Revista Chilena de Historia Natural
ISSN: 0716-078X
editorial@revchilhistnat.com
Sociedad de Biología de Chile
Chile

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Revista Chilena de Historia Natural, vol. 79, núm. 1, 2006, pp. 29-40
Sociedad de Biología de Chile
Santiago, Chile

Revista Chilena de Historia Natural
79: 29-40, 2006

Diversity, distribution and floral specificity of tangle-veined flies (Diptera: Nemestrinidae) in north west Patagonia, Argentina

Diversidad, distribución y especificidad floral de nemestrínidos (Diptera) en el noroeste de la Patagonia, Argentina

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ABSTRACT

Tangle-veined flies (Nemestrinidae) constitute a primitive and rather widespread family among Diptera. The genus *Trichophthalma* occurs in Australia and South America and is the only one in the family with a typically Gondwanian, disjoint distribution. The ecology and distribution of most southern South American species of this genus remains virtually unknown. We studied the diversity, distribution and flower specificity of flower-visiting species of the genus *Trichophthalma* in the temperate forests of southern South America in ten sites along an east-west rainfall gradient (37-40º S) on the eastern slope of the Andes. We recorded nine species of *Trichophthalma*, which showed an overlapped distribution along the gradient and different degrees of floral specificity. Three species are reported for Argentina for the first time and three are first recorded as flower visitors to the local flora. Our results show that while in southern Africa tangle-veined flies are engaged in highly specialized pollination interactions with long-tubed species, the *Trichophthalma* spp. of Patagonia share their flowers with a diverse and rather unspecialized visitor fauna among which several species of flies, bees and birds are present.

Key words: Diptera, Nemestrinidae, *Trichophthalma*, pollination Patagonia.

RESUMEN

Los nemestrínidos constituyen una familia de Dípteros primitiva y de amplia distribución. El género *Trichophthalma* se encuentra en Australia y Sudamérica y es el único en la familia con una distribución disjunta típicamente gondwánica. La ecología y distribución de la mayoría de las especies sudamericanas permanecen virtualmente desconocidas. Estudiamos la diversidad, distribución y especificidad floral de las especies del género *Trichophthalma* de los bosques templados del sur de Sudamérica en diez sitios ubicados a lo largo de un gradiente de precipitación este-oeste (37-40º S) sobre la vertiente occidental de los Andes. Registramos nueve especies de *Trichophthalma*, las cuales mostraron una distribución superpuesta a lo largo del gradiente y diferentes grados de especificidad floral. Tres de las especies fueron registradas por primera vez para Argentina, y tres fueron registradas por primera vez visitando especies de la flora local. Nuestros resultados muestran que mientras en el sur de África los nemestrínidos se involucran en interacciones de polinización altamente especializadas con especies de tubo floral largo, las especies de *Trichophthalma* de Patagonia comparten sus flores con una fauna diversa y poco especializada en la cual están presentes varias especies de moscas, abejas y aves.

Palabras clave: Diptera, Nemestrinidae, *Trichophthalma*, polinización, Patagonia.

INTRODUCTION

Nemestrinidae are picturesque flies (Diptera, Brachycera, Asiloidea) that have the ability to hover, keeping up a high-pitched hum (Cole 1969). They are widespread throughout the globe, but there are some areas of higher concentration: from the Mediterranean to Turkistan, eastern Australia, southern Africa, Chile and Argentina (Bernardi 1973). Thirty years ago there were about 150 described species (Cole 1969), but since then several new species have been added (e.g., Bernardi 1975, 1977) and many might remain undescribed

(Goldblatt & Manning 2000, N. Woodley personal communication).

The family is rather primitive among Diptera and was probably one of the first ones to feed on the nectar of early angiosperms during the early Cretaceous (Willemstein 1987, Mostovski & Martinez Delclos 2000). Fossil records show that Nemestrinidae were already present in the Jurassic in the Palearctic region (Bernardi 1973; Mostovski & Martinez Delclos 2000).

Two extant subfamilies, the Nemestrininae and the Hirmoneurinae, are the most primitive and the most widely distributed. Nemestrininae genera are geographically segregated in South America and Australia (genus *Trichophthalma*), southern Africa (*Prosoeca* and *Stenobasipteron*) and the Palearctic region (*Nemestrinus* and *Stenopteromyia*, with a branch that, later, reached Africa, giving rise to *Moegistorhynchus*) (Bernardi 1973). In South America, several species of Nemestrinidae belonging to the sub-families Hirmoneurinae (represented by the genus *Hirmoneura*) and Trichopsideinae (*Neorhynchocephalus* spp.) have also been described.

Trichophthalma occurs in Australia and South America and is the only case in the family (though not in nature, see Raven & Axelrod 1974, 1975 and references therein) of a genus with such a disjunct (typically Gondwanian) distribution. This genus has 45 Australian species and 21 species described for southern South America (Argentina, Chile and Uruguay) (Bernardi 1973, 1975).

In spite of its primitiveness, *Trichophthalma* shows a rather specialized character (shared by all Nemestrininae): the proboscis is always well developed and it can range between 1.4 to 7 times the height of the head (as measured by Angulo 1971), being sometimes longer than the whole insect, as in *T. scalaris* of Chile (Angulo 1971). Species with long proboscides are able to reach nectar hidden in deep flower tubes, which has lead to remarkably specialized mutualisms (Goldblatt & Manning 2000, Johnson & Steiner 2000, and references therein).

In spite of their widespread distribution and nectar-feeding habit, pollination by tangle-veined flies is a most unusual phenomenon that has only been reported for southern Africa and South America (for the first time by Marloth 1908 and Edwards 1930, respectively). However, unlike southern African species, which have received much attention (Goldblatt & Manning 2000, and references therein), the ecology and distribution of most southern South American species remains virtually unknown (Peña 1996).

Trichophthalma is a diverse genus within the temperate forests of southern South America (Stuardo 1939, Angulo 1971, Bernardi 1973). These forests extend over a narrow strip from ca. 35 to 55º S latitude over much of southern Chile and the eastern slope of the Patagonian Andes in Argentina (Donoso Zegers 1993, Arroyo et al. 1996). In this region, there is a strong rainfall gradient (Paruelo et al. 1998a) which encompasses a striking shift in vegetation in less than 150 km in an east-west direction from xeric desert shrubland to grass-shrub steppe, leading to a low stature tree cover and finally closed canopy forest (Movia et al. 1982, Paruelo et al. 1998b, Austin & Sala 2002).

As part of a community-level survey in NW Patagonia (Argentina) (Devoto et al. 2005), we focused on the diversity and distribution of flower-visiting Nemestrinidae and their floral specificity along the rainfall gradient mentioned above.

MATERIAL AND METHODS

The study was carried out on the eastern slope of the Patagonian Andes within the Nahuel Huapi and Lanín national parks in Argentina, approximately between 39-40º S and 71-72º W. The study sites encompassed from humid *Nothofagus*-dominated forests (close to the Valdivian rainforests of Chile) to the easternmost outskirts of *Austrocedrus*-dominated dry forests on the border of the grass-shrub Patagonian steppe (Paruelo et al. 1998b). From the Andes and eastward through the region, the amount of annual rainfall decreases exponentially reaching less than 200 mm per year in most of the central portion of Patagonia (Paruelo et al. 1998a, Soriano 1983). A characteristic of the temperature pattern throughout the region is the NW-SE distribution of the isotherms, determined mainly by the presence of the Andes (Paruelo et al. 1998a). Mean annual temperatures in the study region range from ca. 10 ºC on the eastern side to ca. 8 ºC on the western side (Movia et al. 1982).

Within the described region, we selected ten sites encompassing an annual rainfall from 700 to 2,550 mm (a ca. 3.6-fold change) and a 0.4-fold change in altitude (Table 1, Movia et al. 1982). General patterns of variation at the community level have been described elsewhere (Devoto et al. 2005). In the present work, we focused on the diversity, distribution and floral specificity of Nemestrinidae.

At each site, 3-5 well-trained observers recorded flower-visitors to the local flora over a period of 7-8 days in mid-December. Additionally, a reduced team of one to two observers re-visited most sites in mid-January and/or mid-December of a later year (see Table 1 for details). We sampled on several plants at different times of the day and on different days. Every flower-visiting tangle-veined flies observed were captured, the only exception being *T. niveibarbis* at two sites (see Table 2 for details) which was extremely abundant and only a few individuals were caught. We pinned insects for later identification at the laboratory. We made determinations using available keys and descriptions (Stuardo 1939, Angulo 1971, Bernardi 1973) and comparing with reference collections at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires) and Museo de La Plata (La Plata) whenever possible. At Caviahue, fieldwork was non-systematic and performed by one observer on a single trip of two days in December. The results from this site are shown, but not included in statistical analyses. All the material is deposited at our department. For our analysis, we included information from comparable studies in the same area from Argentina and Chile (Edwards 1930, Stuardo 1939, Angulo 1971, Bernardi 1973, Riveros et al. 1991, Aizen et al. 2002, Vázquez & Simberloff 2002, 2003, 2004, Smith-Ramírez et al. 2005).

Quality of the data set

Species turnover in pollinator communities can be very significant over time and space (e.g., Williams et al. 2001, Potts et al. 2003, Herrera 2005). Spatial variability was accounted for by sampling in several sites encompassing much of the environmental variation of the region. The complete absence of species of *Trichophthalma* in the two driest sites (in spite of the considerable sampling effort employed there, see Results) suggests that samplings included the total longitudinal distribution of Nemestrinidae, at least on the eastern hang of the Andes. Regarding seasonal variation, we believe that the relatively short sampling window we used did not seriously flaw our data given the unimodal and strongly seasonal reproductive phenology of the communities studied, where the activity of most plants and pollinators is markedly concentrated in December and, to a lesser extent, in January (Smith-Ramírez & Armesto 1994, Riveros & Smith-Ramírez 1996). A similar phenological pattern has been described also for the steppe habitats on the driest sites of the gradient (Soriano et al. 1976). A third concern is that our survey may undersample inter-annual variation. We hope to have partially circumvented this problem by sampling six out of ten sites in at least two different seasons (Table 1). Unfortunately, four sites were sampled for only one season (though two of them were visited twice within the same season) due to logistical reasons (our laboratory and the study region are 1,500 km apart).

Finally, we evaluated whether the uneven sampling effort among sites (Table 1) had affected the number of species recorded at each site (Table 2). However, the correlation between total sampling effort and the number of species of *Trichophthalma* recorded at each site was not significant ($P = 0.998$, $R^2 = 0.000001$, curve not shown).

RESULTS

Diversity and distribution of Nemestrinidae in NW Patagonia

In eight out of ten communities surveyed (see Table 1 for details), we recorded tangle-veined flies visiting flowers of the local flora (Table 2, see Table 3 for a description of plants visited). Overall, we recorded nine different species of *Trichophthalma* (including two undescribed taxa: specie nova 1 and 2, Table 2), which showed an overlapped distribution along the gradient (Table 2). Three of the species were previously unrecorded for Argentina (*T. andina*, *T. porteri* and *T. niveibarbis*, comparing with the only lists of species published by Stuardo 1939 and Bernardi 1973). After standardization for sampling effort, the variation in species number throughout the gradient adjusted to a second-degree polynomial function with a maximum at ca. 1.700 mm (Fig. 1). Eastward and westward from this point, diversity of tangled-veined flies decreased towards both ends of the gradient. In the two driest sites, LL and CT, we found no species of Nemestrinidae foraging on flowers.

Floral specificity

Tangle-veined flies showed different degrees of floral-specificity and visited on average 1.88 plant species (range = 1-4, Tables 3 and 4). Considering the previous records for Nahuel Huapi (NH) region (*T. amoena* visiting *Berberis buxifolia*, *B. darwinii*, *Ribes magellanicum* and *Schinus patagonicus*, and *T. jaffueli* visiting *Alstroemeria aurea* and *Rosa eglanteria*; Vázquez & Simberloff 2003, 2004) the mean rises to 2.3 (range 1-6). The most generalist species was *T. amoena,* which visited six different plant species throughout its range (considering data from Table 3 and from Vázquez & Simberloff 2003, 2004). Some species had wide distribution ranges and visited several plant species throughout the gradient (*T. jaffueli*, Table 3), whereas others had more narrow ranges and visited a single plant species across their distribution (e.g., *T. niveibarbis*, Table 3). A few additional records were not included in our analysis as they were too far from our study area (*T. philippii* on *Chaetanthera microphylla* and *Stachys albicaulis* in the subandean scrub of central Chile, Arroyo et al. 1982; *T. porteri* on *Trevoa quinquenervia* at Fundo Santa Lara, Quillota, Chile, D. Medan unpublished results; *T. herbstii* and *T. commutata* on *Eucryphia cordifolia* at Chiloé, Chile, Smith-Ramírez et al. 2005; *T. jaffueli* on *Senecio patagonicus* at Lago Argentino, Santa Cruz province, Argentina, D. Medan unpublished results). There was no significant relationship between the length of the proboscides of the captured species of *Trichophthalma* and the number of plant species they were recorded visiting ($P = 0.276$, $F_{1,7} = 1.39$; $R^2 = 0.16$; from data on Table 3).

TABLE 1

Dates of field observations, geographic coordinates, mean annual rainfall and altitude of ten study sites in NW Patagonia, Argentina. Sampling effort was calculated as fieldwork days x number of persons participating in fieldwork x number of hours of observations per day

Fechas de observaciones de campo, coordenadas geográficas, precipitación media anual y altitud de diez sitios de estudio en el NO de Patagonia, Argentina. El esfuerzo de muestreo se calculó como número de días de trabajo de campo x número de personas participantes en el trabajo de campo x número de horas de observaciones por día

Site (abbreviation)	Lago Queñi (LQ)	Paso Puyehue (PP)	Lago Tromen (LT)	Arroyo Pedregoso (AP)	Vda. de Barriga (VB)	Villa Traful (VT)	Lago Huechulafquen (LH)	Caviahue CA)	La Lipela (LL)	Confluencia Traful (CT)
Date of field observations	Dec 1999 Jan 2000	Dec 2001	Dec 1998 Dec 2003	Dec 2001 Dec 2002 Jan 2003	Dec 1997 Dec 2003	Dec 2001 Dec 2002 Jan 2003	Dec 1997 Dec 2003	Jan 2002	Dec 2000 Jan 2001	Dec 2001 Dec 2002 Jan 2003
Geographic coordinates	40º09’ S, 71º43’ W	40º44’ S, 71º53’ W	39º34’ S, 71º26’ W	40º37’ S, 71º35’ W	39º45’ S 71º22’ W	40º39’ S, 71º21’ W	39º48’ S, 71º12’ W	37º51’ S, 71º01’ W	40º48’ S, 71º06’ W	40º43’ S, 71º05’ W
Mean annual rainfall (mm)	2,550	2,000	1,750	1,700	1,450	1,250	1,050	1,000	750	700
Altitude (m)	800	950	1,000	870	970	900	780	1,653	735	727
Sampling effort (h)	304	48	180	68	32	92	232	4	320	92

TABLE 2

Distribution of *Trichophthalma* species along a rainfall gradient in NW Patagonia, Argentina. Presence-absence data are based on our own field records and previous studies († Bernardi 1973, ‡ Vázquez & Simberloff 2003, 2004). Although for some species field records were discontinuous along the gradient, we assumed their presence in intermediate sites (§). For our own records, numbers indicate the quantity of individuals caught at each site. Captures of *T. niveibarbis* at LT and VB were kept to a minimum. CH = records from several sites on the Chilean slopes of the Andes at ca. the same latitude (Stuardo 1939, Angulo 1971, Bernardi 1973), PB = Puerto Blest, LQ = Lago Queñi, PP = Paso Puyehue, LT = Lago Tromen, AP = Arroyo Pedregoso, VB = Viuda de Barriga, VT = Villa Traful, LH = Lago Huechulafquen, C = Caviahue, LL = La Lipela, CT = Confluencia Traful. Annual rainfall values (mm) are given for each site. For simplicity, records from previous studies were assigned, when possible, to one of our own sites with equivalent annual rainfall

Distribución de especies de *Trichophthalma* a lo largo de un gradiente de precipitación en el NO de Patagonia, Argentina. Los datos de presencia-ausencia se basan en nuestros propios registros de campo y en estudios previos († Bernardi 1973, ‡ Vázquez & Simberloff 2003, 2004). A pesar de que para algunas especies los registros de campo resultaron discontinuos a lo largo del gradiente, asumimos su presencia en sitios intermedios (§). Para nuestros propios registros, los números indican la cantidad de individuos capturados en cada sitio. La abundancia de *T. niveibarbis* en LT y VB está subestimada debido a que las capturas se restringieron a un mínimo. CH = registros de varios sitios en la vertiente chilena de los Andes a aproximadamente la misma latitud (Stuardo 1939, Angulo 1971, Bernardi 1973), PB = Puerto Blest (3.000 mm), LQ = Lago Queñi, PP = Paso Puyehue, LT = Lago Tromen, AP = Arroyo Pedregoso, VB = Viuda de Barriga, VT = Villa Traful, LH = Lago Huechulafquen, C = Caviahue, LL = La Lipela, CT = Confluencia Traful. Se proporcionan los valores de precipitación media anual (mm) de cada sitio. Por simplicidad los registros de estudios previos fueron asignados cuando fue posible a uno de nuestros propios sitios con precipitación equivalente

Species	CH	PB	LQ	PP	LT	AP	VB	VT	LH	C	LL	CT
Mean annual precipitation (mm)		3,000	2,550	2,000	1,750	1,700	1,450	1,250	1,050	1,000	750	700
T. philippii Rondani	†	†	4	§	3	§	2					
T. nubipennis Rondani	†		4									
T. amoena Bigot	†			2 ‡	‡	‡	†	§	†			
T. jaffueli Stuardo Ortiz	†			‡	‡	6‡	§	1	§	4		
T. porteri Stuardo Ortiz	†				4							
T. sp. 1					2							
T. niveibarbis (Bigot)	†				4	§	10					
T. andina (Philippi)	†					1						
T. sp. 2									1			

Flower-visitors overlap and floral characters

Plants visited by tangle-veined flies were also visited by an average of 17.38 additional species (range: 2-65, Table 3) among which Diptera, Hymenoptera, Coleoptera, Lepidoptera and birds were present (Fig. 2). The diversity of the visitor assemblage of the plants visited by tangle-veined flies varied markedly among species and sites (Fig. 2). For instance, whereas three animal species visited *Cerastium arvense*, *Discaria chacaye* received visits from 65 additional species. As an example of inter-site variation, *Embothrium coccineum* received 10 species of flower visitors at LT (four Hymenoptera, two Diptera, two Nemestrinidae and two birds, including one hummingbird species; Fig. 2) and 19 at LQ (eight Diptera, six Hymenoptera, two Coleoptera, one Lepidoptera, one Nemestrinidae and one hummingbird; Fig. 2).

TABLE 3

Summary of records of interactions between *Trichophthalma* species and local flora in NW Patagonia, Argentina. Numbers on the intersections of rows and columns indicate the number of species of additional flower visitors that share the floral resources (columns) with the species of tangle-veined flies (rows). LQ = Lago Queñi, PP = Paso Puyehue, LT = Lago Tromen, AP = Arroyo Pedregoso, VB = Viuda de Barriga, VT = Villa Traful, LH = Lago Huechulafquen, C = Caviahue. The lengths (and range) of the proboscides of *Trichophthalma* species is also indicated

Resumen de registros de interacciones entre especies de *Trichophthalma* y la flora local en el NO de Patagonia, Argentina. Los números en la intersección entre filas y columnas indican el número de especies de visitantes florales adicionales que comparten los recursos florales (columnas) con las especies de Nemestrínidos (filas). LQ = Lago Queñi, PP = Paso Puyehue, LT = Lago Tromen, AP = Arroyo Pedregoso, VB = Viuda de Barriga, VT = Villa Traful, LH = Lago Huechulafquen, C = Caviahue. Se presenta también longitud (y el rango) de la probóscide de las especies de *Trichophthalma*

Trichophthalma species (number of individuals)	Mean length (range) of the proboscides (mm)	Site	Host plant										
			Ab	Al	Be	Bg	Ca	C	Dc	Ev	Ec	Gp	Hr
T. amoena (2)	4.93 (4.59-5.27)	PP		9								12	
T. andina (1)	6.36	AP											9
T. porteri (4)	4.98 (4.71-5.21)	LT			7				65				
T. jaffueli (9)	5.39 (3.99-10.05)	AP					2						9
		VT						5					
		C								0			
T. niveibarbis (13)	7.73 (5.87-10.00)	LT									9		
T. nubipennis (4)	7.15 (6.86-7.34)	LQ								30			
T. philippii (9)	8.89 (7.74-11.00)	LT									9		
		LQ							46		18		
T. sp. 1 (2)	3.72 (3.44-4.00)	LT			7	32							
T. sp. 2 (1)	5.95	LH	9										

TABLE 4

Shape and length of the flower tube of plant species visited by species of *Trichophthalma* in NW Patagonia, Argentina. Characters are based on Correa (1969-1999) and our own data (†). Ab: *Adesmia boronioides*; Al: *Azara lanceolada*; Be: *Berberis empetrifolia*; Bg: *Buddleja globosa*; C: *Carduus sp.*; Ca: *Cerastium arvense*; Dc: *Discaria chacaye*; Ec: *Embothrium coccineum*; Ev: *Escallonia virgata*; Gp: *Gaultheria phillyreaefolia*; Hr: *Hypochaeris radicata*

Forma floral y longitud del tubo floral de las especies de plantas visitadas por especies de *Trichophthalma* en el NO de Patagonia, Argentina. La caracterización se basa en Correa (1969-1999) y en datos propios (†). Ab: *Adesmia boronioides*; Al: *Azara lanceolada*; Be: *Berberis empetrifolia*; Bg: *Buddleja globosa*; C: *Carduus sp.*; Ca: *Cerastium arvense*; Dc: *Discaria chacaye*; Ec: *Embothrium coccineum*; Ev: *Escallonia virgata*; Gp: *Gaultheria phillyreaefolia*; Hr: *Hypochaeris radicata*

Species	Family	Floral shape	Flower tube length (mm)
Adesmia boronioides J. D. Hooker	Fabaceae	Papilionate	7-10
Azara lanceolata J. D. Hooker	Flacourtiaceae	Brush	0
Berberis empetrifolia Lam.	Berberidaceae	Concave disc	0
Buddleja globosa Hope	Buddlejaceae	Bell-shaped	3.5-6
Cerastium arvense L.	Caryophyllaceae	Concave disc	0
Carduus sp.	Asteraceae	Tubular	12
Discaria chacaye (G. Don.) Tortosa	Rhamnaceae	Tubular	1
Escallonia virgata (Ruiz et Pavón) Persoon	Escalloniaceae	Flat disc	0
Embothrium coccineum J.R. & G. Forster	Proteaceae	Tubular	14†
Gaultheria phillyreaefolia (Pers.) Sleumer	Ericaceae	Urceolate	4
Hypochaeris radicata L.	Asteraceae	Tubular	10

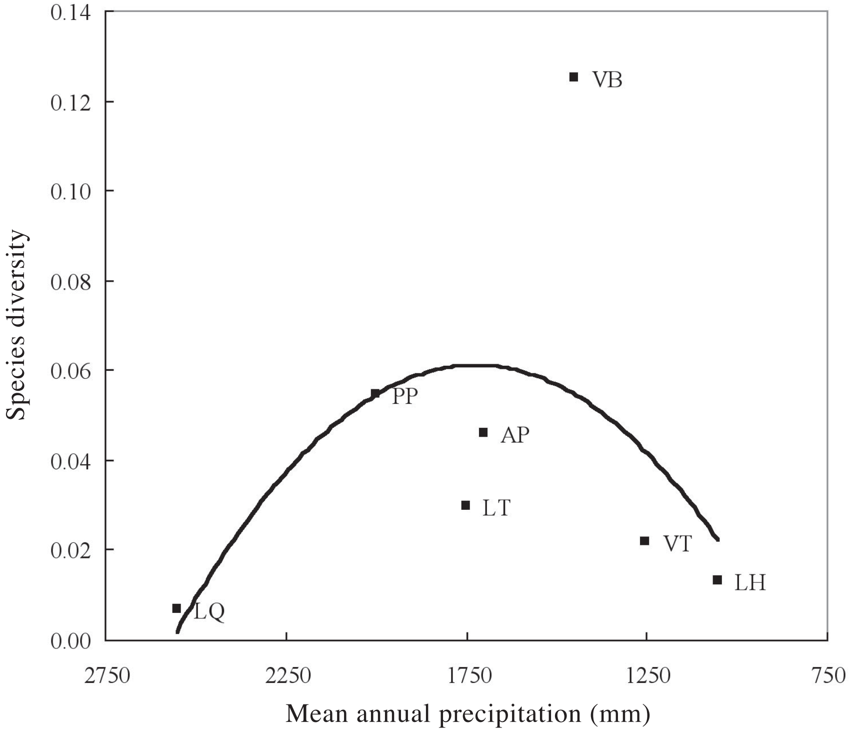


Fig. 1: Diversity (γ) of *Trichophthalma* species along a rainfall gradient in north west Patagonia, Argentina. See Table 2 and its references for further details on source of the data. From left to right, sites are ordered by decreasing mean annual precipitation (Pre) to better reflect their actual geographic position (Pre decreases to the east). In addition to our own data, we only used registers of which sampling effort employed was provided (Vázquez & Simberloff 2002). Field data on species richness was standardized for sampling effort at each site. A second-degree polynomial function was fitted to the transformed data ($\gamma = 9 \times 10^{-8}\,Pre^2 + 0.0003\,Pre - 0.1955$, $R^2 = 0.314$).

Diversidad (γ) de especies *Trichophthalma* a lo largo de un gradiente de humedad en el noroeste de la Patagonia, Argentina. Ver la Tabla 2 y sus referencias para más detalles sobre la fuente de los datos. De izquierda a derecha los sitios están ordenados por precipitación media anual (Pre) decreciente para reflejar mejor su posición geográfica real (Pre decrece hacia el este). Además de los datos propios, solo se utilizaron registros que proporcionaran el esfuerzo de muestreo empleado (Vázquez & Simberloff 2002). La riqueza registrada a campo fue estandarizada por el esfuerzo de muestreo en cada sitio (Tabla 1). Se ajustó a los datos transformados una función polinomial de segundo grado ($\gamma = 9 \times 10^{-8}\,Pre^2 + 0.0003\,Pre - 0.1955$, $R^2 = 0.314$).

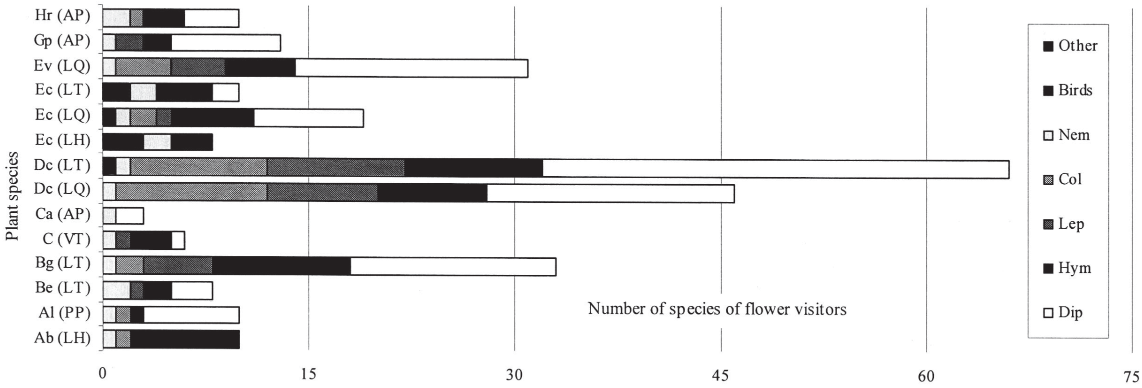
DISCUSSION

Our study adds a considerable amount of information on the ecology of Nemestrinidae at the temperate forests of southern South America on the Argentinean side of the Andes. Together with new records for Argentina of already described species and the finding of two undescribed taxa, we reported several pollination interactions with the local flora.

There are a few previous records of tangle-veined flies visiting flowers of the local Patagonian flora (Edwards 1930, Stuardo 1939, Riveros et al. 1991, Vázquez & Simberloff 2003, 2004, Smith-Ramírez et al. 2005). However, these could be only partially incorporated into our analysis mainly because of lack of detail on sampling effort employed and on the identity of the plant and animal species involved (Vázquez & Simberloff 2002, 2003, 2004 constitutes an exception on this regard) or because they were made too far from our study sites (e.g., Smith-Ramírez et al. 2005). Considering community level data available for six of our sites (Devoto et al. 2005, no data available for VB and C), Nemestrinidae visited on average 10.9 % (range = 3.5-17.4) of all the plant species that received visits from any pollinator taxa during fieldwork. Comparable values reported for the region of 12.9 % (of 31 plant species at Puyehue, Chile, Riveros et al. 1991), 3.8 % (of 26 plant species at Chiloé, Chile, Smith-Ramírez et al. 2005) and

14.2 % (average from eight communities of 15 plants each at Nahuel Huapi, Argentina, Vázquez & Simberloff 2002), suggest Nemestrinidae are possible pollinators of a substantial portion of the anthophilous plant species of the temperate forests of southern South America, although further research on their effectiveness as pollinators is required to confirm this.

This study proves valuable in light of the present scarcity of information on the ecology of the Patagonian species of Nemestrinidae. Throughout eight sites, we recorded nine species belonging to the genus *Trichophthalma* visiting flowers of the local flora. Of the nine species, three were unrecorded for Argentina (*T. andina*, *T. porteri* and *T. niveibarbis*) and two other (represented by three captured individuals that did not fit into the available keys for the genus) are here considered as yet undescribed taxa. *Trichophthalma nubipennis* had been reported for Argentina but is here first recorded as visitor to the local flora (Table 3). Overall, we found in the field 7 of the 21 species of *Trichophthalma* described for southern South America (Argentina, Chile and Uruguay; Bernardi 1973, 1975), besides the two undescribed species mentioned above.



	Ab (LH)	Al (PP)	Be (LT)	Bg (LT)	C (VT)	Ca (AP)	Dc (LQ)	Dc (LT)	Ec (LH)	Ec (LQ)	Ec (LT)	Ev (LQ)	Gp (AP)	Hr (AP)
Dip		7	3	15	1	2	18	34		8	2	17	8	4
Hym	8	1	2	10	3		8	10	3	6	4	5	2	3
Lep			1	5	1		8	10		1		4	2	
Col	1	1		2			11	10		2		4		1
Nem	1	1	2	1	1	1	1	1	2	1	2	1	1	2
Birds									3	1	2			
Other								1						

Fig. 2: Composition of the complete flower-visitor assemblage of plants visited by tangle-veined flies in NW Patagonia, Argentina. The numbers in the table indicate the total amount of species of each order recorded and they correspond to the lengths of the bars above. Plant species: Hr = *Hypochaeris radicata*, Gp = *Gaultheria phillyreaefolia*, Ec = *Embothrium coccineum*, Ev = *Escallonia virgata*, Dc = *Discaria chacaye*, Be = *Berberis empetrifolia*, Bg = *Buddleja globosa*, Ca = *Cerastium arvense*, C = *Carduus* sp., Al = *Azara lanceolada*, Ab = *Adesmia boronioides*. The site where interactions were recorded is indicated between brackets beside the plant species. AP = Arroyo Pedregoso, LQ = Lago Queñi, LT = Lago Tromen, LH = Lago Huechulafquen, VT = Villa Traful, PP = Paso Puyehue.

Composición del elenco completo de visitantes florales de las plantas visitadas por nemestrínidos en el noroeste de la Patagonia, Argentina. Los números en la tabla inferior indican la cantidad total de especies de cada orden registradas y se corresponden con la longitud de las barras superiores. Especies vegetales: Hr = *Hypochaeris radicata*, Gp = *Gaultheria phillyreaefolia*, Ec = *Embothrium coccineum*, Ev = *Escallonia virgata*, Dc = *Discaria chacaye*, Be = *Berberis empetrifolia*, Bg = *Buddleja globosa*, Ca = *Cerastium arvense*, C = *Carduus* sp., Al = *Azara lanceolada*, Ab = *Adesmia boronioides*. Los sitios en que las interacciones fueron registradas se indican entre paréntesis a continuación del nombre de las plantas. AP = Arroyo Pedregoso, LQ = Lago Queñi, LT = Lago Tromen, LH = Lago Huechulafquen, VT = Villa Traful, PP = Paso Puyehue.

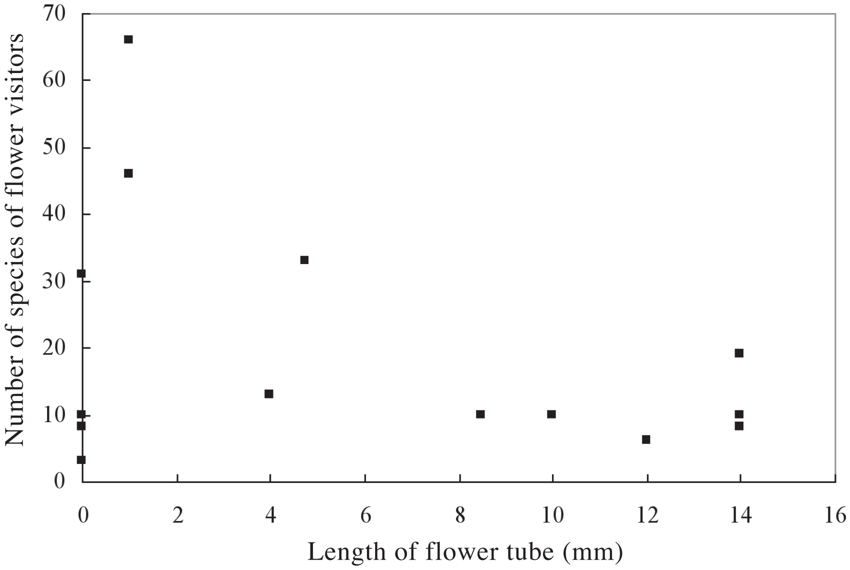


Fig. 3: Relationship between the length of the flower tube of plant species visited by tangle-veined flies (data from Table 4) and their total number of species of flower visitors in north west Patagonia, Argentina.

Relación entre la longitud del tubo floral de las especies de plantas visitadas por nemestrínidos (datos de la Tabla 4) y su número total de especies de visitantes florales en el noroeste de la Patagonia, Argentina.

Most notably, it is reported for the first time in South America (second time worldwide, Manning 2004) a pollination interaction between tangle-veined flies and a Proteaceaous plant (*T. niveibarbis* and *T. philippii* pollinating *E. coccineum*, Table 3). This is interesting in the light of the common Gondwanian origin and present Austral distribution of both families, which suggests an ancient origin for this mutualism (Montaldo et al. 1999)[1]. To our knowledge, this is also the first report of pollination interactions between Nemestrinidae and two other plant genera with Gondwanian distribution (*Discaria* and *Gaultheria*, Table 3).

The pattern of species richness of Nemestrinidae along the precipitation gradient roughly followed a bell-shaped distribution, with highest abundances achieved at intermediate points of the gradient (~1,700 mm) and decreasing towards both its driest and wettest ends (Fig. 1). The complete absence of Nemestrinidae at the driest sites of the gradient is in accordance with the regional (and global) pattern followed in general by all Diptera, whose diversity shows a marked decrease in dryer environments (Devoto et al. 2005). However, it should be considered that *Trichophthalma* species were absent from the driest sites because the plant species they feed on at other sites were not present there. While this may be true for four species (*T. amoena*, *T. porteri*, *T. nubipennis* and *T.* sp. 2) the absence of the remaining five species cannot be attributed to this cause; i.e. in the drier sites there are plant species which *Trichophthalma* spp. visited somewhere else in the region (e.g., *E. coccineum* for *T. philippii* and *T. niveibarbis*). Moreover, at the drier places two of the absent *Trichophthalma* species would have alternative plants to feed on which are congeneric with their original host plants (e.g., *Discaria articulata* for *T. porteri*).

Among *Trichophthalma* species of the eastern slope of the Andes, we found a very weak correspondence between plant distribution and their Nemestrinidae visitors. Our data (Table 2) shows that the longitudinal distribution of a given species of tangle-veined flies can sometimes encompass a marked

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[1] MONTALDO NH, GG ROITMAN, M DEVOTO & D MEDAN (1999) Biología reproductiva de *Embothrium coccineum* (Proteaceae) en la Provincia de Neuquén. XIX Reunión Argentina de Ecología, Tucumán, Libro resúmenes: 106.

change in rainfall and in the accompanying vegetation (e.g., rainfall measures on the western range limits of *T. philippii, T. jaffueli* and *T. amoena* double those of the eastern limits).

Nemestrinidae of southern Africa

In southern Africa pollination by Nemestrinidae is well-documented (Marloth 1908, Vogel 1954, Johnson & Steiner 1995). Ten species of Nemestrinidae belonging to the genera *Moegistorhynchus*, *Prosoeca* and *Stenobasipteron* have been reported to participate in highly specialized pollination interactions with an exclusive guild of species with long floral tubes (Manning & Goldblatt 1996, 1997, Goldblatt & Manning 2000, Manning 2004).

In comparison, the Patagonian Nemestrinidae result much less specialized since they share their floral resources with a diverse and little specialized fauna (Fig. 2 and Table 3). A cause for this can be envisioned in the morphology of the flowers on which tangle-veined flies feed in Patagonia: their open or short-tubed flowers do not hinder the access of other species to the floral resources (Table 4), unlike the long-tubed African guild (Goldblatt & Manning 2000). However, in Patagonia the species with longer flower tubes seem to have a lower maximum number of flower visitors (i.e. they are more specialized) than the shorter-tubed species, although this trend is not significant ($P = 0.06$, $F_{1,6} = 4.90$, $R^2 = 0.44$; Fig. 3). On the other side, there is a notorious contrast between the morphology of African Nemestrinidae, which have proboscides at least 15 mm long (as described by Goldblatt & Manning 2000), and the Patagonian species of Nemestrinidae that we captured whose proboscides range between 3.7 and 8.8 mm in length (Table 3).

Nemestrinidae of eastern Australia

Nemestrinidae are also remarkably abundant in Australia where *Trichophthalma* is the dominant genus (45 species, Bernardi 1975). At the montane rainforests of eastern Australia there are at least 19 species belonging to this genus (Williams 2002). These sites constitute a relict environment closely resembling the temperate forests of southern South America. Unfortunately, there seems to be a lack of studies on the ecology of tangle-veined flies, including *Trichophthalma*, in Australia. Further research there is likely to allow for interesting comparisons with the "South American connection" of the family.

We hope that this paper will encourage further research on Nemestrinidae and their associated flowers. For example, the co-existence of this ancient group with more 'modern' hummingbirds in the visitor assemblage of the 'ornithophilous' (yet also Gondwanian as Nemestrinidae) *E. coccineum* is an interesting scenario that may allow for the testing of hypothesis by evolutionary biologists (Thompson 1998, Gomulkiewicz et al. 2003). Overall, much remains to be understood about the distribution, floral associations and general ecology of the species of Nemestrinidae of southern South America.

ACKNOWLEDGEMENTS

We thank A. Basilio, M. Chamer, G. Gleiser, V. Medan, N. H. Montaldo, G. G. Roitman, L. Rossi and J. P. Torretta for their help in the field and laboratory. An earlier version of this paper benefited from comments by two anonymous reviewers. This work was financed by grants from UBACyT and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). A graduate research scholarship granted by the University of Buenos Aires to M. D. is also gratefully acknowledged. Diego Medan is associated to the CONICET.

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Editor Asociado: Audrey Grez
Recibido el 7 de abril de 2005; aceptado el 8 de junio de 2005