"Jejenes" (Diptera: Simuliidae) of Nahuel Huapi National Park, Patagonia, Argentina: Preliminary results

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"Jejenes" (Diptera: Simuliidae) del Parque Nacional Nahuel Huapi, Patagonia, Argentina: Resultados preliminares

■ **ABSTRACT.** The Simuliidae is a family of Diptera with approximately 2072 described species worldwide. The females of the majority of the species feed from vertebrates' blood, which makes them a significant plague that affects both men as well as cattle, birds, and other vertebrates. The objective of this paper is to create an inventory of Simuliidae and to reveal certain aspects of the biology and distribution of this family of aquatic insects in the Nahuel Huapi National Park. Moreover, information on the zoogeography of Simuliidae in Patagonia is provided. Five genera, 3 subgenera and 32 species Simuliidae are recorded from Patagonia: *Cnesia* (three spp.), *Cnesiamima* (one sp.), *Gigantodax* (14 spp.), *Paraustrosimulium* (one sp.), *Simulium* (*Ectemnaspis*) (one sp.), *S.* (*Psaroniocompsa*) (one sp.) and *S.* (*Pternaspatha*) (11 spp.), At present, we have collected all five genera, one subgenus of *Simulium* (*Pternaspatha*), and 19 species of Simuliidae in the park, which amounts to 57% of the Simuliidae fauna in this area. Puerto Blest, a characteristic area of the High-Andean phytogeographical province (humid forest), showed the highest diversity of Simuliidae.

KEY WORDS. Jejenes. Simuliidae. Nahuel Huapi National Park. Patagonia.

■ **RESUMEN.** Los simúlidos pertenecen a una familia de Diptera (Simuliidae) con alrededor de 2.072 especies descritas a nivel mundial. Las hembras de la mayoría de las especies se alimentan con sangre de vertebrados, lo cual las convierte en importantes plagas que afectan tanto al hombre como al ganado, aves y otros vertebrados. Los objetivos de este trabajo son llevar a cabo un inventario de Simuliidae y dar a conocer algunos aspectos de la biología y la distribución de esta familia de insectos acuáticos en el Parque Nacional Nahuel Huapi, Argentina. Además, se proporciona información sobre la biogeografía de Simuliidae en la Patagonia. Cinco géneros, un subgénero y 32 especies de simúlidos han sido registrados para Patagonia: *Cnesia* (3 spp.), *Cnesiamima* (1 sp.), *Gigantodax* (14 spp.), *Paraustrosimulium* (1 sp.), *Simulium* (*Ectemnaspis* (1 sp.), *S.* (*Psaroniocompsa*) (1 sp.) y *Simulium* (*Pternaspatha*) (11 spp.). Hasta el presente, se han colectado los cinco géneros, un subgénero *(Pternaspatha*) y 19 especies de Simuliidae en el PNNH, lo

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cual representa el 57% de la fauna de Simuliidae en esta área. La mayor diversidad de Simuliidae se encontró en Puerto Blest, zona característica del bosque de la provincia fitogeográfica Alto-Andina.

PALABRAS CLAVE. Jejenes. Simuliidae. Parque Nacional Nahuel Huapi. Patagonia.

INTRODUCTION

The Simuliidae ("blackflies" or "jejenes" as they are commonly known) is a family of Diptera containing 2072 formally named species worldwide (Adler & Crosskey, 2008; 2009) of which 12 genera and approximately 359 species are found in the Neotropical Region (Coscarón & Coscarón-Arias, 2007). The female in the majority of species requires a blood meal for egg maturation and it is this requirement that makes species in this family important as biting pests and in the transmission of parasites in the blood and skin in both man and warm blooded animals (Crosskey, 1990). The most important parasite transmitted by simuliid blackflies is the nematode *Onchocerca volvulus* (Leuckart), which is responsible for the human disease known as "onchocerciasis or river blindness". At present, 37 million people are estimated to carry *O. volvulus*, with 90 million being at risk in Africa (Basánez *et al.*, 2006). They are also responsible for the transmission to humans of the less pathogenic nematode *Manzonella ozzardii* Manson (Shelley *&* Coscarón, 2001). Blackflies or jejenes are also well-known vectors of haematozoa parasites (*e.g, Leucocytozoon* Danilewsky) and arboviruses to a variety of both domesticated and wild animals. Massive blackflies attacks have been known to cause mortality in cattle, pigs, and sheep, which is attributed to toxic shock from the salivary injections during their bite (Currie & Adler, 2008). Other economic impacts caused by blackflies are weight loss, reduced milk production, malnutrition and impotence (Adler *et al.*, 2004; Currie & Adler, 2008).

Apart from their medical importance, the fact that all simuliid species breed in running water makes the family economically important in terms of environmental monitoring of freshwater contamination, particularly because immature stages (larvae and pupae) are highly susceptible to both organic and inorganic pollution (*e.g.* effluent from sugar mills, slurry from farms, insecticide and fertiliser run off from farms and plantations) (Anthony Shelley, pers. comm.). In addition, blackflies are key organisms in aquatic ecosystems as they are an important food source for many vertebrates (*e.g.*, salmonids) and invertebrates (*e.g.*, Plecoptera) (Currie & Adler, 2008). Furthermore, the filter-feeding of the larva plays an important role in stream ecologies due to their ability to remove particulates and dissolved organic matter from the water column and egested it as nutritious faecal pellets (Currie & Adler, 2008; Malmquivist *et al.*, 2001; 2004).

In Argentina, the jejenes fauna or Paquitas is relatively well known mainly due to the efforts of Coscarón (1987; 1991), Coscarón & Coscarón-Arias (2007), Coscarón & Wygodzinsky (1972) and Wygodzinsky & Coscarón (1967; 1973a, b; 1989). Studies of Simuliidae of Patagonia were first initiated by Edwards (1931) and Wygodzinsky (1953, 1958). In this area the Simuliidae are renowned for the attacks they inflict on people and equines, and the fauna shows a high level of endemicity (Coscarón-Arias, 2002). Nonetheless, the Simuliidae fauna within the National Park Nahuel Huapi (NHNP) is still poorly known. The park comprises a wide variety of habitats and is considered a classical representation of the zoogeographical region of Patagonia. This paper augments the preliminary results obtained for the family Simuliidae, which

has been included as a target group in a multidisciplinary project funded by the Darwin Initiative, UK. The projects' basic aim was to undertake baseline research on the wetland invertebrate fauna of northern Patagonia. The distribution and biology of species of Simuliidae in the park is also reviewed.

Previous work on the Simuliidae fauna of Patagonia. The first studies of Simuliidae in Patagonia date back to Blanchard (1852) and Bigot (1888). Philippi (1865) also dealt with the fauna of Chile, which is biogeographically related to Argentina. In these papers the latter authors briefly described four species. The first comprehensive study on Simuliidae in Patagonia is the revision of Edwards (1931). Edwards described nine species new to science, commented on the species previously described by Blanchard, Bigot and Philippi [he also dealt with *S. moorei* (Silva Figueroa), now a synonym of *Paraustrosimulium anthracinum* (Bigot), and produced one of the first supraspecific classification systems in Simuliidae. It is worth mentioning a rather neglected paper by Edwards in 1927, in which he gave an account of his field trip from the city of Bariloche (Argentina) to the town of Los Andes (Chile), and provided a detailed insight into the flora and fauna of the region at that time. Enderlein (1925, 1934) also examined material of some species of Simuliidae from South America, and erected several new genera and species of which the genera *Cnesia* Enderlein (for *C. dissimilis* (Edwards), as *S. gynandrum* (Edwards), the type species) and *Gigantodax* Enderlein (type species *G. bolivianus* Enderlein) are still valid.

Impetus for the study of Simuliidae in Patagonia was given by Coscarón & Wygodzinsky (1962; 1972), Wygodzinsky & Coscarón (1962; 1967) and Wygodzinsky (1953; 1958). The former paper (Coscarón & Wygodzinsky, 1962) was the first publication in which the Simuliidae were treated in a cladistic framework, although no phylogenetic trees were provided. Subsequently, the latter authors produced a series of publications in which they described numerous new species and/or redescribed other taxa poorly known in Argentina (e.g., Coscarón, 1985; Wygodzinsky & Coscarón, 1967; 1973a-b; 1989). The revision of Wygodzinsky & Coscarón (1973a) still remains the most complete study for the New World "Prosimulinii". In the latter revision, the authors erected the genera *Araucnephia* Wygodzinsky & Coscarón, *Araucnephioides* Wygodzinsky & Coscarón, *Cnesia* and *Mayacnephia* Wygodzinsky & Coscarón, and also discussed the taxonomic position of the genera *Gigantodax*, *Lutzsimulium* D'Andretta & D'Andretta, *Paraustrosimulium* Wygodzinsky & Coscarón, and *Tlalocomyia* Wygodzinsky & Díaz Nájera [all these genera now belong to the tribe Simuliini, and *Mayacnephia* is a synonym of *Tlalocomyia*; see Adler & Crosskey, 2008]. The reviews of Dumbleton (1963) and Mackerras & Mackerras (1948) on the Australian Simuliidae fauna and the genus *Austrosimulium* Tonnoir, are pivotal in our understanding of the zoogeographical relationships of the Subantarctic simuliid fauna. The taxonomic position of *Paraustrosimulium* was discussed in comparison to that of *Austrosimulium* (Smart, 1945; Stone, 1963).

The control of the Simuliidae in Patagonia has already been reviewed by Coscarón-Arias (1989; 1998a), who also studied the cytotaxonomy of three species of the genus *Gigantodax*: *G. chilensis* (Philippi), *G. fulvescens* (Blanchard), and *G. marginalis* (Edwards), and of *Cnesia dissimilis* in the Lanin National Park (Coscarón-Arias, 1998b). Coscarón-Arias (2000) also studied the cytotaxonomy of *Simulium limay* Wygodzinsky, a species also found in Nahuel Huapi National Park. In 2002, Coscarón-Arias reviewed all species found in Patagonia, and provided a checklist together with an identification key to separate all genera and species based on immature stages. Information on the taxonomy, biology and distribution of all Simuliidae found in Patagonia may be found in Coscarón (1991) and, more recently, in Coscarón & Coscarón-Arias (2007), except for the genus *Gigantodax*. The latter can be found in Wygodzinsky & Coscarón (1989).

Coscarón-Arias (2002) recorded five genera (*Cnesia*, *Cnesiamima* Wygodzinsky & Coscarón, *Gigantodax*, *Paraustrosimulium*, and *Simulium* Latreille), three subgenera of *Simulium* (*Ectemnaspis* Enderlein, *Psaroniocompsa* Enderlein, and *Pternaspatha* Enderlein) and 34 species of Simuliidae from Patagonia. However, this number has now been reduced to 32 due the recent synonymy of *Simulium bonaerense* Coscarón & Wygodzinsky with *Simulium jujuyense* (Paterson & Shannon) by Hernández *et al*. (2007), and *Simulium walterwittmeri* Wygodzinsky with *S. limay* by Coscarón & Coscarón Arias (2007).

MATERIAL AND METHODS

The NHNP and the National Reserve Nahuel Huapi are located between latitude 40° 08′ and 41° 35′ south and longitude 71° 02′ and 71° 57′ west in Argentina. Brooks *et al.* (2009) provided the characterisation of climate, drainage, geology, topography, and vegetation following the publications of Martin & Mermoz (2005) and Monjeau (2006). Therefore, the reader should consult the latter publications for further details.

Collecting field trips were made in the summer season (October to February) in 2006-2007 and 2007-2008 (Fig. 1). Numerous running water courses were sampled for Simuliidae in different vegetation zones of the NHNP. The collecting, rearing and dissection techniques, and terminology used are those detailed in Shelley *et al.* (1989; 1997), Hernández & Shelley (2005) and Hernández *et al.* (2007) [see also "Systematics and Taxonomy of Blackflies, www.blackflies.info" by Hernández, 2007]. Adults collected in Malaise trap and larvae obtained by kick-sampling techniques were also examined for this study. We have followed the classification system of Adler & Crosskey (2008) for the generic and subgeneric arrangements in this paper. All specimens collected during the course of this project are housed at The Natural History Museum, London, UK (BMNH), and Museo La Plata, Argentina (MLP). Further material has been examined from Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (NMHU), National Museum of Natural History, Washington, USA (USNM), and the Canadian National Collection, Ottawa, Canada (CNC).

RESULTS AND DISCUSSION

Coscarón-Arias (2002) and Coscarón & Coscarón-Arias (2007) recorded five genera and 32 species of Simuliidae for Patagonia (see Hernández *et al.*, 2007). At present, we have collected all five genera (*Cnesia*, *Cnesiamima*, *Gigantodax*, *Paraustrasimulium*, and *Simulium*), a subgenus of *Simulium* (*Pternaspatha*) and 19 species in the NHNP (Table I), which amount to 57% of the Simuliidae fauna in Argentina. We have failed to find *Simulium jujuyense* (as *S. bonaerense*) and *S. wolffhuegeli* (Enderlein) in the park. However, this is hardly surprising as both species are characteristic of hotter climate towards the northern areas of Rio Negro Province, and the phytogeographical provinces of Monte, Espinal and Pampeana (Roig-Juñent & Coscarón, 2001). In addition, *Gigantodax trifidus* Wygodzinsky & Coscarón, *Gigantodax minor* Wygodzinsky & Coscarón, and seven species of the subgenus *Pternaspatha* have also not been collected in the park (see Table I), which highlights the need to continue the survey of Simuliidae in this area. A field trip was made in November 2008 to collect in new water courses to the south of the park and localities near Bariloche, especially Lake Guillelmo, from where Edwards (1931) described several species of *Gigantodax.*

The immature stages (larvae and pupae) of most of the species of Simuliidae were found in cold, clear, fast flowing water streams in NHNP, except for *Paraustrosimulium anthracinum* that was collected in slow flowing, murky water stream in Isla Victoria. The area of the Valdivian forest (Puerto Blest) showed a higher diversity of Simuliidae, with *Gigantoda*x being the most frequent genus. *Cnesia dissimilis* and *Simulium* (*Pternaspatha*) *nemorale* Edwards are the

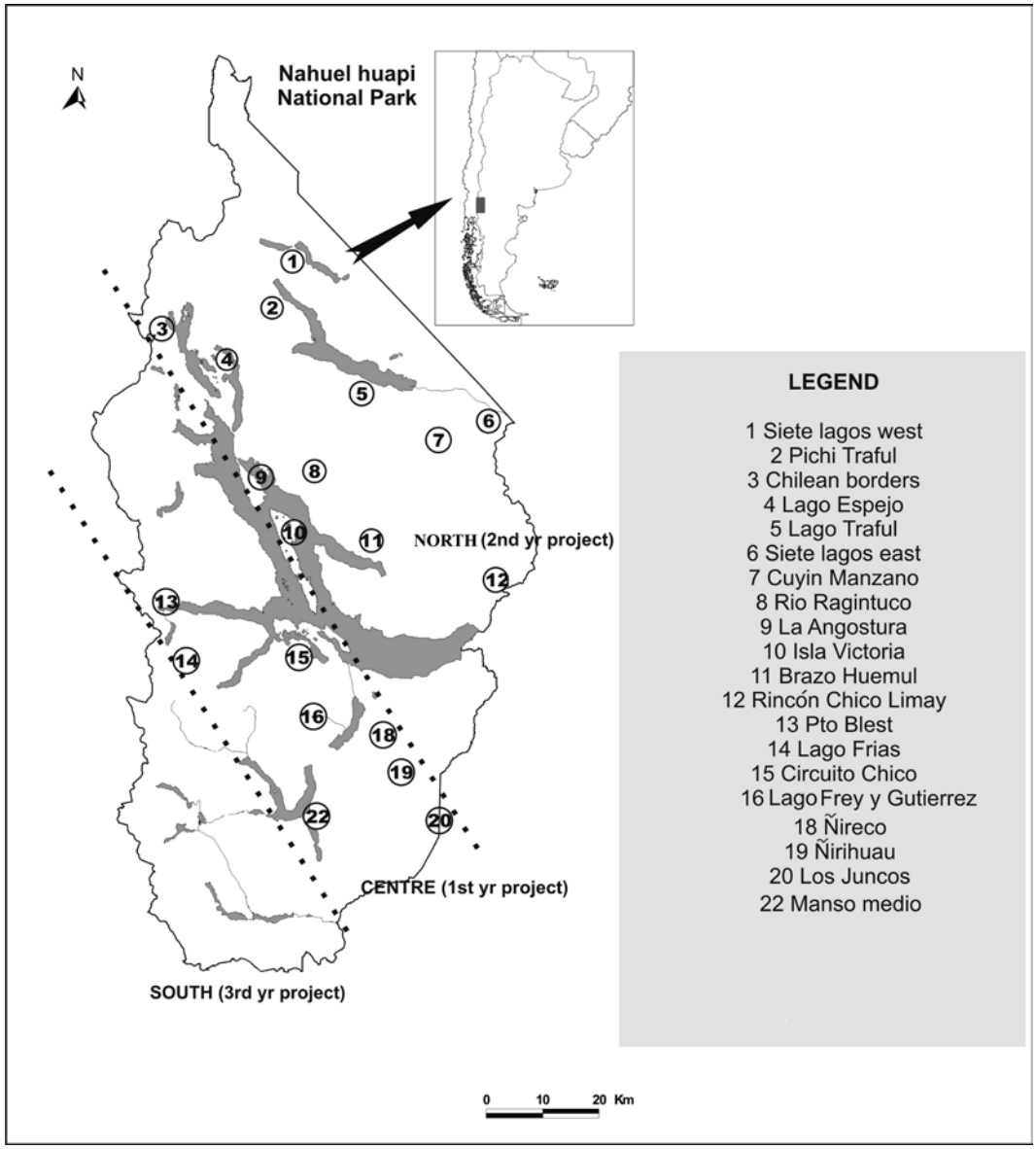

Fig. 1. Main collecting areas for Simuliidae in Nahuel Huapi National Park, northern Patagonia, Argentina, in the north and central parts of the park.

most abundant species in the park appearing in more than 50% of the total sites sampled up to March 2008 (184 collecting sites). They have a wider distribution in the park extending from the *Nothofagus* Blume forests to the Low Steppe and urban areas nearby. The genus *Gigantodax* is the most diverse in the park with 11 species recorded in this area (see Table I). Two species were collected biting humans in the park, *P. anthracinum* and *S. nemorale*. The former species (as *S. moorei*) was recorded as man-biting in the Taitao Peninsula in Chile by Silva Figueroa (1917), while Edwards (1931) recorded "the painful bite causing swelling of the hand". However, Wygodzinsky & Coscarón (1973a) stated that they had never recorded anthropophilous behaviour in this species during their studies in Patagonia. We only collected a few females of *P. anthracinum*

TABLE I. Checklist of Simuliidae recorded for Patagonia by Coscarón-Arias (2002) and Coscarón & Coscarón-Arias (2007) and those recorded at the Nahuel Huapi National Park, Argentina in this study.

Genus/Species	Coscarón-Arias (2002) and Coscarón & Coscarón-Arias (2007)	This study
Cnesia dissimilis (Edwards, 1931)	X	X
C. pusilla Wygodzinsky & Coscarón, 1973	X	X?
C. ornata Wygodzinsky & Coscarón, 1973	X	X
Cnesiamima atroparva (Edwards, 1931)	X	X
Gigantodax antarcticus (Bigot, 1888)	X	X
G. araucanius (Edwards, 1931)	X	X
G. brophyi (Edwards, 1931)	X	X
G. carmenae Wygodzinsky & Coscarón, 1989	X	X
G. dryadicaudicis Wygodzinsky & Coscarón, 1989	X	X
G. chilensis (Philippi, 1865)	X	X
G. femineus (Edwards, 1931)	X	X
G. fulvescens (Blanchard, 1852)	X	X
G. igniculus Coscarón & Wygodzinsky, 1962	X	X
G. marginalis (Edwards, 1931)	X	X
G. minor Wygodzinsky & Coscarón, 1989	X	—
G. rufidulus Wygodzinsky & Coscarón, 1989	X	X
G. rufescens (Edwards, 1931)	X	X
G. shannoni (Edwards, 1931)	X	X
G. trifidus Wygodzinsky & Coscarón, 1989	X	—
Paraustrosimulium anthracinum (Bigot, 1888)	X	X
Simulium (Pternaspatha) annulatum Philippi, 1865	X	X
S. (*Pter.*) *barbatipes* (Enderlein, 1934)	X	—
S. (*Pter.*) *caprii* Wygodzinsky & Coscarón, 1967	X	—
S. (*Pter.*) *diamantinum* Coscarón & Coscarón-Arias, 1996	X	—
S. (*Pter.*) *limay* Wygodzinsky, 1958	X	X
S. (Pter.) *nemorale* (Edwards, 1931)	X	X
S. (*Pter.*) *nigristrigatum* (Enderlein, 1930)	X	—
S. (*Pter.*) *pichii* Wygodzinsky & Coscarón, 1967	X	—
S. (*Pter.*) *simile* Silva Figueroa, 1917	X	—
S. (*Pter.*) *stelliferum* Coscarón & Wygodzinsky, 1972	X	—
S. (*Pter.*) *strigidorsum* (Enderlein, 1934)	X	—
S. (*Psaroniocompsa*) *jujuyense* (Paterson & Shannon, 1927)	X	—
S. (*Psilopelmia*) *wolffhuegeli* (Enderlein, 1922)	X	—
TOTAL	32	19

in the Challhuaco area, although they did not display a marked anthropophily. On the contrary, *S. nemorale* was very common and highly anthropophilic, biting voraciously in Puerto Blest area, Challhuaco, and the transition forests (ecotone) at Rio Nirihuau.

In general, the Simuliidae fauna of the NHNP and Patagonia shows a high degree of endemism with *Cnesia*, *Cnesiamima, Paraustrosimulium* (together with the Chilean taxa *Araucnephia, Araucniphiodes*) only found in this region (Coscarón & Coscarón-Arias, 1995). The genus *Gigantodax* is the only taxon that is widely distributed from south USA, along the Mesoamerican mountain range, northern South America (Venezuela) to Tierra del Fuego (Coscarón & Miranda-Esquivel, 1998; Pinto-Sánchez *et al.*, 2005; Wygodzinsky & Coscarón, 1989). The subgenus *Pternaspatha* is highly

specious in Patagonia and the Andes, with a single species (*Simulium cotopaxi* Wygodzinsky & Coscarón) recorded from Ecuador between 3000-4000m of altitude (Wygodzinsky & Coscarón, 1979; see also Coscarón & Coscarón-Arias, 1996a-b). The biogeography and distribution of the Simuliidae in Patagonia and the Neotropical Region have been reviewed by several authors (e.g., Coscarón & Coscarón-Arias, 1995; Roig-Juñent & Coscarón, 2001), who postulate that the existing fauna suffered a main vicariant event correlated with marine introgression. These authors also stated that the close relationship of Simuliidae with taxa from other continents showed that this family was widely distributed in Gondwana before its fragmentation. Phylogenetical analysis have revealed that the Patagonian Simuliidae fauna is more closely related to the taxa found in the temperate forests of New Zealand, Australia, and areas of southeast Asia (e.g., Gil-Azevedo & Maia-Herzog, 2007; Roig-Juñent & Coscarón, 2001; Wygodzinsky & Coscarón, 1973a-b), which are consistent with the distribution patterns in other insect groups (see detailed review in Morrone, 2006).

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LITERATURE CITED

1. ADLER, P. H. & R. W. CROSSKEY. 2009. World blackflies (Diptera: Simuliidae): a fully revised edition of the taxonomic and geographical inventory. http://entweb.clemson.edu/biomia/pdfs/ blackflyinventory.pdf. [109 pp] [last accessed 24.March.2009].
2. ADLER, P. H. & R. W. CROSSKEY. 2008. World blackflies (Diptera: Simuliidae): a fully revised edition of the taxonomic and geographical inventory. http://entweb.clemson.edu/biomia/pdfs/ blackflyinventory.pdf. [105 pp] [last accessed 5.September.2008].
3. ADLER, P. H., D. C. CURRIE & D. M. WOOD. 2004. *The black flies (Simuliidae) of North America*. Cornell University Press, Ithaca, New York.
4. BASÁNEZ, M. A., S. D. S. PIO, T. S. CHURCHER, L. P. BREITLING, M. P. LITTLE & M. BOUSSINESQ. 2006. River Blindness: A success history under threat? *PloS Medicine* 3: 1454-1460.
5. BIGOT, E. 1888. Diptères. *In*: *Mission Scientifique du Cap Horn 1882-1883*. Vol. 6, Zoologie. Gauthier-Villars et fils, Paris, 45 pp.
6. BLANCHARD, E. 1852. Fauna chilena: Diptera. *In*: Gay, C. (ed.), *Historia Física y Política de Chile. Zoología*, vol. 7, Imprenta de Maulde et Renou, Paris, 353 pp.
7. BROOKS, S. J., L. M. HERNÁNDEZ, J. MASSAFERRO, G. R. SPINELLI & M. PENN. 2009. Capacity building for freshwater insect studies in northern Patagonia, Argentina. *Rev. Soc. Entomol. Argent.* 68 (1-2) (This issue).
8. COSCARÓN, S. 1985. Sobre la larva de *Cnesiamina atroparva* Edwards y su significado para interpretar las relaciones filogenéticas de los simúlidos notogeicos (Diptera - Insecta). *Bol. Soc. Biol. Concepción* 56: 67-70.
9. COSCARÓN, S. 1987. *El género Simulium Latreille en la Región Neotropical: Análisis de los grupos supraspecíficos, especies que los integran y distribución geográfica (Simuliidae, Diptera)*. Museu Paraense Emílio Goeldi, 112 pp.
10. COSCARÓN, S. 1991. *Fauna de Agua Dulce de la República Argentina. 38. Insecta, Diptera. 2. Simuliidae.* Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires.
11. COSCARÓN-ARIAS, C. L. 1989. Estudios citotaxonómicos y bioecológicos de Simuliidae (Diptera, Insecta) de Argentina. Tesis doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata, 293 pp.
12. COSCARÓN-ARIAS, C. L. 1998a. Los Simúliudos y su control en el Valle del río Negro y Neuquén. *Rev. Soc. Entomol. Argent.* 58: 276-281.
13. COSCARÓN-ARIAS, C. L. 1998b. The polyteme chromosomes of *Cnesia dissimilis* (Edwards) and three species of *Gigantodax* Enderlein (Diptera: Simuliidae) from Lanin National Park (Argentina). *Mem. Inst. Oswaldo Cruz* 93: 445-458.
14. COSCARÓN-ARIAS, C. L. 2000. The salivary gland chromosomes of the black fly *Simulium (Pternaspatha) limay* (Diptera: Simuliidae) from Argentina. *Rev. Colomb. Entomol.* 26: 137-143.
15. COSCARÓN-ARIAS, C. L. 2002. Los simúlidos de Patagonia (Simuliidae, Diptera, Insecta). *In*: O.D. Salomón (Comp.). *Actualizaciones en Antropología Sanitaria Argentina. Serie de Enfermedades Transmisibles, Publicación Monográfica 2,* Fundación Mundo Sano, Buenos Aires.
16. COSCARÓN, S. & C. L. COSCARÓN-ARIAS. 1995. Distribution of Neotropical Simuliidae (Insecta, Diptera) and its areas of endemism. *Rev. Acad. Colomb. Cien.* 19: 717-732.

17. COSCARÓN, S. & C. L. COSCARÓN-ARIAS. 1996a. On *Simulium* (*Pternaspatha*), with description of a new species (Diptera-Simuliidae). *Mem. Inst. Oswaldo Cruz* 91: 703-710.
18. COSCARÓN, S. & C. L. COSCARÓN-ARIAS. 1996b. Análisis cladístico de *Simulium (Pternaspatha)* Enderlein con datos sobre su distribución geográfica (Diptera: Simuliidae). *Acta Ent. Chilena* 20: 71-82.
19. COSCARÓN, S. & C. L. COSCARÓN-ARIAS. 2007. Neotropical Simuliidae (Diptera: Insecta). *In*: Adis, J., J. G. Arias, G. Rueda-Delgado & K. M. Wantzen (eds.), *Aquatic Biodiversity in Latin America*, Vol 3, Pensoft, Moscow-Sofia.
20. COSCARÓN, S. & D. R. MIRANDA-ESQUIVEL. 1998. *Pedrowygomyia* a new neotropical Prosimuliini genus (Diptera: Simuliidae): *Gigantodax* s. lat. split of into two genera. *Entomol. Scand.* 29: 161-168.
21. COSCARÓN, S. & P. WYGODZINSKY. 1962. Simuliidae (Diptera-Insecta) de Tierra del Fuego, Patagonia e Isla de Juan Fernández. *Acta Zool. Lilloana* 18: 281-333.
22. COSCARÓN, S. & P. WYGODZINSKY. 1972. Taxonomy and distribution of the black fly subgenus *Simulium* (*Pternaspatha*) Enderlein (Simuliidae, Diptera, Insecta). *Bull. Am. Mus. Nat. Hist.* 147: 201-240.
23. CROSSKEY, R. W. 1990. *The Natural History of Black Flies.* John Wiley & Sons. Chichester. ix + 711pp.
24. CURRIE, D. C. & P. H. ADLER. 2008. Global diversity of black flies (Diptera: Simuliidae) in freshwater. *Hydrobiologia* 595: 469-475.
25. DUMBLETON, L. J. 1963. The classification and distribution of the Simuliidae (Diptera) with particular references to the genus *Austrosimulium. N. Z. J. Sci.* 3: 320-357.
26. EDWARDS, F. W. 1927. Insect collecting in the southern Andes. *Nat. Hist. Mag.* 1, iii-125.
27. EDWARDS, F. W. 1931. Simuliidae. *In*: Diptera of Patagonia and South Chile. *British Museum (Natural History), London* 2: 121-154.
28. ENDERLEIN, G. 1925. Weitere Beiträge zur Kenntnis der Simuliiden und Verbreitung. *Zool. Anz.* 62: 201-211.
29. ENDERLEIN, G. l934. Aussereuropäische Simuliiden aus dem Wiener Museum. *Sitz.Ges. Naturf. Freunde Berlin* 1934:190-195.
30. GIL-AZEVEDO, L. H. & M. MAIA-HERZOG. 2007. Preliminary considerations on phylogeny of Simuliidae genera from Southern Hemisphere (Insecta, Diptera). *Zootaxa* 1643: 39-68.
31. HERNÁNDEZ, L. M., A. J. SHELLEY, A. P. A. LUNA DIAS & M. MAIA-HERZOG. 2007. New specific synonymies and taxonomic notes on Neotropical black flies (Diptera: Simuliidae) belonging to the subgenera *Chirostilbia* Enderlein, *Hemicnetha* Enderlein, *Inaequalium* Coscarón & Wygodzinsky, *Psaroniocompsa* Enderlein and *Psilopelmia* Enderlein. *Zootaxa* 1506: 1-80.
32. HERNÁNDEZ, L. M. 2007. Systematics and taxonomy of blackflies. www.blackflies.info/ last accessed 28.August.2008].
33. HERNÁNDEZ, L. M. & A. J. SHELLEY. 2005. New specific synonymies and taxonomic notes on Neotropical blackflies (Diptera: Simuliidae). *Zootaxa* 853: 1-46.
34. MACKERRAS, I. M. & M. J. MACKERRAS. 1948. Revisional notes on Australasian Simuliidae (Diptera). *Proc. Linn. Soc. N. S. W.* 73: 429-439.
35. MALMQUIVIST, B., P. H. ADLER, K. KUUSELA, R. W. MERRIT & R. S. WOTTON. 2001. Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos* 92: 35-43.
36. MALMQUIVIST, B., P. H. ADLER, K. KUUSELA, R. W. MERRIT & R. S. WOOTON. 2001. Black flies in the boreal biome, key organisms in both terrestrial and aquactic environments; a review: *Ecoscience* 11: 187-200.
37. MONJEAU, A. 2006. Perfil de Área protegida Argentina, Parque Nacional Nahuel Huapi. *Parks Watch, Fortaleciendo las Áreas Protegidas para conservar la Biodiversidad* [pdf unnumbered pages report].
38. MARTIN, C. E. & M. MERMOZ. 2005. Mapa de vegetación del Parque y la Reserva Nacional Nahuel Huapi. *An. Parques Nacionales* 17: 51-62.
39. MORRONE, J. J. 2006. Biogeographic area and trasition zones od Latin America and the Caribbean Islands based on panbiogeographic and cladistic analysis of the entomofauna. *Ann. Rev. Entomol.* 51 : 467-494.
40. PHILIPPI, R. A. 1865. Aufzähliug der chileninschen Dipteren. *Verh. Zool, Bot. Ges. Wien.* 15: 595-782.
41. PINTO-SÁNCHEZ, N.R., D.R. MIRANDA-ESQUIVEL & P. MUÑOZ DE HOYOS. 2005. Phylogenetic analysis of *Gigantodax* (Diptera: Simuliidae). *Insect Syst. Evol.* 36: 1-25.
42. ROIG-JUÑENT, S. R. & S. COSCARÓN. 2001. Biogeographical history of the Neotropical and Neantarctic Simuliidae (Diptera). *Rev. Mus. Argent. Cs. Nat.* 3: 119-134.
43. SHELLEY, A.J. & S. COSCARÓN, S. 2001. Simuliid blackflies (Diptera: Simuliidae) and ceratopogonid midges (Diptera: Ceratopogonidae) as vectors of *Mansonella ozzardi* (Nematoda: Onchocercidae) in northern Argentina. *Mem. Inst. Oswaldo Cruz* 96: 451-458.
44. SHELLEY, A. J., M. ARZUBE & C. A. COUCH. 1989. The Simuliidae (Diptera) of the Santiago onchocerciasis focus in Ecuador. *Bull. Br. Mus. Nat. Hist.* (*Entomol.*) 58: 79-130.
45. SHELLEY, A. J., C. A. LOWRY, M. MAIA-HERZOG, A. P. A. LUNA DIAS & M. A. P. MORAES. 1997. Biosystematic studies on the Simuliidae (Diptera) of the Amazonia onchocerciasis focus of Brazil. *Bull. Br. Nat. Hist. Mus.* (*Entomol.*) 66: 1-121.
46. SILVA FIGUEROA, C. 1917. Dos nuevos simúlidos de Chile. *Bol. Mus. Nac. Chile* 10: 28-35.
47. SMART, J. 1945. The classification of the Simuliidae (Diptera). *Trans. R. Entomol. Soc. Lond.* 95: 463-532.
48. STONE, A. 1963. An annotated list of genus-group names in the family Simuliidae (Diptera). *U. S. Dep. Agric. Tech. Bull.* 1284: 1-28.
49. WYGODZINSKY, P. 1953. Sobre algunos simúlidos argentinos (Diptera). *Anales del Instituto de Medicina Regional, Tucumán* 3: 293-320.
50. WYGODZINSKY, P. 1958. Notas y descripciones de Simuliidae patagónicos y andinos (Diptera). *Acta Zool. Lilloana* 16: 121-148.
51. WYGODZINSKY, P. & S. COSCARÓN. 1962. On the relationships and zoogeographical significance of *Austrosimulium anthracinum* (Bigot), a black fly from southern South America (Diptera, Simuliidae). *Pac. Insects* 44: 1-244.
52. WYGODZINSKY, P. & S. COSCARÓN. 1967. A review of *Simulium* (*Pternaspatha*) Enderlein (Simulide, Diptera). *Bull. Am. Mus. Nat. Hist.* 136: 42-116.
53. WYGODZINSKY, P. & S. COSCARÓN. 1973a. A review of the Mesoamerican and South American black flies of the tribe Prosimuliini (Simuliinae, Simuliidae). *Bull. Am. Mus. Nat. Hist.* 151:129-200.
54. WYGODZINSKY, P. & S. COSCARÓN. 1973b. Notes on South American black flies of the tribe Prosimuliini (Simuliinae, Simuliidae, Diptera). *Am. Mus. Novit.* 2529: 1-9.
55. WYGODZINSKY, P. & S. COSCARÓN. 1979. Description of a black fly of the subgenus *Simulium* (*Pternaspatha*) from the High Andes of Ecuador (Diptera, Simuliidae). *Am. Mus. Novit.* 2670: 1-9.
56. WYGODZINSKY, P. & S. COSCARÓN. 1989. A revision of the blackfly genus *Gigantodax* Enderlein (Simuliidae, Diptera, Insecta). *Bull. Am. Mus. Nat. Hist.* 189: 1-269.