor*: (0) absent; (1) present, without canal; (2) with a canal where the embolus fits; (3) massive, with canal. State (1) was not represented across the taxa, thus the

- character states were recoded as follows: (0) absent; (1) present, with canal; (2) massive. Massive primary conductor is a synapomorphy of (*Selknamia* + *Negayan*). le = 3; ci = 0.66; ri = 0.87.
 76. *Translucent vertical lamina on C*. Autapomorphic.
 77. *Prolateral process on C, crossing the canal*. This character was recoded, because in *N. puno* and *N. cerronegro* the prolateral process on C is reduced. Recoded states are: (0) absent; (1) reduced; (2) present. Process present is a synapomorphy of *Selknamia minima* and of (*N. tridentata* + *N. coccinea*). Ambiguously reduced in *N. puno* and *N. cerronegro*; absent in *N. tata*. le = 4; ci = 0.5; ri = 0.33.
 78. *Apex of C displaced close to the median apophysis* (Ramírez 1997). le = 2; ci = 0.5; ri = 0.
 79. *Secondary conductor (C2)*: (0) absent; (1) fused to anterior dorsal margin of tegulum; (2) free. C2 is lost in (*Selknamia* + *Negayan*). le = 5; ci = 0.4; ri = 0.5.
 84. *Canal on C2*: (0) absent; (1) present, short; (2) deep, long, arising under the PMA, *Gayenna* type. State (2) was not counted in the analysis, as it is only scored for the other amaurobioidine tribe, *Gayennini*. le = 3; ci = 0.33; ri = 0.
 92. *C2 Josa type* (hypertrophied and complex, Ramírez 2003: 20). Autapomorphic.
 95. *Embolus very long*. Synapomorphy of *Negayan*, also a parallel gain in *Josa*. le = 2; ci = 0.5; ri = 0.87.
 96. *Basal process on embolus*. Autapomorphic.
 97. *Shape of basal process of embolus*: (0) flattened; (1) thin, hyaline; (2) membranous, expansible; (3) complex; (4) spine-like; (5) thick, conical; (6) *Gayennini* type (not scored in the analysis). Ambiguous. Basal process thick and conical (state 5) is a potential synapomorphy of *Negayan*. le = 7; ci = 0.71; ri = 0.6.
 98. *Base of embolus flattened*: (0) unmodified, approximately cylindrical; (1) flattened (Ramírez 1995b). Autapomorphic.

Epigyne

100. *Epigastrium partially sclerotized*. Autapomorphic.
 102. *Epigyne projecting posteriorly*. Autapomorphic.
 111. *Posterior notch between the lateral lobes (LF)*. le = 1; ci = 1; ri = 1.
 112. *Posterior depressions on LF*. Difficult to score in some *Negayan* females as the lateral lobes are no longer recognizable. The plesiomorphic condition is 'absent', and the depressions arise in (*N. coccinea* + *N. tridentata*) (shallow in the latter, Ramírez 2003). le = 3; ci = 0.33; ri = 0.33.
 113. *LF projecting posteriorly*. Arises independently in *Josa*, *N. argentina*. and (*N. coccinea* + *N. tridentata*). le = 3; ci = 0.33; ri = 0.5.

Spermathecae and ducts

115. *Copulatory openings on epigastric furrow*. Independently gained in several groups, present in *N. cerronegro*. le = 5; ci = 0.2; ri = 0.2.

116. *Copulatory ducts (CD) slender.* Independently gained in *Selknamia*, *N. puno*, and (*N. cerronegro* + *N. tucuman*). le = 4; ci = 0.25; ri = 0.25.

117. *CD coiled along longitudinal axes.* Convergent gain in many groups within the subfamily Amaurobioidine. Coiled CD are also convergent in *Negayan*, present in all but one (*N. cerronegro*) of its species. le = 4; ci = 0.25; ri = 0.66.

118. *CD extremely coiled.* Independently gained in *Josa* and *N. enrollada*. le = 2; ci = 0.5; ri = 0.

123. *Duct of the accessory bulb:* (0) short; (1) long. (The length of the duct of AB is markedly different between *Josa* species, and the rest of Amaurobioidini; Ramirez 2003: 22). le = 1; ci = 1; ri = 1.

124. *Spermathecae spherical:* (0) irregular; (1) approximately spherical. le = 2; ci = 0.5; ri = 0.

125. *Spermathecae contiguous:* (0) separate; (1) contiguous. Synapomorphy of *Negayan*, reverts only in *N. tucuman*. Independently gained in other groups. le = 4; ci = 0.25; ri = 0.72.

126. *Fertilization duct (FD) coiled along with the CD.* Autapomorphic.

127. *FD distant from epigastric furrow.* le = 4; ci = 0.25; ri = 0.4.

Sexual behaviour

128. *Copulatory plug* (See Ramírez 2003; for a justification of this character). le = 2; ci = 0.5; ri = 0.

Spines (see Ramírez 2003, for spination patterns and explanation of character states).

Tibia I

132. *Supplementary ventral spines on tibia I:* (0) 2-2-2 or less; (1) 2-2-2-2 or more. Autapomorphic.

133. *v p1-x-x.* Autapomorphic.

134. *v r1-x-x.* le = 2; ci = 0.5; ri = 0.

136. *v x-p1-x displaced prolaterally.* le = 1; ci = 1; ri = 1.

138. *v xap:* (0) 2ap; (1) p1ap; (2) 0ap. le = 7; ci = 0.28; ri = 0.72.

Metatarsus I

140. *v x-p1-x.* le = 3; ci = 0.33; ri = 0.

141. *v x-r1-x.* le = 3; ci = 0.33; ri = 0.

142. *p 1-x.* le = 2; ci = 0.5; ri = 0.

Tibia II

146. *v p1-x-x.* le = 2; ci = 0.5; ri = 0.83.

147. *v r1-x-x.* Autapomorphic.

148. *v x-p1-x.* le = 1; ci = 1; ri = 1.

150. *v p1ap.* le = 3; ci = 0.33; ri = 0.6.

151. *v r1ap.* le = 2; ci = 0.5; ri = 0.85.

152. *p x-1.* le = 5; ci = 0.2; ri = 0.

Metatarsus II

153. *p d1-x-x.* Autapomorphic.

154. *p x-1-x.* le = 1; ci = 1; ri = 1.

156. *d p1ap.* Autapomorphic.

Patella III

158. *r d1.* le = 5; ci = 0.2; ri = 0.5.

Tibia III

160. *v p1-x-x.* le = 1; ci = 1; ri = 1.

162. *v x-p1-x.* Autapomorphic.

163. *v x-r1-x.* le = 3; ci = 0.33; ri = 0.6.

164. *v x-x-p1.* Autapomorphic.

165. *v x-x-r1.* Autapomorphic.

Metatarsus III

166. *v 2-x-x.* Autapomorphic.

167. *v x-p1-x.* le = 3; ci = 0.33; ri = 0.66.

168. *v x-r1-x.* le = 3; ci = 0.33; ri = 0.33.

169. *v ap:* (0) 2; (1) p1; (2) 1; (3) 0. le = 7; ci = 0.28; ri = 0.

170. *Preening comb on metatarsi III and IV.* le = 5; ci = 0.2; ri = 0.2.

171. *p d1-x-x.* le = 3; ci = 0.33; ri = 0.66.

172. *p x-1-x.* le = 2; ci = 0.5; ri = 0.

173. *p x-x-1.* le = 2; ci = 0.5; ri = 0.

174. *r d1-x-x.* le = 4; ci = 0.25; ri = 0.62.

175. *r x-1-x.* le = 2; ci = 0.5; ri = 0.66.

176. *r x-x-1.* le = 2; ci = 0.5; ri = 0.

177. *d x-p1-x.* le = 1; ci = 1; ri = 1.

178. *d x-x-p1.* le = 4; ci = 0.25; ri = 0.

179. *d x-x-r1.* le = 3; ci = 0.33; ri = 0.33.

Patella IV

180. *r d1.* le = 4; ci = 0.25; ri = 0.7.

Tibia IV

181. *v p1-x-x.* Autapomorphic.

182. *v r1-x-x.* le = 2; ci = 0.5; ri = 0.

184. *v x-r1-x.* le = 1; ci = 1; ri = 1.

186. *v x-x-r1.* Autapomorphic.

Metatarsus IV

188. *v r1-x-x.* le = 2; ci = 0.5; ri = 0.

190. *v x-r1-x.* le = 4; ci = 0.25; ri = 0.25.

191. *p d1-x-x.* le = 4; ci = 0.25; ri = 0.57.

192. *p x-1-x.* le = 3; ci = 0.33; ri = 0.

193. *p x-x-1.* le = 2; ci = 0.5; ri = 0.

194. *r d1-x-x.* le = 3; ci = 0.33; ri = 0.06

195. *r x-1-x.* le = 4; ci = 0.25; ri = 0.

196. *r x-x-1.* le = 2; ci = 0.5; ri = 0.

197. *d x-p1-x.* le = 3; ci = 0.33; ri = 0.66.

198. *d x-x-p1.* le = 2; ci = 0.5; ri = 0.5.

199. *d x-x-r1.* le = 2; ci = 0.5; ri = 0.

Appendix 2.

List of new characters proposed in this analysis

Description of the 15 characters proposed in this study, with a brief summary of their evolution, optimized on the tree in Fig. 1. Numeration follows Ramírez (2003); new characters are added after the original ones. Length (le) and consistency (ci) and retention (ri) indexes are reported in each character. New multistate characters are considered unordered.

Epigynum

200. Number of posterior epigynal pouches: (0) none; (1) one (Fig. 10B); (2) two (Fig. 11B). Two pouches arose independently in *Negayan cerronegro*, *Gamakia hirsuta* and *Ferrieria ebinata*. One pouch is autapomorphic in *N. puno*. le = 4; ci = 0.5; ri = 0.

201. Direction of coiling axis of copulatory ducts: (0) longitudinal (Figs 12C and 13C); (1) divergent, towards the laterals (Fig. 8B); (2) convergent, towards the centre (Fig. 16C). Convergent coiling axis is an autapomorphy of *N. tarapaca*. Divergent axis is a parallel gain in *N. puno* and *N. coccinea*. le = 3; ci = 0.66; ri = 0.

202. Direction of the first portion of copulatory ducts: (0) convergent (Fig. 7C); (1) parallel (Fig. 11C); (2) divergent (Fig. 10C). The direction of the copulatory ducts is considered according to the male embolus run, i.e. from the copulatory openings to the spermathecae. Accordingly, convergent means the first portion of the copulatory duct (before joining the accessory bulb duct) runs towards the centre of the epigynum. Convergent copulatory ducts are shared by most *Negayan* species. le = 8; ci = 0.25; ri = 0.

203. Location of accessory bulbs in relation to the spermathecae: (0) dorsal; (1) same; (2) ventral (Fig. 11C). Related to the position of the accessory bulbs in the dorsal-ventral axis in relation to the spermathecae. Although it ambiguously optimizes at *Negayan* node, dorsal accessory bulbs are shared by most *Negayan* species, except for *N. coccinea* and *N. cerronegro* (ventral). le = 7; ci = 0.28; ri = 0.37.

204. Accessory bulbs: (0) lateral, apart from each other (1) central, close and located between the spermathecae. Lateral accessory bulbs are shared by almost all amaurobioidine representatives, except *Aysenoides terricola* and *Acanthoceto acupicta*. le = 3; ci = 0.33; ri = 0.33.

Male palp

205. Sudden inclination of the retrolateral tibial apophysis (RTA) towards copulatory bulb: (0) absent; (1) present (Fig. 9E, 11E and 13E). Inclined RTA is a synapomorphy of *Negayan* (excluding *N. paduana*); reverts to absent in *N. tata*. le = 2; ci = 0.5; ri = 0.8.

206. Length of RTA 'Negayan type': (0) short, up to tip of PMA (Fig. 10E); (1) long, surpassing the PMA, variable in the

median apophysis area (Fig. 9E). Long RTA is plesiomorphic in *Negayan*. Short RTA is a potential synapomorphy of the most inclusive node that excludes *N. ancha*, only reverting in *N. coccinea*. The difference between the heights in the RTA is quite marked. le = 2; ci = 0.5; ri = 0.66.

207. Sudden narrowness in RTA 'Negayan type': (0) absent, width of apophysis remains more or less constant (Fig. 11F); (1) median, narrowness in the middle height in the RTA (Fig. 13F); (2) apical, very close to the sinuous tip (Fig. 12F). Median narrowness in the RTA is shared by all *Negayan* species, except in *N. paduana*, *N. tata* (apical) and *N. cerronegro* (absent). le = 3; ci = 0.66; ri = 0.

208. Lobe associated with the base of the median apophysis: (0) absent; (1) present, membranous lobe. Arises independently in *N. excepta* and *N. tata*. le = 2; ci = 0.5; ri = 0.

209. Ventral fold prolateral to PMA: (0) absent; (1) membranous (Fig. 12I); (2) slightly sclerotized (Fig. 13G). The ventral fold is lost in *N. puno*. Ambiguous optimizations within *Negayan*. le = 4; ci = 0.5; ri = 0.5.

Somatic morphology

210. Two anterior dorsal yellow dots on abdomen: (0) absent; (1) present. Dots are absent in *N. enrollada*. le = 5; ci = 0.20; ri = 0.

211. Shape of the two anterior dorsal yellow dots on abdomen: (0) circular; (1) extended along half abdomen or less; (2) extended along more than half abdomen. Dots are extended along more than half abdomen in *N. excepta*. le = 7; ci = 0.28; ri = 0.16.

212. Degree of sclerotization of anterior lateral spinnerets (ALS): (0) normal, same sclerotization as the other spinnerets; (1) slightly sclerotized. Slightly sclerotized ALS are synapomorphy of *Negayan* (excluding *N. paduana*), and revert to normal in the most inclusive node that excludes *N. ancha*. ALS slightly sclerotized is secondary gained in *N. tarapaca*. le = 4; ci = 0.25; ri = 0.25.

213. Basal spines on the dorsal femoral surface in male legs: (0) normal, as long as distal spines; (1) long, longer than distal spines, but equal to median ones; (2) very long, longer than distal and median spines. Very long basal spines are synapomorphy of *Negayan*, reverting independently to long in *N. tridentata*, *N. tata* and *N. puno*. Spines revert to normal in *N. argentina*. le = 9; ci = 0.22; ri = 0.36.

214. Number of retromarginal cheliceral teeth in male: (0) two; (1) three; (2) four or more. Polymorphic in some *Negayan* species. le = 6; ci = 0.33; ri = 0.42.

215. Number of promarginal cheliceral teeth in male: (0) three; (1) four; (2) five or more. Three teeth are shared by most of the taxa scored here, four teeth present in *N. coccinea*. Autapomorphic.