



Restriction of the Type Locality “Los Puentes”, Ecuador, for Several Species of Arachnida, Gastropoda and Plants

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“Los Puentes” in northwestern Ecuador has been cited as the type locality for several spider, gastropod, and plant taxa. Yet, earlier works ambiguously described it as “near Quito,” leading to confusion about its location. By examining historical documents, maps, and an official decree, I verify that “Los Puentes” lies near Nanegalito, Pichincha province, on the northwestern slopes of the Western Cordillera of the Andes of Ecuador, at 1200–1500 m elevation. I formally restrict the type locality for multiple species, including *Isomeria bourcieri lutea* Cousin 1887 (Gastropoda: Labyrinthidae), *Guestieria locardi* Jousseaume 1887 (Gastropoda: Scolodontidae), *Proserpinella cousini* Jousseaume 1887 (Gastropoda: Proserpinellidae), *Mesembrinus vesperus* Jousseaume 1887 (Gastropoda: Achatinidae), *Idiophthalma robusta* Simon 1889 (Arachnida: Barychelidae), *Eurypelma (Lasiodora) augusti* Simon 1889 (Arachnida: Theraphosidae), *Eurypelma (Lasiodora) vespertinus* Simon 1889 (Arachnida: Theraphosidae), *Asplundia nonoensis* Harling 1958 (Pandanales: Cyclanthaceae), and *Blakea eriocalyx* Wurdack 1979 (Myrtales: Melastomataceae), ensuring taxonomic clarity.

The precise definition of a type locality is fundamental in nomenclature, as it directly influences the stability of species names and underpins accurate assessments of distribution, ecology, and conservation status (ICZN 1999). When original locality descriptions are ambiguous or erroneous, subsequent researchers may misinterpret the geographical context where species exist, potentially leading to confusion in scientific literature. In northwestern Ecuador, “Los Puentes” has historically been cited as the type locality of several taxa of spiders, gastropods, and plants (Cousin 1887; Harling 1958; Jousseaume 1887; Simon 1889; Wurdack 1979) (Table 1). Yet, statements that it lies near Quito have complicated its precise location. This study resolves these inconsistencies by clarifying the exact location of “Los Puentes” and formally restricting the type locality for nine taxa, thereby promoting taxonomic clarity and supporting ongoing research in biogeography and conservation.

Cousin (1887) and Jousseaume (1887) were the earliest taxonomists to describe new taxa from specimens collected at “Los Puentes”. These included *Isomeria bourcieri lutea* Cousin 1887, *Guestieria locardi* Jousseaume 1887, *Mesembrinus vesperus* Jousseaume 1887, and *Proserpinella cousini* Jousseaume 1887 (Table 1). In Cousin’s most renowned publication, *Faune malacologique de la République de l’Équateur* (Cousin 1887), he regularly cited “Los Puentes, près Guala” [Los Puentes, near Guala] when discussing the distributions of several species (e.g., *Cyclophorus esmeraldensis*, *Mesembrinus visendus*, *Porphyrobaphe irroratus*, *Drymaeus petasites*, *Ammonoceras flora*, *Psadara selenostoma*, *Isomeria bourcieri*, and *Obeliscus cuneus*), noting that he found *Bourciera helicinaeformis* “Dans le chemin de Quito à Guala, vers Hacienda de Los Puentes” [On the road from Quito to Guala, towards Hacienda de Los Puentes]. Elsewhere, Cousin referred to “Los Puentes (paroisse de Calacoli[sic], prov. de Pichincha [sic])” [Los Puentes (parish of Calacalí, prov. of Pichincha)] for *Eurytus taylorianus*. Cousin also included details about the altitude of Los Puentes, stating “more or less 1500 m” for *M. visendus* and “about 1500 m” for *O. cuneus*. Pilsbry (1906) echoed this information, citing the locality as “Los Puentes near Guala at about 1500 meters... (Cousin)” for *O. cuneus*, based on Cousin’s (1887) statement.

Collections from Los Puentes during that period were primarily carried out by Auguste Edouard Cousin (Paris, 1835–Quito, 1899, see Breure 2020, Correoso Rodríguez 2020, Jarrín 2021, 2024). “Los Puentes” was one of the farms owned by the Cousin family in Ecuador, where they had sugar cane plantations (Jarrín 2021). In describing *Mesembrinus vesperus* (now *Zoniferella vespera*), Jousseaume (1887) noted that “A single example of this species was collected by our colleague, Mr. A. Cousin, in his property of Los Puentes, near Quito” (Cisneros-Heredia & Valencia 2023). Correoso Rodríguez (2020) likewise reported that “Los Puentes” was in northwestern Pichincha and that Auguste Cousin acquired the farm in 1866. Breure (2020) indicated that the label accompanying the types of *Proserpinella cousini* read “Los

Puentes San Fernandino”. However, photographs of those labels showed the inscription “Los Puentes S. Fernando” and not “Fernandino” (Breure 2020: figs. 31–32).

Later, Paul Rivet appears to have collected there during his expeditions of the Second Geodesic Mission to Ecuador, as Germain (1907, 1911) noted specimens of *Bulimus (Porphyrobaphe) irroratus* from “Los Puentes, road of Gualea”. Francisco Cousin, son of Auguste Cousin, was a friend of Rivet (Jarrín 2021, 2024) and likely hosted him at Cousin family’s farm in Los Puentes.

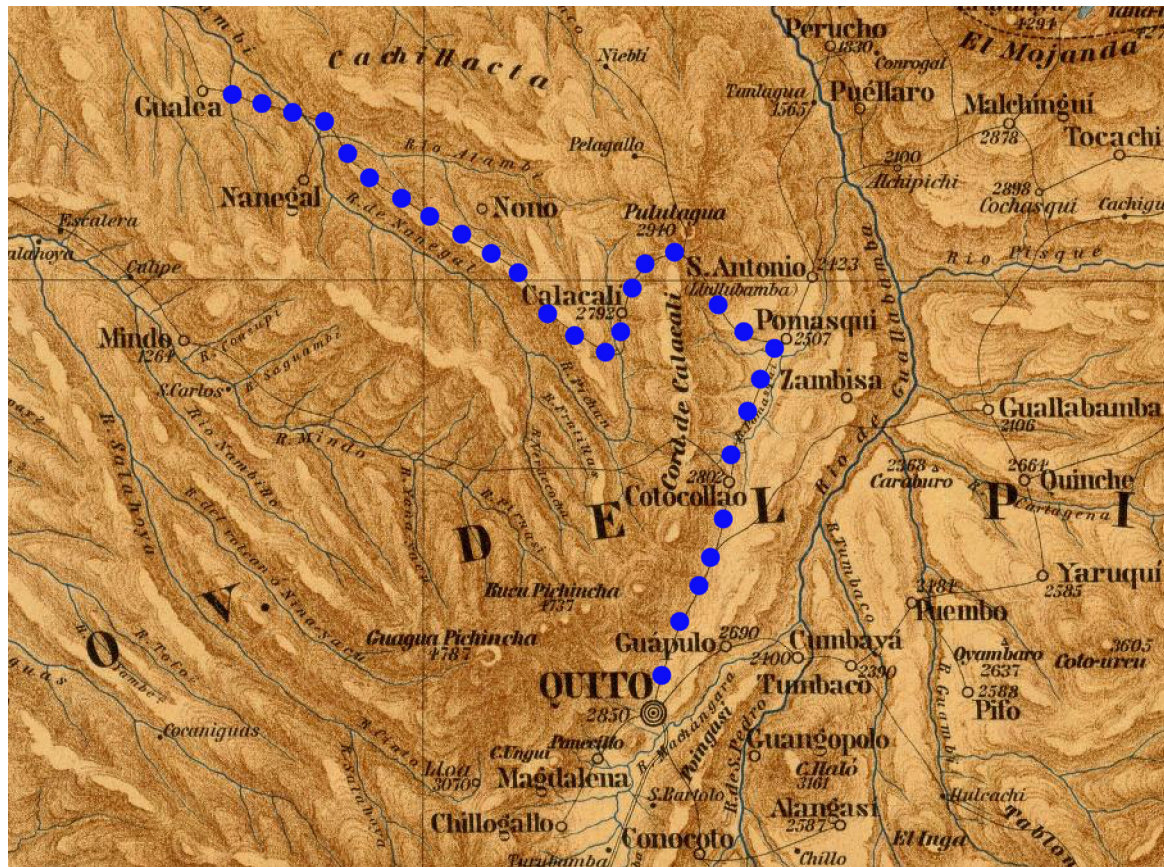


FIGURE 1. Section of the Carta Geográfica del Ecuador by Theodore Wolf (1892) indicating the Quito–Gualea bridle path (blue dots). Dark lines indicate roads and bridle paths.

Erik Asplund, collecting in August 1955, obtained at least 23 plant specimens at “Los Puentes”, including the holotypes of *Asplundia nonoensis* Harling, 1958 and *Blakea eriocalyx* Wurdack, 1979, now deposited at the Herbarium of the Naturhistoriska Riksmuseet. He recorded the type locality of these species as “Vicinity of Nanegal, Los Puentes” and “Los Puentes (near Nanegal towards Nono)”. He wrote “Los Puentes near Nanegal” or “Los Puentes on road from Nono to Nanegal” on labels of other specimens, referencing the elevation for all his specimens at ca. 1200 m.

Although most historical references to “Los Puentes” specified that it was on the western slopes of the Western Cordillera of the Andes in northern Ecuador, some authors have been misled by statements indicating that it was “near Quito”, which would place it within the inter-Andean valley of Quito (Hoya de Guayllabamba). For instance, Jousseume (1887) reported that Los Puentes was “near Quito” and Cousin (1887) wrote “Los Puentes, county of Quito” for *Isomeria cymatodes* and *Cyclotus fischeri*. Similarly, Correoso Rodríguez (2010) noted that *Rhodea aequatoria* was recorded from “Los Puentes near Quito” but also mentioned that this locality was in the lower basin of the River Guayllabamba.

Simon (1889), using specimens collected by A. Cousin, described three species of spiders from “Los Puentes” (Table 1). He reported the type localities of *Idiophthalma robusta* Simon, 1889 and *Eurypelma (Lasiodora) augusti* Simon, 1889 (now *Pamphobeteus augusti*) as “Los Puentes, près Quito” [Los Puentes, near Quito] and listed specimens of *Diplura longicauda* Ausserer, 1871 (now *Linothele longicauda*)—whose type locality is Quito—from “Los Puentes, near Quito”. Regarding *Cyclosternum schmardae*, Simon (1889) wrote, “nous l’avons en outre reçu de Los Puentes et de Rumipamba, aux environs de Quito, par M. A. Cousin” [we also received it from Los Puentes and Rumipamba, in the surroundings of Quito, from Mr. A. Cousin], implying that, like Rumipamba, Los Puentes was also situated within the inter-Andean valley of

Quito. Consequently, Petrunkevitch (1911) cited only Quito as the type locality of *Pamphobeteus augusti* and *Idiophthalma robusta*. Sherwood *et al.* (2022) similarly listed Quito as the type locality of *Pamphobeteus augusti* (Simon, 1889) while mentioning “Los Puentes” in the remarks and placed *Pamphobeteus vespertinum* (Simon, 1889) in the “West Ecuador dry forest” ecoregion, which would overlap with Quito. In a subsequent publication, Sherwood *et al.* (2023) re-evaluated “Los Puentes” based on an earlier version of the present study (Cisneros-Heredia & Valencia, 2022). “Los Puentes” was misspelt by Petrunkevitch (1911) when referring to the type locality of *Eurypelma (Lasiadora) vespertinum* (now *Pamphobeteus vespertinus*), and by Bertani *et al.* (2008) as “Los Fuentes” for the same species (Sherwood *et al.* 2022).

TABLE 1. List of species with the type locality of “Los Puentes” in Ecuador, in chronological order of their original descriptions.

Original species name	Current species name	Taxonomic classification
<i>Isomeria bourcieri lutea</i> Cousin, 1887	<i>Isomeria bourcieri lutea</i> Cousin	Animalia: Mollusca: Gastropoda: Labyrinthidae
<i>Guestieria locardi</i> Jousseume, 1887	<i>Guestieria locardi</i> Jousseume	Animalia: Mollusca: Gastropoda: Scolodontidae
<i>Mesembrinis vesperus</i> Jousseume, 1887	<i>Zoniferella vespera</i> (Jousseume)	Animalia: Mollusca: Gastropoda: Achatinidae
<i>Proserpinella cousini</i> Jousseume, 1887	<i>Archecharax cousini</i> (Jousseume)	Animalia: Mollusca: Gastropoda: Proserpinellidae
<i>Idiophthalma robusta</i> Simon, 1889	<i>Idiophthalma robusta</i> Simon	Animalia: Arthropoda: Arachnida: Barychelidae
<i>Eurypelma (Lasiadora) augusti</i> Simon, 1889	<i>Pamphobeteus augusti</i> (Simon)	Animalia: Arthropoda: Arachnida: Theraphosidae
<i>Eurypelma (Lasiadora) vespertinus</i> Simon, 1889	<i>Pamphobeteus vespertinus</i> (Simon)	Animalia: Arthropoda: Arachnida: Theraphosidae
<i>Asplundia nonoensis</i> Harling, 1958	<i>Asplundia nonoensis</i> Harling	Plantae: Angiospermae: Pandanales: Cyclanthaceae
<i>Blakea eriocalyx</i> Wurdack, 1979	<i>Blakea eriocalyx</i> Wurdack	Plantae: Angiospermae: Myrtales: Melastomataceae

The species of *Linothele* reported by Simon (1889) as *L. longicauda* likely does not belong to that taxon, given that *L. longicauda* is restricted to the inter-Andean basin of Quito (Ausserer 1871; Drolshagen & Bäckstam 2021; Dupérré *et al.* 2023; Peñaherrera-R *et al.* 2023). The specimen mentioned by Simon (1889) should be re-examined to determine if it corresponds to a previously described *Linothele* known from the northwestern slopes of the Andes of Ecuador (although, except for *L. zaia* Dupérré & Tapia, 2015, all others are known from much higher or lower elevations) or if it represents an undescribed species.

Historical documents provide additional evidence to clarify the precise location of “Los Puentes” by showing how travellers traversed the route between Quito and Gualea. The map by Wolf (1892) indicates a bridle path connecting Quito with Gualea, transversing north across the inter-Andean valley of Quito through the towns of Cotacollao and Pomasqui before ascending the Western Cordillera of the Andes via the mountain pass between the Casitagua and Pululahua mountains toward Calacalí and Nono, then descending the western slopes of the Andes to Nanegal and Gualea (Fig. 1). An executive decree issued by Eloy Alfaro, then president of Ecuador, on 14 June 1898 (Valdivieso 1898) also clarifies the location of Los Puentes. The decree, included in a report by Ricardo Valdivieso for the Ministry of Public Works presented to the Congress of 1899, was in response to requests for improving the local bridle path and noted that the farm “Los Puentes” was in the parish of Nanegal and on the Quito-Nono-Gualea road:

[Translation of the decree excerpt]

Art. 1º Repair the bridle path from Gualea to Nono.

Art. 2º For this work, the owners of rustic estates of the parish of Gualea will contribute, once only, with 7% of the value of their properties. The farms “Chiquilpe” of the parish of Nono and “Los Puentes” of Nanegal will contribute the same amount.

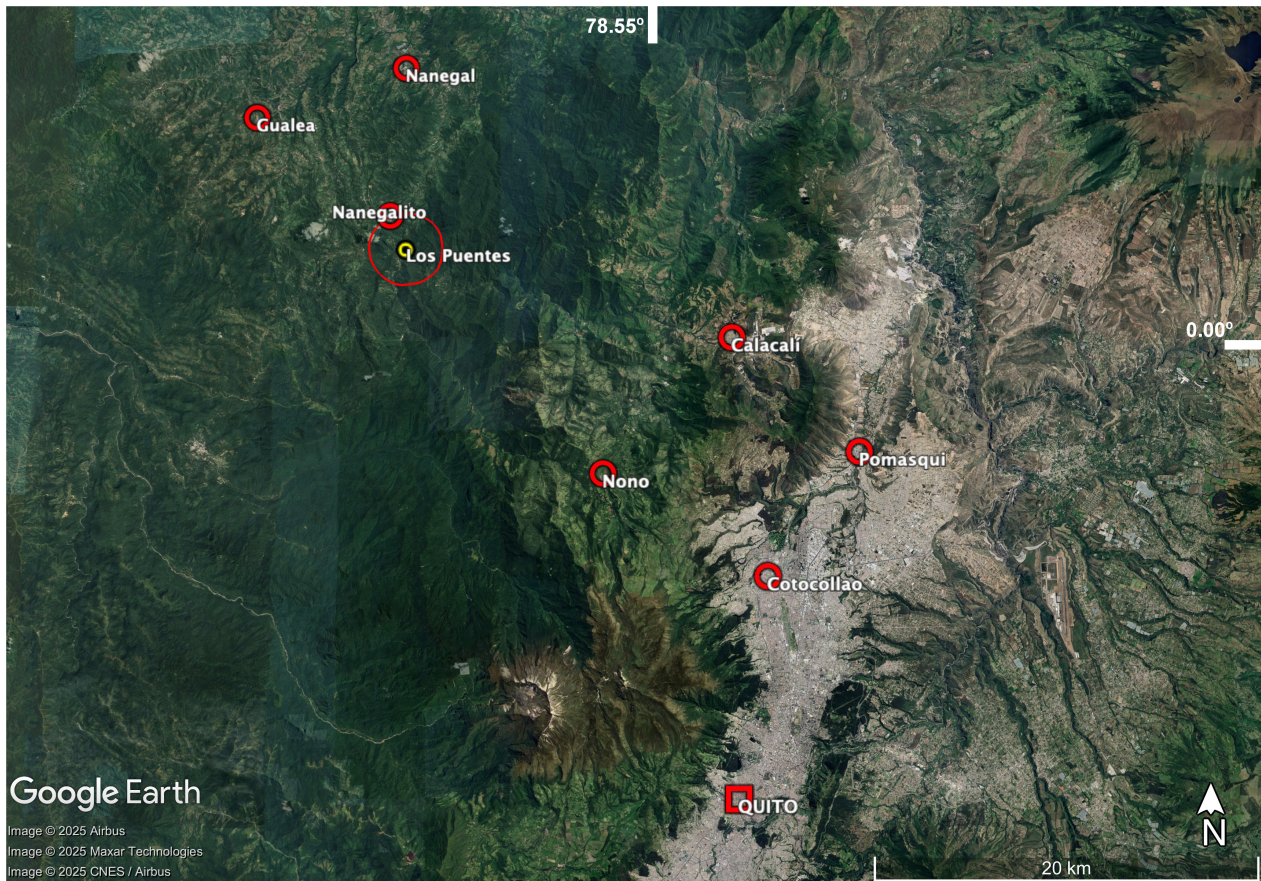


FIGURE 2. Map showing the location of “Los Puentes”, near Nanegalito, on the western slopes of the Western Cordillera of the Andes of northern Ecuador, at 1200–1500 m elevation, Pichincha province, Republic of Ecuador (red circle and yellow dot, coordinates focus point: 0.0458, -78.6742, radius: 2 km). Other localities mentioned in the text and Fig. 1 are also shown. A KMZ file showing these localities is available here: <https://doi.org/10.6084/m9.figshare.19297532>. Map images: Google, Landsat/Copernicus, Airbus, CNES/Airbus, Maxar Technologies.

During the second half of the 20th century, parts of the Quito-Nono-Guala bridle path served as the basis for constructing the Quito-Nono-Nanegalito road and later the Calacali-Nanegalito-Puerto Quito highway. “Los Puentes” literally means “the bridges” in Spanish. Although many bridges existed along the old bridle path from Quito to Guala in the 19th century, there is only one locality known by that name in the region. It is now classified as a neighbourhood of the parish of Nanegal (DIPLA 2023; GAD Pichincha 2017; IGM 1990) and lies near a confluence of rivers where large bridges were historically built. About 2 km northeast of this locality is an area referred to as “San Fernando Cuatro Hermanos”, which likely corresponds to the “S. Fernando” cited for *Proserpinella cousini*.

According to the recommendation of the International Code of Zoological Nomenclature (ICZN 1999, see discussion by Cisneros-Heredia 2017), I restrict the type localities of *Isomeria bourcieri lutea* Cousin 1887 (Gastropoda: Labyrinthidae), *Guestieria locardi* Jousseume 1887 (Gastropoda: Scolodontidae), *Proserpinella cousini* Jousseume 1887 (Gastropoda: Proserpinellidae), *Mesembrinis vesperus* Jousseume, 1887 (Gastropoda: Achatinidae), *Idiophthalma robusta* Simon 1889 (Arachnida: Barychelidae), *Eurypelma (Lasiodora) augusti* Simon 1889 (Arachnida: Theraphosidae), *Eurypelma (Lasiodora) vespertinus* Simon 1889 (Arachnida: Theraphosidae), *Asplundia nonoensis* Harling 1958 (Pandanales: Cyclanthaceae), and *Blakea eriocalyx* Wurdack 1979 (Myrtales: Melastomataceae) and all other species whose type specimens were collected at the Cousin family farm “Los Puentes” in northwestern Ecuador, to the following locality: Los Puentes, near Nanegalito, on the western slopes of the Western Cordillera of the Andes of northern Ecuador, Pichincha province, Republic of Ecuador (coordinates focus point: 0.0458, -78.6742, radius: 2 km) (Fig. 2). The elevation of all Asplund’s plant collections is ca. 1200 m, while the elevation of the gastropods and spiders is ca. 1500 m.

The newly restricted type locality is described as a circle, defined by a central focus point and a radius covering the maximum distance the site is expected to lie (i.e., the point-radius method, Wieczorek *et al.* 2004). A KMZ file showing this locality is available here: <https://doi.org/10.6084/m9.figshare.19297532>.

Although I have conducted an exhaustive search to find taxa described from “Los Puentes”, I suggest that researchers working with specimens collected by Cousin and cited as coming from Quito check the original labels and museum catalogues, to confirm the correct provenance, especially those deposited in the National Museum of Natural History in Paris, where much of the material collected by Cousin is expected to be deposited.

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References

- Ausserer, A. (1871) Beiträge zur Kenntniss der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 21, 117–224.
- Bertani, R., Fukushima, C.S. & Da Silva Jr, P.I. (2008) Two new species of *Pamphobeteus* Pocock 1901 (Araneae: Mygalomorphae: Theraphosidae) from Brazil, with a new type of stridulatory organ. *Zootaxa*, 1826 (1), 45–58.
<https://doi.org/10.11646/zootaxa.1826.1.3>
- Breure, A.S.H. (2020) Type material of taxa described by Cousin and Jousseume in the Royal Belgian Institute of Natural Sciences, Brussels. *Folia Malacologica*, 28, 95–113.
<https://doi.org/10.12657/folmal.028.005>
- Cisneros-Heredia, D.F. (2017) The type localities of *Anolis aequatorialis* Werner, 1894 (Sauria: Iguania: Dactyloidae) and *Pristimantis appendiculatus* (Werner, 1894) (Amphibia: Anura: Craugastoridae). *Zootaxa*, 4216 (2), 190–196.
<https://doi.org/10.11646/zootaxa.4216.2.5>
- Cisneros-Heredia, D.F. & Valencia, R.F. (2022) Comments on snails of the genus *Zoniferella* from Ecuador (Mollusca: Achatinidae), with restriction of the type locality ‘Los Puentes’ for several species of Gastropoda and Arachnida. *Biorxiv*, 2022.03.03.482746.
<https://doi.org/10.1101/2022.03.03.482746>
- Cisneros-Heredia, D.F. & Valencia, R.F. (2023) Comments on snails of the genus *Zoniferella* from Ecuador (Mollusca: Achatinidae). *ACI Avances en Ciencias e Ingenierías*, 15, e3121.
<https://doi.org/10.18272/aci.v15i2.3121>
- Correoso Rodríguez, M. (2010) Nuevo reporte y localidades de *Rhodea cousini* Jousseume, 1900 (Gastropoda: Subulinidae) para el Ecuador. *Revista Geoespacial*, 7, 45–51.
- Correoso Rodríguez, M. (2020) *Moluscos y arte en Ecuador*. Casa de la Cultura Ecuatoriana, Quito, 88 pp.
- Cousin, A. (1887) Faune malacologique de la République de l’Équateur. *Bulletin de la Société Zoologique de France*, 12, 187–287.
- DIPLA (2023) *Escuelas Régimen Costa, Distrito Metropolitano de Quito*. Dirección de Planificación y Ambiente, Gobierno de la Provincia Pichincha, Quito. [map]
- Drolshagen, B. & Bäckstam, C.M. (2021) A taxonomic review of the mygalomorph spider genus *Linothele* Karsch, 1879 (Araneae, Dipluridae). *Zoosystema*, 43, 163–196.
<https://doi.org/10.5252/zoosystema2021v43a10>
- Dupérré, N. & Tapia, E. (2015) Descriptions of four kleptoparasitic spiders of the genus *Mysmenopsis* (Araneae, Mysmenidae) and their potential host spider species in the genus *Linothele* (Araneae, Dipluridae) from Ecuador. *Zootaxa*, 3972 (3), 343–368.
<https://doi.org/10.11646/zootaxa.3972.3.3>
- Dupérré, N., Tapia, E. & Bond, J.E. (2023) Review of the spider genus *Linothele* (Mygalomorphae, Dipluridae) from Ecuador—An exceptional case of speciation in the Andes. *Arthropoda*, 1, 68–341.
<https://doi.org/10.3390/arthropoda1030010>
- GAD Pichincha (2017) *Mapa político y vial*. Gobierno Autónomo Descentralizado Provincia de Pichincha, Quito. [map]
- Germain, L. (1907) Sur quelques mollusques de la République de l’Équateur (Mission de M. le Dr. Rivet). *Bulletin du Muséum National d’Histoire Naturelle*, 1, 52–68.
- Germain, L. (1911) *Étude sur les mollusques terrestres et fluviatiles recueillis par M. le Dr. Rivet*. In: *Mission du Service Géographique de l’Armée pour la mesure d’un Arc de Méridien Équatorial en Amérique du Sud sous le contrôle scientifique de l’Académie des Sciences 1899–1906. Tome 9 Zoologie*. Gauthier-Villars, Imprimeur-Libraire du Bureau des Longitudes, de l’École Polytechnique, Paris, C77 pp. [pp. C1–C77]

<https://doi.org/10.5962/bhl.title.980>

- Harling, G.W. (1958) Monograph of the Cyclanthaceae. *Acta Horti Bergiani*, 18, 1–428.
- ICZN (1999) *International Code of Zoological Nomenclature. 4th Edition*. International Trust for Zoological Nomenclature, London. Available from: <https://www.iczn.org/the-code/the-code-online/> (accessed 9 April 2025)
- IGM (1990) *Carta topográfica: Calacalí CT-EII-E4*. Instituto Geográfico Militar, Quito. [map]
- Jarrín, M.J. (2021) La red erudita de Paul Rivet en el Ecuador: Agentes, saberes y objetos. *Boletín de la Academia Nacional de Historia*, 99, 145–168.
- Jarrín, M.J. (2024) La collection Auguste Cousin (1835-1899) et son itinéraire entre l'Équateur et Paris. In: Richard, N. (Ed.), *Amateurs en sciences: une histoire par les collections*. Actes des congrès nationaux des sociétés historiques et scientifiques. Éditions du Comité des travaux historiques et scientifiques, Paris, pp. 19–33.
<https://doi.org/10.4000/books.cths.18297>
- Jousseaume, F. (1887) Mollusques nouveaux de la République de l'Équateur. *Bulletin de la Société Zoologique de France*, 12, 165–186.
- Peñaherrera-R, P., Guerrero-Campoverde, A., León-E, R.J., Pinos-Sánchez, A. & Cisneros-Heredia, D.F. (2023) A new species of *Linothele* Karsch, 1879 (Araneae: Dipluridae) from south-eastern Ecuador. *Arachnology*, 19, 713–720.
<https://doi.org/10.13156/arac.2023.19.4.713>
- Petrunkévitch, A. (1911) A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. *Bulletin of the American Museum of Natural History*, 29, 1–809.
<https://doi.org/10.5962/bhl.title.23819>
- Pilsbry, H.A. (1906) XVIII. Achatinidae: Stenogyrinae and Coeliaginae *Manual of conchology structural and systematic*. Conchological Department, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, 357 pp.
- Sherwood, D., Gabriel, R., Brescovit, A.D. & Lucas, S.M. (2022) On the species of *Pamphobeteus* Pocock, 1901 deposited in the Natural History Museum, London, with redescription of type material, the first record of *P. grandis* Bertani, Fukushima & Silva, 2008 from Peru, and the description of four new species (Araneae: Theraphosidae). *Arachnology*, 19, 650–674.
<https://doi.org/10.13156/arac.2022.19.3.650>
- Sherwood, D., Gabriel, R., Peñaherrera-R, P., León-E, R.J., Cisneros-Heredia, D.F., Brescovit, A.D. & Lucas, S.M. (2023) *Pamphobeteus* Pocock, 1901: Redescriptions, new species and records, description of a missing sex, with taxonomic notes and changes in *Megaphobema* Pocock, 1901 (Araneae: Theraphosidae). *Arachnology*, 19, 894–930.
<https://doi.org/10.13156/arac.2023.19.6.894>
- Simon, E. (1889) Révision des Avicularidae de la République de l'Équateur. *Actes de la Société Linnéenne de Bordeaux*, XLII, 399–404.
- Valdivieso, R. (1898) *Informe del Ministerio de Obras Públicas, Agricultura, etc. al Congreso ordinario de 1898*. Tipografía de la Escuela de Artes y Oficios, Quito, 233 pp.
- Wieczorek, J., Guo, Q. & Hijmans, R. (2004) The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. *International Journal of Geographical Information Science*, 18, 745–767.
<https://doi.org/10.1080/13658810412331280211>
- Wolf, T. (1892) Carta geográfica del Ecuador. Map. Instituto Geográfico de H. Wagner & E. Debes, Leipzig.
- Wurdack, J.J. (1979) Certamen Melastomataceae XXX. *Phytologia*, 43, 339–355.