

Historical review

Francisco Campos-Rivadeneira and Roberto Levi-Castillo: Their lives and contributions to the study of mosquitoes (Diptera: Culicidae) in Ecuador

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The study of mosquitoes is important in the prevention of vector-borne diseases. In Ecuador, the study of local mosquito biodiversity was pioneered by two entomologists whose contributions span through the first half of the 20th century, Francisco Campos-Rivadeneira and Roberto Levi-Castillo.

Both of them contributed to general aspects of Entomology and to particular insights in mosquito taxonomy. Their publications and discoveries were recognized by the international scientific community but went unnoticed in South America during their time. Today, very few citizens remember the names and contributions of these two scientists.

Here, we provide an overview of their lives, a summary of their contributions, and we conclude with a broader outlook on the practice of science in Latin America during their time.

Keywords: Culicidae/classification; disease vectors; entomology/history; Ecuador.

Francisco Campos-Rivadeneira y Roberto Levi-Castillo: sus vidas y contribuciones al estudio de los mosquitos (Diptera: Culicidae) en Ecuador

El estudio de los mosquitos es una importante tarea en la prevención de las enfermedades transmitidas por vectores. En Ecuador, el conocimiento de la biodiversidad local de mosquitos se inició con dos entomólogos pioneros que trabajaron a inicios del siglo XX: Francisco Campos-Rivadeneira y Roberto Levi-Castillo.

Ambos hicieron importantes contribuciones en el campo de la Entomología en general y de la taxonomía de los mosquitos en particular. En su época, sus aportes fueron reconocidos por la comunidad científica internacional, pero pasaron desapercibidos en la región suramericana. Hoy en día, son muy pocos los que recuerdan los nombres y los aportes de estos dos hombres de ciencia.

En este artículo, se presenta una breve biografía de ambos científicos y un resumen de sus contribuciones, y se establece en perspectiva la situación de la práctica de la ciencia en Latinoamérica durante la época.

Palabras clave: Culicidae/clasificación; vectores de enfermedades; entomología/historia; Ecuador.

The study of mosquito populations and their distribution is an important component in the prevention of vector-borne diseases. This is particularly important nowadays given the increasing frequency of mosquito-transmitted diseases and the emergence of new arboviruses (for example, chikungunya, Zika) (1-5).

The seminal contributions of Roberto Levi-Castillo and Francisco Campos-Rivadeneira (Levi-Castillo R. Provisional List of the Culicidae, Simuliidae, Phlebotomus, and Culicoides of Ecuador. Proceedings, Tenth International Congress of Entomology, Montreal, August 17-25, 1956. Section on Medical and Veterinary Entomology. 1958, Vol. 3, p. 867-71) (6-8) remained isolated and inactive in the timeline of mosquito vector research in Ecuador for an extended period. The study of mosquitoes in Ecuador has regained attention with both ecological (9-15) and taxonomic studies (16-19) only recently.

The current estimated number of mosquito (Diptera: Culicidae) species in Ecuador is 244 (12,17,20-22). However, this estimate is expected to increase

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in the next few years given the sustained efforts of local researchers to explore the ample diversity of habitats and complex geography of Ecuador (23,24). This process of discovery will be accelerated by the availability of new molecular methods that allow differentiating what once were cryptic and unknown mosquito species (18,25,26).

Both entomologists, Francisco Campos-Rivadeneira (figure 1A) and Roberto Levi-Castillo (figure 1B), were born in the port city of Guayaquil and they pioneered the study of mosquito vectors and established the seeds for the development of Medical Entomology in Ecuador during the 20th century (8). Although the works of these pioneering entomologists have been acknowledged to some extent in a handful of publications (8,12), no complete assessment has been made on the scientific efforts and contributions of these two Ecuadorian scientists, especially in regards to our understanding of mosquito biodiversity and taxonomy.

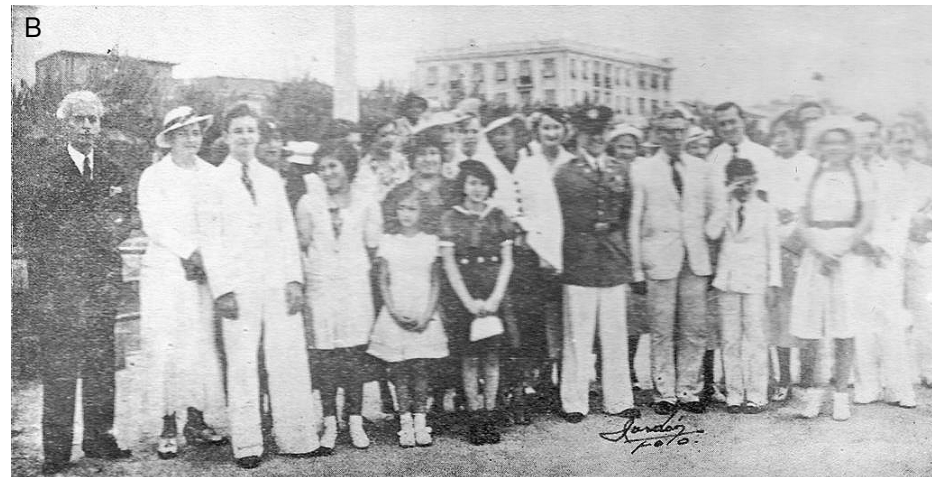


Figure 1. A. Portrait of Francisco Campos-Rivadeneira in 1935

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B. Picture of a young Roberto Levi-Castillo (third from the left) in Guayaquil after his arrival from the United States in 1938.

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Here we provide a biography and historical assessment on the lives of these two Ecuadorian scientists and we provide a comprehensive list of the scientific literature regarding their entomological studies, in particular, their contributions to the study of mosquitoes in Ecuador. We believe the lives of both Ecuadorian entomologists can serve as a case study on the cultural and economic conditions in Ecuador and other countries in South America, which throughout the 20th century experienced a unique and difficult history for the development of science. The system proposed by Reinert (27) for abbreviations of mosquito generic-level taxa is used throughout the text.

Francisco Campos-Rivadeneira

Campos-Rivadeneira was born in Guayaquil, in the province of Guayas (coastal Ecuador), on January 11th, 1879. His father was Francisco Campos Coello and his mother Manuela Rivadeneira Olvera. He grew up in a catholic and traditional family along with six other siblings and he never completed high school (28,29). His father's family had a long tradition of intellectuals,

which included physicians, bibliographers, and antiquarians. His father was an outstanding humanist and thinker of his time, who held important academic and political positions throughout his life, including director of the *Biblioteca Municipal* in Guayaquil, secretary of the *Banco Nacional*, head of Guayaquil's most important high school, minister of Education, professor, journalist, and politician (30).

From an early age and encouraged by his father, Campos-Rivadeneira developed a strong interest in the natural world. He and his father used to take long excursions through Guayaquil and its rural outskirts, where they would look for all kinds of animals, particularly insects. Given his shy and introverted personality, a young Campos-Rivadeneira spent most of his time collecting insects and learning from books. Having left aside formal instruction, his love for insects drove him to acquire knowledge on the principles of Entomology and other scientific disciplines. Given the social limitations of his time and society, Campos-Rivadeneira self-taught scientific mastery on Entomology was remarkable. At only 16 years of age, he was hired to teach geography at the *Colegio Nacional Vicente Rocafuerte* (28,29). He also received instruction from the Jesuit priest Luis Sodiro, who was a renowned botanist, and from whom Campos-Rivadeneira probably acquired much of his curiosity for nature (31).

In 1895, after the liberal revolution in Ecuador (32), his father was given the position of principal at the *Colegio San Vicente del Guayas*. From this new position, his father established the *Museo de Ciencias Naturales* and bought a collection of zoological, botanical, and mineralogical specimens from France. Endorsed by his father, Campos-Rivadeneira was soon appointed as museum director. This academic position may have given Campos-Rivadeneira an adequate environment to further his interests in the study of insects and allowed him to house his private collections into the museum he directed, which included beetles and a large variety of metals and precious stones. In 1899, he started editing a "Guía rápida del museo" which included information on insects. He wished to share the love and admiration he had for the local fauna with the citizens of Guayaquil (29).

In 1900, after publishing an article on Ecuadorian entomology, he was invited to the Latin American Scientific Conference in Buenos Aires. Tragically, a year later the museum collections under his aegis were destroyed in a fire that burned to ashes most of the *Colegio Nacional Vicente Rocafuerte*. Despite this setback, Campos-Rivadeneira continued making expeditions and publishing the results of his findings. Considering his efforts to elevate national science, president Lizardo García awarded him the title of "*Zoólogo del Estado*". The museum was re-opened after a year of inactivity following the fire (28,29).

In 1902, he was appointed as professor of Natural Sciences and lectured on the subject of Hygiene at the *Facultad de Medicina* of the *Universidad de Guayaquil*. He was a kind and inspiring professor who soon became popular among his students, especially during the entomological expeditions that he liked to share with his pupils. His publications on Entomology started to appear more frequently on local magazines, which remain as historical proof of his expertise on a wide range of entomological groups (for example, butterflies, crickets, and beetles) and fields in the natural sciences (taxonomy, morphology, and behavior, among others). In 1907, his sustained contributions to Ecuadorian entomology granted him a membership to the Entomological Society of Cornell, Pennsylvania (28).

From 1907 onwards, most of his studies focused on agricultural pests and in 1917, he was recognized as a member of the Entomological Society of America. In 1920, his interest on medical entomology strengthened and he edited a book entitled "Entomología médica: nuestras principales especies de mosquitos y el modo de extinguirlos". This book is considered a pioneering effort to inform the local population of Ecuador about the risks of malaria and its vectors. This was followed by a publication on the mosquito fauna of Guayaquil and its surroundings (7). In 1926, he was visited by Emilio J. Pampana, a physician from the Royal College of Physicians and Surgeons of London, with whom he edited a paperback on the anti-malaria campaign in Guayaquil. In 1940, due to his scientific trajectory and productivity, he was appointed Chief of the *Servicio Entomológico* at the *Instituto Nacional de Higiene* (currently known as *Instituto Nacional de Investigación en Salud Pública Leopoldo Izquieta Pérez*), a position that he held until the last days of his life (28,29).

Campos-Rivadeneira had a prolific career and collaborated with many foreign researchers in the field of Entomology. His network of collaborators is exemplified on the many taxa that have been named after him, such as the genus *Camposiana* Townsend 1915 (Diptera: Tachinidae), *Camposiella* Hebard 1924 (Orthoptera: Tettigoniidae), and *Campostrecha* Mello Leitão 1937 (Arachnida: Ammostrechidae), a species of water strider, *Hebrus camposi* (Hemiptera: Hebridae) (33), as well as many species of tiger beetles (34,35). Most of his articles were published in the *Revista del Colegio Nacional Vicente Rocafuerte* (36,37).

The prints of this magazine are few and rare nowadays, held only in a few century-old universities in Ecuador and the central archives of the Ecuadorian government. In an enjoyable quirk of history, Campos-Rivadeneira wrote an article on *Morpho* butterflies in 1946, which was subject to severe criticism from a young and yet unknown Roberto Levi-Castillo.

Despite having been a prolific researcher subject to numerous recognitions and honors, his salary never reflected his achievements and his life was marked by poverty. After the widespread introduction of DDT as a generic pesticide to control insect populations, he was convinced that his work on agricultural entomology was not relevant anymore. This led to a period of self-inflicted isolation and confinement within the walls of his museum collection, which at that time was housed at the *Instituto Nacional de Higiene*.

Campos-Rivadeneira passed away on May 5th, 1962. During his career, he described approximately 150 species of insects that were previously unknown to science. After his death, his beloved museum collection was neglected and eventually lost (28,29). Ten years after his death, a group of biologists and scholars in Quito founded the *Sociedad de Amigos de la Naturaleza Francisco Campos*. This Society promoted the research and conservation of Ecuador's biodiversity and many relevant researchers at the time became members. In 1992, the Congress of Ecuador condecorated the Society for its contributions and also for helping to establish the *Museo Ecuatoriano de Ciencias Naturales* and the *Fundación Natura* (J. M. Carrión, personal communication).

Roberto Levi-Castillo

Levi-Castillo was born in Guayaquil on January 29th, 1921. Resembling Campos-Rivadeneira, Levi-Castillo's family was also part of a legacy of intellectuals and artists. His father was Roberto Levi Hoffman, who during the 19th century attended his postgraduate studies under the guidance of Robert

Koch and Paul Ehrlich. Levi Hoffman arrived in Ecuador in 1909 to work as the chief chemist for the Guayaquil laboratory and throughout the years became an influential person in many affairs related to the social, political, and commercial life of this city.

Levi-Castillo initiated his basic studies at a local school but was soon sent by his family to continue them in Europe. As a teenager, his father enrolled him at the Riverside Military Academy in Gainesville, GA, and he later moved to the Hollywood Military Academy in Pensacola, FL. He graduated in 1937 as a U.S. Army Air Force Reserve Second Lieutenant. He returned to Ecuador in 1938, and to obtain a locally recognized bachelor title, he completed an additional year of studies at the *Colegio Nacional Vicente Rocafuerte*. Soon after his return to Guayaquil, he was appointed as *ad honorem* instructor at the *Escuela de Aviación Militar* (38).

After finishing high school, he enrolled at the *Universidad de Guayaquil* and studied two simultaneous degrees: In chemistry and pharmaceuticals and in medicine. With the start of the international tensions that led to World War II, he was called by the military to enroll as an army reserve officer. During the Ecuador-Perú war of 1941, he was garrisoned at a military base in the province of El Oro, where he took part in war actions. At some point during this armed conflict, he and two other cadets deserted and traveled to the Andean city of Cuenca. There, he had an emergency surgery due to a tooth infection which was further aggravated by a piece of gauze that was not removed. A severe infection required him to travel back to Guayaquil in sought of better medical treatment but was left with a cavity in his palate that required him to travel to the United States to receive proper treatment (38).

Perhaps taking advantage of his unplanned return to the United States, in 1942 he continued to study at Cornell Medical College. In 1943, he visited the *Escuela de Medicina Tropical* at the *Universidad de La Habana* in Cuba for an eight-month period. Once finished his training in Cuba, he returned to Cornell and received instruction as a US Army Special Forces Official under the leadership of Major William Barby (who was a decorated World War II war hero). That same year, he was assigned to missions in the allied countries and Italy. His tour of duty included Dundee (Scotland), North Africa, Sicily, Naples, and Anzio, where he helped to combat typhus fever outbreaks as a medical officer. Having an active role in the Sanitary Corps, he also went to Greece and Provence (France) to help control malaria outbreaks (38).

In 1944, he traveled to Fort Leavenworth, Kansas, to attend a Higher Command and Staff Course. Later that year, he returned to Guayaquil where he continued his studies at the *Escuela de Química y Farmacia*. He had an active role in many strikes against the *Concejo Universitario* to demand the upgrade of the School to the status of Faculty. During this time he also collaborated with Francisco Campos-Rivadeneira, with whom he took part in many excursions near Guayaquil city. As a result of this collaboration, he published several papers on the taxonomy of *Anopheles* (39-41). Then, in 1945, he set up the collaboration with the Public Health Inter-American Cooperative Service of the US government and moved to Quito where he worked as an epidemiologist and medical entomologist under Jaime Rivadeneira Dávila. During 1945, he published several important papers on the malaria vectors of the Ecuadorian Andean valleys (42,43), a region where the disease was endemic at that time, but where it was later eradicated (44). In regards to his pioneering findings on the biology of *Anopheles pseudopunctipennis*, the primary vector species at the

highlands of Ecuador at that time, he would remark, “My findings were widely discussed by foreign scientists, meanwhile, here in Ecuador people call me ‘Doctor Mosquito’ and make fun of me” (38).

Later, in 1946, he married a Dominican woman called Martina Bello Germán (38) and moved back to Guayaquil where he started his own research center at the now traditional “El Paraíso” neighborhood. His publications were greatly appreciated by the international scientific community due to the thoroughness of his analyses. He complemented his taxonomical and zoological descriptions with scientific illustrations and microphotographs taken with his camera, which he retrofitted to his microscope. He was fluent in Spanish, English, German, French, and Italian.

In 1947, he was appointed as a chemistry teacher at the *Colegio Nacional Vicente Rocafuerte*. This was a time during which he exchanged correspondence and maintained a healthy scientific controversy with the renowned Francisco Campos-Rivadeneira. His relationship with Campos-Rivadeneira was one of respect and cooperation. Moreover, Levi-Castillo acknowledged him as his mentor and a renowned entomologist (39). In 1949, he published two important scientific papers summarizing what was currently known at the time about South American malaria vectors, including his own original findings (45,46), and also a preliminary list of *Culex* mosquito species from Ecuador (47). During the early 1950s, he published several papers on the mosquito fauna responsible for the transmission of yellow fever in Ecuador and South America (48-52). In December of 1951, he received a doctorate title in Chemistry and Pharmaceutics. His thesis research was an analysis of the resistance of *Culex quinquefasciatus* to insecticides. He would later publish his results in a local journal (53).

In 1952, he was appointed as editor in chief of the *Revista Ecuatoriana de Entomología y Parasitología*. He also received the international “Carlos Finlay” medal, granted by the *Sociedad Cubana de Medicina Tropical*. The following ten years would be the most productive of his career, a time during which he traveled through the country collecting and cataloging the mosquito diversity of the Ecuadorian coast, the highlands, the Amazonian region, and the Galápagos Islands. The “Distribution of *Haemagogus* mosquitoes in Ecuador” (54), the description of several new species (55-64), and inventories of the Ecuadorian mosquito fauna are amongst some of its most influential papers (6,47,65-66). Regarding other topics, he researched the possible use of the green algae *Chara fragilis* as a biological control for mosquito larvae (67,68). Nevertheless, he did not find evidence of larvicidal properties. He designed a special box to transport live mosquito larvae and pupae collected from the field (69). He was also a pioneer in the use of male genitalia for the identification of mosquito species (39,70) and was the first to use polyvinyl alcohol to prepare microscope slides of mosquito larvae, pupae, and male genitalia (71). Polyvinyl alcohol provides a superior medium that does not require the previous dehydration of specimens (72).

After divorcing his wife and getting remarried to Blanca Muñoz Aguirre, his promising scientific career ended abruptly in 1962. Disappointed by the lack of scientific interest in his young students and after a university strike that made him realize it would be nearly impossible to form new entomologists, he decided to retire from this field. This fateful decision can be understood and explained through this statement: “I understood that my way of thinking was ahead of the local culture and that entomology could not be the reason of my life any more in a society that doesn’t have the economic resources to finance my diverse

research interests. That is why I left science, sold all my equipment, burned down all my books, and abandoned the thing that brought me so much joy and illusion one day, to give way to other realities and, in search for them, I found in philately a new horizon. Immediately, I dedicated myself fervently to it and managed to gather various collections since I had a considerable fortune" (38).

Among his stamp collections, he held the "Scadta" and the "Panagra", which are some of the most valuable and rare stamp series of Ecuador. In 1960, he won the bronze medal at the Albert Hall International Exposition in London. In the long run, he became highly praised by international philatelic societies and recognized as the owner of the best and most complete collection of Ecuadorian stamps. Between 1959 and 1966, he wrote a weekly column at the "El Telégrafo" newspaper from Guayaquil where he would discuss various topics on philately (73).

In 1970, he made a leap into the study of history by collaborating with the historian Julio Estrada Icaza at the *Archivo Histórico del Guayas*. Soon afterward, his friend, the rear admiral Carlos Monteverde Granados, hired him to work at the *Instituto de Historia Marítima* and published several articles in the Institute's journal. In 1991, he became a member of the *Asociación de Historiadores Ecuatorianos* and in 1997, of the *Academia Nacional de Historia*.

Another important facet of his life was his involvement in Freemasonry, in which he was an active member at the Pythagoras Lodge in Washington, D.C., since 1946. He later enrolled at the Texas, Missouri, Kansas, New York, and Iowa lodges. His association to Freemasonry in Ecuador was through the "Luz de América No. 5" Lodge. His essays on masonry were published at "*Ars Quatuor Coronatorum*" (London), which was an important research journal on the history of Freemasonry.

During the 1990s, he moved with his family to Ecuador's capital city, Quito, where he devoted himself to the investigation of historical subjects. He continued to write columns for national newspapers and the journal of the *Universidad de Guayaquil*. He passed away on October 29th, 2006, at the age of 85. Versatile, self-taught, polyglot, and passionate, his production is scattered in different journals and newspapers of the world.

Conclusions

The contributions of Campos-Rivadeneira and Levi-Castillo to the study of disease-transmitting mosquitoes in Ecuador

During their prolific career, Campos-Rivadeneira and Levi-Castillo reported a total of 158 mosquito species for Ecuador, of which 12 were previously unknown in this country (supplementary material). Given the current estimate of approximately 252 mosquito species present in Ecuador (12,15,17,20,21), both scientists described approximately 63 % of the total mosquito fauna. Considering the rapid pace at which the study of mosquito diversity discovers new species, the contributions of contemporary and future researchers will slowly reduce the considerable bias towards what both Campos-Rivadeneira and Levi-Castillo did for entomology in Ecuador (11,12,14,22). Nevertheless, both remain as the most prolific discoverers of mosquitoes in this country.

Campos-Rivadeneira reported a total of 32 mosquito species in Ecuador, 27 of these as new geographical records locally. Most of his specimens were collected in Guayaquil and its surroundings (Durán, Posorja, El Salado) or from nearby cities like Quevedo or Machala. He reported the presence of

Aedes vexans in the Galápagos Islands. However, this was most likely a misidentification with the only native mosquito species that was known to be present in the archipelago at the time, *Ae. taeniorhynchus* (74). In 1954, Levi-Castillo claimed that *Haemagogus equinus*, previously reported by Campos-Rivadeneira (75), was not present in Ecuador and that most likely was misidentified with *Hg. panarchys* or *Hg. spegazzini* (76).

In 1918, Harrison G. Dyar described *Ae. camposanus* based on specimens from Guayaquil sent by Campos-Rivadeneira (77). However, in 1928, Dyar synonymized *Ae. camposanus* with *Ae. euplocamus* (78) only to be brought back from synonymy by Levi-Castillo (79,80). More recently, Arnell synonymized it again as *Ae. euplocamus* (81) and nowadays it is a synonym of *Ae. scapularis*. In 1925, Dyar described *Culex camposi*, a new species, and named it after Campos-Rivadeneira (82). Nevertheless, Lane categorized it as a variety of *Cx. coronator* (83) only to be recognized later again as a valid species by Bram (84). Throughout his career, Campos-Rivadeneira published at least 52 scientific papers dealing with different insect groups; further searches might reveal additional publications. However, we remain confident that we have included all of his publications dealing with mosquito taxonomy hereby.

Levi-Castillo reported a total of 136 species, of which 99 were new geographical records in Ecuador. His specimens were collected throughout all the Ecuadorian territory, from the highlands to the western and eastern lowlands. Yet, some of his collections require confirmation since for some specimens there is no specific reported locality and no other reference collections exist (*Anopheles peryassui*, *Hg. laecotaeniatus*, *Cx. originator*, etc.). Levi-Castillo described 14 new mosquito species for science with specimens from Ecuador, these are *An. gomezdelatorrei*, *Hg. soperi*, *Cx. babahoyensis*, *Cx. guayasi*, *Cx. quitensis*, *Limatus andinus*, *Li. guayasi*, *Trichoprosopon andinum*, *Tr. cotopaxense*, *Wyeomyia esmeraldasii*, *Wy. aequatoriana*, *Wy. amazonica*, *Toxorhynchites aequatorianus*, and *Uranotaenia equatorianna*. Many of these have not been recorded again since their original description (2).

In 1959, *Tx. aequatoriannus* was listed as *nomen dubium* by Stone (85). While Stone does not give a reason for this change, it was most likely due to his lack of access to inspect type specimens. *Tr. cotopaxense* was originally described as *Tr. cotopaxensis* by Levi-Castillo and was later renamed by Stone (86); then, Zavortink categorized this species as *nomen dubium* advocating that its description seemed to include characteristics from at least three other species and most likely no type specimens exist (87). Other species described by Levi-Castillo were later synonymized by Stone (85); these are *Ae. garciai* (60) (synonym of *Psorophora cingulata*), *Hg. garciai* (88) (synonym of *Hg. boshelli*), *Cx. azuayus* Levi-Castillo, 1954 (61) (synonym of *Cx. nigripalpus*) and *Wy. aequatorialis* Levi-Castillo, 1952 (55) (synonym of *Wy. aphobema*). Levi-Castillo also described two subspecies of *An. anopheles pseudopunctipennis*: *An. Ano. pseudopunctipennis* ssp. *levicastilloi* (1944a) and *An. Ano. pseudopunctipennis* ssp. *rivadeneirai* (1945b) which to the present day are still recognized as valid (20).

Given Levi-Castillo's contributions to dipterology, in 1945, John Lane described *Cx. levicastilloi* from specimens probably sent by Levi-Castillo from Ecuador (89). Interestingly, there is also a mosquito from Madagascar, *Mymomyia (Ingramia) levicastilloi* described by French entomologist Alexis Grjebine (1918-1988) in 1986 (90). Levi-Castillo probably met Grjebine in 1943 during his tour of duty around Europe (see section above).

For the most part, and concurring with the report by Zavortink (87), mosquito specimens of Levi-Castillo that were kept at the *Centro Ecuatoriano de Investigaciones Entomológicas* (CIEI), in Guayaquil seem to have been lost. To our knowledge, the only existing collection by Levi-Castillo seems to be the slides deposited at the U.S. National Entomology Collections (USNM) as reported by Zavortink (87), and some adult types deposited at this same museum (*Cx. babahoyensis* and *Hg. soperi*) (20). The whereabouts of the remaining specimens are currently unknown. It might be possible that his collection at the CIEI suffered a fate similar to that of his books when Levi-Castillo decided to abandon his entomological studies. Throughout his career, Levi-Castillo published a total of 65 papers, and we are confident that we have searched and included if not all, most of his production, particularly that dealing with mosquito taxonomy. Interestingly, both Campos-Rivadeneira and Levi-Castillo published their studies as single authors in the majority of their publications.

A comment on the practice of science in Latin America during the first half of the 20th century

The reasons for the success or failure of both Campos-Rivadeneira and Levi-Castillo as scientists rely on a shared set of characteristics that appropriately represent the cultural and economic conditions that permeated most of the 20th century in Ecuador and that affected how science and technology developed in this country.

Both Campos-Rivadeneira and Levi-Castillo lived at a time when the fate of Latin American countries was determined by an intense focus on the export of unprocessed materials and goods with little added value in knowledge and technology (91,92). As a consequence, the majority of the population in Ecuador remained excluded from the development of new ideas, which reinforced their detachment from scientific inquiry and innovation and, thus, were not agents of societal change (93).

The lives and accomplishments as scientists of both Campos-Rivadeneira and Levi-Castillo share common ground in the fact that both were able to transcend the limitations of their time and society by privileged social and economic conditions. Their families belonged to a favorable combination of strong intellectual traditions, foreign higher education, and auspicious social connections. Even under such unique circumstances, both scientists performed under conditions defined by limited resources, low salaries, inadequate equipment, small libraries, isolation from scientific networks, and political instability (94), which have historically plagued the practice of science in Latin America.

The dependence on foreign education and cultural and professional connections to Europe and North America was also an essential component of the lives and professional careers of these Ecuadorian scientists. Without such foreign influence and support, it would have been nearly impossible for both to accomplish the productivity and notoriety for which they are now remembered at least within the narrow spectrum of Ecuadorian entomologists and historians. The exogenous influence in the contributions to science by Campos-Rivadeneira and Levi-Castillo was also related to how Latin American countries invested in science as an engine for rapid economic development. Contrary to the medical focus that characterized the research of these two scientists, very few success stories are known from Latin American scientists in theoretical and non-applied sciences (95).

It has not been our intention to discuss the lives of these two scientists within a robust philosophical framework on the history of Latin American science, akin to the elaborate discussions in the field such as those of Saldaña (95). Nonetheless, we believe the lives of both Campos-Rivadeneira and Levi-Castillo could be considered as generalized paradigms that represent not only the political and social standards for the practice and development of science during the first half of the 20th century in Ecuador, but also as figures that exemplify the overall conditions for the practice of science throughout most of the Latin American history. We could argue that, until recently, to be a successful scientist in Ecuador and most parts of Latin America, one needed to share similar conditions to the lives of both scientists discussed in this manuscript, including social and political connections enabling the support of government authorities to fund science activities directly connected to economic and productive concerns.

One should also regret the anticlimactic end of the scientific careers of both Campos-Rivadeneira and Levi-Castillo. Despite their sustained efforts to nurture and capitalize their individual scientific interests, they were never able to establish a self-sustained school of thought, through students and pupils who could have kept alive and improve on their contributions. This failure may have been related to the poor record of Ecuadorian higher education institutions, which for the most part of the 20th century subsisted in a system which was ‘impossible to explain, to evaluate, nor to defend on grounds of equity, efficiency, quality or its contribution to national development’ (96).

The lives of Campos-Rivadeneira and Levi-Castillo are examples of fortitude and perseverance through difficult times, something that has characterized many Latin American scientists. It is through these difficulties and continuous struggle against the adversities of their culture and economies that it is possible to represent at least a particular aspect of the history of science in Latin America.

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Supplementary material

List of mosquito species collected, described, and reported by F. Campos-Rivadeneira and R. Levi-Castillo for Ecuador. For each species, the collection localities reported on their publications are listed.

Subfamily Anophelinae

Genus *Anopheles* Meigen, 1818

Subgenus *Anopheles* Meigen, 1818

1. *Anopheles (Anopheles) apicimacula* Dyar & Knab, 1906. Guayas, El Oro, Los Ríos, Manabí, and Esmeraldas (1). No specific locality data (2).
2. *Anopheles (Anopheles) eiseni* Coquillett, 1902. Esmeraldas, Manabí, Guayas, Los Ríos, El Oro, Chimborazo, Pichincha, Azuay, Cañar, Loja, Cotopaxi, Imbabura, and Carchi. Up to 2000 m (1). No specific locality data (2).
3. *Anopheles (Anopheles) mediopunctatus* Lutz, 1903. Guayas: Guayaquil and its surroundings (3). Esmeraldas, Los Ríos, Manabí, and Guayas (1). No specific locality data (Levi-Castillo 1958).
4. *Anopheles (Anopheles) neomaculipalpus* Curry, 1931. Cañar, Azuay, and Loja (2).
5. *Anopheles (Anopheles) peryassui* Dyar & Knab, 1908. No specific locality data (2).
6. *Anopheles (Anopheles) pseudopunctipennis* Theobald, 1901. Guayas: Guayaquil and its surroundings (3). Guayas: Milagro (4). From sea level up to 2500 m (1).
7. *Anopheles (Anopheles) pseudopunctipennis* ssp. *Levicastilloi* Levi-Castillo 1944. Type locality: Ecuador, Guayas, from Bucay to Progreso (5). Guayas: Bucay (1). Coastal lowland regions up to 300 MASL; provinces of Esmeraldas, Manabí, Los Ríos, Guayas, and El Oro (1). No specific locality data (5).
8. *Anopheles (Anopheles) pseudopunctipennis* ssp. *rivadeneirai* Levi-Castillo 1945. Type locality: Ecuador, Inter-Andean region valleys up to 2500 MASL, provinces of Carchi, Imbabura, Pichincha, Cotopaxi, Tungurahua, Chimborazo, Cañar, Azuay, and Loja (1). Pichincha: Los Chillós Valley (6). No specific locality data (2).
9. *Anopheles (Anopheles) punctimacula* Dyar & Knab, 1906. Guayas: Guayaquil and its surroundings, Chobo, Barraganetal, San Rafael (3,7). Guayas: Guayaquil (8). Guayas: Milagro (4). El Oro, Los Ríos, Esmeraldas, Manabí, Guayas, up to 280 m (1).
10. *Anopheles (Anopheles) shannoni* Davis, 1931. No specific locality data (2).

Subgenus *Kerteszia* Theobald, 1905

11. *Anopheles (Kerteszia) boliviensis* (Theobald, 1905). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (1).
12. *Anopheles (Kerteszia) homunculus* Komp, 1937. No specific locality data (2).
13. *Anopheles (Kerteszia) neivai* Howard, Dyar & Knab, 1913. Guayas: Guayaquil, Posorja (3,7). Esmeraldas, Manabí, Guayas, El Oro, Los Ríos (1).

Subgenus *Lophopodomyia* Antunes, 1937

14. *Anopheles (Lophopodomyia) gomezdelatorrei* Levi-Castillo, 1955. Type locality: Ecuador, Carchi, Chiltazon, altitude 2,880 m, cave (2,9).
15. *Anopheles (Lophopodomyia) squamifemur* Antunes, 1937. No specific locality data (2).
16. *Anopheles (Lophopodomyia) vargasi*. Gabaldón, Cova García & López, 1941. No specific locality data (2).

Subgenus *Nyssorhynchus* Blanchard, 1902

17. *Anopheles (Nyssorhynchus) albimanus* Wiedemann, 1820. Guayas: Guayaquil (8). Guayas: Guayaquil, Durán, San Rafael, Posorja (3). Guayas: Milagro (4). Guayas, El Oro, Manabí, Los Ríos, Esmeraldas (1). No specific locality data (2).
18. *Anopheles (Nyssorhynchus) aquasalis* Curry, 1932. Esmeraldas, Guayas, Manabí, Santa Elena: Palmar, El Oro (1).
19. *Anopheles (Nyssorhynchus) argyritarsis* Robineau-Desvoidy, 1827. No specific locality data (2).
20. *Anopheles (Nyssorhynchus) darlingi* Root, 1926. No specific locality data (2).
21. *Anopheles (Nyssorhynchus) oswaldoi* (Peryassú, 1922). No specific locality data (2).
22. *Anopheles (Nyssorhynchus) rangeli* Gabaldón, Cova García & López, 1940. No specific locality data (2).
23. *Anopheles (Nyssorhynchus) strodei* Root, 1926. No specific locality data (2).

Subgenus *Stethomyia* Theobald, 1902

24. *Anopheles (Stethomyia) acanthotorynus* Komp, 1937. No specific locality data (2).
25. *Anopheles (Stethomyia) kompi* Edwards, 1930. No specific locality data (2,10).

Genus *Chagasia* Cruz, 1906

26. *Chagasia bathana* (Dyar, 1928). Guayas: Road to Salinas, Manabí (1). No specific locality data (2).

Subfamily Culicinae

Genus *Aedeomyia* Theobald, 1901

Subgenus *Aedeomyia* Theobald, 1901

27. *Aedeomyia (Aedeomyia) squamipennis* (Lynch Arribáizaga, 1878). Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Yaguachi, Milagro, Salitre (11). Guayas, Los Ríos, El Oro (12).

Genus *Aedes sensu* Meigen, 1818

Subgenus *Georgecraigius* Reinert, Harbach & Kitching, 2006

28. *Aedes (Georgecraigius) fluviatilis* (Lutz, 1904). Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Arajuno, Shell-Mera (11). No specific locality data (2).

Subgenus *Howardina* Theobald, 1903

29. *Aedes (Howardina) albonotatus* (Coquillett, 1906). Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé (11). Pichincha, Imbabura, Bolivar and Chimborazo (10). No specific locality data (2).
30. *Aedes (Howardina) pseudodominicii* Komp, 1936. Napo (formerly Napo-Pastaza): Ila, Napo, Tena (11). Napo (formerly Napo-Pastaza) (10).
31. *Aedes (Howardina) quadrivittatus* (Coquillett, 1902). Azuay, Cañar, Pichincha, and Imbabura (10). No specific locality data (2).
32. *Aedes (Howardina) sexlineatus* (Theobald, 1901). Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Arajuno (11).

Subgenus *Ochlerotatus* Lynch Arribáizaga, 1891

33. *Aedes (Ochlerotatus) angustivittatus* Dyar & Knab, 1907. Napo (formerly Napo-Pastaza): Tena, Ila, Napo;

- Pastaza (formerly Napo-Pastaza): Puyo (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
34. *Aedes (Ochlerotatus) euplocamus* Dyar & Knab, 1906. Guayas: Milagro (4).
35. *Aedes (Ochlerotatus) fulvus* (Wiedemann, 1828). Guayaquil and its surroundings (3,7).
36. *Aedes (Ochlerotatus) milleri* Dyar, 1922. Cañar, Loja, Chimborazo, Cotopaxi, Pichincha, Imbabura, Azuay: Cuenca, Río Tomebamba, 2600 m (13); Monay, Paute, Girón, Azogues, and Biblián (14). No specific locality data (2).
37. *Aedes (Ochlerotatus) scapularis* (Rondani, 1848). Guayas: Guayaquil, El Salado, Durán (3,7). Guayas: Guayaquil (8). Guayas: Milagro (4). Guayas: Guayaquil, Chongón, Puná, Yaguachi, Milagro; Napo (formerly Napo-Pastaza): Tena, Ila, Napo (11). Guayas, El Oro, Los Ríos, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
38. *Aedes (Ochlerotatus) serratus* (Theobald, 1901). Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé, Viche (11). Guayas, Manabí, Esmeraldas, Pichincha, Los Ríos, and Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
39. *Aedes (Ochlerotatus) taeniorhynchus* (Wiedemann, 1821). Guayas: Guayaquil, Durán, Posorja (3,7). Guayas: Milagro (4). Guayas: Guayaquil, Yaguachi, Milagro, Puná (11). Guayas, Manabí, Esmeraldas, El Oro, Galápagos (10). No specific locality data (2).

Subgenus *Protomacleaya* Theobald, 1907

40. *Aedes (Protomacleaya) metoecopus* Dyar, 1925. Guayas: Guayaquil and its surroundings (3). Guayas, Manabí, Los Ríos (10). No specific locality data (2).
41. *Aedes (Protomacleaya) terreus* (Walker, 1856). Guayas: Guayaquil, Yaguachi, Milagro, Pascuales, Chongón, Progreso; Manabí: Chone, Calceta, Santa Ana; Esmeraldas: Quinindé (11).

Genus *Coquillettidia* Dyar, 1905

Subgenus *Rynchotaenia* Brethés, 1910

42. *Coquillettidia (Rynchotaenia) nigricans* (Coquillett, 1904). Los Ríos (10). No specific locality data (2).

Genus *Culex* Linnaeus, 1758

Subgenus *Aedinus* Lutz, 1904

43. *Culex (Aedinus) amazonensis* (Lutz, 1905). No specific locality data (2).

Subgenus *Anoediopora* Dyar, 1923

44. *Culex (Anoediopora) conservator* Dyar & Knab, 1906. No specific locality data (2).
45. *Culex (Anoediopora) originator* Gordon & Evans, 1922. No specific locality data (2).

Subgenus *Carrollia* Lutz, 1905

46. *Culex (Carrollia) babahoyensis* Levi-Castillo, 1953. Type locality: Ecuador, Los Ríos: Juan Montalvo, Hacienda "Mora" (15,16). Los Ríos (10). No specific locality data (2).
47. *Culex (Carrollia) bihaicola* Dyar & Nuñez Tovar, 1927. Santo Domingo de los Tsáchilas: Santo Domingo de los Colorados (formerly part of Esmeraldas); Esmeraldas: Quinindé (11). Guayas, Manabí, Esmeraldas, and Pichincha (10).
48. *Culex (Carrollia) infoliatu*s Bonne-Wepster & Bonne, 1920. Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Puyo, Shell-Mera, Mera (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

49. *Culex (Carrollia) iridescens* Lutz, 1905. Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (17). Napo (formerly Napo-Pastaza): Tena, Ila, Napo, Canelos; Pastaza (formerly Napo-Pastaza): Puyo, Canelos (11). No specific locality data (2).
50. *Culex (Carrollia) metempsytus* Dyar, 1921. Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Arajuno, Shell-Mera (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17).
51. *Culex (Carrollia) secundus* Bonne-Wepster & Bonne, 1920. Pastaza (formerly Napo-Pastaza): Tena, Arajuno, Shell-Mera (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
52. *Culex (Carrollia) urichii* (Coquillett, 1906). Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Arajuno (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

Subgenus *Culex* Linnaeus, 1758

53. *Culex (Culex) archegus* Dyar, 1929. Azuay: Cuenca, Monay (11). Azuay: Cuenca (18,19).
54. *Culex (Culex) articularis* Philippi, 1865. Azuay, Cañar, Chimborazo y Loja (10). No specific locality data (2).
55. *Culex (Culex) camposi* Dyar, 1925. Synonym: *Culex coronatorcamposi*, resurrected from syn *coronator* Bram, 1967. Guayas: Guayaquil, Chongón, Yaguachi, Milagro; Los Ríos: Baba, Vinces, Babahoyo, Mocache, Palenque, Quevedo; El Oro: Machala, Puerto Bolívar, Santa Rosa, La Emerenciana, Piñas, Portovelo (11). Guayas, El Oro, Los Ríos (10,17). No specific locality data (2).
56. *Culex (Culex) chidesteri* Dyar, 1921. Napo: Tena, Ila (11). Napo, Orellana, Pastaza (formerly Napo-Pastaza), Morona-Santiago and Zamora-Chinchipe (10,17).
57. *Culex (Culex) coronator* Dyar & Knab, 1906. Guayas: Guayaquil, Durán (3,7). Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Puyo (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
58. *Culex (Culex) guayasi* Levi-Castillo, 1953. Type locality: Ecuador, Babahoyo, Los Ríos(10,20). Los Ríos (10). No specific locality data (2).
59. *Culex (Culex) levicastilloi* Lane, 1945. El Oro: Machala, Santa Rosa, La Emerenciana, Puerto Bolívar(11).El Oro (10). No specific locality data (2).
60. *Culex (Culex) maracayensis* Evans, 1923. No specific locality data (2).
61. *Culex (Culex) mollis* Dyar & Knab, 1906. Guayas: Guayaquil, Tenguel; El Oro: Machala, Puerto Bolívar; Los Ríos: Babahoyo, Vinces, Palenque; Esmeraldas: Esmeraldas, Táchina, Limones; Manabí: Jipijapa, Chone, Santa Ana, Calceta; Napo (formerly Napo-Pastaza): Ila, Napo, Tena (11). Guayas, El Oro, Los Ríos, Manabí, Esmeraldas, Napo (formerly Napo-Pastaza) and Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
62. *Culex (Culex) nigripalpus* Theobald, 1901. Guayas: Guayaquil and its surroundings (3,7). Guayas: Milagro (4). Guayas: Guayaquil, Yaguachi, Milagro, Venecia, Pascuales, Tenguel, Puná, Chongón, Progreso, Balzar; El Oro: Machala, Puerto Bolívar, Pasaje; Manabí: Portoviejo, Manta; Esmeraldas: Táchina, Quinindé; Los Ríos: Vinces, Mocache, Palenque, Quevedo, Baba, Babahoyo; Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Shell-Mera (11). Guayas, El Oro, Manabí, Los Ríos, Esmeraldas, Napo (formerly Napo-Pastaza), and Morona-Santiago (formerly Santiago-Zamora) (10,17). Azuay: Zhurucuchu and Lullucchas regions (21). No specific locality data (2).
63. *Culex (Culex) quinquefasciatus* Say, 1823. Guayas: Guayas: Guayas: Guayaquil, Durán. Naranjal (3,7). Guayas: Milagro (4). Bolívar (formerly part of Los Ríos): Balsapamba; Guayas: Guayaquil, Chongón, Yaguachi, Milagro, Venecia, Naranjito, Bucay, Progreso, General Villamil, Pascuales, La Toma, Manglaralto, Tenguel,

Puná, Balzar, Daule; Los Ríos: Babahoyo, Baba, Vinces, Jujan, Mocache, Palenque, Quevedo, La Angélica, Barreiro, Montalvo, Playas de Vinces; Esmeraldas: Esmeraldas, Táchina, Quinindé, Río Verde, Limones; El Oro: Machala, Puerto Bolívar, La Emerenciana, Bellavista, Santa Rosa, El Guabo, Pasaje; Manabí: Portoviejo, Manta, Bahía, Junín, Chone, Calceta, Santa Ana, Jipijapa, Puerto Cayo, Machalilla, San Vicente (11). Guayas, El Oro, Los Ríos, Manabí, Esmeraldas, Islas Galápagos, Napo (formerly Napo-Pastaza), and Morona-Santiago (formerly Santiago-Zamora) (10,17). Guayas: Guayaquil (22). No specific locality data (2).

64. *Culex (Culex) quitensis* Levi-Castillo, 1953. Type locality: Ecuador, Pichincha, Quito (18). Cotopaxi, Pichincha, and Imbabura (10). No specific locality data (2).

65. *Culex (Culex) usquatissimus* Dyar, 1922. Guayas: Guayaquil and its surroundings (3).

Subgenus *Melanoconion* Theobald, 1903

66. *Culex (Melanoconion) albinensis* Bonne-Wepster & Bonne, 1920. No specific locality data (2).

67. *Culex (Melanoconion) bastagarius* Dyar & Knab, 1906. Napo (formerly Napo-Pastaza): Tena, Napo; Pastaza (formerly Napo-Pastaza): Puyo (11). Los Ríos, Guayas, Napo (formerly Napo-Pastaza) (10). Morona-Santiago (formerly Santiago-Zamora) (17). No specific locality data (2).

68. *Culex (Melanoconion) comatus* Senevet & Abonnenc, 1939. No specific locality data (2).

69. *Culex (Melanoconion) conspirator* Dyar & Knab, 1906. Guayas: Guayaquil and its surroundings (3). Guayas, Los Ríos, Manabí, Esmeraldas, and El Oro (17). No specific locality data (2).

70. *Culex (Melanoconion) distinguendus* Dyar, 1928. Napo (formerly Napo-Pastaza): Tena (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

71. *Culex (Melanoconion) dunni* Dyar, 1918. Napo (formerly Napo-Pastaza): Tena, Napo, Ila (11). Los Ríos, Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

72. *Culex (Melanoconion) eastor* Dyar, 1920. Pastaza (formerly Napo-Pastaza): Arajuno (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

73. *Culex (Melanoconion) educator* Dyar & Knab, 1906. Pastaza (formerly Napo-Pastaza): Mera, Shell-Mera, Puyo (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

74. *Culex (Melanoconion) elevator* Dyar & Knab, 1906. Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Puyo (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

75. *Culex (Melanoconion) erraticus* (Dyar & Knab, 1906). Los Ríos (10). No specific locality data (2).

76. *Culex (Melanoconion) innovator* Evans, 1924. No specific locality data (2).

77. *Culex (Melanoconion) inhibitor* Dyar & Knab, 1906. Napo (formerly Napo-Pastaza): Tena, Ila, Napo (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

78. *Culex (Melanoconion) iolambdis* Dyar, 1918. No specific locality data (2).

79. *Culex (Melanoconion) madininensis* Senevert, 1936. No specific locality data (2).

80. *Culex (Melanoconion) phlogistus* Dyar, 1920. Los Ríos(10). No specific locality data (2).

81. *Culex (Melanoconion) pilosus* Lee, 1946. Guayas: Guayaquil and its surroundings (3,7). Guayas, Guayas: Guayaquil, Yaguachi, Milagro, Pascuales; Los Ríos: Baba, Babahoyo, Vinces, Mocache; El Oro: Machala, Santa Rosa, Pasaje, La Emerenciana, Bellavista; Esmeraldas: Esmeraldas, Limones, Río Verde, Táchina; Napo (formerly Napo-Pastaza):Ila, Napo, Tena; Pastaza (formerly Napo-Pastaza): Arajuno (11). Guayas, El Oro, Los Ríos, Manabí, Esmeraldas, Napo (formerly Napo-Pastaza) and Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

82. *Culex (Melanoconion) plectoporpe* Root, 1927. No specific locality data (2).
83. *Culex (Melanoconion) putumayensis* Matheson, 1934. Pastaza (formerly Napo-Pastaza): Arajuno (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
84. *Culex (Melanoconion) saramaccensis* Bonne-Wepster & Bonne, 1920. Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (17).
85. *Culex (Melanoconion) spissipes* (Theobald, 1903). No specific locality data (2).
86. *Culex (Melanoconion) taeniopus* Dyar & Knab, 1907. Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Puyo (11). Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
87. *Culex (Melanoconion) theobaldi* (Lutz, 1904). Los Ríos, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Subgenus *Microculex* Theobald, 1907

88. *Culex (Microculex) chryselatus* Dyar & Knab, 1919. Napo (formerly Napo-Pastaza): Tena; Pastaza: Arajuno (11). Napo, (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
89. *Culex (Microculex) imitator* Theobald, 1903. Napo (formerly Napo-Pastaza): Tena, Napo; Pastaza (formerly Napo-Pastaza): Shell-Mera, Arajuno (11). Guayas, Los Ríos, Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).
90. *Culex (Microculex) stonei* Lane & Whitman, 1943. Napo (formerly Napo-Pastaza): Tena, Napo; Pastaza (formerly Napo-Pastaza): Arajuno (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Subgenus *Phenacomyia* Harbach & Peyton, 1992

91. *Culex (Phenacomyia) corniger* Theobald, 1903. Guayas: Guayaquil, San Rafael (23). Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón, Pascuales, Puná; Los Ríos: Vinces, Mocache, Quevedo; Esmeraldas: Esmeraldas, Limones; El Oro: Machala, Puerto Bolívar, Santa Rosa; Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Puyo, Shell-Mera, Mera, Arajuno (11). Guayas, El Oro, Manabí, Los Ríos, Esmeraldas, Napo (formerly Napo-Pastaza), and Morona-Santiago (formerly Santiago-Zamora) (10,17). No specific locality data (2).

Subgenus uncertain

92. *Culex (Subgenus uncertain) aikenii* Aiken & Rowland, 1906. *Nomen dubium* (24). Los Ríos (10). No specific locality data (2).
93. *Culex (Subgenus uncertain) ocellatus* Theobald, 1903. Napo (formerly Napo-Pastaza): Tena, Ila; Pastaza (formerly Napo-Pastaza): Arajuno (11). Napo (formerly Napo-Pastaza), Morona-Santiago (17).

Genus *Haemagogus* Williston, 1986

Subgenus *Conopostegus* Dyar, 1925

94. *Haemagogus (Conopostegus) leucocelaenus* (Dyar & Shannon, 1924). Napo (formerly Napo-Pastaza): Tena, Ila, Napo (11). Napo (formerly Napo-Pastaza) (10).
95. *Haemagogus (Conopostegus) leucotaeniatus* (Komp, 1938). Esmeraldas: Quinindé (11). Esmeraldas, Manabí, and Pichincha (10). No specific locality data (2).

Subgenus *Haemagogus* Williston, 1986

96. *Haemagogus (Haemagogus) albomaculatus* Theobald, 1903. Guayas: El Salado (7).

97. *Haemagogus (Haemagogus) boshelli*. Osorno-Mesa, 1944. Synonym: *Haemagogus garciai* Levi-Castillo, 1955. Esmeraldas: Isla de Changuaral (12,25). No specific locality data (2).
98. *Haemagogus (Haemagogus) equinus* (Theobald, 1903). Guayas: El Salado (7). Later, Levi-Castillo (26) claimed that this species was absent from Ecuador.
99. *Haemagogus (Haemagogus) janthinomys* Dyar, 1921. Napo (formerly Napo-Pastaza), Morona-Santiago (formerly Santiago-Zamora) (27). Esmeraldas (26). No specific locality data (2).
100. *Haemagogus (Haemagogus) panarchys* Dyar, 1921. Guayas: Guayaquil and its surroundings (3). Guayas: Milagro (4). Guayas: Guayaquil, Guayaquil-Salinas road Km.3, Chongón or Colonche Mountain Range(28). Guayas: Guayaquil, Chongón, Progreso, Yaguachi, Milagro (11). Guayas, El Oro, Los Ríos, Manabí (10,12). "Chongón or Colonche Mountain Range" (actually includes the provinces of Guayas, Manabí, and Esmeraldas) (29). No specific locality data (2)..
101. *Haemagogus (Haemagogus) soperi* Levi-Castillo, 1955. Type locality: Ecuador, Los Ríos, Juan Montalvo (30). Esmeraldas; Manabí; El Oro: Santa Rosa (31). No specific locality data (2).
102. *Haemagogus (Haemagogus) spegazzinii* Brethés, 1912. Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé, Viche; Manabí: Santa Ana, Chone, Jama, Calceta; Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Puyo, Arajuno, Shell-Mera, Mera (11). Santo Domingo de los Tsáchilas: Santo Domingo de los Colorados (32).

Genus *Limatus* Theobald, 1901

103. *Limatus andinus* Levi-Castillo, 1954. Type locality: Ecuador, Los Ríos, Valencia (33). No specific locality data (2).
104. *Limatus durhamii* Theobald, 1901. Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón, Progreso, Yaguachi, Milagro (11). Guayas, Los Ríos, Manabí, Esmeraldas, and El Oro (10).
105. *Limatus guayasi* Levi-Castillo, 1954. Type locality: Ecuador, Guayas, El Empalme (33). No specific locality data (2).

Genus *Lutzia* Theobald, 1903

Subgenus *Lutzia* Theobald, 1903

106. *Lutzia (Lutzia) allostigma* (Howard, Dyar & Knab, 1915). No specific locality data (2).
107. *Lutzia (Lutzia) bigoti* Bellardi, 1862. No specific locality data (2).

Genus *Mansonia* Blanchard, 1901

Subgenus *Mansonia* Blanchard, 1901

108. *Mansonia (Mansonia) humeralis* Dyar & Knab, 1916. Napo (formerly Napo-Pastaza): Tena; Pastaza (formerly Napo-Pastaza): Canelos, Arajuno (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
109. *Mansonia (Mansonia) indubitans* Dyar & Shannon, 1925. El Oro: Machala, La Emerenciana, Bellavista, Santa Rosa; Manabí: Manta, Bahía de Caraquez, Chone, Calceta, Canuto (11). Guayas, El Oro, Manabí, Los Ríos, Esmeraldas (10). No specific locality data (2).
110. *Mansonia (Mansonia) pseudotitillans* Theobald, 1901. Guayas and Los Ríos (10). No specific locality data (2).
111. *Mansonia (Mansonia) titillans* (Walker, 1848). Guayas: Guayaquil (8). Guayas: Guayaquil, El Salado, Durán, Posorja; Los Ríos: Quevedo (3,7,34). Guayas: Guayaquil, Samborondón, Yaguachi, Milagro; Esmeraldas: Quinindé, Esmeraldas, Limones; Manabí: Jipijapa, Chone (11). No specific locality data (2).
112. *Mansonia (Mansonia) wilsoni* (Barreto & Coutinho, 1944). Manabí (10). No specific locality data (2)

Genus *Onirion* Peyton & Harbach, 2000

113. *Onirion personatum* (Lutz, 1904). Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé, Viche (11). Manabí, Esmeraldas, Los Ríos, Guayas, and Pichincha (10). No specific locality data (2).

Genus *Orthopodomyia* Theobald, 1904

114. *Orthopodomyia fascipes* (Coquillett, 1906). Napo (formerly Napo-Pastaza): Tena (11). Guayas, Los Ríos, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Genus *Psorophora* Robineau-Desvoidy, 1827

Subgenus *Grabhamia* Theobald, 1903

115. *Psorophora (Grabhamia) cingulata* Fabricius, 1805. Napo: Tena, Dos Ríos (35). No specific locality data (2).

116. *Psorophora (Grabhamia) confinnis* (Lynch Arribalzaga, 1891). Guayas, Manabí, Los Ríos(10). No specific locality data (2).

Subgenus *Janthinosoma* Lynch Arribálzaga, 1891

117. *Psorophora (Janthinosoma) cyanescens* (Coquillett, 1902). Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza: (formerly Napo-Pastaza): Puyo, Mera, Shell-Mera, Arajuno (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

118. *Psorophora (Janthinosoma) ferox* (Humboldt, 1819). Guayas: Guayaquil and its surroundings (3,7). Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Mera, Shell-Mera, Arajuno; Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé, Viche (11). Guayas, El Oro, Manabí, Esmeraldas, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

119. *Psorophora (Janthinosoma) lutzii* (Theobald, 1901). Guayas, Manabí, Los Ríos, Esmeraldas (formerly Napo-Pastaza) (10). No specific locality data(2).

Subgenus *Psorophora* Robineau-Desvoidy, 1827

120. *Psorophora (Psorophora) ciliata* Fabricius, 1794. Napo (formerly Napo-Pastaza): Tena, Ila, Napo (11). Manabí, Esmeraldas, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Genus *Sabethes* Robineau-Desvoidy, 1827

Subgenus *Peytonulus* Harbach, 1991

121. *Sabethes (Peytonulus) fabricii* Lane & Cerqueira, 1942. No specific locality data (2).

122. *Sabethes (Peytonulus) identicus* Dyar & Knab, 1907. Manabí: Santa Ana, Chone, Calceta, Canuto, Eloy Alfaro, Flavio Alfaro, Jama, Portoviejo, Colón, Junín, Jipijapa (11). Guayas, Manabí, Los Ríos (10). No specific locality data (2).

Subgenus *Sabethes* Robineau-Desvoidy, 1827

123. *Sabethes (Sabethes) bipartipes* Dyar & Knab, 1906. Guayas (Dyar 1925). Guayas: Guayaquil, Durán, Posorja (3,7,8). Guayas: Milagro (4). Guayas: Guayaquil, Pascuales, Yaguachi, Milagro, Chongón, Progreso, Cerecita, Nobol, Durán, Balzar, Daule (11). Guayas, El Oro, Manabí, Los Ríos (10). No specific locality data (2).

124. *Sabethes (Sabethes) cyaneus* (Fabricius, 1805). Esmeraldas: Quinindé; Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados (11). Manabí (10). No specific locality data (2).

Subgenus *Sabethoides* Theobald, 1903

125. *Sabethes (Sabethoides) chloropterus* (von Humboldt, 1819). Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón (11). Guayas, El Oro, Los Ríos, Manabí(10). No specific locality data (2).

Genus *Trichoprosopon* Theobald, 1901

126. *Trichoprosopon andinum* Levi-Castillo, 1953. Described as *andinus* (36). Type locality: Ecuador, Cotopaxi, Macuchi (36). No specific locality data (2).
127. *Trichoprosopon compressum* Lutz, 1905. Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé (11). Guayas, Los Ríos, Manabí, and Esmeraldas (10). No specific locality data (2).
128. *Trichoprosopon cotopaxense* Levi-Castillo, 1953. Described as *cotopaxensis*. Changed to *cotopaxense* (37). *Nomen dubium* possible syn. *Trichoprosopon digitatum* & *Johnbelkinia ulopus* (38). Provisionally accepted name (39). *Nomina dubia* (40). Type locality: Ecuador, Cotopaxi, Macuchi (36). No specific locality data (2)
129. *Trichoprosopon digitatum* (Rondani, 1848). Guayas: Guayaquil, Naranjal; El Oro: Machala (3,7). Guayas: Guayaquil, Chongón, Progreso, Tenguel, Puná; Santo Domingo de los Tsáchilas (formerly part of Esmeraldas): Santo Domingo de los Colorados; Esmeraldas: Quinindé (11). Guayas, Manabí, Esmeraldas, Pichincha, and Los Ríos (10). No specific locality data (2).
130. *Trichoprosopon evansae* Antunes, 1942. Napo (formerly Napo-Pastaza): Tena, Ila (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
131. *Trichoprosopon lanei* (Antunes, 1937). Synonym: *Goeldia lanei* Antunes, 1937. Napo (formerly Napo-Pastaza): Tena, Ila, Napo; Pastaza (formerly Napo-Pastaza): Puyo (11). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).
132. *Trichoprosopon vonplesseni* (Dyar & Knab, 1906). Napo (formerly Napo-Pastaza): Tena (11). Napo (formerly Napo-Pastaza) (10,41). No specific locality data (2).

Genus *Toxorhynchites* Theobald, 1901Subgenus *Lynchiella* Lahille, 1904

133. *Toxorhynchites (Lynchiella) bambusicola* Knight & Rozeboom, 1946. No specific locality data (2).
134. *Toxorhynchites (Lynchiella) haemorrhoidalis* (Fabricius, 1787). No specific locality data (2).
135. *Toxorhynchites (Lynchiella) haemorrhoidalis superbus* (Fabricius, 1787). Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón, Nobol, Puná, Tenguel (11). Guayas, Manabí, Los Ríos (10). No specific locality data (2).
136. *Toxorhynchites (Lynchiella) hypoptes* Knab, 1907. Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón, Puná (11). Guayas, Manabí, Esmeraldas, and Los Ríos (10). No specific locality data (2).
137. *Toxorhynchites (Lynchiella) theobaldi* (Dyar & Knab, 1906). No specific locality data (2).
138. *Toxorhynchites aequatorianus* Levi-Castillo, 1953. *Nomen dubium* (42). Type locality: Ecuador, Los Ríos: Pichilingue (43). No specific locality data (2).

Genus *Uranotaenia* Lynch Arribálzaga, 1891Subgenus *Uranotaenia* Lynch Arribálzaga, 1891

139. *Uranotaenia (Uranotaenia) aequatorianna* Levi-Castillo, 1953. Type locality: Los Ríos, Babahoyo (10). No specific locality data (2)
140. *Uranotaenia (Uranotaenia) geometrica* Theobald, 1901. Guayas: Guayaquil and its surroundings (3). Guayas: Guayaquil, Chongón, Nobol, Pascuales, Puna, Tenguel; El Oro: Machala, Santa Rosa, La Emerenciana, Tendales (11). Guayas, El Oro, Los Ríos, and Manabí (10). No specific locality data (2).
141. *Uranotaenia (Uranotaenia) leucoptera* (Theobald, 1907). Los Ríos (10). No specific locality data (2).

142. *Uranotaenia (Uranotaenia) lowii* Theobald, 1901. Guayas: Guayaquil and its surroundings (3,7). Bolívar (formerly part of Los Ríos): Balsapamba; Guayas: Guayaquil, Chongón, Nobol, Pascuales, Puna, Tenguel; El Oro: Machala, Pasaje, Santa Rosa, La Emerenciana, Bellavista; Manabí: Portoviejo, Manta, Chone, Santa Ana, Junín, Calceta, Tosagua, Bahía de Caraquez, San Vicente, Jipijapa, Paján; Esmeraldas: Esmeraldas, Quinindé, Río Verde, Táchina; Santo Domingo de los Tsáchilas: Santo Domingo de los Colorados (formerly part of Esmeraldas); Los Ríos: Babahoyo, Montalvo, Barreiro, Baba, Vines, Mocache, Palenque, Jujan (11). Guayas, Los Ríos, Manabí, Esmeraldas (10). No specific locality data (2).
143. *Uranotaenia (Uranotaenia) pulcherrima* Lynch Arribálzaga, 1891. Guayas: Guayaquil and its surroundings (3). Los Ríos and Guayas (10). No specific locality data (2).
144. *Uranotaenia (Uranotaenia) sapphirina* (Osten Sacken, 1868). Guayas: Guayaquil (8). Los Ríos and Guayas (10). No specific locality data (2).

Genus *Wyeomyia* Theobald, 1901

Subgenus *Dendromyia* Theobald, 1903

145. *Wyeomyia (Dendromyia) complosa* (Dyar, 1928). No specific locality data (2).

Subgenus *Dodecamyia* Dyar, 1918

146. *Wyeomyia (Dodecamyia) aphobema* Dyar, 1918. Synonym: *Wyeomyia aphobema* var. *aequatorialis* Levi-Castillo, 1952. Napo (formerly Napo-Pastaza): near Tena (10,44) "mendeley": {"formattedCitation": "(10,44). No specific locality data (2).

Subgenus *Hystatomyia* Dyar, 1919

147. *Wyeomyia (Hystatomyia) esmeraldasii* (Levi-Castillo, 1955). Described as *Phoniomyia esmeraldasii* by Levi-Castillo (1955). Type locality: Ecuador, Esmeraldas, Island of Changuaral, Ancón de Sardinias Bay (30). No specific locality data (2).

Subgenus *Miamyia* Dyar, 1919

148. *Wyeomyia (Miamyia) codiocampa* Dyar & Knab, 1907. Manabí, Esmeraldas, Guayas, Los Ríos, and El Oro (10). No specific locality data (2).

Subgenus *Nunezia* Dyar, 1928

149. *Wyeomyia (Nunezia) bicornis* (Root, 1928). Pastaza (formerly Napo-Pastaza): Arajuno (11). Manabí, Esmeraldas, and Napo (formerly Napo-Pastaza) (10).

Subgenus *Phoniomyia* Theobald, 1903

150. *Wyeomyia (Phoniomyia) lassalli* (Bonne-Wepster & Bonne, 1921). Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

151. *Wyeomyia (Phoniomyia) splendida* Bonne-Wepster & Bonne, 1919. Manabí, Esmeraldas, and Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Subgenus *Wyeomyia* Theobald, 1901

152. *Wyeomyia (Wyeomyia) melanopus* Dyar, 1919. No specific locality data (2).

153. *Wyeomyia (Wyeomyia) scotinomus* (Dyar & Knab, 1907). Napo (formerly Napo-Pastaza): Tena (11). Manabí, Esmeraldas, Los Ríos, and Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

Subgenus uncertain

154. *Wyeomyia* (Subgenus uncertain) *aequatorianna* Levi-Castillo, 1954. Type locality: Ecuador, Los Ríos, Hacienda Pichilingue (33). No specific locality data (2).

155. *Wyeomyia* (Subgenus uncertain) *amazonica* Levi-Castillo, 1954. Type locality: Ecuador, Napo, Tena. Pastaza (33). No specific locality data (2).
156. *Wyeomyia* (Subgenus uncertain) *chalcocephala* Dyar & Knab, 1906. No specific locality data (2).
157. *Wyeomyia* (Subgenus uncertain) *flui* (Bonne-Wepster & Bonne, 1920). No specific locality data (2).
158. *Wyeomyia melanocephala* Dyar & Knab, 1906. . Napo (formerly Napo-Pastaza): Tena, Ila; Pastaza (formerly Napo-Pastaza): Arajuno (11). Manabí, Esmeraldas, Guayas, Los Ríos, Napo (formerly Napo-Pastaza) (10). No specific locality data (2).

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