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A FORMAL NOMENCLATURE AT THE RANK OF SUBGENUS FOR NEOTROPICAL *PIPER* (PIPERACEAE)

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ABSTRACT

A formal nomenclature is provided, at the taxonomic rank of subgenus, for the major Neotropical clades recognized within the genus *Piper* (Piperaceae). Many of these names have been used informally at this rank, but most have not been validly published or the names are actually illegitimate. Of the nine subgenera recognized, two new names and five new combinations are required. Relevant discussion is provided and, where appropriate, lectotypification and synonymy.

In two publications concerning the phylogeny of the genus *Piper*, Jaramillo et al. (2008, 2024) identified eight or nine (respectively), monophyletic, Neotropical clades. Unfortunately, many of the names assigned to these clades have never been formally recognized, at least at the rank of subgenus, which is what was informally proposed in their recent publication (Jaramillo et al. 2024; see "Key to Subgenera of Neotropical Pipers"). Most of those names were originally published at the rank of genus (e.g., *Enckea* Kunth, *Ottonia* Sprengel, *Peltobryon* Klotzsch ex Miq., *Pothomorphe* Miq., and *Schilleria* Kunth) and several were eventually recognized at the rank of subgenus and especially section. However, a few of these genera (e.g., *Enckea, Peltobryon*, and *Schilleria*) are technically illegitimate, superfluous names. To clarify this situation (with synonymy, explanation, and lectotypification), a complete nomenclatural accounting at the level of subgenus is provided (in alphabetical order), following the rank recognized/suggested in the publication by Jaramillo et al. (2024). This will allow for their proper use at the rank of subgenus in any future publications where a more extensive taxonomic hierarchy below the level of genus might be of value.

1. **Piper** subg. **Gonistum** (Raf.) Bornst., **comb. nov.** Basionym: *Gonistum* Raf., Sylva Tellur. 85. 1838. **TYPE SPECIES:** *Gonistum unguiculatum* (Ruiz & Pav.) Raf. Basionym: *Piper unguiculatum* Ruiz & Pav., Fl. Peruv. 1: 34–35, t. 57b. 1798. **LECTOTYPE** (designated here): **PERU.** Habitat in Pozuzu et Chincahao nemoribus, *Ruiz & Pavón s.n.* (MA–810991, online image!; isolectotypes: BM–939032, online image!, FI–011387, online image!, G–169981!, MA–810988, 810989, 810990, online images!, P–614509, 614510, online images!).

   Amalago Raf., Sylva Tellur. 84. 1838, pro parte. **TYPE SPECIES:** not designated.

   Enckea Kunth, Linnaea 13: 590–592. 1840. **TYPE SPECIES:** not designated.

   Arctottonia Trel., Proc. Amer. Philos. Soc. 69: 315. 1930. *Piper* subg. *Arctottonia* (Trel.) Standl. & Steyerm., Fieldiana, Bot. 24(3): 275. 1952. **TYPE SPECIES:** *Piper muelleri* C. DC., Prodr. 16(1): 243. 1869. **TYPE: MEXICO.** Veracruz, Orizaba, in 1853, *Müller 180* (holotype: BR–659817!; isotypes: G-DC–00320842!, GH–00005472!, ILL fragment–00008300!, LE–00001482!, NY–00250946, online image!).

Notes. The more commonly used name of *Enckea* was proposed by Kunth, but without a type designation. Fourteen species were included in his treatment, most of which were new combinations based on species previously recognized in *Piper*. Several names were later added to the genus,

primarily by Miquel (1843-1844). Unfortunately, one of the names originally included in Kunth's publication was *Enckea unguiculata* (Ruiz & Pav.) Kunth, based on *Piper unguiculatum* Ruiz & Pav. from Peru. This same name served as the basionym of the type species of the new monotypic genus *Gonistum* Raf. Because the name *Gonistum* predates that of *Enckea* (1838 vs. 1840), and circumscription of *Enckea* by Kunth included the type of a previously published, legitimate genus, the name *Enckea* is superfluous, as Kunth should have used the name *Gonistum* instead (although I suspect he was completely unaware of the Rafinesque publication). As such, the name *Enckea* cannot serve as the basionym for recognition at any other rank, as *Gonistum* would be the basionym of choice. Because many of the clades identified in Jaramillo et al. (2008, 2024) are currently suggested for recognition at the rank of subgenus (see Jaramillo et al. 2024) within *Piper*, formal combination of *Gonistum* at the level of subgenus is required, as accomplished above.

Ruiz & Pavón did not designate a specific collection to serve as the type of *Piper unguiculatum*, other than mentioning the locality of their collection as "Habitat in Pozuzu et Chincahao nemoribus." Several collections identified as *Piper unguiculatum* exist in the Ruiz & Pavón herbarium in Madrid (MA), which is the repository of their original material. Duplicate collections exist in other herbaria, most likely via sale of some of the original material by Pavón to Aylmer Lambert (circa 1816), whose herbarium was sold after his death in 1842 to other interested buyers (see Miller 1970 for further details). I have seen many of these collections via the Global Plants Database on JSTOR, which are cited throughout the manuscript as "online images." I have chosen one of the original collections at MA to serve as a lectotype, as it displays important features for identification, including both leaf surfaces, and inflorescences at various stages of development, including young fruits.

The genus *Arctottonia* was proposed by Trelease (1930) as a segregate from *Piper* to accommodate the species from Mexico and northern Central America with palmately veined leaves, and pedicellate flowers and fruits. In his view these species represented the North American counterpart to a similar group, the genus *Ottonia*, from South America. Bornstein (1989) completed a taxonomic revision of this group, ultimately recognizing 14 species in this subgenus, while noting that members are closely related to those in *Enckea*. Subsequent molecular analysis (see Jaramillo et al. 2008, 2024) confirmed these suspicions, as *Arctottonia* was determined to be non-monophyletic, embedded within the *Enckea* lineage. Only four species were ever formally recognized in *Arctottonia*, and all of them have previous names in *Piper* (see Bornstein 1989 for details).

The genus *Amalago* Raf. is included here, in part, as several of the species mentioned in the protologue are considered members of subg. *Gonistum* based on their erect, shrubby habit, palmately veined leaves, spicate inflorescences, and typically 5- or 6-staminate, bisexual flowers that do not form bands around the rachis. The circumscription of *Amalago* appears to be conflicted as it includes two quite disparate entities, *Piper amalago* L. from the Neotropics (recognized as *Amalago antillana* Raf., a nomen novum to avoid creating a tautonym), which properly fits the description provided here; and *Piper malamiris* L. [*Amalago malmiri* (L.) Raf.; *Cubeba malamiri* (L.) Miq., *Chavica malamiris* (L.) Miq.], a species from the Paleotropics (India, Sri Lanka?) that is apparently a scandent shrub with leaves best described as multiplinerved with five to nine main veins all arising within the lowermost 5–8 mm of the blade, and unisexual flowers on dioecious individuals (as is typical for pipers of the Paleotropics).

2. **Piper** subg. **Lepianthes** (Raf.) Bornst., **comb. nov.** Basionym: *Lepianthes* Raf., Sylva Tellur. 85. 1838. **LECTOTYPE SPECIES:** *Lepianthes umbellata* (L.) Raf. ex Ramamoorthy, Fl. Hassan Dist. 52. 1976. Basionym: *Piper umbellatum* L., Sp. Pl. 1: 30. 1753. **LECTOTYPE:** Plumier, Descr. Pl. Amér. 53, t. 73. 1693 (designated by Huber, Revis. Handb. Fl. Ceylon 6: 289. 1987).

Pothomorphe Miq., Bull. Sci. Phys. Nat. Néerl. 2: 447, 450. 1839. *Piper* sect. *Pothomorphe* (Miq.) C. DC., Prodr. 16(1): 240, 331. 1869 (as "*Potomorphe,"* a correctable error). **LECTOTYPE**

SPECIES: *Pothomorphe umbellata* (L.) Miq., designated by Britton & Wilson, Sci. Surv. Porto Rico 5: 229. 1924.

Heckeria Kunth, Linnaea 13: 564. 1840. **TYPE SPECIES** not designated. *Piper* sect. *Heckeria* Benth. & Hook. f., Gen Pl. 3(1): 131. 1880, as a replacement name for *Heckeria* Kunth (not Raf.). *Piper* subg. *Heckeria* (Benth. & Hook. f.) Standl., Contr. U.S. Natl. Herb. 23: 145. 1920.

Notes. Rafinesque created the new genus *Lepianthes*, citing several species previously recognized in *Piper*, including *P. umbellatum*, but did not explicitly make the formal combination in *Lepianthes* (only implied). This was later accomplished, inadvertently, by Ramamoorthy as noted above. The name *Heckeria* Kunth is technically an illegitimate, superfluous name as he included the type of *Lepianthes* among the species included in *Heckeria*. Therefore, he should have used the earlier name of *Lepianthes*.

There has been controversy concerning the lectotypification of *Lepianthes*, with Wilbur (1985, 1987) and Jones and Lamboy (1986) offering different perspectives. However, as noted in the publication by Saralegui Boza (2004) for the Flora of Cuba, it does appear as though Rafinesque actually chose *Piper umbellatum* as the type species, although he did not validate this by making the combination in *Lepianthes*. I am following the interpretation in Saralegui Boza, which makes *Lepianthes* the earliest available name at the rank of subgenus.

Members of this lineage are erect subshrubs or shrubs (only climbing in *Piper multiplinervium* C. DC.), usually with leaves membranous and palmately veined (only pinnate in *Piper auritum* Kunth), the petioles sheathing. Flowers and floral bracts are tightly organized in distinct bands around the rachis and the fruits are typically obovoid.

3. **Piper** subg. **Macrostachys** (Miq.) Bornst., **comb. nov.** Basionym: *Artanthe* Miq. sect. *Macrostachys* Miq., Syst. Piperac. 378, 391. 1844. **LECTOTYPE SPECIES** (designated here)**:** *Piper obliquum* Ruiz & Pav. **TYPE: PERU.** "In Cuchero sylvis ad Cayumba terminum," *Ruiz & Pavón s.n.* (holotype: P?; isotypes: BM–000993730, right-hand specimen!, MA–810973, online image!).

Notes. In the *Tropicos* database, this taxon is listed at the rank of section within *Piper*. This is an unfortunate error, as it is clearly first mentioned in Miquel's *Systema Piperacearum* of 1843-1844 as a section within the genus *Artanthe*.

Tebbs (1989) listed the type of *Artanthe* sect. *Macrostachys* as *Piper obliquum*, but she offered no explanation. One can surmise that she simply chose the first name listed under that section (*Artanthe magnifica*) on page 391 of Miquel's *Systema*, but that is hardly an appropriate rationale (the name *Piper obliquum* is actually listed in synonymy under *Artanthe magnifica*, but that is an illegitimate name as Miquel was obligated to use the first available epithet, which means this taxon should have been called *Artanthe obliqua* (Ruiz & Pav.) Miq.). I have maintained the choice of Tebbs, but only because this species is one of the more common and widely recognized elements within sect. *Macrostachys*, with a range from Mexico to Brazil as commonly circumscribed (see Tebbs 1989; Callejas 2001; Bornstein and Coe, in press). Members of subg. *Macrostachys* are generally easy to recognize based on their medium to large shrub or tree-like habit; large, membranous to chartaceous, pinnately veined leaves, with petioles typically sheathing for most of their length and leaf bases often strongly asymmetrical; inflorescences usually very long (20+ cm) and pendulous, with flowers and associated floral bracts forming distinct bands around the rachis. In this regard, *Piper obliquum* is an excellent representative to serve as a lectotype species, as it clearly displays all of these features.

4. **Piper** subg. **Ottonia** (Spreng.) Standl., Contr. U.S. Natl. Herb. 23(1): 146. 1920. Basionym: *Ottonia* Spreng., Neue Entdeck. Pflanzenk. 1: 255. 1820. *Piper* subsect. *Ottonia* (Spreng.) Benth. & Hook. f., Gen Pl. 3(1): 131. 1880. **TYPE SPECIES:** *Ottonia anisum* Spreng. **LECTOTYPE**

(designated here): **BRAZIL.** Rio de Janeiro, 1816, *Kulenkamp s.n.* (LE–00001499, online image!; possible isolectotype: LE–00001498, online image!).

Notes. In his original publication of the genus *Ottonia*, Sprengel only included one species, *Ottonia anisum*. Although an exact specimen is not cited as a potential type, he did mention a collection from eastern Brazil, apparently housed in the herbarium of Karl Heinrich Mertens, whose entire herbarium was acquired by the St. Petersburg Botanic Gardens (LE) upon his death in 1830. Two collections exist in the herbarium at LE, both of which were annotated by Ricardo Callejas (in 1985) as *Piper anisum* (Spreng.) Angely. Callejas completed his Ph.D. thesis entitled "Taxonomic revision of *Piper* subgenus *Ottonia* (Piperaceae)" in 1986, but it was never formally published. A type verification label by Callejas is affixed to the Kulenkamp specimen (mentioned above) with the designation as a lectotype, but neither was this formally accomplished via publication. Thus, lectotypification is required.

Members of this subgenus are primarily found in the lowland forests of Brazil, especially in the Atlantic Forests, with one species (*Piper darienense* C. DC.) occurring as far north as Nicaragua. They are small to medium-sized shrubs with pinnately veined leaves, usually with two callosities (thickenings), one on each side of the petiole at the very base of the blade. The inflorescences consist of fairly loosely organized flowers and associated floral bracts that do not form bands around the rachis, the flowers either pedicellate or sessile. In essence, they are the South American counterpart to subg. *Gonistum*, which share these basic morphological features but with palmately veined leaves.

5. **Piper** subg. **Oxodium** (Raf.) Bornst., **comb. nov.** Basionym: *Oxodium* Raf., Sylva Tellur. 85. 1838. **TYPE SPECIES:** *Oxodium callosum* (Ruiz & Pav.) Raf. Basionym: *Piper callosum* Ruiz & Pav., Fl. Peruv. 1: 34, t. 53a. 1798. **LECTOTYPE** (designated here): **PERU**. Habitat in nemoribus Pillao ad Chacahuassi, *Ruiz & Pavón s.n.* (MA–810928, online image!; isolectotypes: B herbarium Willdenow–00653-010, online image!, HAL–101681, online image!, MA–910929 and MA–810930, online images!, fragment at U–01801271, online image!).

Schilleria Kunth, Linnaea 13: 676. 1839. **TYPE SPECIES:** not designated.

Peltobryon Klotzsch ex Miq., Syst. Piperac. 46, 369. 1844. *Piper* sect. *Peltobryon* (Klotzsch ex Miq.) Benth. & Hook. f., Gen. Pl. 3(1): 130. 1880. **TYPE SPECIES:** not designated.

Notes. Similar to the situation for *Enckea*/*Gonistum*, the genus name *Schilleria* is illegitimate and superfluous. Kunth included *Schilleria callosa* (Ruiz & Pav.) Kunth among the 47 species he attributed to *Schilleria*, which is based on the name *Piper callosum* Ruiz & Pav. As indicated above, this is the basionym of the new monotypic genus *Oxodium* published a year earlier by Rafinesque.

For the genus *Peltobryon*, Miquel included the name *Peltobryon callosum* (Ruiz & Pav.) Miq. (with *Piper callosum* and *Schilleria callosa* listed as synonyms) among the five species recognized. Because *Oxodium* predates *Schilleria* (1838 vs. 1839) and *Peltobryon* (1838 vs. 1844) and the circumscriptions of *Schilleria* and *Peltobryon* included the type species of a legitimately published genus, they are superfluous names that cannot serve as basionyms at any other rank. Formal combination of *Oxodium* at the rank of subgenus is required, as accomplished above.

As was the case for *Piper unguiculatum*, lectotypification is required for the type of *Piper callosum*. Again, the original herbarium of Ruiz & Pavón is housed at MA, and several type specimens are located therein. Among these possible lectotypes I have chosen one specimen (MA–810928) that provides all of the features typically necessary for proper identification, including leaves with both surfaces readily visible, flowers at various stages of maturation, and at least a few fruits at early stages of development.

6. **Piper** subg. **Palmatinervium** Bornst., **nom. nov.** **TYPE SPECIES:** *Piper cinereum* C. DC., J. Bot. 4: 214. 1866. **TYPE: COLOMBIA**. Chocó, *Triana s.n. (1820?)* (holotype: G-DC–00206081, online image!; isotype: BM–000993719, online image!).

Notes. In both phylogenetic analyses by Jaramillo et al. (2008, 2024), this monophyletic lineage is identified as the *"Piper sanctum/Piper cinereum* complex," with no formal name applied. To rectify this situation, I am proposing the name indicated above, which refers to the type of leaf venation found in members of this small clade.

Besides *Piper cinereum*, which occurs from southern Panama to northern South America, the other, more common species included in this lineage is *Piper patulum* Bertol. (Nuovi Ann. Sci. Nat. 1(1): 410. 1838), a species ranging from southern Mexico to central Panama, and with a rather checkered nomenclatural/taxonomic history (see Ramirez-Amezcua 2016 and Bornstein and Coe, in press, for more specific historical details). In brief, this species was long known by the misapplied name of *Piper sanctum* (Miq.) Schltdl. ex C. DC., which is actually a synonym of *Piper auritum*, as properly recognized by Ramirez-Amezcua (2016). Ramirez-Amezcua (2016) used the name *Piper commutatum* Steud. (Nomencl. Bot. (ed. 2) 2: 340. 1841) for this species, not realizing there was the earlier name of *Piper patulum* from 1838.

Both species have membranous to chartaceous, palmately veined leaves; those of *Piper cinereum* have cordate leaf bases on both monopodial and sympodial axes, while those of *Piper patulum* are cordate along the monopodial axes but basally rounded to cuneate along the sympodial axes. The inflorescences in both species are elongate spikes with flowers and floral bracts forming distinct bands around the rachis. The fruits are rounded (when viewed from the apex), the spikes eventually distally curved or pendulous in fruit.

Both type specimens have labels that indicate the collection number as "1820," with the specimen at BM also indicating that it was collected in March 1853. The original protologue does not include a collection number or date of collection, only that it was housed in the de Candolle herbarium (now G-DC).

7. **Piper** subg. **Pennistylosum** Bornst., **nom. nov.** **TYPE SPECIES:** *Piper phytolaccifolium* Opiz in Presl, Reliq. Haenk. 1(3): 151. 1828 (as "*phytolaccaefolium*", a correctable spelling). *Artanthe phytolaccifolia* (Opiz) Miq., Syst. Piperac. 534. 1844; *Peltobryon phytolaccifolium* (Opiz) Presl, Abh. Königl. Böhm. Ges. Wiss. Ser. 5, 6: 584. 1851. **TYPE: ECUADOR.** Guayaquil, *Haenke s.n.* (holotype: PR; isotypes: PRC–450176 and PRC–450577, online images!).

Notes. The lineage identified in Jaramillo et al. (2008, 2024) as "Peltobryon" requires a new name as *Peltobryon* is an illegitimate, superfluous name as explained under item #5 (*Piper* subg. *Oxodium*). I have created a name that reflects two common attributes for members of this clade - leaves pinnately nerved throughout their length, and the presence of a stylose ovary. Besides these features, a typical member of this lineage possesses membranous leaves, often marginally ciliate and glandular-dotted; inflorescences erect, but often pendulous in fruit; and anthers usually with an expanded, glandular connective. These features are all found in *Piper phytolaccifolium*, which is why it was chosen as the type species. It is a broadly distributed species (as commonly circumscribed; see Burger, 1971; Steyermark 1984; Callejas 2001; Bornstein and Coe, in press), ranging from southern Mexico to northern South America (Colombia, Ecuador, Peru, Venezuela).

8. **Piper** subg. **Pleiostachyopiper** (Trel.) M.A. Jaram., Syst. Bot. 49: 274. 2024. Basionym: *Pleiostachyopiper* Trel., Proc. Amer. Philos. Soc. 73(5): 328–329, pl. a. 1934. **TYPE SPECIES:** *Pleiostachyopiper nudilimbum* (C. DC.) Trel. Basionym: *Piper nudilimbum* C. DC., Verh. Bot. Vereins Prov. Brandenburg 47: 113. 1905. **TYPE: BRAZIL**. Amazonas, Juruá Miry, Rio Juruá,

in July 1901, *Ule 5708* (holotype: B–apparently destroyed, photo at F!, US!, partial tracing at G-DC–00321380!; isotypes: CORD–00002256, online image!, G!, HBG–509639, online image!, K!, NY!).

Notes. Based on a phylogenetic analysis using ITS sequence data, Jaramillo et al. (2024) established that two species, *Piper globirhachis* M.A. Jaram. and *Piper nudilimbum*, constitute a distinct lineage, sister to subg. *Oxodium*. They recognized this lineage as subg. *Pleiostachyopiper*, resurrecting a name first used by Trelease as a segregate genus from *Piper*. In a separate phylogenetic analysis involving multiple nuclear genes, Hastings et al. (in press) also have confirmed the segregate status of *Piper nudilimbum*, similarly suggesting a close relationship with members of the clade *Schilleria* (= *Oxodium*).

Both members of this lineage are small shrubs with chartaceous, palmately veined leaves, very short inflorescences (usually < 1 cm) with flowers and floral bracts not forming bands around the rachis, stylose ovaries, and fruits embedded in the rachis. See Jaramillo et al. (2024) for additional details.

9. **Piper** subg. **Radula** (Miq.) Bornst., **comb. nov.** Basionym: *Artanthe* sect. *Radula* Miq., Syst. Piperac. 378–379, 426. 1844. *Piper* sect. *Radula* (Miq.) Tebbs ex Verdc., Fl. Trop. E. Africa, Piper 3. 1996. **LECTOTYPE SPECIES** (designated here): *Piper aduncum* L. **LECTOTYPE:** Plumier, Descr. Pl. Amér. t. 77. 1693 (designated by Saralegui Boza, Fl. Republ. Cuba, ser. A, Pl. Vasc. 9(3): 81. 2004).

Notes. Similar to the situation for *Piper* subg. *Macrostachys*, the *Tropicos* database incorrectly lists *Radula* as a section within the genus *Piper*. As indicated by the citation information above, Miquel first mentioned this name in his *Systema Piperacearum* of 1843-1844 as a section within the genus *Artanthe*.

Tebbs (1993) listed the type of sect. *Radula* Miq. as *Piper radula* Kunth (currently recognized as *Piper bredemeyeri* Jacq.; Tebbs 1993, Callejas 2020) but offered no explanation. Similar to the situation for *Piper* subg. *Macrostachys* (see explanation above under that name), it appears that she simply chose the first species listed under *Artanthe* sect. *Radula* on page 426 of Miquel's *Systema* (*Artanthe radula* (Kunth) Miq.). Again, this seems insufficient as rationale for the choice of a lectotype. Instead, I have chosen a different species mentioned in Miquel's treatment, *Piper aduncum* (= *Artanthe adunca* (L.) Miq., Comm. Phytogr. 2: 49–50. 1840.; Syst. Piperac. 449. 1844.). This is perhaps the most broadly distributed species in subg. *Radula* and possibly the entire genus, as it occurs throughout the Neotropics and has also been introduced in the southeastern USA as well as several areas in the Paleotropics (e.g., Africa, Asia, Malaysia, and Oceania). It displays many of the features typically associated with members of this section or subgenus, including membranous, pinnately veined leaves, these often scabrous above, erect inflorescences (sometimes distally curved at anthesis as in *Piper aduncum*), and flowers plus associated floral bracts tightly arranged within the inflorescence, forming distinct bands around the rachis.

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