mutant's retinal degeneration as well as light's involvement in the give-and-take between rhabdomeres and endosomes (Chinchore *et al*., 2009). Using immunocytochemistry, they found that light exposure moves rhodopsin from rhabdomeres to Rab7-positive endosomes; an overload in endosomes caused by tenacious arrestin binding was offered as the explanation for degeneration in the norpA mutant. They also found that 13 hours of darkness allowed rhodopsin to be cleared from endosomes while newly synthesized rhodopsin transport into the rhabdomere continued.

We quantified rhodopsin using photometry of the deep pseudopupil in live white-eyed flies to replicate our earlier finding (Zinkl *et al*., 1990) and to confirm Chinchore *et al*.'s (2009) finding that a return to dark re-establishes rhodopsin in the rhabdomere. The accompanying figure (bottom) shows a substantial rhodopsin decrease for light-reared flies when compared with dark-reared flies. We further show a higher rhodopsin level in light-reared flies that had been returned to the dark for 1 day and for 2 days.

In summary, we used confocal microscopy and microscope photometry, both based on photoreceptor imaging in living flies, to confirm that room light levels of illumination cause rhodopsin to move from rhabdomeres into endosomes and that a return to darkness re-establishes the full amount of rhodopsin in rhabdomeres.

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Review of reported *Drosophila* species (Diptera: Drosophilidae) in montane habitats in Colombia.

Villamizar, Carolina[1], and Diana Álvarez[2]. [1]Bióloga, Pontificia Universidad Javeriana. carito.villamizar@gmail.com; [2]Laboratorio de Genética de Poblaciones Molecular y Biología Evolutiva, Departamento de Biología, Pontificia Universidad Javeriana.
E-mail: dalvarez@javeriana.edu.co

Introduction

Even with the advances in biology the total number of the world's insect species remains unknown. With only 20% of the insects known globally, it is clear that there is much yet to be learned about insect communities. Furthermore, gaining knowledge about more of the remaining 80% to effectively determine real biodiversity will help entomologists and other biologists better understand insect evolution (Grimaldi and Engel, 2005). One of the most advanced fauna inventories are the insects of the order Diptera, because they are disease vectors and other species used as biological models like *Drosophila*. There are descriptions of sister species that are morphologically identical but divergent at the DNA level. The Drosophilidae family represent the 3% of the species assuming that the order Diptera have 120,000 species approximately.

Of the 3,800 species described in the Drosophilidae family, 1,600 belong to the *Drosophila* genus (Grimaldi and Engel, 2005; Wheeler, 1981; Bachli *et al*., 2004). As in other taxonomic groups, new discoveries have contributed to the evolutionary reconstruction of the family and the

genus which appropriately has changed over time. For example, the review of the Drosophilidae family made by Grimaldi (1990) proposed that the genus was made of 15 subgenera, while Markow and O'Grady (2006), based on recent phylogenetic studies, proposed a modification of the taxonomic relations made by Trockmorton (1975) for the *Drosophila* subgenera. The most relevant changes are in the species radiations; the first one, considered to be the most basal, is the *virilis-repleta*. This radiation includes the groups: *annulimana*, *bromeliae, canalinea, carbonaria, carsoni, coffeata, dreyfusi, melanica, mesophragmatica, nannoptera, peruviana, polychaeta, repleta, robusta, tumiditarsus* and *virilis.* The second radiation, *immigrans-tripunctata,* includes the groups *calloptera, cardini, guarani, immigrans, pallidipennis, quinaria, testácea* and *tripunctata*. The *Drosophila* and *Sophophora* (*melanogaster, saltans, obscura* and *willistoni*) subgenera represent more than 90% of the total diversity of the *Drosophila* genus (Markow and O'Grady, 2006).

Val *et al*.'s literature review of the *Drosophila* genus studies conducted in the Neotropical region (1981) indicate that *repleta*, *mesophragmatica*, *cardini*, *saltans* and *willistoni* are the most studied species groups. They have different evolutionary patterns and have adapted to different environments. The *repleta* group is the largest of the *virilis-repleta* radiation and is found in deserts and open formations associated with cactaceae. The *mesophragmatica* group, in the same radiation, is found only in Andean mountain systems. The *cardini* group, from the *inmigrans-tripunctata* radiation, has species distributed on islands and on the mainland, in woods and open formations. The *saltans* and the *willistoni* groups, from the *Sophophora* subgenus, also inhabit woods and open formations (Val *et al.,* 1981).

The first records of Drosophilids reported for Colombia date back to 1960, when Heed and Carson collected Drosophilids associated with plants, identifying species from the *onychophora* and *flavopilosa* groups (Heed and Carson, 1960; Hunter, 1979). This and other studies (Hunter, 1979, 1988, 1992) have provided important contributions to the study of the *Drosophila* genus. Hunter determined early on that *mesophragmatica* and *obscura* were the most common groups. Also, in Colombia, genetic studies of *Drosophila pseudoobscura bogotana* have showed this subspecies to be a model for the study of population divergence at the infra specific level (Alvarez, 1993, 2003; Alvarez *et al*., 2002). This is an endemic subspecies recognized from studying 25 allozymes in Colombian populations (from "La Sabana de Bogota") and comparing them to North American ones (Ayala and Dobzhansky, 1974). Currently, there is insufficient Drosophilid species data in Colombia to establish if *Drosophila pseudoobscura bogotana* is present in other montane habitats different from "La Sabana de Bogota". The objective of this work is to obtain a theoretical basis for diversity of *Drosophila* species found in montane habitats (>1600 m) of Colombia based on information available for this genus.

Material and Methods

We reviewed the scientific literature to identify the species groups that can be found in Colombia. Species groups with Neotropical distributions were based on the work of Val *et al*. (1981). From Markow and O'Grady's 2006, work, which is a taxonomic key for the species maintained in stock centers, we established the species that can be present in Colombia. Two additional sources of information that we used were the Taxodros database (http://taxodros.unizh.ch/), that specializes in organizing taxonomic information of the *Drosophila* genus across the world and Flybase (http://flybase.bio.indiana.edu/) that lists the species phylogeny of the Drosphilidae family. In Taxodros we retrieved all the geographical coordinates and altitudinal records for Colombia. In the end, only species of the *Drosophila* genus were considered and those

with altitudes higher than 1600 m. The stocks centers that maintain *Drosophila* strains were revised, too.

Results and Discussion

There are 35 genera of Drosophilidae in the neotropics. Within the *Drosophila* genus, the subgenera most studied and with the largest representation are *Drosophila* and *Sophophora* with 275 and 58 species, respectively. According to Val *et al*. (1981), it can be deduced that Colombia can have 47 species of the subgenus *Drosophila* (not including the *repleta* group) and 23 species of the subgenus *Sophophora* (Table 1). Val *et al.* (1981) did not consider *coffeata* group, and *peruviana* does not have a Colombian distribution. Thus, 24% of the Neotropical species can be found in Colombia for both subgenera. However, this value is an underestimate, because the *repleta* species are not considered. According to Markow and O'Grady (2006), from the 29 species groups of *Drosophila* genus, 15 species groups are found wholly or partly in the neotropics (Table 1).

Table 1. Species of Neotropical distribution that include Colombia. * Neotropical species groups as in Markow and O'Grady, 2006.

Species groups (species #)	Species in Colombia	Geographic distribution
Drosophila subgenus, *virilis-repleta* radiation		
annulimana (8)*	*D. annulimana*	Brazil, Bolivia and Colombia
	D. breuerae	Colombia
bromeliae (1)*	*D. bromeliae*	From Mexico to Colombia
canalinea (5)*	*D. canalinea*	From Mexico to Southern of Brazil
	D. canalinioides	From El Salvador to Venezuela
castanea (1)	*D. castanea*	From Mexico to Colombia and Venezuela
dreyfusi (5)*	*D. briegeri*	Panama, El Salvador, Colombia and Brazil
flavopilosa (16)	*D. acroria, D. crossoptera, D. incompta, D. melina*	Central and South America
funebris (introducida)	*D. funebris*	Cosmopolitan
mesophragmatica (9)*	*D. brncici, D. gasici, D. mesophragmatica, D. viracochi*	Only Andean including Colombia
polychaeta (1)	*D. polychaeta*	From USA to Brazil
repleta (73)*	*grupo mercaptorum*	Brazil and Bolivia
	grupo fasciola	Mexico and South America
virilis (introduced)	*D. virilis*	Wide distribution in the Neotropics
xanthopallescens (1)	*D. aureopallescens*	Panama and Colombia
Drosophila subgenus, *inmigrans-tripunctata* radiation		
calloptera (8)*	*D. lindae*	Colombia, Peru and Bolivia
	D. schildi	From Costa Rica to Colombia and Venezuela, and Brazil
	D. calloptera	From Mexico to Brazil
cardini (16)*	*D. cardinoides*	From Mexico to Brazil
	D. neomorpha	From Mexico to Colombia
	D. polymorpha	From Guatemala to Brazil
	D. neocardini	Colombia and Brazil
	D. cardini	From USA to Brazil and Chile
guarani (9)*	*D. griseolineata*	Colombia, Bolivia and Brazil
inmigrans (introducida)	*D. inmigrans*	Cosmopolitan

pallidipennis (1)*	*2 subspecies*	Central America, Peru and Brazil
tripunctata *	*D. setula*	From Central America to Northern South American
I subgroup (6)		
II subgroup (10)	*D. unipunctata*	From Mexico to Northern South American
	D. mediodelta	From Central America to Colombia
III subgroup (20)	*D. trapeze*	From Mexico to Northern South American
	D. crocina	From Mexico to Brazil
	D. converga, D. mediopictoides	From Central America to Northern South America
	D. mediopicta, D. mediostriata, D. nigricincta	From Central America to Brazil
	D. bandeirantorum	Brazil and Colombia
IV subgroup (15)	*D. metzii*	From Mexico to Northern South America
	D. medioparva, D. pellewae, D. trifiloides, D. tristriata	From Central America to Northern South America
	D. leticiae	Colombia
Sophophora subgenus		
melanogaster (introduced 5)*	*D. ananassae*	Wide distribution in the Neotropics
	D. malerkotliana	Wide distribution in the Neotropics
	D. melanogaster	Cosmopolitan
	D. simulans	Cosmopolitan
	D. kikkawaii	Wide distribution in the Neotropics
obscura (7)*	*grupo affinis, D. tolteca*	From Mexico to Bolivia
	D. pseudoobscura pseudoobscura	From USA to Colombia
	D. pseudoobscura bogotana	Colombia
saltans (21)*	*D. emarginata*	From Mexico to Colombia, Venezuela, Ecuador and Peru
	D. parasaltans	Colombia and Brazil
	D. septentriosaltans	Colombia
willistoni (23)*	*D. willistoni willistoni*	USA and Mexico south to Brazil
	D. tropicalis tropicalis	From El Salvador to Brazil and Bolivia
	D. paulistorum (super especie)	Colombia
	D. bocainensis	From Brazil and Argentina to Colombia and Venezuela
	D. megalagitans	Colombia
	D. pseudobocainensis (tipo 2)	Colombia (Popayan)
	D. nebulosa	From USA, Mexico south to Brazil and Peru
	D. funnipennis	From El Salvador to Brazil
	D. capricorni	From Panama to Brazil south
	D. sucinea	From Mexico to Colombia
	D. changuinolae	From Panama to Colombia (Amazon)
	D. mangabeirai	From Central America, Puerto Rico south to Brazil

Using Taxodros, we found 234 Drosophilid species for Colombia. Of these, that inhabit altitudes higher than 1600 m, 87 species belong to the *Drosophila* genus; one from the *Siphlodora* subgenus, 64 species from the *Drosophila* subgenus, and 22 species within the *Sophophora* subgenus (Table 2). Among the *Drosophila* subgenus, there are 48 species belonging to Neotropical species groups expected for Colombia and 16 species from groups that were not previously considered for Colombia: (*Siphlodora* (subgenus), *rubifrons*, *onychophora* and *sticta*). There are no Taxodros records for the groups *bromeliae, castanea*, *polychaeta*, and *xanthopallescens* of the *Drosophila* subgenus in Colombia. The registries are from nine different departments (states), the majority of which came from Cundinamarca, followed by Cauca and Tolima. Within the *Drosophila* subgenus,

the *onychophora* group was the most frequent, followed by the *repleta* and *tripunctata* groups. *Willistoni* was the most common group within the subgenus *Sophophora* (Table 2). Unfortunately, some inconsistences in the coordinates and name localities occur within the Taxodros registers.

Table 2. Registered *Drosophila* species for Colombia in Taxodros above 1600 m.* Subgenera and species groups not considered for Colombia previously.

Species groups(species #)	Species	Departments (localities)
Siphlodora subgenus (1)*		
	D. flexa	Antioquia (Medellin, Rionegro, Sonsón)
Drosophila subgenus, *virilis-repleta* radiation		
annulimana (2)	*D. annulimana, D. gibberosa*	Cundinamarca (Cota)
canalinea (2)	*D. canalinea*	Cundinamarca (Cota)
	D. panamensis	Cundinamarca (Facatativá)
dreyfusi (1)	*D. briegeri*	Cundinamarca (Cota)
flavopilosa (2)	*D. melina*	Cauca (Popayán)
	D. acroria	Cundinamarca (Cota)
funebris (1)	*D. funebris*	Cundinamarca (Cota)
mesophragmatica (7)	*D. mesophragmatica, D. viracochi*	Boyaca (Paipa), Cauca (Caloto), Cundinamarca (Cota, La Calera), Nariño (Pasto), Tolima (Roncevalles)
	D. gasici	Cauca (Caloto), Cundinamarca (Cota, La Calera), Nariño (Pasto), Tolima (Roncevalles)
	D. altiplanica, D. orkui, D. pavani	Cundinamarca (Cota)
	D. brncici	Cundinamarca (Cota, La Calera), Boyaca (Paipa), Nariño (Pasto), Tolima (Roncevalles)
repleta (10)	*D. fulvimacula*	Cundinamarca (Fusagasugá)
	D. hydei	Cundinamarca (Cota, Fusagasugá)
	D. longicornis, D. martensis, D. pararepleta, D. starmeri, D. uniseta	Cundinamarca (Zipaquirá)
	D. mercatorum	Cundinamarca (Cota), Tolima (Roncevalles)
	D. paranaensis, D. repleta	Cundinamarca (Cota, Facatativá, Fusagasugá)
virilis (1)	*D. virilis*	Cundinamarca (Cota)
Drosophila subgenus, *inmigrans-tripunctata* radiation		
calloptera (2)	*D. calloptera*	Cundinamarca (Fusagasugá)
	D. schildi	Meta (Lisbia)
cardini (4)	*D. polymorpha*	Cauca (Popayán, Caloto), Cundinamarca (Zipaquirá, Fusagasugá)
	D. cardini, D. cardinoides	Cundinamarca (Cota, Fusagasugá, Zipaquirá)
	D. parthenogenetica	Cundinamarca (Facatativá)
guarani (2)	*D. griseolineata*	Cundinamarca (Cota, Cáqueza, Fusagasugá), Cauca (Caloto), Tolima (Roncevalles)
	D. guaramunu	Cundinamarca (Cota), Cauca (Caloto), Tolima (Roncevalles)
inmigrans (1)	*D. immigrans*	Boyaca (Paipa), Cundinamarca (Cota, Fusagasugá, La Calera), Nariño (Pasto), Tolima (Roncevalles)
pallidipennis (1)	*D. pallidipennis*	Cundinamarca (Fusagasugá)
rubifrons (1)*	*D. popayan*	Cauca (Popayán)
tripunctata (13)	*D. argenteifrons*	Cundinamarca (Facatativá)
	D. bandeirantorum	Boyaca (Paipa), Cauca (Caloto), Cundinamarca (Cota, Fusagasugá, La Calera), Nariño (Pasto), Tolima (Roncevalles)

	D. crocina, D. mediodelta, D. mediopictoides	Cundinamarca (Cota)
	D. cundinamarca	Cundinamarca (Zipaquirá)
	D. mediostriata	Cundinamarca (Fusagasugá)
	D. metzii	Cundinamarca (Cota, Facatativá)
	D. setula	Cundinamarca (Fusagasugá)
	D. tripunctata	Cundinamarca (Cota, Fusagasugá), Meta(Lisbia)
	D. albicans, D. angustibucca, D. mediostriata	Meta (Lisbia)
onychophora (13)*	*D. acuminanus, D. arane, D. bifurcada, D. bomarea, D. carablanca, D. choachi, D. colmenares, D. franii, D. margarita*	Cundinamarca (Cota)
	D. arboloco, D. freilejoni	Cundinamarca (Cota, La Calera)
	D. desbaratabaile	Cundinamarca (Cota), Nariño (Pasto)
	D. chisaca	Cundinamarca (La Calera)
sticta (1)*	*D. sticta*	Cundinamarca (Facatativá)
Sophophora subgenus		
melanogaster (4)	*D. ananassae*	Cundinamarca (Cota, Fusagasugá), Santander (Chicamocha)
	D. melanogaster	Boyaca (Duitama, Paipa), Cauca (Caloto) Cundinamarca (Cota, Fusagasugá, La Calera, Zipaquirá) Meta (Lisbia), Nariño (Pasto), Santander (Chicamocha), Tolima (Roncevalles)
	D. simulans	Cundinamarca (Cota, Fusagasugá)
	D. kikkawaii	Cundinamarca (Cota)
obscura (3)	*D. azteca*	Cundinamarca (Cota)
	D. pesudoobscura bogotana	Cundinamarca (Cota, Facatativá, Zipaquirá)
	D. pseudoobscura	Boyaca (Duitama, Paipa, Sogamoso, Tunja) Cundinamarca (Facatativá, Cota, Zipaquirá, La Calera, Sutatausa, Salto del Tequendama), Norte de Santander (Pamplona)
	D. tolteca	Cundinamarca (Cota, Fusagasugá), Tolima (Roncevalles)
saltans (4)	*D. emarginata, D. prosaltans*	Cundinamarca (Cota, Fusagasugá)
	D. saltans	Cundinamarca (Cota)
	D. sturtevanti	Cundinamarca (Facatativá, Fusagasugá)
willistoni (11)	*D. sucinea*	Boyaca (Paipa), Cauca (Caloto), Cundinamarca (Fusagasugá), Nariño (Pasto), Tolima (Roncevalles)
	D. pseudobocainensis	Cauca (Popayán)
	D. bocainensis	Cundinamarca (Zipaquirá)
	D. capricorni	Cundinamarca (Cota, Fusagasugá), Meta (Lisbia)
	D. equinoxialis	Cundinamarca (Facatativá, Fusagasugá, Cota), Caldas (Manizales)
	D. fumipennis	Cundinamarca (Fusagasugá), Meta(Lisbia)
	D. nebulosa	Cundinamarca (Facatativá), Meta (Lisbia)
	D. paulistorum	Cundinamarca (Cota, Fusagasugá), Santander (Malaga)
	D. willistoni	Cundinamarca (Facatativá, Fusagasugá, Cota), Caldas (Manizales), Santander (Malaga)
	D. parabocainensis	Meta (Lisbia)
	D. tropicalis	Cundinamarca (Fusagasugá)

In Flybase there are two refereed stock centers of *Drosophila*: Ehime (http://kyotofly.kit.jp/cgi-bin/ehime/index.cgi) and UC San Diego (https://stockcenter.ucsd.edu/info/welcome.php). The first one is specialized in Asiatic strains and the majority of these 914 are from Japan. San Diego (previously in Tucson) holds strains and preserves specimens from 240

species belonging to 30 species groups, 24 from the *Drosophila* subgenus and 11 from the *Sophophora* subgenus. Combined, within these stocks there are 33 strains with geographic origins from Colombia. Twelve of the species are from *Drosophila* and 9 are from *Sophophora* (Table 3). But of these species, only 7 are from locations above 1600 m. Thus, only 4.7% of the total number of species for the subgenus *Drosophila* and 18% for the subgenus *Sophophora* are represented in relation to the number expected for montane habitats. These strains were deposited in the stock center more than 50 years ago.

Table 3. Drosophila strains at UC San Diego with geographic origin of Colombia. * localities above 1600 m.

Species groups (species #)	Species (strain #)	Localities
Drosophila subgenus		
polychaeta (1)	*D. polychaeta* (1)	Leticia
repleta (5)	*D. eohydei* (3)	Santa Marta, 1956; Bucaramanga (isoline); Bucaramanga (ethanol)
	D. fulvimacula (2)	Villavicencio, 1956; Leticia, 1960
	D. hydei (3)	Villavicencio, 1956; Villavicencio, BAC library
	D. mercaptorum (2)	Palmira; Manizales*, 1963
	D. paranaensis (2)	Villavicencio, 1956; Leticia
cardini (1)	*D. cardinoides* (2)	Santa Marta, 1956; Bucaramanga, 1953
guarani (1)	*D. griseolineata* (1)	Medellín*
inmigrans (1)	*D. inmmigrans* (1)	Palmira
pallidipenis (1)	*D. pallidipennis* (1)	Bucaramanga, 1953
tripunctata (2)	*D. mediostrata* (2)	Leticia, 1956; Palmira, 1960
	D. unipunctata (1)	Medellín*, 1955
Sophophora subgenus		
melanogaster (2)	*D. kikkawai* (2)	Leticia (isoline); Genome 2010
	D. melanogaster (1)	Bogotá*, 1962
obscura (1)	*D. pseudoobscura* (2)	Bogotá*, 1960; Bogotá*, 1976 (SC)
	D. p. bogotana (1)	Bogotá*, 1978 (w-)
saltans (3)	*D. emarginata* (1)	Medellín*, 1955
	D. prosaltans (1)	Leticia, 1960
	D. sturtevanti (1)	Bucaramanga, 1956
willistoni (3)	*D. capricorni* (1)	Palmira, 1960
	D. nebulosa (1)	Palmira, 1955
	D. sucinea (1)	Medellín*, 1958

With these results it is evident that the information about the species with geographic distributions in Colombia is very incomplete. The expected neotropical species come from a literature review that is incomplete due to artificial patterns of distribution, artifacts of sampling techniques, and differences in the spatial and temporal designs in the revised works (Val *et al.,* 1981). On the other hand, the work of Markow and O´Grady (2006) is, as they say, biased because they only worked with the species in the stocks centers, although this is actually one of the most useful works on *Drosophila*. The inconsistencies in the coordinates in Taxodros can be due to the methods used for geo positioning, which add more bias to the data. In the stock centers there are few Colombian strains, and they were deposited more than 50 years ago. At the present time there are no new taxonomic *Drosophila* studies in montane habitats in Colombia. Thus, there is a void of information of this species.

According to our literature analysis, if a sampling were undertaken in Columbian montane habitats, we would expect to find species from the following species groups: *repleta, cardini, guarani, inmigrans, pallidipenis, tripunctata, melanogaster, obscura, saltans,* and *willistoni*. Other species groups we expect to find from the *virilis-repleta* radiation, but not present in the stock center, are: *annulimana, bromeliae, canalinea, dreyfusi, flavopilosa, funebris, mesophragmatica,* and *virilis*. Similarly, from the *inmigrans-tripuntata* radiation we expect to find *calloptera* and *rubifrons*. There are also species groups that were only found in one source of information but can probably be found in Colombia: *casatanea, xantopallecens, macroptera, quinaria, onycophora,* and *sticta*.

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Genetic markers of the *Va*/*Ba* balanced lethal strain of *Drosophila subobscura*.

Araúz, P. A., C. Pegueroles, G. Calabria, L. Serra, J. Balanyà, M. Pascual, and F. Mestres. Dept. de Genètica. Facultat de Biologia. Universitat de Barcelona. E-mails: pedroargon@hotmail.es; cintapq@gmail.com; gemma.calabria@gmail.com; lserra@ub.edu; jbalanya@ub.edu; martapascual@ub.edu; fmestres@ub.edu

The *Va*/*Ba* strain, constructed by Sperlich *et al*. (1977), is the only balanced lethal strain in *D. subobscura.* It allows the production of homozygous O chromosomes and has been a useful tool not only to analyse chromosomal viabilities but also to obtain homokaryotypic lines (Mestres and Serra, 2008). Besides the morphological dominant mutations *Va* (*Varicose*) and *Ba* (*Bare*), other genetic markers have been characterized in this strain, some of them by our group and not described previously. Here we present a list of these markers.