REINSTATEMENT AND EXPANSION OF THE GENUS PERISTETHIUM (LORANTHACEAE)¹

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Abstract

The genus *Peristethium* Tiegh. (Loranthaceae) is re-established to comprise five species previously placed in *Struthanthus* Mart. (*P. aequatoris* (Kuijt) Kuijt, *P. leptostachyum* (Kunth) Tiegh., *P. lojae* (Kuijt) Kuijt, *P. polystachyum* (Ruiz & Pav.) Kuijt, and the new nomenclatural combination presented here, *P. tortistylum* (Kuijt) Kuijt). Also included are five species from *Cladocolea* Tiegh. (*P. archeri* (A. C. Sm.) Kuijt, *P. peruviense* (Kuijt) Kuijt, and *P. primarium* (Kuijt) Kuijt), with two transferred as new nomenclatural combinations herein, *P. nitidum* (Kuijt) Kuijt and *P. roraimense* (Steyerm.) Kuijt). Additionally, five new species are described and illustrated (*P. attenuatum* Kuijt, *P. colombianum* Kuijt, *P. confertiflorum* Kuijt, *P. lamprophyllum* Kuijt, and *P. palandense* Kuijt). The genus *Peristethium* thus consists of 15 species and a key is provided for the genus. It is characterized by pairs of conspicuous, often caducous, chaffy scale leaves at the base of the mostly determinate inflorescences, and by lateral inflorescence units that are triads and/or ebracteolate single flowers called monads (in one case, partly pentads). Some species have bisexual flowers while others are dioecious; flowers are either tetramerous or hexamerous, and one pentamerous species is included (*P. nitidum*). The minute anthers are sessile or nearly so, placed far above the middle of the petals. Geographically, the genus reaches from northern Bolivia to Costa Rica, with two rare, narrow endemics on Mt. Roraima in Venezuela and the Pakaraima Mountains.

Key words: Cladocolea, IUCN Red List, Neotropical Loranthaceae, Peristethium, Struthanthus.

The genus Struthanthus Mart. (Loranthaceae) was initially established for a number of South American species (Martius, 1830). The protologue describes the inflorescence as a spike or raceme of paired triads, the flowers being stated as bisexual and the anthers dorsifixed on slender filaments. However, Eichler (1868) would correct Martius's diagnosis by pointing out that Struthanthus species are dioecious, the aborted organs of the opposite sex present in both unisexual flower types. Eichler referred to nine Mesoamerican species Martius had not known and added 10 new species for South America in Flora Brasiliensis. Numerous further species have been described in the meantime from various Neotropical regions. Struthanthus has not been monographedonly local treatments have been published—and the total number of species is thus not precisely known. In 1895, Van Tieghem maintained the genus Spirostylis C. Presl ex Schult. & Schult. f. segregated earlier from Struthanthus by Presl (in Schultes & Schultes f., 1829), and would add two segregate genera, Eichlerina Tiegh. and Peristethium Tiegh. These three segregate genera have not been recognized by subsequent workers, except for Peristethium

as a monotypic genus in Engler and Krause (1935). Struthanthus as a whole ranges from northwestern Mexico to Bolivia and Argentina, being absent from the Caribbean.

It has been noted for some time that Struthanthus is a paraphyletic assemblage (Kuijt, 1975b). My morphological study of inflorescences in the family suggested that at least three separate intergeneric bridges seemed to exist between the genus and Cladocolea Tiegh. (Kuijt, 1981b: 9-12). Each of these bridges consisted of at least two bridgehead species (see Kuijt, 1975b: 279-281). One intermediate species was placed in Struthanthus, the other in Cladocolea, suggesting that at least part of Struthanthus was derived from Cladocolea-like ancestors. The most prominent of these bridging intermediaries involved at least S. leptostachyus (Kunth) G. Don and C. archeri (A. C. Sm.) Kuijt. Other related species discovered since that time seemed to reinforce the bridge concept of species with intermediate morphologies. Recent study, nevertheless, especially of the new species to be described herein, has led to a fundamental reevaluation of the intergeneric connection. From these new insights it

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is herewith proposed to realign the species involved in the C. archeri-S. leptostachyus intergeneric bridge as a separate genus, for which the name Peristethium is available. This includes the assignment of several species to Peristethium thus far resident in Struthanthus (S. aequatoris Kuijt, S. leptostachyus, S. polystachyus (Ruiz & Pav.) G. Don, and S. tortistylus Kuijt) or in Cladocolea (C. archeri, C. nitida Kuijt, C. peruviensis Kuijt, C. primaria Kuijt, and C. roraimensis (Steyerm.) Kuijt). Additionally, five newly discovered species from Andean South America are herein described and illustrated. As now constituted by these 15 species, the genus Peristethium demonstrates coherent, structural, and geographic integrity. Several features, seen in individual species, are unique or nearly so in New World Loranthaceae, even in the family generally, and include an inflorescence most often terminated by a single flower that is preceded by at least one pair of lateral 1-flowered units called monads, an inflorescence bearing a number of basal pairs of papery (often caducous or partially caducous) scale leaves, and extremely small, mostly sessile and basifixed anthers that are positioned near the tips of the subtending petals. The combination of these features is unique in Loranthaceae. Peristethium includes both dioecious species as well as some with bisexual flowers; unusual in Neotropical Loranthaceae, some species are tetramerous and others hexamerous.

In retrospect, it can be seen that Peristethium as a natural assemblage has been glimpsed in the past without being properly appreciated. The protologue of Struthanthus tortistylus Kuijt suggested an affinity to P. leptostachyum (Kunth) Tiegh. and P. polystachyum (Ruiz & Pav.) Kuijt, these species then still being placed in Struthanthus (as S. leptostachyus and S. polystachyus; Kuijt, 2003a). A study of foliar sclerenchyma pointed in the same direction, suggesting taxonomic connections between P. archeri (A. C. Sm.) Kuijt, P. leptostachyum, and the two new nomenclatural combinations presented here, P. primarium (Kuijt) Kuijt and P. roraimense (Steyerm.) Kuijt (as Cladocolea primaria and C. roraimensis; Kuijt & Lye, 2005). Parallel statements are to be found in the protologue of C. primaria (Kuijt, 1987a). The present treatment resolves such ambiguities.

Van Tieghem's protologue of *Peristethium* (Van Tieghem, 1895) is exceedingly sparse and based on the original *Loranthus leptostachyus* Kunth alone. He repeated Martius's error by describing the flowers as bisexual, even though this had been corrected by Eichler (1868). The new genus was founded primarily

on the several pairs of partly persistent, chaffy bracts that envelop the young inflorescence, but Van Tieghem, without providing any details, also stated that the stamens are of one type; in reality, they are always placed at two somewhat different heights. Van Tieghem's errors (as applied to the only species then recognized) were repeated by Engler and Krause (1935), who added a further one, namely the threadlike shape of the filaments, all of which are said to be of equal length. As indicated in the generic diagnosis below, bisexual flowers are characteristic of at least one species not known to the above authors, and anthers are sessile or nearly so, threadlike filaments not being present.

The rationale for recognizing Peristethium as a segregate from Struthanthus and as here circumscribed is based on several structural characters. The most prominent among these is the above-mentioned development of several to many pairs of conspicuous chaffy scale leaves at the base and along the inflorescence axis, the axial ones (bracts) subtending triads and monad. Most of the scales along the fertile axis tend to be caducous, but basal scale leaves often persist. No species of Struthanthus possess such scale leaves, but several other, unrelated Neotropical Loranthaceae show similar but much smaller and mostly deciduous scale leaves along the lower inflorescence axes, as in Panamanthus Kuijt. In the Old World, a similar, independent evolution of modified scalelike leaves below the flowers has occurred, as in Diplatia Tiegh., Tolypanthus (Blume) Blume, and several other genera (Kuijt, 1981b). However, the scale leaves in these Old World genera are much larger, often brightly colored, and not deciduous. The above-mentioned scale leaves are to be distinguished from the more inconspicuous pairs of prophylls at the base of axillary ramifications of some mistletoes, e.g., Psittacanthus mayanus Standl. & Steverm. and P. sonorae (S. Watson) Kuijt (Kuijt, 2009).

A second important generic character in *Peristethium* is the occurrence in each inflorescence of a single morphologically terminal flower, commonly flanked by one or more pairs of ebracteolate monads. The inflorescence is thus determinate. Paucity of materials has prevented me from confirming this aspect in some species accepted here for *Peristethium*. In at least one unrelated species, *Struthanthus deppeanus* (Schltdl. & Cham.) G. Don in Mexico, the same determinate pattern exists (Kuijt, 1981b), but elsewhere in small-flowered genera in the Loranthaceae this is known only in *Cladocolea*.

A third important generic feature in *Peristethium* is the sessile or nearly sessile, exceedingly small anther, inserted well above the middle of the petal that bears it. Struthanthus characteristically has larger, versatile anthers on long, slender filaments. The other small-flowered genera in the Loranthaceae possess entirely different androecia, especially Dendropemon (Blume) Rchb. (Kuijt, 2011a) and many species of the genus *Passovia H.* Karst.; the latter have minute anthers, but can scarcely be held as related to Peristethium. The small size of the anthers, and the prominent sterile anthers in male plants, for example, of P. leptostachyum, can be problematic in the determination of sex, as shown by the errors made by Van Tieghem (1895) and Engler (1897) in referring to that species as having bisexual flowers. Nevertheless, species with bisexual flowers as well as dioecious species exist in *Peristethium*. Further, the slender shape of the seedling in *Peristethium*, lacking a swollen haustorial pole, has also emerged as a contrasting feature vis-à-vis most other small-flowered genera. Finally, the existence of foliar sclerenchyma is a common denominator for those species that have been investigated (Kuijt & Lye, 2005). The profusion of stellate foliar sclereids is especially remarkable in P. roraimense, where much of the leaf mesophyll consists of such cells.

The variation in inflorescence structure seen in Peristethium is in general agreement with the evolutionary trends previously outlined for the Loranthaceae (Kuijt, 1981b). In that study, I concluded that the evolution of their inflorescences led from monads to aggregation as triads, and that this process begins at the base of the inflorescence. This latter tendency corresponds to the change from plants with bisexual flowers to a dioecious condition, and that hexamery was derived from tetramery. With regard to triadization, we may see all stages in the process represented in extant species of *Peristethium*. For example, P. archeri, P. peruviense (Kuijt) Kuijt, and P. roraimense have strictly monadic inflorescences. In P. primarium, P. palandense Kuijt, and several others, triads are present basally while monads are found subterminally and variably. Finally, P. confertiflorum may have only triads, with the additional, unanticipated production of some pentads. With the exception of P. primarium, all tetramerous species also exclusively have monadic inflorescences, thus combining two putatively ancestral conditions.

The curiously contorted style described and illustrated for *Peristethium polystachyum* and *P. tortistylum* Kuijt (Kuijt) has equivalents in several other Neotropical genera. The majority of Mesoamerican species of *Cladocolea* show this feature, seen more strongly in the female flower than the male

(Kuijt, 1975b). In Mexico, it is also known in Struthanthus; in fact, the generic synonym Spirostylis was based on this stylar twisting in what is now known as S. interruptus (Kunth) G. Don (Kuijt, 1975a). Struthanthus tortistylus from Ecuador (2003a) was published before it was realized that contorted styles are also characteristic of female P. polystachyum, a fact not previously mentioned in the literature. One further species with strongly contorted styles, an as yet undescribed species of Struthanthus from Peru, has recently been discovered. Thus we can be assured that there are at least three instances in which this curious, unexplained feature has evolved independently in Neotropical, small-flowered genera. The phenomenon is not known from other Loranthaceae in either the New or Old Worlds, with the solitary exception of *Ileostylus micranthus* (Hook. f.) Tiegh. of New Zealand (Barlow, 1966). The biological significance of contorted styles is not known, but it may bear a relation to the extraordinary behavior of the embryo sac known from Loranthaceae generally (see Kuijt, 1969, for a summary).

As now constituted, Peristethium also has convincing geographical integrity: its species range from Amazonian Bolivia north through the Andes into Costa Rica, with two endemic, highly localized outliers on Mt. Roraima and the Pakaraima Mountains (Fig. 1). It is generally accepted that the upper regions of the tepuis of Venezuela and Guyana environmentally correspond to the paramo life zone of the northern Andes (Berry et al., 1995), and the existence of the two rare species, P. roraimense and P. nitidum (Kuijt) Kuijt, in the Mt. Roraima area is not unexpected. The phylogenetic affinities of Peristethium with other small-flowered genera in the Loranthaceae are at present unclear, although the coherence of Psittacanthinae, which also includes the large-flowered genera Aetanthus (Eichler) Engl. and Psittacanthus Mart., has received molecular affirmation (Vidal-Russell & Nickrent, 2008; Nickrent et al., 2010). However, the precise relationships among the various genera remain to be elucidated. Morphological information, especially the occurrence of tetramerous flowers, determinate inflorescences, and monads lacking bracteoles, at present suggests an affinity of Peristethium with Cladocolea.

TAXONOMIC TREATMENT

Peristethium Tiegh., Bull. Soc. Bot. France 42: 175. 1895. TYPE: Peristethium leptostachyum (Kunth) Tiegh. [≡ Loranthus leptostachyus Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 440. 1818 (1820)].

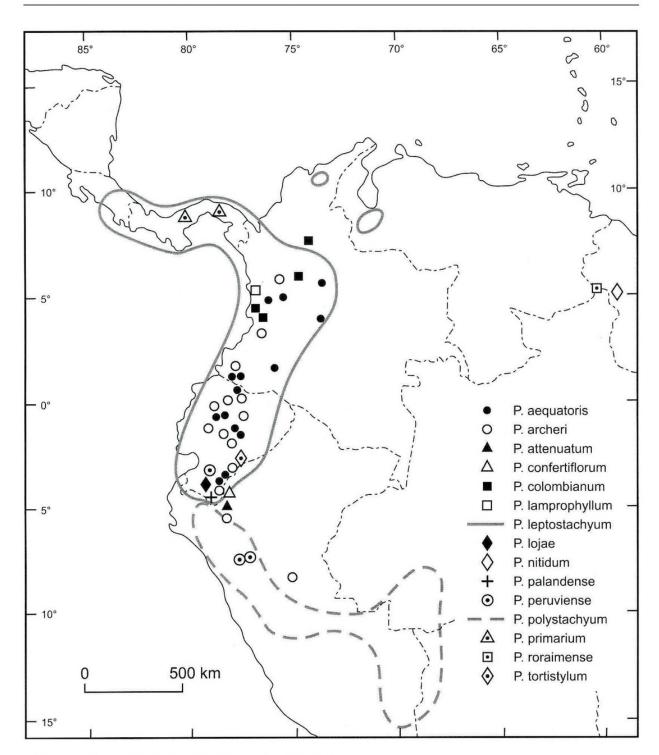


Figure 1. Geographic distribution of the species of Peristethium.

Struthanthus Mart., p.p., Flora 13: 102–106. 1830. TYPE: Struthanthus syringifolius (Mart.) Mart. [≡ Loranthus syringifolius Mart.].

Plants sparsely branched, unisexual when dioecious or bisexual, percurrent (monopodial), rarely determinate; internodes terete to quadrangular, smooth or with numerous rounded lenticels; epicortical roots present on some branches (and at the base of the plant) at least in *Peristhemium aequatoris*

(Kuijt) Kuijt, *P. archeri*, *P. leptostachyum*, and *P. lojae* (Kuijt) Kuijt. Leaves paired, ovate to elliptical, apex mostly acute to acuminate; petiolate. Inflorescences in units as monads or triads or mixed (as in the new species presented here, *P. confertiflorum*, with some pentads), the uppermost inflorescence section mostly with monads and terminating in a single flower, the monads ebracteolate; basal inflorescence bracts large, yellowish, chaffy or thick (as in *P. primarium*), bracts caducous where subtending

flowers, variably persistent or caducous at the base; monads, triads, and pentads (when present) pedunculate or more commonly sessile. Flowers tetramerous or hexamerous (P. nitidum the only pentamerous exception); anthers minute, ± isomorphic, 4-loculate, basifixed, placed just below the petal tip, at 2 different heights, sessile or nearly so, sometimes with a small connectival horn; style straight (the upper portion convoluted in female *P. polystachyum* and *P.* tortistylum (Kuijt) Kuijt); style absent in male flowers (P. peruviense (Kuijt) Kuijt, P. roraimense, and P. polystachyum) or present (in other species); stigma capitate, often oblique; anthers/staminodia absent in female (P. roraimense) or present (in other species). Fruit a 1-seeded berry, the seed enveloped by viscin, endosperm present, hexangular at least in P. leptostachyum but unknown in others, embryo dicotyledonous, slender, torpedo-shaped, the radicular pole not swollen. Pollen grains oblate, and moderate in size, the amb basically triangular (see the discussion below).

Distribution. Peristethium is a genus of 15 species, ranging from northern Amazonian Bolivia and adjacent Brazil (Acre) through Peru, Ecuador, Colombia, and Venezuela, and into Panama and Costa Rica, with one endemic species on Mt. Roraima, and a second rare species in the nearby Pakaraima Mountains (Fig. 1).

Etymology. The genus name is taken from the Latin for "peri-," meaning "surrounding, around," and "-stethium" for "collar or involucre."

Discussion. In addition to the generic characters in the above description, the anatomical circumscription of *Peristethium* is apparently significant. Foliar sclerenchyma appears to supply another generic distinction from Struthanthus, but I can provide only a glimpse of this feature. The presence of astrosclereids in the mesophyll of P. leptostachyum (as S. leptostachyus), in contrast to nearly all other Struthanthus species, was first mentioned in Kuijt (1964). The possible taxonomic utility of foliar sclereids was then raised with reference to some of the species placed in *Peristethium* (Kuijt, 1981b). Peristethium roraimense is especially noteworthy in this regard, as much of its leaf mesophyll consists of astrosclereids with many bulbous arms (noted as Cladocolea roraimensis; Kuijt, 1975b). Foliar sclereids are known to occur also in a couple of unrelated Mexican Struthanthus species (Kuijt & Lye, 2005), but are not of the same type. At present, the occurrence of foliar astrosclereids seems to buttress the taxonomic integrity of Peristethium.

Pollen. I have been able to study the pollen of three species, Peristethium aequatoris, P. leptostachyum, and P. lojae, and significant palynological differences exist between species even in such a modest sample (Fig. 2). The first two species are generally similar, but P. lojae is different in several respects. This is interesting in that it fully supports its separate status as a species, a question that was by no means securely established in Kuijt (1986), where the suspicion remained that P. lojae might be no more than an extreme form of *P. leptostachyum*. The pollen of all three species reported here is oblate and moderate in size (slightly more than 20 µm diameter). The outline of the pollen grain in polar view, or amb (Erdtman, 1952), is basically triangular, that of P. aequatoris and P. leptostachyum sometimes slightly concave, and that of P. lojae more commonly a little convex. The surface in all three species is essentially psilate, being very slightly verrucate between lobes. The margo is especially smooth and somewhat raised. Peristethium aequatoris and P. leptostachyum have isopolar pollen, but the situation in P. lojae is not clear. Micrographs for P. lojae show many grains with a distinctive, psilate apocolpial field, but many others without. I have established that at least some individual grains are heteropolar in this respect. It is not possible at this time to ascertain whether this is true for all grains. The variation in the size, shape, and prominence of the apocolpial field urges caution in this regard. The P. lojae apocolpial field ranges from circular to nearly triangular and is also somewhat variable in size. The grains of *P. aequatoris* and P. leptostachyum differ from each other in that the colpae of the former are wide, yet so shallow as to be inconspicuous, and the equatorial areas between lobes are a little more roughly ornamented than in *P*. leptostachyum. In both cases we are concerned with a diploporate condition. A polar view of many P. aequatoris grains demonstrates that the colpae are so shallow as to leave some uncertainty of their polar fusion (Fig. 2A). The pollen grains of P. lojae can immediately be recognized as being different from those of the other two species studied here. The colpae are transequatorial and very deep, with distinctly raised, smooth margins along their full length. Thus a polar view shows deeply notched lobes (Fig. 2C, D). The grains of *P. lojae* have three rather than six pores, each situated at the equator. The striking apocolpal fields described above also clearly separate P. lojae from the other two species studied. Apocolpal fields such as that of P. lojae have previously been reported from several other smallflowered, Neotropical genera (Feuer & Kuijt, 1985), as has heteropolarity, sometimes in the same population as isopolarity.

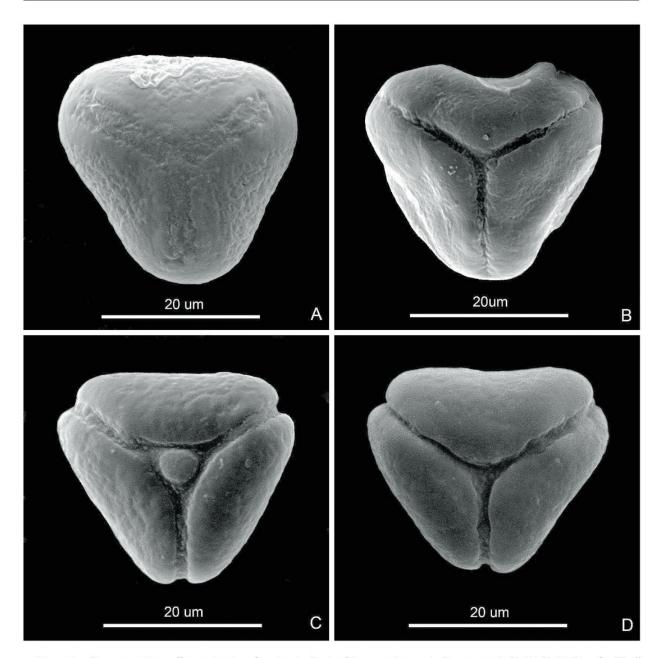


Figure 2. Representative pollen grains in polar view in *Peristethium* species. —A. *P. aequatoris* (Kuijt) Kuijt (*Van der Werff & Gudiño 107033*, UC). —B. *P. leptostachyum* (Kunth) Tiegh. (*Foster & Terborgh 6166*, UC). —C, D. *P. lojae* (Kuijt) Kuijt, showing two opposite polar views (*Lewis et al. 2953*, UC).

Sex distribution. The sex distribution in species of Peristethium continues to be ambiguous in some cases, partly because the anthers are exceedingly small at least when compared to those of other Neotropical genera, especially Struthanthus. It is only when fruiting specimens also carry evident, pollenbearing anthers that flowers can be securely regarded as bisexual as in P. archeri. Similarly, a species is clearly dioecious where the anthers or styles are completely missing in some specimens, as exemplified in P. peruviense, P. roraimense, and (at least most) P. polystachyum. Monoecious species are unknown in Neotropical Loranthaceae, except in two Oryctina Tiegh. species (Kuijt, 1981a) and

(questionably) in *Cladocolea coriacea* Kuijt (Kuijt, 1987b). It is thus certain that both dioecious species and species with bisexual flowers coexist in *Peristethium*. The same duality characterizes *Cladocolea* and the genus previously known as *Phthirusa* Mart. (Kuijt, 1975b, 2011b). Unfortunately, there remain some species in *Peristethium* where limited materials do not allow us to ascertain sexual distribution, therefore sex distribution is not utilized in the keys below.

Summary of distinctive features. Since most species of *Peristethium* have earlier been placed in *Struthanthus* or *Cladocolea*, it is useful to underline

the distinctive features of the genus *Peristethium*. The most significant of these is the cluster of mostly chartaceous and caducous bracts at the base of the inflorescence and this aspect is striking on at least the larger species. No species of Struthanthus or Cladocolea has such obvious bracts. The unrelated, monotypic genera Gaiadendron G. Don and Panamanthus have minute bracts at the base of the inflorescence, but these are not chaffy, and are not followed by similar, caducous bracts in the rest of the inflorescence. The minute, basifixed anthers, placed well above the petal's middle, are either sessile or on exceedingly short filaments, as seen on upper anthers. The androecium in Peristethium is also distinctive, even though sessile anthers occur exceptionally in Struthanthus, as in S. condensatus Kuijt (Kuijt, 1980: fig. 18), in some Passovia species (Kuijt, 2011b), and in Cladocolea (e.g., C. alternifolia (Eichler) Kuijt; Kuijt, 2003a). As seen in Peristethium, the subterminal monads and terminal flowers are known only in one Mexican species of Struthanthus, S. deppeanus (Kuijt, 1981b: figs. 4.2-4.3), but predominate in *Cladocolea*. Triads are not known in *Cladocolea* except for one probably teratological instance in C. pedicellata Kuijt (Kuijt, 1975b: fig. 28b). The pentads of P. confertiflorum are unique in the family. Finally, the slender embryo and angular endosperm are at least very unusual in New World Loranthaceae, but have not been documented for all *Peristethium* species. A striking feature without equivalence in other Loranthaceae is the absence of even a rudimentary style in most or all male flowers of three species, P. peruviense, P. polystachyum, and P. roraimense. In these species, the base of the flower shows a circular cushion, probably a nectary, with a small, central depression. Otherwise, the solitary, other instance may be the taxonomically isolated C. coriacea from Venezuela (Kuijt, 1987b), where the lack of a style in male flowers has not been documented convincingly.

Another, but perhaps more subtle contrast between Struthanthus and Peristethium is the sequence in which flowers open. As pointed out in an earlier survey of the Loranthaceae (Kuijt, 1981b), indeterminate inflorescences flower exclusively from the base upward and, in long inflorescences, young or

mature fruits may be in evidence at proximal nodes while distal flowers are still in bud. Determinate inflorescences, in contrast, develop basipetally and tend to open the terminal flower first, or all the flowers will open more or less simultaneously. The latter is especially evident in *P. confertiflorum*, *P. leptostachyum*, and *P. polystachyum*.

The shape of the mature *Peristethium* embryo has emerged as a distinctive generic character. In all species of Struthanthus (and many Dendropemon, Oryctanthus (Griseb.) Eichler, and Passovia species) seen by me, especially at the time of fruit maturation, the young seedling or embryo has a massively expanded haustorial disk (Kuijt, 1982). Nothing of the sort is true in P. archeri (described herein), P. colombianum Kuijt (Fig. 6E), P. leptostachyum, P. polystachyum (Fig. 15E), or P. primarium in which the radicular pole is slender and not in the least expanded (Kuijt, 1975a: fig. 2d; 1987a: fig. 5b). The seedling at that stage is torpedo-shaped, lacking any expansion of the radicular, haustorial pole. The seedling of Cladocolea is somewhat similar but is not as narrow and slender as that of Peristethium (Kuijt, 1975a). Other Neotropical but unrelated genera with slender embryos are Gaiadendron, Notanthera (DC.) G. Don, Panamanthus, and Tripodanthus (Eichler) Tiegh. (Kuijt, 1982).

In female (i.e., fruit-bearing) specimens of *Peristethium aequatoris*, which make up the great majority of specimens seen, the anthers are fully formed but exceedingly small and clearly do not contain pollen, even though the sterile pollen sacs seem to open. In both this species and some others, sex distribution may thus be difficult to ascertain. A plant with all flowers in the fruiting stage cannot reveal whether it is a female plant or whether its flowers are bisexual.

Epicortical roots, as stated in the above generic description, have been noted in at least two species. Those in *Peristethium archeri* may be at least 25 cm (*Neill et al. 5909*, UC) and may reach several meters in *P. leptostachyum* as noted in Costa Rica and Panama (Kuijt, 1964).

Because of the several generic changes that have occurred in the group in recent decades, Table 1 is provided to facilitate the identification of specimens.

TAXONOMIC KEY TO THE SPECIES OF PERISTETHIUM

- Leaf apex rounded to slightly emarginate; petals 5; known from the Pakaraima Mountains only 9. P. nitidum
 Leaf apex not rounded or emarginate; petals 4 or 6; not known from the Pakaraima Mountains.
 - 2a. Inflorescence bearing monads only; flowers tetramerous.

 - 3b. Flowers sessile; shoots percurrent; northern Peru to Colombia, or Mt. Roraima.

Table 1. Morphological comparison of genera within the Struthanthus complex. M = Monads, T = triads, NA = not applicable.

	Inflorescence type	Monads or triads	Bracteoles on monads	Plant sexuality	No. of petals	Basal inflorescence bracts
Cladocolea Tiegh.	det.*	M	_	bisexual/dioecious	(4)6(5)	_
Dendropemon (Blume) Rchb.	indet.	M	+	bisexual	6	-
Maracanthus Kuijt	indet.	M	+	bisexual/dioecious	6	_
Oryctanthus (Griseb.) Eichler	indet.	M	+	bisexual	6(4)	_
Oryctina Tiegh.	indet.	M	+	bisexual/dioecious/ monoecious	6	-
Panamanthus Kuijt	indet.	M	+	bisexual	6	_
Passovia H. Karst.	indet.	T	NA	bisexual/dioecious	6(4)	_
Peristethium Tiegh.	det.	M/T	_	bisexual/dioecious	4(6)	+
Phthirusa Mart.	NA	T	NA	bisexual	4	_
Pusillanthus Kuijt	indet.	T	NA	bisexual	4	_
Struthanthus Mart.	indet.*	T	NA	dioecious	6*	-

^{*}Exceptions occur in species within these genera.

- 4b. Leaves thin or somewhat coriaceous, apex acute to attenuate, venation evident; northern Peru to Colombia.

 - 5b. Leaves < 10 cm, somewhat coriaceous, apex abruptly acute to nearly obtuse, lowest lateral veins prominent, reaching at least to the middle of the blade; inflorescence 3–4 cm ... 2. P. archeri
- 2b. Inflorescence bearing triads and (some species) subterminal monads; flowers hexamerous or tetramerous.
 - 6a. Lateral triad flowers as well as monads and triads short-pedicellate 1. P. aequatoris
 - 6b. All flowers and triads sessile or essentially so (but see *P. confertiflorum*).

 - 7b. Flowers hexamerous; style straight, convoluted, or lacking; Costa Rica to Bolivia.

 - 8b. Triad pairs 12 or fewer, not densely crowded; pentads lacking; both triads and monads sessile, not deflected; Costa Rica to Bolivia.

 - 9b. Flowers not sunken in nodal cups, subtending nodes not swollen; both male and female flowers with straight styles (except in *P. tortistylum*), or style unknown.
 - 10a. Subterminal monads mostly 2 to 8 pairs.

 - 11b. Internodes quadrangular or keeled; inflorescence up to 8 cm (as inferred from infructescence length); style unknown 10. *P. palandense*
 - 10b. Subterminal monads 1(to 2) or lacking.

 - 12b. Internodes on leaf-bearing stems mostly 0.5 cm thick or less (but see *P. colombianum*), with pustular or elongated lenticels; inflorescence axis developing prominent lenticels in fruit; knoblike growths in leaf axils absent; inflorescences with terminal flower and 1 or 2 pairs of subterminal monads.

- 13b. Infructescences not obviously crowded; leaf-bearing internodes mostly 0.5 cm thick or less, developing pustular lenticels; Costa Rica to Ecuador.
- Peristethium aequatoris (Kuijt) Kuijt, comb. nov. Basionym: Struthanthus aequatoris Kuijt, Fl. Ecudaor, 24: 149–151. 1986. TYPE: Ecuador. Pichincha: Cantón Quito, along rd. betw. Tandayapa & Mindo, 9–10 km beyond Tandayapa, 2530 m, 16 Dec. 1979, T. B. Croat 49355 (holotype, MO-3096226!; isotypes, UC-1956802!, UC-1956803!). Figure 3.

Plants dioecious, leggy, sparsely branched, glabrous; internodes straight, slightly quadrangular to carinate, smooth without lenticels, to 9(13) cm; bearing occasional basal epicortical roots. Leaves to 12×10 cm, thin, broadly lance-ovate to nearly elliptical, apex obtuse to abruptly attenuate-cuspidate or slightly acuminate, base mostly truncate, venation pinnate, evident, with 2 to 4 or more lateral veins reaching at least halfway to the apex, midvein running into the apex; petiole 1–1.5 cm. Inflorescences 1 to 3 per leaf axil, each inflorescence largely triadic, 5–14 cm; inflorescence bearing 8 to 14 pairs of triads followed by 1 pair of monads, and 1 terminal flower; triad and monad peduncles 1-2 mm, median flower of triads sessile, lateral flowers on pedicels ca. 1 mm; basal inflorescence bracts several pairs, small, ± persistent; floral bracts and bracteoles caducous; peduncle 1-2 cm. Flowers hexamerous, flower buds yellowish or greenish white, apex rounded, 6.5 mm; petals ca. 4.5 mm; male flower with anthers nearly 1 mm, at 2 different heights near the bud apex, not overlapping, with slender style and undifferentiated stigma; female flower as the male but more slender, sterile anthers 1 mm, well-formed and even dehiscing; style 4 mm; stigma capitate. Fruit an ovoid berry, dull orange-red, to 10 mm and 5.5 mm thick when mature.

Distribution. Collections of Peristethium aequatoris have been seen only from Colombia. It grows in elevations ranging from 160 to 4000 m.

Discussion. The protologue of Struthanthus aequatoris (Kuijt, 1986) contained some errors that must be corrected. Most importantly, Peristethium aequatoris does indeed have chaffy bracts at the base

of the inflorescence, but they are small and early caducous, and are obvious only at the earliest stages of inflorescence development. Similar, but somewhat smaller, caducous chaffy bracts subtend the triads and monads and can be seen at the tip of expanding inflorescences. In the protologue it was suggested that the species might also be present in neighboring Colombia. This is indeed the case, as numerous collections cited below indicate.

Additional specimens examined. COLOMBIA. Caqueta: 63 km N of Florencia near border with Huila, Gentry et al. 9181 (MO). Chocó: Cerro del Torrá, Silverstone-Sopkin et al. 4454 (MO, UC); carr. Ansermanuevo-San José del Palmar, border of Valle del Cauca, Alto del Galápago, Forero et al. 2882 (MO). Nariño: Mpio. Ricuarte, Corregimiento Chucunéz, Reserva Natural La Planada, Roldán 1603 (UC); 7 km from Chucunés, 1°5′N, 78°1′W, Gentry & Keating 59728 (MO); Reserva Natural La Planada, a 7 km de Chucunés, Benavides 8709 (MO); Corregimiento Chucunés, Reserva Natural La Planada, Roldán 1601 (HUA, MO), 1602 (MO), 1603 (MO); trail from La Planada to Pielapí, 1°4′N, 78°2′W, Gentry et al. 63655 (MO); Isla de los Osos, 1°10′N, 77°50′W, Benavides 9733 (MO); trayecto San Isidro-La Planada, 1°10′N, 77°58′W, Benavides 9230 (MO). Riseralda: Santa Rosa de Cabal, along rd. to Termales, borders of Río San Eugenio, Wijninga & Wolf 548 (UC). Santander del Sur: 4 km below Palo Blanco W of Vélez, Luer et al. 10103 (MO, UC). ECUADOR. Carchi: Mira, 0°50'N, 78°11'W, Tirado et al. 1282 (UC); above Maldonado, Van der Werff & Gudiño 10858 (UC); Tulcán-Maldonado, W of Tufino, Van der Werff & Gudiño 10703 (UC). Cotopaxi: Cantón Sigchos, 35 km de Sigchos, 0°32′4″S, 78°58′43″W, Ramos et al. 6862 (UC). Morona-Santiago: Cantón Gualaquiza, Cordillera del Cóndor, 3°27'S, 78°22'W, Gentry 80344 (UC). Napo: SW of Cosanga, Orellana, Parque Nac. Yasuní, 0°30″S, 77°52′W, *Dik* 476 (UC). **Pichincha:** vic. of Bellavista Scientific Research Station and 1.2 km S of Bellavista, 0.3-1 km W of Tandayapa-Mindo rd., 00°01′16″S, 78°41'07"W, Croat et al. 96475 (MO, UC): 1.7-2.1 km beyond Bellavista, 0°01′02″S, 78°44′07″W, Croat 94632 (MO, UC); Tandayapa-Mindo rd., 7.2 km S of Tandayapa, 0°0′24"S, 78°40'W, Croat et al. 96505 (MO, UC); vic. of Bellavista, Km. 12 on rd. from Tandayapa to Mindo, 0°01′02″S, 78°44′49″W, Croat 94573 (MO, UC); carr. Nanegalito-Armenia, Loma de San José, La Vuelta Brava, 0°5′N, 78°40′W, Zak & Jaramillo 3221 (K ex MO); carr. Quito-Mitad del Mundo, Calacalí-Nanegalito, betw. Calacalí & Nanegalito, Freire-F. et al. 631 (NY); Cantón Quito, 0°4'N, 78°39'W, Webster et al. 30484 (UC); old rd. Quito-

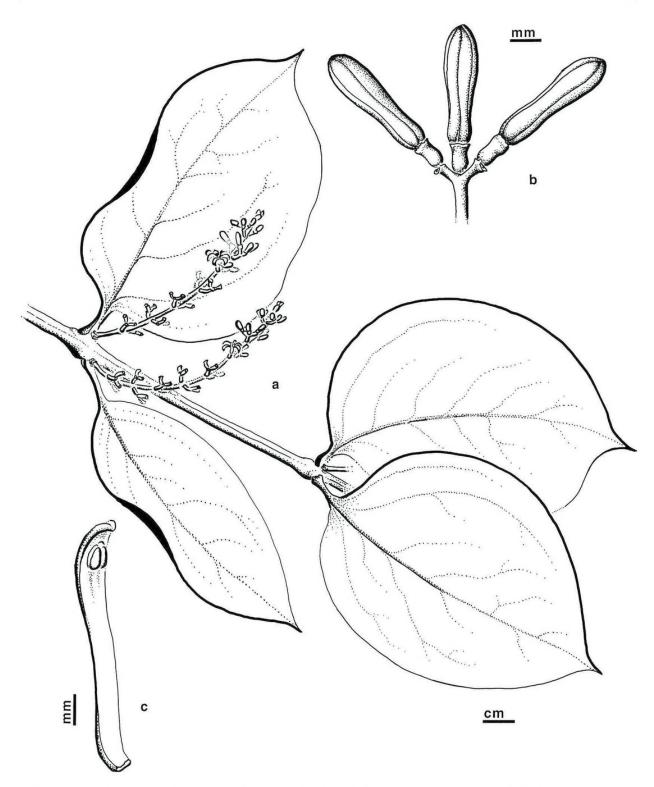


Figure 3. Peristethium aequatoris (Kuijt) Kuijt. —A. Habit. —B. Triad. —C. Petal and stamen. Drawn from Croat et al. 96475 (UC). Scale bars: A = 1 cm; B, C = 1 mm.

Santo Domingo de los Colorados, 6–11 km W of San Juan de Chiriboga, 0°15′S, 78°45′W, Luteyn & Boom 8479 (NY, UC); 0°13′53″N, 78°48′10″W, Zak 1102 (K, UC); 1155 (UC); Reserva Río Guajalito, near Chiriboga, along old rd. Quito–Santo Domingo, on Lauraceae, Van der Werff et al. 12218 (F, UC); carr. Quito–San Juan–Chiriboga, Empalme, Km. 59, Zak 1205 (K, UC); 1307 (UC); carr. Quito–Chillogallo–San Juan–Chiriboga, 29–32 km from Chillogallo, 0°17′S, 78°41′W, Freire-F. et al. 1514 (NY); old rd.

Quito-Nono, Mindo, 9 km S of Tandayapa toward Mindo, 0°N-S, 78°43′W, Luteyn et al. 8834 (NY); Reserva Florística-Ecológica Río Guajalito, Km. 59 de la carr. antigua Quito-Santo Domingo de los Colorados rd., estribaciones occidentales del Volcán Pichincha, 0°13′53″S, 78°48′10″W, Jaramillo & Zak 7916 (K ex MO, UC); main entrance from Quito-Santo Domingo rd., 3.5 km from hwy., Croat 72027 (MO). Zamora-Chinchipe: Zamora, Palacios & Tirado 13400 (UC).

2. Peristethium archeri (A. C. Sm.) Kuijt, comb. nov. Basionym: Oryctanthus archeri A. C. Sm., Bull. Torrey Bot. Club 59: 516–517. 1932. Cladocolea archeri (A. C. Sm.) Kuijt, J. Arnold Arbor. 56: 277–281. 1975. TYPE: Colombia. Antioquia: 18 km N of Medellín, 2000 m, Jan. 1931, W. A. Archer 1521 (holotype, US-0151740!). Figure 4.

Plants rather large, glabrous, percurrent; stems long and straight, branching only from older wood, angular and smooth when young, becoming stout and terete, with numerous conspicuous, round lenticels of uniform size; internodes 4.5-8 cm; epicortical roots present at the base, occasionally on the stems, to 25 cm. Leaves decussate, $3-10 \times 2-5$ cm, somewhat coriaceous, ovate, apex abruptly acute to nearly obtuse, base rounded to truncate, midvein prominent as a groove, running into apex, with prominent lateral veins, the lowest ones often running more than halfway to the apex; petiole 4-8 mm, canaliculate. Inflorescences several per leaf axil; each inflorescence mostly 3-4 cm, with ca. (3 to)5 pairs of ebracteolate, sessile monads and a single terminal flower; floral bracts acute, to nearly 3 mm, naviculate, mostly caducous but some persisting; with several pairs of small, chartaceous scale leaves at the base. Flowers tetramerous, bisexual, sessile, yellowish green, the mature bud nearly 6 mm, blunt; petals 4.5 mm, 4(or 5); each with 1 sessile anther, anthers placed at 2 different heights, both above the middle but all of similar shape, having 4 pollen sacs with blunt projecting connective; pollen smooth, somewhat 3-lobed but lacking evident surface markings; ovary 1.5×1.5 mm, with irregularly denticulate calyculus; style straight and rather stout, 3 mm; stigma weakly differentiated, oblique. Fruit ovoid, "rose red when young, becoming blue with grevish bloom" (Archer 1521, in sched.), 6×4 mm thick, with blunt apex; embryo dicotylous, 3 mm, narrow, the radicular pole not expanded.

Distribution. Collections of Peristethium archeri have been seen only from Colombia. This species grows in elevations ranging from 500 to 2500 m.

Dicussion. The original concept of Peristethium archeri (Smith, 1932) and my subsequent description and illustration for the Flora of Ecuador (Kuijt, 1986) were based on northern material, the type from Colombia. It has since developed that the species is exceedingly variable further south in Ecuador, both in leaf shape and the size of inflorescences, and intermediates to P. attenuatum Kuijt may occur.

Peristethium archeri, as here circumscribed, is a variable species in terms of leaf shape and inflorescence size and composition. Its possible intermediates to P. attenuatum are alluded to below. In Colombia (especially in Antioquia), a very small form occurs that may, in fact, represent an unrecognized species. Its leaves are no more than 6×2 cm and are narrowly ovate with an attenuate apex and obtuse base. Most strikingly, its inflorescences and infructescences (including flowers and fruits) are at most 1 cm, are completely sessile in the leaf axils, and regularly bear only seven flowers, including the terminal one. Below, I list the two most striking specimens I have encountered and that I place in P. archeri only provisionally; they were collected in essentially the same locality (Roldán et al. 747 and 1120, MO). Possible intermediates to larger P. archeri, also from Antioquia, have been noted, as in Roldán 1063 (MO). In the first specimen, fruits are described as orange and black, in the second, pink to black.

Additional specimens examined. COLOMBIA. Antioquia: Mpio. Frontino, carr. Nutibara-La Blanquita, Sector Murrí, 6°45′N, 76°21′W, on Compositae, Roldán et al. 747 (MO); Km. 14, on Ericaceae, Roldán et al. 1120 (MO); La Sierra, 18 km N of Medellín, on Tournefortia fuliginosa Kunth, Archer 1058 (US); Cordillera Central, near Porcesito, Río Medellín valley, Hodge 6842 (US). Chocó: Mpio. Carmen de Atrato, 6°1'N, 76°7'W, Roldán & Luteyn 1054 (UC). Nariño: 1°15′N, 78°9′W, Gentry et al. 55201 (UC). Valle: Mpio. Cairo, Cerro del Ingles, Cordillera Central, Serranía de las Paraguas, Silverstone-Sopkin et al. 2753 (F); shores of Río Bugalagrande, Calamar, Cuatrecasas 20506 (F); Cordillera Occidental, W slope, Hoya del Río Dagua, La Elsa, La Cristalina, Cuatrecasas 15244 (F, UC); Hoya del Río Cali, Quebrada Honda, camino a Miralindo, Cuatrecasas 18430 (F); Paraguas, cerca de frontera con Dpto. Chocó, Silverstone-Sopkin 3837 (F). San Pablo: Km. 16, Cali-Buenaventura, Restrepo 24 (UC); Finca Zingara, Km. 18, Restrepo 6 (UC). ECUADOR. Imbabura: Lita, Acosta Solís 12200 (F), Madison et al. 4999 (SEL). Morona-Santiago: Cantón Huamboya, Shankaimi, 1°58'S, 77°49'W, Palacios 11418 (MO, UC). **Pastaza:** Mera, *Harling et al.* 9845 (S); on Miconia Ruiz & Pav., Asplund 19166 (S). Pichincha: near Santo Domingo, Fagerlind & Wibom 1758 (S); Chaupi, Dodson & Thien 1852 (UBC, UC). Tungurahua: Río Negro, bank of Río Pastaza, on Banara guianensis Aubl., Asplund 18624 (S). Zamora-Chinchipe: Cantón Zamora, Romerillos Bajo, E border of *Podocarpus* Natl. Park, Quebrada Neva, Fundación Maquipucuna, 4°11'S, 78°55'W, Clark et al. 3337 (MO, UC); El Pangui, Cordillera del Cóndor, near Cóndor military post, on Ecuador-Peru border, 3°38′20″S, 78°23'29"W, Neill et al. 14516 (UC ex MO). PERU. Amazonas: Bagua, 4°55′S, 78°19′W, Rodríguez et al. 1012 (UC); Imaza, Díaz et al. 7972 (UC). Cuzco: Paucartambo, Nuñez 8076 (UC). **Huánuco:** Prov. Pachitea, near Pucallpa, Wallnöfer 18-26388 (UC); SW slope of Río Llulla Pichis watershed, ascent of Cerro La Sira, on Melastomataceae, Dudley 13450 (F). Piura: Prov. Huancabamba, Díaz et al. 2751 (UC).



Figure 4. Peristethium archeri (A. C. Sm.) Kuijt. —A. Habit. —B. Young inflorescence. —C. Young infructescence. —D. Bud and floral dissection. A, B, and D drawn from Palacios 11418 (UC); C drawn from Neill et al. 14516 (UC). Scale bars: A=1 cm; B-D=1 mm.

3. Peristethium attenuatum Kuijt, sp. nov. TYPE: Peru. Amazonas: Prov. Bagua, Distr. Imaza, Tayu Mujaji, Comunidad de Wawas, sobre una capa esponjosa de raices y materia orgánica, Campau Uwejush, 5°15′56″S, 78°22′07″W, 1200 m, 21 Oct. 1997, R. Vásquez, Lirio & Pitug 24633 (holotype, MO-4922779!). Figure 5.

Haec species quoad surculos percurrentes, inflorescentiam monades tantum gerentem, bracteas persistentes etiam flores sessiles bisexuales tetrameros *Peristethio archeri* (A. C. Sm.) Kuijt arcte affinis, sed ab eo foliis tenuibus majoribus apice plerumque attenuatis venis lateralibus basalibus non elevatis, inflorescentia breviore atque calyculo inconspicuo distinguitur.

Plants percurrent, glabrous; internodes 3-6 cm, terete (somewhat quadrangular in coastal Ecuador), bearing reddish brown, pustular lenticels when young. Leaves to 16×5 cm, paired, ovate, thin, apex long-acuminate, base truncate-cordate, venation pinnate, midvein running into the apex, lateral veins obscure; petiole ca. 7 mm. Inflorescence 6-8 mm, determinate, not expanding in fruit; above with 3 pairs of ebracteolate, sessile monads, and a single terminal flower; flower bracts caducous; inflorescence bracts at least 4 pairs, acute, chaffy, persistent. Flowers sessile, bisexual, tetramerous, greenish white, 5 mm including 1 ovary, 1.5 mm with nearly smooth calveulus; petals 4.3 mm; anthers sessile, placed 2.5 mm above the base of the petals; style straight, 3 mm, placed on a small, raised portion; stigma capitate, distinct, oblique. Fruit 3×2 mm, ellipsoid, purplish or bluish green (Vásquez et al. 34633, in sched.), calyculus indistinct.

Distribution. Collections of Peristethium attenuatum have been seen from Ecuador and Peru. This species grows in elevations ranging from 100 to 1550 m.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. Peristethium attenuatum is closely related to P. archeri in having persistent inflorescence bracts, tetramerous bisexual flowers, and only monads. Peristethium archeri can be distinguished by having smaller, non-attenuate, thicker leaves and much longer, more floriferous and elongated inflorescences, and a distinctly erose calyculus. As mentioned under P. archeri, intermediates between it and P. attenuatum may occur.

Many of the Ecuadorian specimens cited below derive from northwestern Ecuador, being thus far removed (ca. 500 km) from the type locality, but they nevertheless seem to be conspecific with it, even though the young internodes are distinctly quadrangular rather than terete.

Paratypes. ECUADOR. Carchi: vic. of Peñas Blancas, 6.6 km N of El Chical along trail to Tobar Donosa, 0°58′38″N, 78°11′53″W, Croat 94862 (MO, UC); along rd. betw. El Chical & Tulcán, 15.4 km E of El Chical, 0°54′04″N, 78°05′50″W, Croat 94954 (MO, UC); Parroquia Tobar Donoso, Reserva Ethnica Awá Sabalera, 0°55′N, 78°32′W, Aulestia et al. 759 (MO). Esmeraldas: Km. 8, Lita—Altotambo, Dodson & Gentry 17542 (UC). Quinindé: Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, Monkey Bone Trail, 0°21′N, 79°44′W, Pitman & Bass 1084 (MO), Pitman et al. 809 (MO); ridge of La Loma de los Guerrilleros, Clark 2931 (MO); Río Palaví Awá encampment, 01°07′N, 78°37′W, Hoover et al. 4073 (MO), 00°58′N, 78°16′W, Hoover et al. 3102 (MO).

4. Peristethium colombianum Kuijt, sp. nov. TYPE: Colombia. Valle del Cauca: Mpio. Buenaventura, vía Buenaventura—Cali, 300 m, on Cecropia Loefl., 14 Apr. 2007, D. Macias & B. R. Ramírez 5001 (holotype, CAUP!; isotype, CUVC!). Figure 6.

Haec species quoad habitum robustum atque folia grandia apice acuminata *Peristethio leptostachyo* (Kunth) Tiegh., quoad inflorescentiam magnam densissimam *P. confertifloro* Kuijt similis, sed a hoc inflorescentia pentadibus carente atque triadibus monadibusque sessilibus non deflexis, ab illo internodiis crassioribus lenticellis elongatis notatis, foliis in sicco fuscatis, inflorescentia magna densa squamis basalibus attenuatis subtenta atque bracteolis acicularibus triades monadesque subtendentibus distinguitur.

Plants quite robust, dioecious; stem internodes terete, bearing numerous, small, slender, elongated lenticels, to 7 cm and to 10 mm diam. when leafbearing. Leaves to 20 × 10 cm, leathery, lanceolateovate to nearly elliptical, apex acuminate, base truncate, dull on both sides, turning dark when dry, venation pinnate or nearly so, midrib strongly raised on abaxial side, running into apex, with 2 or more strong basal lateral veins; petiole 1 cm, stout. Male inflorescence at least 3 cm, axis quadrangular, bearing 7 to 9 pairs of triads, 1 or 2 pairs of subterminal monads with acicular bracteoles, and 1 terminal flower; female inflorescence subtended by at least 6 pairs of caducous, acute, brittle and stiff, papery scale leaves, to 8 cm in fruit, its axis to 2.5 mm thick at the base, with large lenticels, bearing up to 12 pairs of crowded, completely sessile triad pairs and 1 pair of subterminal monads, at least some with whiplike bracteoles 1 mm, followed by a single terminal, sessile flower. Flowers hexamerous, not

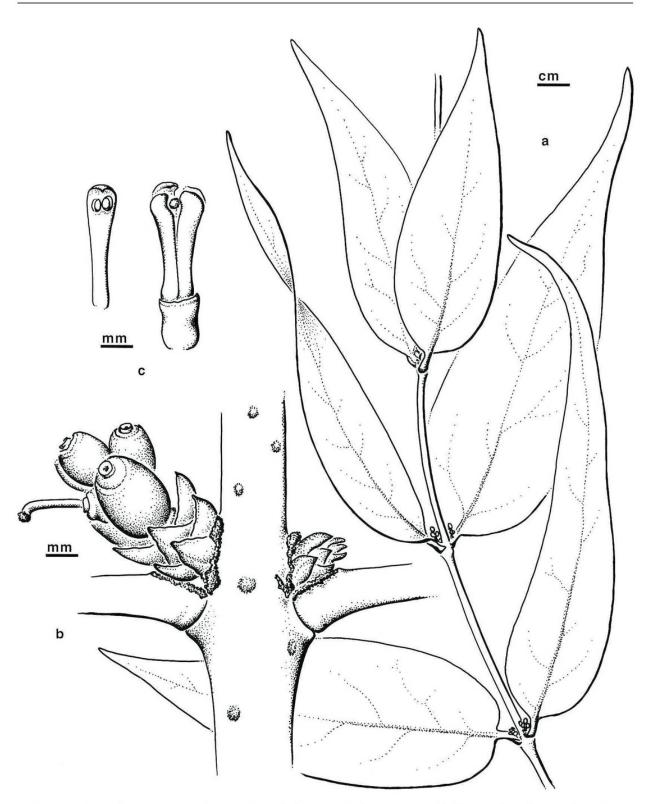


Figure 5. Peristethium attenuatum Kuijt. —A. Leafy shoot. —B. Infructescence. —C. Flower and petal. Drawn from Vásquez et al. 34633 (MO). Scale bars: A = 1 cm; B, C = 1 mm.

placed in nodal cups, subtending nodes not swollen; male flower bud 5 mm, ovary 1 mm, with coarsely dentate calyculus; anthers 0.7 mm, slightly biseriate, sessile above the middle of the petals; sterile style nearly as long as the petals, slightly curved in the middle but essentially straight; stigma undifferenti-

ated. Female flower unknown. Fruit ellipsoid to obovoid, reddish brown (Macias & Ramírez P. 5001, CAUP), 7×5 mm, apex truncate, calyculus inconspicuous; embryo 5 mm, extremely slender, the 2 cotyledons 2 mm, strap-shaped, the radicular end without swelling.

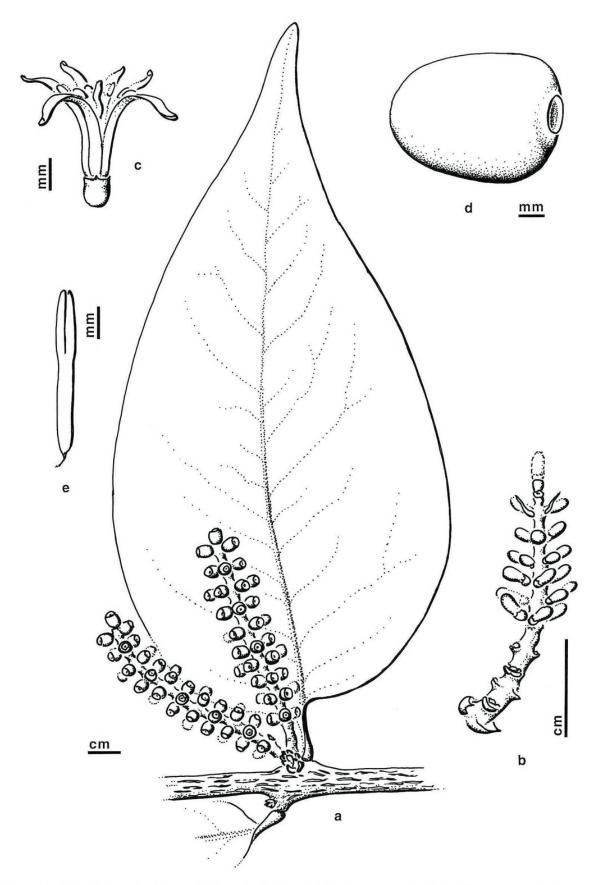


Figure 6. Peristethium colombianum Kuijt. —A. Habit and infructescences. —B. Male inflorescence —C. Open male flower. —D. Fruit. —E. Embryo. A, B drawn from Macias P. & Ramírez P. 5001 (CAUP); C–E drawn from Daly & Betancur 5344 (UC). Scale bars: A, B=1 cm; C-E=1 mm.

Distribution. Collections of Peristethium colombianum have been seen only from Colombia. This species grows in elevations ranging from 10 to 1700 m.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. It is unfortunate that the available material of this strikingly robust species lacks female flowers. The plants are similar to Peristethium leptostachyum, sharing a robust habit, similarly large leaves at least 18 cm long, with attenuate apices. Peristethium colombianum is distinguished by the massive, densely crowded infructescence axes with numerous triads; large, acuminate, dark-drying leaves are also distinctive, as are the attenuate basal scales of the inflorescence. In P. leptostachyum, there are many pairs of chaffy, pale bracts subtending the inflorescences, but acicular bracteoles subtend the triads and monads in P. colombianum. The only other known species of Peristethium with such large, densely crowded inflorescences is *P. confertiflorum*, which differs from *P. colombianum* in having distinct, deflected triad peduncles and occasional pentads. The fruits of the type are said to be reddish brown (Daly & Betancur 5344, in sched.), but this is likely an immature coloration, as the mature fruits are bluepurple, in at least most species of Peristethium.

Paratypes. COLOMBIA. Antioquia: Valley of Río Anorí, vic. of Planta Providencia, 35 km SW of Zaragoza, area surrounding confluence of Quebrada LaTirana & Río Anorí, W slope, 7°18′N, 75°4′W, Waide 62113 (UC); Mpio. San Carlos, corregimiento El Jordán, trocha Los Planes entre carr. alto de Samaná–Quebrada La Villa, Embalse de Punchiná, alrededores de Quebrada La Selva, Velásquez & Zora 231 (UC); Mpio. San Luis, Piedra de Castillón, SW of town, ridge top leading to peak, 6°1′N, 75°1′W, Daly & Betancur 5344 (UC). Valle: Bajo Calima, 15 km N of Buenaventura, Cartón de Colombia concession, 3°56′N, 77°8′W, Gentry & Juncosa 40481 (MO, UC); same previous locality, Gentry et al. 53667 (UC); Puerto Marizalde, Río Nanay, forest behind town, mostly Campnosperma Thwaites swamp, 3°15′N, 77°28′W, Gentry & Juncosa 40565 (UC).

5. Peristethium confertiflorum Kuijt, sp. nov. TYPE: Peru. Cajamarca: San Ignacio, Distr. San José de Lourdes, Poblado Los Llanos, 5°5′33″S, 78°50′22″W, 2002 m, 16 Oct. 2006, J. Perea & V. Flores 2902 (holotype, UC!; isotypes, AMAZ not seen, HUT not seen, MO not seen, MOL not seen, USM not seen). Figures 7, 8.

Haec species quoad folia ovato-elliptica basi truncata Peristethio palandensi Kuijt similis, sed ab eo habitu robusto, internodiis teretibus lenticellis parvis numerosis notatis atque inflorescentia congesta ex triadibus pluribus monadibus paucis ac pentadibus nonnullis constante distinguitur.

Plants presumed dioecious, the type female; stems stout, glabrous, internodes straight, terete, 8-10 cm, 8 mm thick where bearing inflorescences. Leaves to 16 × 8 cm, ovate-elliptic, apex acuminate, base truncate, venation pinnate, midrib reaching apex and strongly raised on abaxial surface; petiole 2 cm. Inflorescence axis lacking lenticels, 6-8 cm; ca. 24 pairs of crowded, somewhat deflected triads and 1 or 2 pairs of subterminal monads and a terminal flower; pairs of pentads present in mid-region of the inflorescence; peduncle ca. 5 mm. Flowers presumed bisexual, hexamerous, flower bud blunt-tipped. Male flowers with anthers 0.5 mm, sessile, placed at 2 different heights just below the tips of the petals; style 3 mm, stout, straight; stigma blunt, poorly differentiated. Female flowers 5 mm including the 1.5 imes 1 mm ovary with finely denticulate calyculus. Fruit not known.

Distribution. Peristethium confertiflorum is only known from the type specimen collected at 2000 m from Cajamarca in Peru.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. The close geographic proximity and similarity in leaf shape might suggest that Peristethium palandense and P. confertiflorum are conspecific, but fundamental differences exist between the two species. Peristethium confertiflorum is an unusually stout plant with terete internodes bearing numerous, small lenticels, while stems of P. palandense are not at all stout (< 5 mm), and has somewhat quadrangular, smooth internodes. More significantly, the inflorescences of the two species are entirely distinct. Peristethium confertiflorum is characterized by numerous triads, with far fewer monads (one or two pairs) distal on a congested inflorescence, especially the tip being crowded. In P. palandense, the inflorescence is more open, with five to eight subterminal monad pairs and no terminal crowding. The occurrence of 5-flowered lateral units (pentads) on the inflorescence in *P. confertiflorum* is a unique feature (see below).

Unfortunately, the sexual condition of *Peristethium* confertiflorum remains uncertain. In the case of the type, the dimensions of the style seem to indicate fruit-producing capacity, but the anthers are of normal size and produce pollen. Its flowers may therefore be presumed as bisexual. The most extraordinary feature of the present species is the

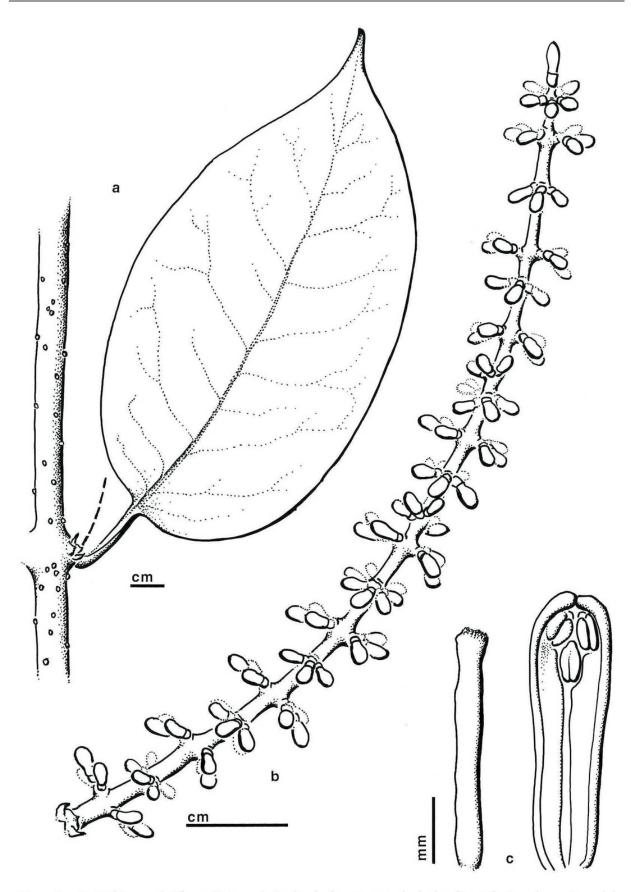


Figure 7. Peristethium confertiflorum Kuijt. —A. Leaf and adjacent stem, the broken line indicating the position of the inflorescence. —B. Inflorescence. —C. Floral dissection. Drawn from Peres & Flores 2902 (UC). Scale bars: A, B=1 cm; C=1 mm.

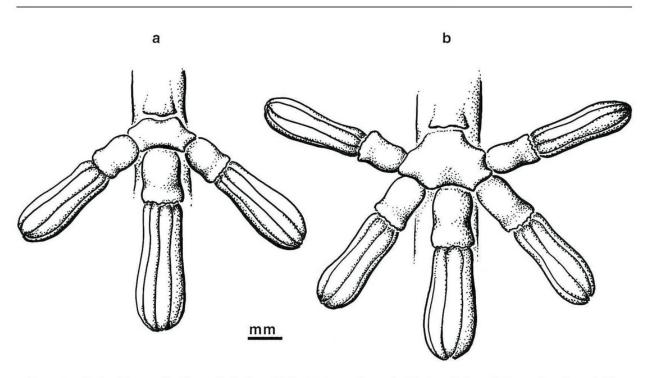


Figure 8. Peristethium confertiflorum Kuijt, lateral inflorescence units. —A. Triad. —B. Pentad. Drawn from Peres & Flores 2902 (UC). Scale bars = 1 mm.

occurrence, usually in the mid-region of the inflorescence, of lateral units that are not triads but pentads, bearing five flowers in a somewhat fanshaped, deflected configuration (Fig. 8). The peduncles of triads and pentads are scarcely recognizable, but are stout structures ca. 1×2 mm. The flowers are placed on this transverse, barlike structure that is placed more or less directly on the inflorescence axis. Most triads and pentads are somewhat deflexed, making it virtually impossible to discern the scar of the subtending bract. As it is, on these lateral units there seems to be no evidence of bracteole-like structures, although these may have fallen very early. Above each unit, the inflorescence axis shows a slightly overhanging, ridgelike lip. The median flower is the largest (and/or oldest) one, flanked on each side by two smaller (and/or younger) ones, all five of the flowers being more or less in the same plane. Having surveyed inflorescence structure of the family generally some years ago (Kuijt, 1981b), I can state that no comparable inflorescence structure is known elsewhere in Loranthaceae. The very rare pentads reported from *Passovia pyrifolia* (Kunth) Tiegh. are of an entirely different structure (Kuijt & Weberling, 1972).

6. Peristethium lamprophyllum Kuijt, sp. nov. TYPE: Colombia. Choco: area of Baudó, lt. side of Río Baudó, 7 km upstream from estuary, on shore opposite Quebrada Caimanerita, 11 Feb.– 29 Mar. 1967, (& fl.), H. P. Fuchs & L. Zanella 22060 (holotype, K!; isotypes, F!, US not seen). Figure 9.

Haec species quoad inflorescentiam triades floresque sessiles gerentem, flores hexameros etiam stylum rectum Peristethio colombiano Kuijt, P. leptostachyo (Kunth) Tiegh. et P. lojae (Kuijt) Kuijt similis, sed ab eis internodiis caulium floriferorum crassis, tumoribus gongylodibus ad axillas foliares prolificantibus, foliis adaxialiter nitidissimis atque inflorescentia axe elenticellato flore terminali ac monadibus subterminalibus ut videtur carente distinguitur.

Plants dioecious; stem internodes to 6 cm long and 1 cm thick when leaf-bearing, terete, with conspicuous knoblike, proliferating swellings in axils, with numerous small, pustular lenticels, to 6 cm and 1 cm thick. Leaves to 15×6 cm, ovate-lanceolate, very shiny above, dull below, apex acute, base obtuse, midvein strongly raised abaxially and grooved adaxially, running into apex, venation pinnate, with numerous lateral, oblique veins, much of the minor venation evident abaxially; distinct stout petiole, 1.5 cm. Male inflorescence axis somewhat keeled, smooth, without lenticels, with nodes not swollen, to 7 cm; 11 pairs of sessile triads, upper 1 or 2 nodes bearing possibly subterminal monads and terminal flower uncertain; basal inflorescence bracts several pairs, whitish, ovate-deltoid, 2×2 mm, apex acute; peduncle ca. 3 mm. Flowers hexamerous, flower buds 5 mm; petals essentially isomorphic; anthers 0.75 mm, sessile at 2 different heights near the petal tips; style 4 mm, slender, straight, stigma weakly developed; ovary 1 mm, apex rounded, calyculus

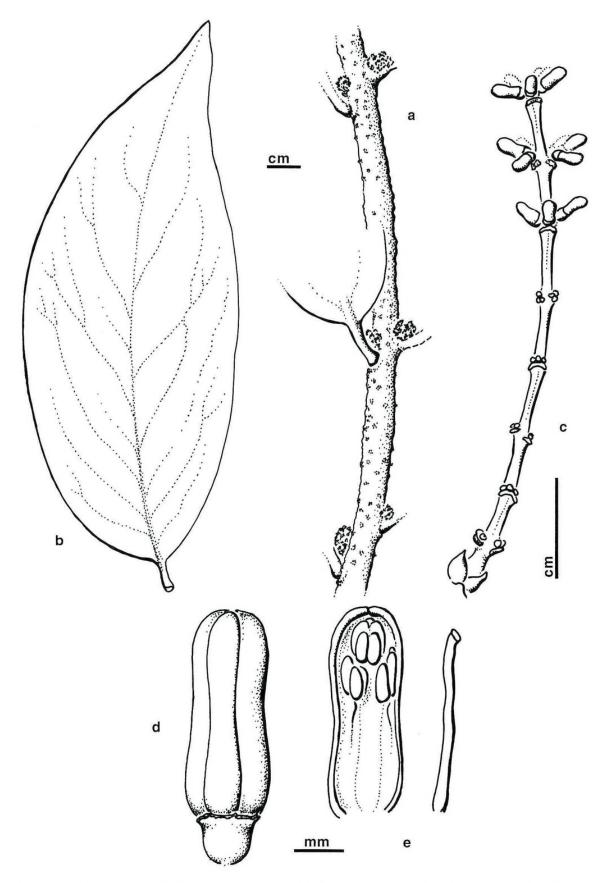


Figure 9. Peristethium lamprophyllum Kuijt. —A. Leaf-bearing stem, showing axillary knobs. —B. Leaf. —C. Inflorescence. —D, E. Mature flower bud and floral dissection. Drawn from Fuchs & Zanella 22060 (K). Scale bars: A-C=1 cm; D, E=1 mm.

with minutely erose, darkened rim; pollen sacs 4, elongated, connectival horns very small or absent. Fruit not known.

Distribution. Peristethium lamprophyllum is only known from the type collection collected in Choco, Colombia.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. Peristethium lamprophyllum undoubtedly is an unrecognized species, even though the available material is sparse and badly fragmented. The stems are extremely stout, to 1 cm in diam., the leaves being strikingly shiny adaxially. The massive axillary knobs are made of numerous inflorescence scars; bract remnants are also very different from the other species here treated in which bracts are often caduous. The new species is similar to P. leptostachyum, which has matte leaves lacking the adaxial luster characteristic of P. lamprophyllum and does not develop the knoblike growths in the leaf axils. Unfortunately, the fragmented condition of the type of P. lamprophyllum denies me the possibility of ascertaining the construction of the inflorescence tip.

7. Peristethium leptostachyum (Kunth) Tiegh., Bull. Soc. Bot. France 42: 175. 1895. Basionym: Loranthus leptostachyus Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 440. 1818 [1820]. Struthanthus leptostachyus (Kunth) G. Don, Gen. Hist. 3: 411. 1834. TYPE: Colombia. "Crescit in andibus Quinduensium, inter Carthago et Buga, alt. 1200 hex. Floret Augusto," Humboldt & Bonpland s.n. (holotype, P!, P at F neg. 39627!; isotype, B†, B† at F neg. 11806!). Figure 10.

Loranthus pyrifolius Willd. ex Schult. f. in Schultes & Schultes, Syst. Veg., ed. 15 bis [Roemer & Schultes] 7: 1647. 1830, syn. nov., nom. illeg. superfl., non Loranthus pyrifolius Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 441. 1818 [1820]. TYPE: s. coll. (B-W 06975-010!).

Phthirusa pittieri K. Krause, Repert. Spec. Nov. Regni Veg. 15: 441–442. 1919, as "Pittieri." TYPE: Panama. Colón: "längs des Rïo Fato in Wäldern und Dickichten, um 10–100 m, als Parasit auf Sloanea-Arten," July–Aug. 1911, H. Pittier 3911 (holotype, B†).

Plants dioecious, large, sparsely branched, the stout branches sometimes reaching several meters in length, 8 mm diam.; stem terete to somewhat ridged when young, bearing numerous pustular, cinnamon-brown lenticels; epicortical roots numerous, long, on stems and base of the plant. Leaves to 18×7 cm

(rarely to 25×10 cm), broadly to narrowly lanceolate to ovate, somewhat thicker and rigid and usually pale green, apex attenuate, sometimes abruptly so, base mostly obtuse to truncate; petiole ca. 1 cm, strongly canaliculate. Inflorescence 1 to more per leaf axil, to 12 cm; with several sterile internodes and at least minute cinnamon-brown lenticels, with 12 or fewer numerous pairs of sessile triads and 1 or 2 pairs of single, sessile, ebracteolate monads and a single terminal flower, monads and triads not sunken in nodal cups; each inflorescence subtended by numerous pairs of chaffy, pale, usually early caducous bracts; floral bracts and bracteoles caducous; peduncle 2 cm. Flowers hexamerous, unisexual, not sunken in nodal cups, buds 4-5 mm; the female flower slender, the male flower clavate; anthers in the male flowers sessile, sometimes with twisted, white hairs directly below, in 2 series at slightly different heights above the middle of the petals; anthers in the female flowers sterile, straplike; stigma capitate, distinct, oblique; style essentially straight, present also in the male flower. Fruit to 7×5 mm, ellipsoid, dull brick red becoming waxy dark blue; seeds with endosperm hexagonal in section, embryo with poorly developed, slender haustorial pole.

Distribution. Collections of Peristethium leptostachyum have been seen from Costa Rica and Panama in Central America, and from Colombia, Ecuador, Peru, and Venezuela in South America. The taxon was collected at elevations ranging from sea level to 2370 m.

Discussion. The two collections from Peru below represent the first authentic records of *Peristethium leptostachyum* for Peru; both, however, are within a few kilometers from the Ecuadorian border.

The distinction between Peristethium leptostachyum and P. polystachyum is not directly obvious, and the two species have frequently been confused (as in Kuijt, 1964, where both species were included within *Struthanthus*); however, there are several clear differences. Peristethium leptostachyum has styles in all flowers, whatever sex; the species has cinnamonbrown lenticels on either the stem or the inflorescence axis (most commonly both, although the lenticels sometimes are minute); and its mature inflorescence nodes are not especially expanded even in fruit. Additionally, the leaves of *P. leptostachyum* tend to be thicker, mostly with a less attenuate apex, than those of P. polystachyum, which tend to be thin and markedly attenuate. The male flowers of P. polystachyum lack any vestige of a style, showing a small central cushion with a slight depression in its place; usually neither the stem internodes nor



Figure 10. Peristethium leptostachyum (Kunth) Tiegh. —A. Habit. —B, C. Male and female flowers, respectively. —D. Mature fruit. —E. Inflorescence (probably male) in earliest stage of expansion. A and D redrawn from Kuijt (1986), with permission from the author; B and C redrawn from Kuijt (1964), with permission from Bot. Jahrb. Syst., http://www.schweizerbart.de; E drawn from Pérez et al. 255 (UC). Scale bar for B, C, and E applies to D. Scale bars: A = 1 cm; B–E = 1 mm.

inflorescence axis of either sex bear lenticels. The upper style of the female flower in P. polystachyum usually has a sigmoid shape in its upper half; the nodes of especially the infructescences are strongly expanded, and the flowers are inserted in conspicuous axial cups. Finally, the geographical range of P. leptostachyum reaches from northern Peru (Piura) and Ecuador to Costa Rica, while P. polystachyum is limited to north-central Peru except for two known nearby Bolivian collections (La Paz, Pando). There may be some possible geographical overlap between the two species.

The difference between male and female flowers is so slight that it is understandable that some earlier workers thought Peristethium leptostachyum had bisexual flowers. In fact, the species is dioecious, even though the male flower has a prominent style, while the female flower bears recognizable, strapshaped or arrowshaped, sterile anthers.

The protologue of *Loranthus leptostachyus* speaks of monads ("Flores solitarii"), but this is probably an error and cannot be confirmed from the two type photographs available at the Field Museum. Peristethium archeri is the only known Colombian Peristethium species with purely monadic inflorescences and does not resemble the above two photographs, differing from P. leptostachyum also in being much smaller (leaves $3-10 \times 2-5$ cm) and having tetramerous, bisexual flowers.

Additional specimens examined. COLOMBIA. Antioquia: Medellín, grounds of the Facultad de Agronomía, on Inga Mill., Cuatrecasas 24282 (US). Magdalena: Alto Río Buritaca, Alto de Mira, por el camino a la Cascada del Río Negro hasta la finca de Merardo, 11°5′N, 73°48′W, Madriñán & Barbosa 267 (F). COSTA RICA. Alajuela: Cinchona, E of Vara Blanca de Sarapiquí, on Eucalyptus L'Hér., Kuijt 2565 (CR, UBC); Canton San Carlos, Villa Quesada, Smith 2583 (GH, MICH); region of Zarcero, Zapote de San Carlos, Smith s.n. (MO); Collines de San Ramon, Tonduz 17733 (CR); entre Río Jesús y El Alto de Ramón, Brenes 17134 (CR). Puntarenas: vic. of Palmar N, along Río Terraba, Allen 5312 (UC, US); Golfito, Kuijt 2558 (CR, UBC). San José: forest along Río Paquita, Dodge & Goerger 9761 (F), Dodge & Goerger 9762 (F, GH, MO); San Isidro del General, on Pithecellobium longifolium (Humb. & Bonpl. ex Willd.) Standl., Kuijt 2445 (CR, UBC); vic. of El General, Skutch 4023 (GH, MO, NY, US), Skutch 4879 (GH, MO, NY, US), Skutch 2618 (GH, MICH, MO, NY, US); La Hondura, Standley 36236 (US), Standley 37950 (US); near Quebradillas, 7 km N of Santa María de Dota, Standley 42989 (US); S of Cartago, Stork 416 (US); forêts du Copey, Tonduz 11669 (CR, GH, NY, US). ECUADOR. El Oro: Km. 11 Atahualpa, Paccha, 03°33′05″S, 79°41′01″W, Vargas et al. 5501 (MO, UC). Imbabura: Cotocachi, Parroquia García Moreno, Reserva Biológico Los Cedros, Sendero El Inca, 0°18'47"N, 78°46'27"W, Vargas et al. 6525 (MO, UC). Manabi: Bosque Protector Cerro Pata de Pájaro, 15 km SE of Pedernales, 0°2′N, 79°57′W, Neill et al. 11315 (MO, UC). Zamora-Chinchipe: Yacuambi, Centro Shuar Kurinta, Cordillera Kunku Naint (Cordillera de la Ciudad), Reserva Tukupi Nunke, Cajekai et al. 782 (UC). PANAMA. Coclé: El Valle de Antón, Allen 3721 (US). Veraguas: vic. Santa Fe, Cerro Tute, Allen 4391 (K). PERU. Piura: Montaña de Cuyas, 10 km NE of Ayábaca, 4°32′S, 79°44′W, Gentry et al. 75113 (MO). Tumbes: Prov. Zarumilla, carr. entre El Caucho y quebrada Naranjal, Díaz et al. 7509 (MO). VENEZUELA. Mérida: Cerra de La Cuchilla, near Zea, Velasco & Ramia 374 (VEN); above Hacienda Agua Blanca, above La Azulita, Stevermark 56088 (F, US, VEN).

8. Peristethium lojae (Kuijt) Kuijt, comb. nov. Basionym: Struthanthus lojae Kuijt, Brittonia 32(4): 526–527, figs. 12–15. 1980. TYPE: Ecuador. Loja: 15 km S of Loja, 2600 m, G. W. Harling 5808 (holotype, S!). Figure 11.

Plants robust, with regular, decussate phyllotaxy; stem internodes mostly 0.5 cm thick or less, straight, 4-angled, rather dark in color, with scattered, large lenticels; adventitious roots occasionally from stem nodes. Leaves 10×5 cm, somewhat coriaceous, lanceolate, apex acute, base rounded to truncate; petiole ca. 15 mm, discrete. Inflorescences 1 per leaf axil, the young fertile axis smooth, with lenticels developing when in fruit; nodes swollen, gradually expanding from ca. 2 cm at anthesis, to 7-11 cm in fruit; with numerous pairs of triads, 1 or 2 pairs of subterminal, ebracteolate monads, and 1 terminal flower; each inflorescence subtended by several pairs of smooth, papery bracts, bracts and bracteoles caducous. Flowers 6.5-8 mm (2-3 mm immature in type), ca. 1/2 of which is ovary with smooth calyculus, not sunken in nodal cups; petals 6, dimorphic, dull to golden yellow; anthers essentially sessile, placed at 2 different heights; style 1 mm, ± straight; stigma stout, weakly differentiated. Fruit obovoid, light violet-red or orange when immature, probably becoming purplish blue, at least 8 mm and 6 mm thick, the calyculus inconspicuous.

Distribution. Peristethium lojae is only known from collections from Ecuador at elevations between 2500 and 2730 m.

The floral features illustrating the Discussion. protologue of Struthanthus lojae (Kuijt, 1980) are immature; in reality, the flowers are nearly twice as long as shown (as in *Lewis et al. 2531*).

The 1980 protologue states that Struthanthus lojae is dioecious, with figure 14 (Kuijt, 1980: 525, my present Fig. 11C) supposedly showing floral details of the female flower. In retrospect, I feel this may well be in error, the flower buds being immature, and that the illustration shows what may be fertile anthers that are as large as others in the genus; if anything, they

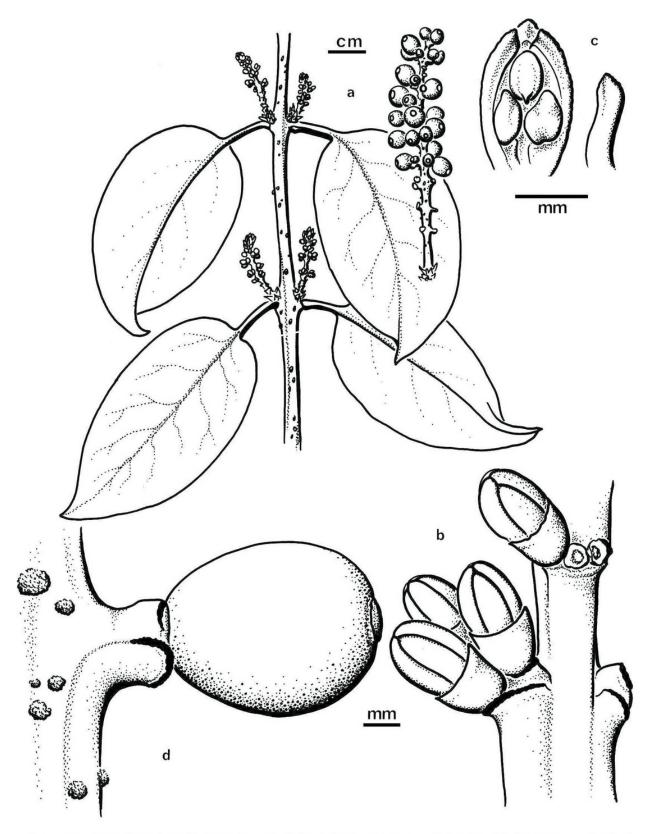


Figure 11. *Peristethium lojae* (Kuijt) Kuijt. —A. Habit and infructescence. —B. Portion of inflorescence. —C. Floral dissection. —D. Mature fruit (reprinted from Kuijt, 1986, with permission from the author). Scale bars: A = 1 cm; B-D = 1 mm.

are larger (6.5–8 mm). The closely related *Peristethium leptostachyum* is similar in general habit. In *P. leptostachyum*, however, the sterile anthers in the female flower are slender, straplike structures, in

contrast to the epipetalous stamens inserted at two levels in *P. lojae*. Since the holotype bears fruit, it may be that *P. lojae*, in contrast to *P. leptostachyum*, has bisexual flowers.

Peristethium lojae is clearly different from P. leptostachyum and others: it is much stouter in all ways, with large clusters of persistent inflorescence bracts; flowers are 8 mm; drying dark (seen in all K specimens). The uncertainty expressed in my 1980 protologue of Struthanthus lojae as to its separation from S. leptostachyus has vanished in the face of its pollen morphology, which, especially in the presence of an apocolpium and in its diplocolpate structure, is completely distinct from that of P. leptostachyum.

Additional specimens examined. ECUADOR. Loja: track from Universidad Nac. Loja to Uritusinga, Km. 8, 4°2′S, 79°12′W, Lewis et al. 2531 (K, UC); Km. 9.5, Lewis et al. 3508 (K, UC); Km. 8 [4°2′S, 79°12′W], Lewis et al. 2953 (K, UC).

9. Peristethium nitidum (Kuijt) Kuijt, comb. nov. Basionym: Cladocolea nitida Kuijt, Novon 13: 74–76. 2003. TYPE: Guyana. Potaro Siparuni Region: Pakaraima Mtns., Mt. Wokomung, ridgeline 0.5 km E of Wokomung escarpment adjacent Ka-Mie-Wah pinnacle, 5°4′N, 59°53′W, 1400–1500 m, 15 Nov. 1993, (♀ fls.), T. W. Henkel, R. Williams, S. Fratello & P. Joseph 4400 (holotype, originally LEA, transferred to UC, UC-1954350!; isotype, US-03368714!). Figure 12.

Plants dioecious, the type female, sparsely branched, glabrous; stems quadrangular at least when young. Leaves regularly paired, to 5×2 cm, obovate, apex rounded to notched, sometimes nearly mucronulate, upper surface very shiny when dry, lower surface dull, venation pinnate, even the minor venation clearly marked; petiole ca. 1 cm, slender. Male plants not known. Female inflorescence 1 per axil, flanked by 2 acute prophylls becoming torn and corky with time, inflorescence including flowers 5-6 mm, determinate, consisting of 7 flowers in 3 decussate pairs and 1 terminal flower; all flowers ebracteolate, at least the lowest ones subtended by 1 caducous bract 2 mm, others apparently ebracteate. Flowers 4.5 mm of which 1 mm ovary with flaring, entire calyculus; petals 5, each with minute, elongate staminodial cushion; style nearly as long as the petals, surrounded basally by a nectary disk; stigma capitate, distinct, prominent, 0.75 mm wide. Fruit not known.

Distribution. Peristethium nitidum is known only from the type specimen, collected in Guyana.

Discussion. The caducous floral bracts, ebracteolate flowers, and minute, determinate inflorescences indicate a more appropriate placement of this rare species in *Peristethium*. It appears to be most closely related to *P. roraimense*, which has very similar inflorescences. Its pentamerous flowers are unique in small-flowered Loranthaceae.

10. Peristethium palandense Kuijt, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: Palanda, cuenca del Río Chinchipe, sector de La Cruz, Palanda, 4°39′54″S, 79°4′56″W, 1840 m, 9 Mar. 2007, W. Quizhpe & A. Wisum 2599 (holotype, UC!; isotypes, MO!, QCNE not seen). Figure 13.

Haec species quoad inflorescentiam triades monades floresque sessiles gerentem, flores hexameros etiam monades subterminales in paribus multis *Peristethio tortistylo* (Kuijt) Kuijt similis, sed ab eo internodiis quadrangularibus carinatisve atque inflorescentia longiore distinguitur.

Plants leggy, glabrous; internodes quadrangular to somewhat keeled, 6–7 cm, < 5 mm thick. Leaves to 14×5 cm, ovate-elliptic, apex cuspidate, base nearly truncate, venation pinnate, the midrib running into the apex and strongly raised on the abaxial surface; petiole 1.5–2 cm, discrete. Inflorescence axis somewhat terete, bearing sparse, yellowish brown, round lenticels, 8 or 9 pairs of well-spaced, sessile triads and 5 to 8 pairs of subterminal monads in open arrangement and 1 terminal flower; peduncles ca. 8 mm. Flowers sessile, presumed bisexual, hexamerous, not sunken in nodal cups, the nodes not expanded. Infructescence to 8.5 cm, subtended by caducous scales. Fruit ellipsoid-obovate, said to be black, truncate apically, 4×2.5 mm.

Distribution. Peristethium paladense is known only from the type collection from Ecuador, which was collected at 1840 m.

IUCN Red List category. The conservation status of Peristethium palandense is Data Deficient (DD) (IUCN, 2001).

Discussion. Peristethium palandense is distinguishable by its cuspidate leaf apices and long inflorescences, and especially the numerous monad pairs in their upper portion. The new species is known from the type collection only, bearing fruit, and regrettably, no flowers.

11. Peristethium peruviense (Kuijt) Kuijt, comb. nov. Basionym: Cladocolea peruviensis Kuijt, Novon 13: 76–77. 2003. TYPE: Peru. San Martín: Rioja–Pomacochas rd., below Venceremos, ca. 20 km NW of Rioja near Restaurant El Amigo, 05°45′S, 77°38′W, 1600 m, 8 Feb. 1984 (♀ fl.), A. Gentry & D. N. Smith 45173 (holotype, MO-

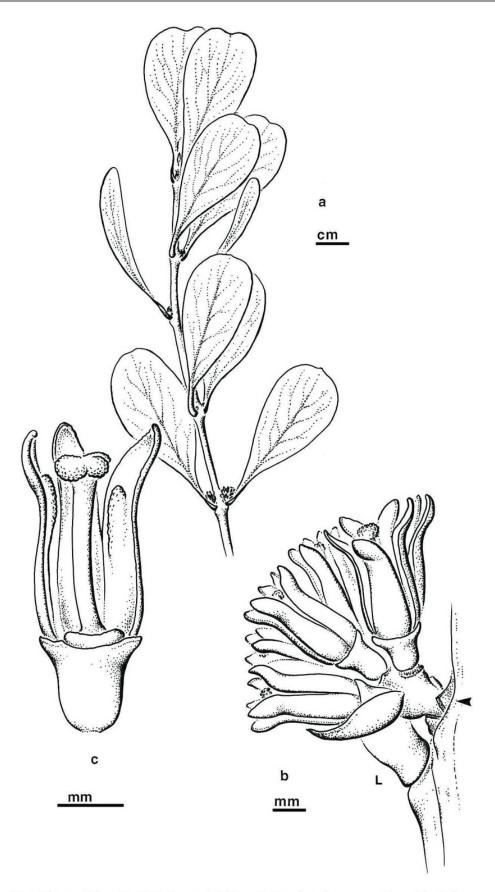


Figure 12. Peristethium nitidum (Kuijt) Kuijt. —A. Habit. —B. Female inflorescence. Five of the 7 flowers are visible, in the axil of a leaf (L); one floral bract is still in place, others have fallen. The arrowhead indicates a split, corky prophyll subtending the inflorescence. —C. Flower, the nearest two petals removed (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: A = 1 cm; B, C = 1 mm.

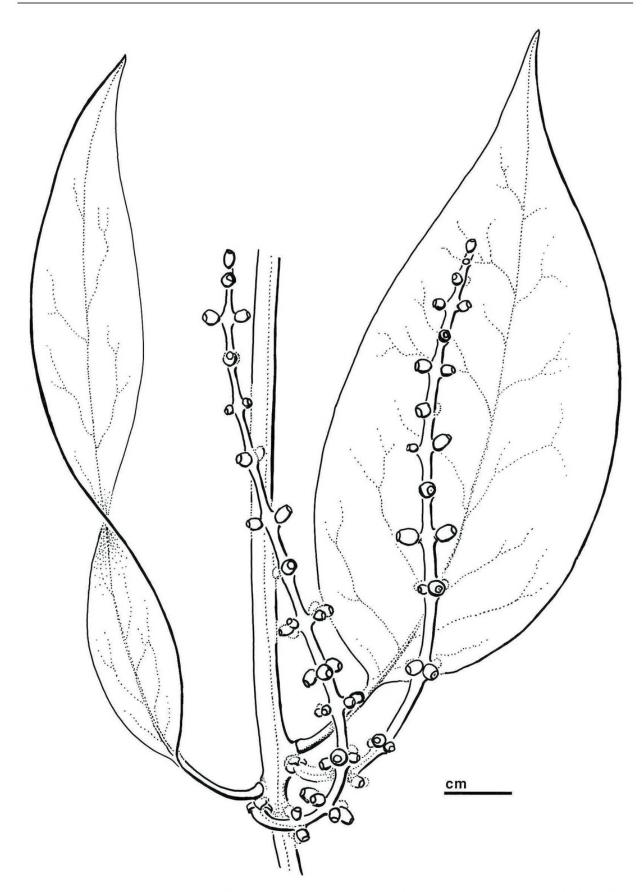


Figure 13. Peristethium palandense Kuijt, habit with young infructescences. Drawn from Quizhpe & Wisum 2599 (UC). Scale bar = 1 cm.

4399772!; isotypes, originally LEA, transferred to UC, UC-1956802!). Figure 14.

Plants dioecious, only the type and female flowers known; stems probably dichotomous, innovations with 3 to 8 pairs of leaves, after which the apex apparently aborts; internodes somewhat angular or grooved, lacking lenticels when leaf-bearing, to 3 cm, older nodes somewhat swollen; phyllotaxy paired. Leaves to 10×5 cm, lanceolate to ovate, shiny above, dull below, apex obtuse to nearly acute, base tapering into indistinct, venation pinnate, evident, with numerous lateral veins; petiole 3-6 mm, flat. Male inflorescence 7-9 mm, on older growth and in leaf axils, subtended by several pairs of yellowish, chaffy bracts, the axis 5 mm; bearing 2 or 3(4) pairs of lateral, ebracteolate flowers and 1 terminal one, each with a pedicel ca. 0.6 mm, the subtending bracts small and caducous, inflorescence base surrounded by corky crater. Mature male flower bud 4.5 mm, slender; ovary 1 mm, calyculus nearly smooth; petals 4, 3.5 mm, strapshaped, scarcely dimorphic; petal with downward leading ridge below anthers; anthers 1 mm, sessile near the petal tips, at 2 slightly different heights, each 4-loculate, apex slightly notched; style lacking in male flower, center of flower with flat, papillate cushion slightly indented centrally. Fruit blue to purple.

Distribution. Peristethium peruviense is known only from six collections from Peru and two from southern Ecuador.

Discussion. The protologue already points out the surprising affinity to *Peristethium roraimense*.

Additional specimens examined. ECUADOR. Zamora-Chinchipe: area of Estación Científica San Francisco, 30 km on rd. Loja–Zamora, E of Ceja Andina, [3°58′18″S, 79°4′44″W], Werner 1591 (UC); on Meliaceae, Bussman et al. 12594 (MO). PERU. Cajamarca: San Ignacio, San José de Lourdes, 5°00′43″S, 78°54′9″W, Campos & Vásquez 6405 (UC ex MO); base del Cerro Picorana, 04°59′25″S, 078°54′5″W, Díaz et al. 10364 (UC ex MO); 10152 (F!-2255039).

12. Peristethium polystachyum (Ruiz & Pav.) Kuijt, comb. nov. Basionym: Loranthus polystachyus Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 3: 50. 1802. Struthanthus polystachyus (Ruiz & Pav.) G. Don, Gen. Hist. 3: 410. 1834, non Phthirusa polystachya Eichler [= Passovia stelis (L.) Kuijt]. TYPE: Peru. s. loc., s.d., Ruiz & Pavon s.n. (holotype, MA not seen, MA at F photo neg. 29465!). Figure 15.

Plants dioecious, percurrent, glabrous; stems sparsely branched, lacking lenticels in the stems, branches to 2 m; internodes 3-8 cm, ± terete; epicortical roots unknown. Leaves paired, $7(-19) \times$ 6(-7.5), apex acuminate to attenuate, base acute, tapering into the petiole, venation pinnate, evident, the midrib running into the apex; petiole 5-10 mm, slender, indistinct. Inflorescences several to many per leaf axil, to 6(10) cm, sometimes elongating to 12 cm, sometimes inflorescence axis with slender, linear lenticels to 5 mm (as in Daly et al. 9901, UC), the base with several pairs of blunt, caducous or eroding scale leaves, terminal flower, and to 3 pairs of subterminal monads in male plants, but conditions uncertain in female ones, triad pairs 10 to 13, the triad peduncle absent. Flowers hexamerous, attached directly to the inflorescence axis, in small cups. Male flower bud to 3.5-4 mm, clavate; the petal below with shoulder-like ridge; anthers nearly 1 mm, basifixed on short (< 0.5 mm) filament, nearly sessile, at 2 different heights, with small connectival horn; ovary 0.5 mm; style absent, the central cushion papillate, with small, central depression, rarely hairlike. Female flower with sigmoid style in upper 1/2 ca. 3 mm; stigma large, capitate; anthers inconspicuous sterile bulges. Fruit ovoid, blue, 6 mm and 3 mm thick, calyculus inconspicuous; fruit-bearing nodes greatly swollen.

Distribution. Peristethium polystachyum is found from northern Peru to Bolivia.

Discussion. Peristethium polystachyum is similar to P. leptostachyum, differing in the contorted style in the female flower and the absence (or near absence) of even a vestigial style in the male, and the knoblike expansion of at least the infructescence nodes, at each node appearing like six stout cupules (see type MA at F. neg. 19645). See also the comments under P. leptostachyum and P. tortistylum.

The collections Janovec & Maceda 2721 (UC) and Schunke V. 5816 (F) appear to have fruits, but in reality are male plants, the ovaries of which have become insect-galled; the same deceptive situation is occasionally seen in some Mexican Struthanthus species.

Boeke 2082 (UC), from Chachapoyas, Amazonas, Peru, is here provisionally listed under *Peristethium polystachyum* but lacks triadic knobs. It has unusually small flowers (petals 3 mm), isomorphic stamens, and an exceedingly slender, hairlike, straight style, but clearly is a male plant, having prominent anthers that occupy much of the flower (Fig. 15C). It may thus represent an unrecognized species.

The two collections from Venezuela cited in Rizzini (1982) belong to *Peristethium leptostachyum* instead (see under that species).

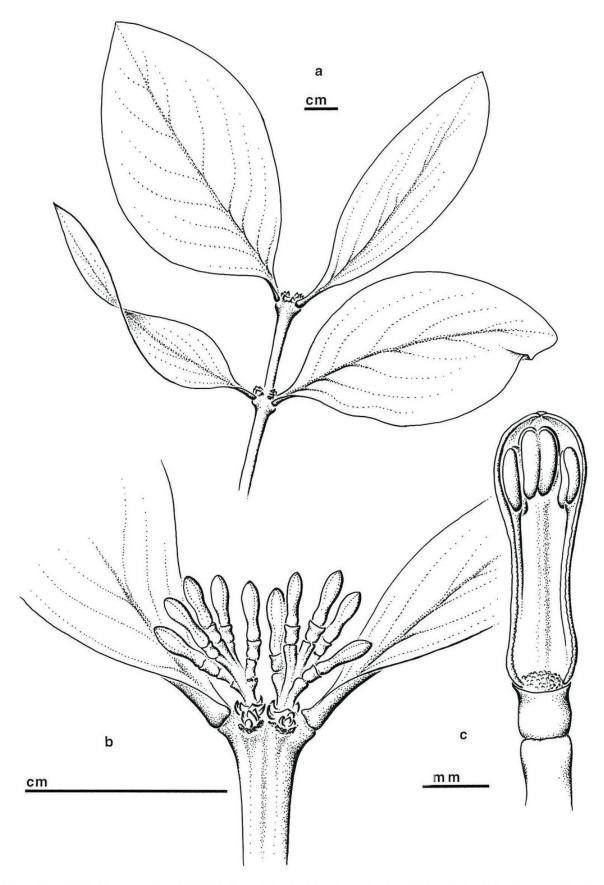


Figure 14. Peristethium peruviense (Kuijt) Kuijt. —A. Leafy, determinate shoot. —B. Two axillary inflorescences at the tip of part A. —C. Male flower, the nearest petal removed to show anthers, basal cushion, and absence of style (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: A, B=1 cm; C=1 mm.

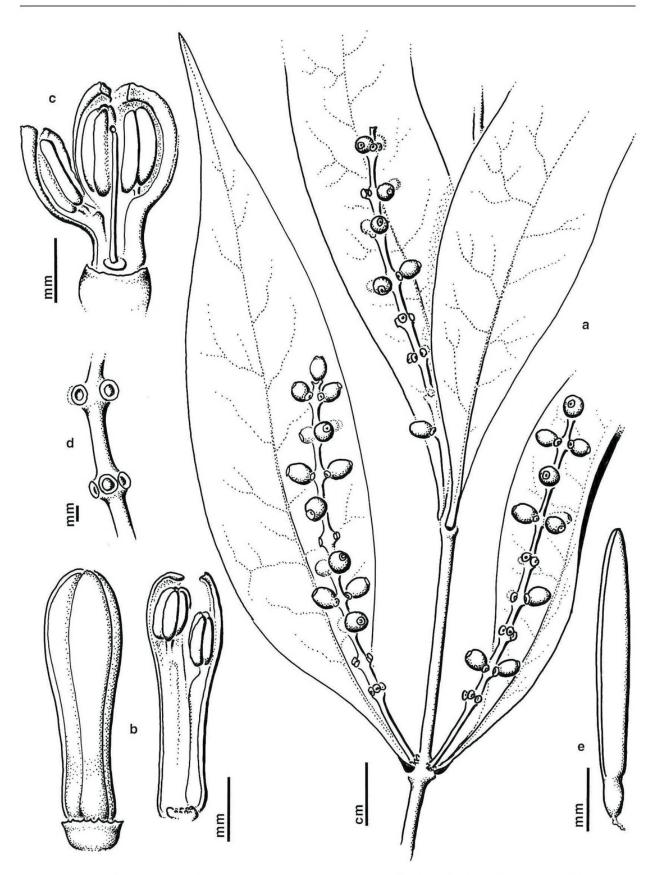


Figure 15. Peristethium polystachyum (Ruiz & Pav.) Kuijt. —A. Habit of fruiting plant. —B. Bud and floral dissection of male flower; note absence of style. —C. Floral dissection of male flower showing threadlike style. —D. Portion of old infructescence showing raised floral cups. —E. Embryo. A drawn from Smith 1862 (UC). B drawn from Foster 6166 (UC). C drawn from Boeke 2082 (UC). D and E drawn from Gentry et al. 70774 (UC). Scale bars: A = 1 cm; B—E = 1 mm.

A specimen from Loreto, Peru, is also tentatively placed here (*Klug 1562*, US). It is similar in appearance and has greatly contorted styles; additionally, the anther and supporting petals are comparable to those of other *Peristethium*. The inflorescence appears to consist of only two to three nodes, at least the basal ones triadic. However, all flowers are pedicellate (pedicels 0.5 mm), as are the triads, conditions that disagree with typical *P. polystachyum*. Unfortunately, the specimen does not yield further definitive characteristics.

Curiously, the female herbarium specimens of *Peristethium polystachyum* seem to greatly outnumber the male ones; at UC, there are only two male specimens, but 12 female ones.

Additional specimens examined. BOLIVIA. La Paz: Alto Madidi, rd. 3-5 km NE of camp, 13°35'S, 68°46'W, Gentry et al. 70774 (UC ex MO). Pando: Nicolás Suárez, ca. de Cobija en las prox. del Aeropuerto, Casas & Susanna 8096 (NY). PERU. Amazonas: Prov. Chachapoyas, Leimebamba-Chilcos trail, Chilcos, Boeke 2082 (MO, NY). Cajamarca: San Ignacio, San José de Lourdes, base del Cerro Picorana, 4°59′25″S, 78°54′5″W, Díaz et al. 10364 (UC); San Ignacio, San José de Lourdes, 5°0′43″S, Campos & Vásquez 6405 (UC). Huánuco: Prov. Huánuco, Chinchao, Pampayacu, 1 km E of Cochero, Schunke V. 5804 (F, NY); possibly in Huánuco, SW slope of Río Hualla Pichis watershed, ascent of Cerro del Sira, 9°25'S, 74°42′W, Dudley 13450 (F); Prov. Leoncio Prado, Distr. Rupa Rupa, E of Tingo María, near Cerro Quemado, J. Schunke V. 10615 (MO). Loreto: near Mishayacu, near Iquitos, Klug 1562 (US). Madre de Díos: rd. to Tambopata, N of Puerto Maldonado, Gentry et al. 19603 (F, MO); Tambopata, outskirts of Puerto Maldonado, 12°35'S, 69°10′W, Gentry & Young 31769 (MO); Prov. Manu, Puerto Maldonado, Los Amigos Biological Station, Madre de Díos River, 7 km upriver from mouth of Río Los Amigos, on Inga Miller, J. Schunke V. 5816 (F); Janovec & Maceda 2721 (UC); Parque Nacional del Manu, Río Manu, Cocha Cashu Station, Foster & Terborgh 6166 (MO). Pasco: Prov. Oxapampa, Palcazo Valley, Cabeza del Mono, 5-6 km W of Iscozacin (10°12'S, 17°14'W), Smith 3819 (NY ex MO); Iscozacin, near confluence of Río Palcazu and Río Iscozacin, Juan Franzen property, 10°12'S, 75°13'W, on Inga, Smith 1906 (NY); on Citrus L., Smith 1862 (NY). Piura: Huancabamba, Prov. Canchaque, Chorro Blanco, Díaz et al. 2751 (MO). **Puno:** Prov. Sandia, 12.5–13.8°S, betw. Río Azata & Colorado, on Calliandra Benth., Núñez & Muños 5248 (F, MO). Ucayali: Prov. Purús, Distr. Purús, abajo del Pto. Esperanza, margen derecho del Río Purús, 10°12′S, 70°57′W, Schunke-Vigo & Graham S14995 (NY).

13. Peristethium primarium (Kuijt) Kuijt, comb. nov. Cladocolea primaria Kuijt, Ann. Missouri Bot. Gard. 74: 511–514. 1987. TYPE: Panama. Panamá: Cerro Jefe, 2 km along rd. to Altos de Pacora from jct. with rd. to peak, low cloud forest, 800 m, 24 May 1981, K. J. Sytsma & S. Knapp 4797 (holotype, MO-3404269!; isotypes,

originally LEA, transferred to UC, UC-1956823!). Figures 16, 17.

Plants sparsely branched, twining, glabrous; stems terete or slightly 4-ridged, often with conspicuous lenticels when older, straight and rather rigid; epicortical roots occasionally present on the stems and probably from the base. Leaves paired, somewhat leathery, broadly lanceolate to ovate, apex mostly blunt or slightly apiculate, venation inconspicuous, midrib conspicuous and running into apex; petioles stout, 10-15 mm. Inflorescences subtended by several pairs of thick, brown scale leaves, solitary in leaf axils, determinate; with 3 or 4(5) pairs of triads, 2 pairs crowded at the base and a pair somewhat higher, followed by a pair of ebracteolate monads and a terminal flower, the basal triads crowded in the leaf axil. Flowers bisexual, pale yellow, 4-partite; petals slightly dimorphic, 2-2.5 mm; anthers very small, placed on upper part of petals, sessile on the shorter petals and with very short filaments on the longer ones; ovary 1.5×1 mm; style \pm straight; stigma capitate, oblique, reaching the petal tips. Fruit ellipsoid, red, becoming dark purple, 6×4 mm; calyculus inconspicuous; embryo dicotylous, slender, the haustorial pole scarcely expanded.

Distribution. Peristethium primarium as described (Kuijt, 1987a) is restricted to the province of Panama, to the Cerro Jefe area; because of this, one disjunct collection is noted from Colón in Panama.

Discussion. The collection from Colón (McPherson & Van der Werff 19998, MO) represents a remarkable disjunction; all other known specimens have been gathered in the Cerro Jefe area. As far as I know, it represents the only known, convincing example of long-distance dispersal within a single landmass; other (very few) instances have been recorded only from pelagic islands, as Phoradendron berteroanum (DC.) Griseb. on the Galápagos Islands, P. piperoides (Kunth) Trel. on Cocos Island (Kuijt, 2003b), and Dendropemon caymanensis Proctor from Little Cayman Island (Kuijt, 2011a). The specimen has slightly larger leaves and internodes, the leaf apex being somewhat acuminate, but the structure of the inflorescence is identical to that of Cerro Jefe material.

Additional specimens examined. PANAMA. Colón: Teck Cominco Petaquilla mining concession, streamside forest by old Petaquilla camp, 8°50′14″N, 80°41′17″W, McPherson & Van der Werff 19998 (MO). Panamá: forest near rd. to Cerro Jefe, near jct. with rd. to Altos de Pacora, Mori & Kallunki 2763 (NY, UC); Cerro Jefe, 6.6 mi. above Goofy Lake, Sytsma et al. 2839 (UC); near radio tower, D'Arcy & Hamilton 14817 (UC); Cerro Jefe, 9°15′N,

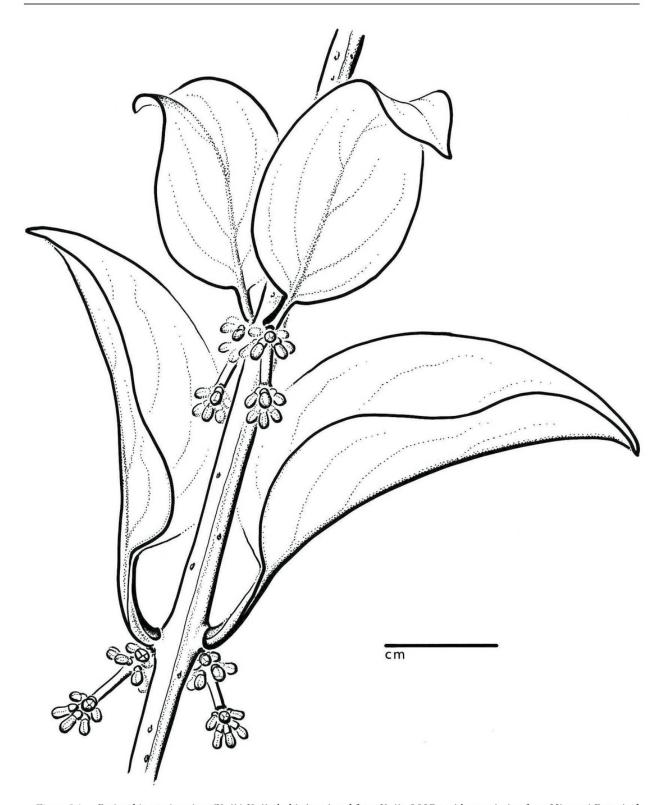


Figure 16. Peristethium primarium (Kuijt) Kuijt, habit (reprinted from Kuijt, 1987a, with permission from Missouri Botanical Garden Press). Scale bar = 1 cm.

79°20′W, Hamilton & D'Arcy 611 (UC). PERU. Loreto: near Mishayacu, near Iquitos, Klug 1562 (US).

14. Peristethium roraimense (Steyerm.) Kuijt, comb. nov. Basionym: *Phthirusa roraimensis* Steyerm., Fieldiana, Bot. 28: 224, 225. 1951. *Cladocolea roraimensis* (Steyerm.) Kuijt, J. Arnold Arbor. 56: 326–327. 1975. TYPE: Venezuela. Bolívar: Mt. Roraima, SW-facing forested slopes betw. Rondón Camp & base of sandstone bluffs, 2040–2255 m, 30 Sept. 1944, *Steyermark* 58943 (holotype, F-1284129!; isotypes, NY-285200!, US!). Figure 18.

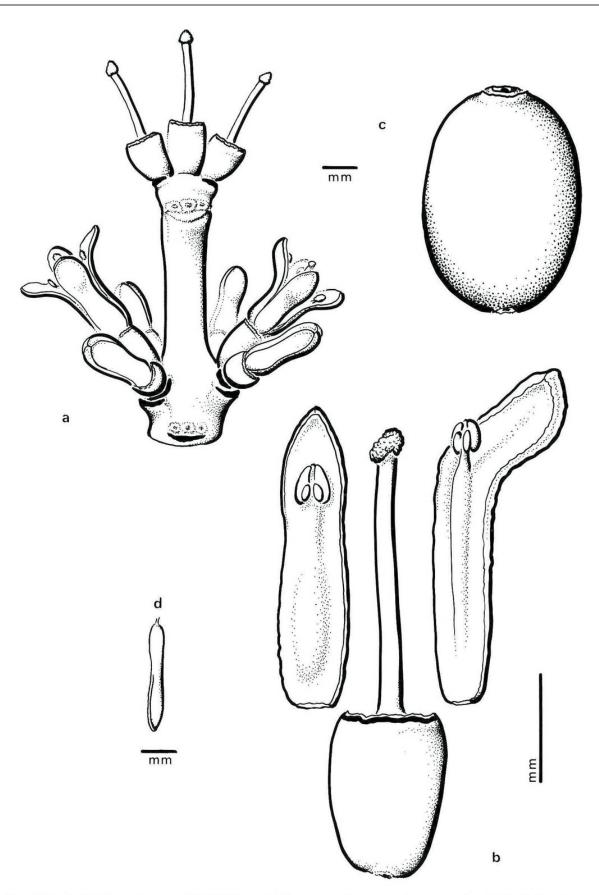


Figure 17. *Peristethium primarium* (Kuijt) Kuijt. —A. Inflorescence, the upper triads removed. —B. Floral dissection. —C. Mature fruit. —D. Embryo (reprinted from Kuijt, 1987a, with permission from Missouri Botanical Garden Press). Scale bars = 1 mm.

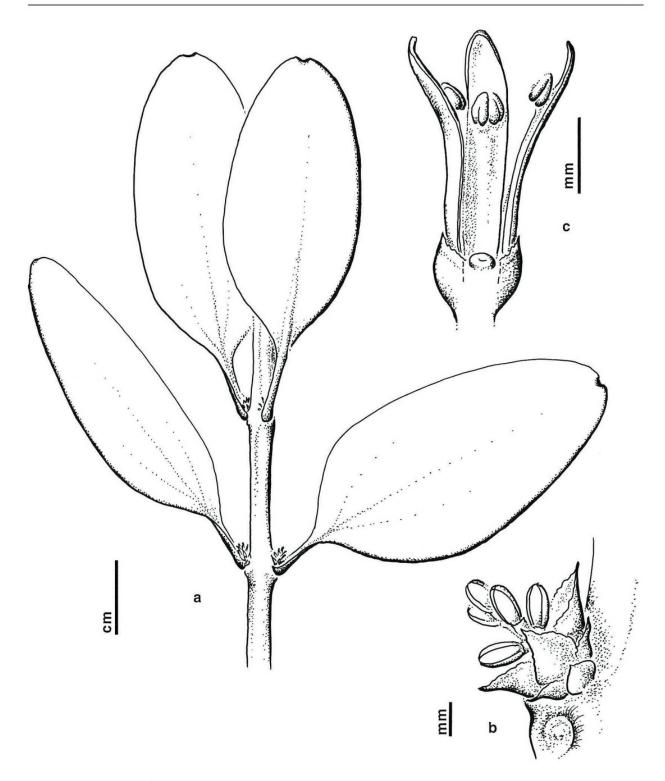


Figure 18. Peristethium roraimense (Steyerm.) Kuijt. —A. Habit, reconstructed. —B. Immature inflorescence above leaf scar. —C. Mature flower, the nearest petal removed to show the central cushion and absence of style (reprinted from Kuijt, 1975b, with permission from the author). Scale bars: A = 1 cm; B, C = 1 mm.

Plants rigid, percurrent; stems somewhat succulent, 2–5 mm thick, bark smooth; internodes rather short (1–3 cm); epicortical roots not seen. Leaves decussate, 40– 50×10 –25 mm, elliptic to ovate to obovate, olive-green to bronze, coriaceous, apex obtuse or more commonly emarginate through loss of a caducous, brown, nail-like tip 1×1 mm, base

obtuse to acute, venation obscure; mesophyll differentiated into sclereids with many bulbous arms; petiole ca. 3 mm, strongly canaliculate. Inflorescence 1 per leaf axil, subtended by several pairs of acute, chartaceous bracts; 1–2 mm; flowers paired, sessile, ebracteolate monads and a single terminal flower; floral bracts caducous. Flowers 7 to 9 per inflores-

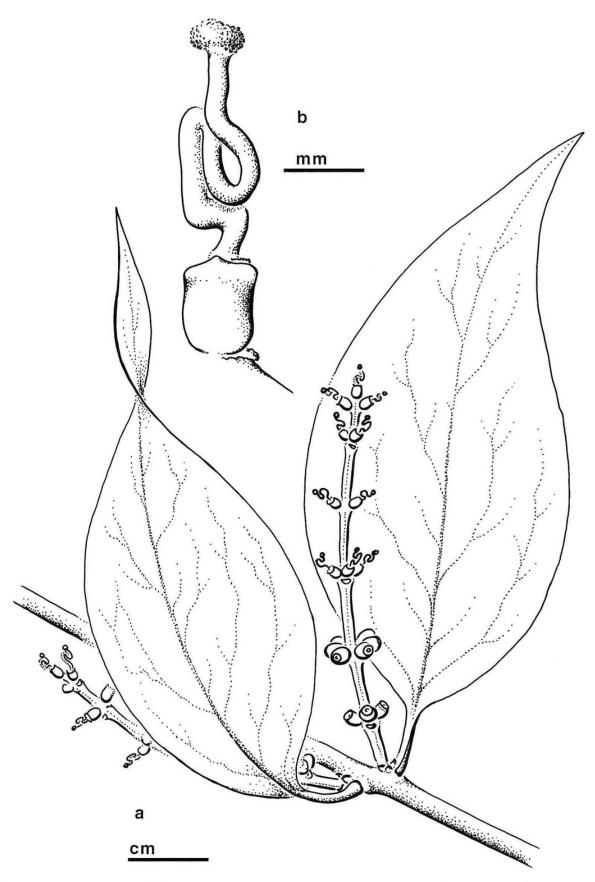


Figure 19. Peristethium tortistylum (Kuijt) Kuijt. —A. Habit of young fruiting plant. —B. Ovary and style (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: $A=1~\mathrm{cm}$; $B=1~\mathrm{mm}$.

cence, yellowish; calyculus prominently 2-dentate; petals 4, each 4 mm; with a sessile anther above the middle in biseriate arrangement; pollen smooth, round-triangular, with little or no evidence of triradiate grooves (colpi); style not seen. Fruit oblong-ovoid, said to be dull blue-green (Steyermark 58943), 7×5 mm, the fruiting axis elongating to ca. 12 mm.

Distribution. In Kuijt (1975b), only two collections of *Peristethium roraimense* are listed, both from exactly the same spot on Mt. Roraima.

Discussion. Peristethium roraimense is perhaps the rarest of all South American mistletoes and is characterized by an exceedingly small inflorescence that nevertheless corresponds in all structural details to that of other species, especially *P. peruviense*. In both species, a style appears to be completely lacking in male flowers. In the protologue, the species is stated to have 5- or 6-merous flowers, but that is in error, as the flowers, again like *P. peruviense* and others, are 4-merous.

Additional specimens examined. Location same as the type, Steyermark 58965 (F, US).

15. Peristethium tortistylum (Kuijt) Kuijt, comb. nov. Basionym: Struthanthus tortistylus Kuijt, Novon 13: 82–83. 2003. TYPE: Ecuador. Pastaza: Kapawí (Amuntai), Río Pastaza, on pasture tree, 2°31'S, 76°48'W, 235 m, 14–20 July 1988, W. H. Lewis, M. Elvin-Lewis, C. E. Cerón, E. J. Kenelly & M. C. Gnerre 13615 (holotype, MO-6323705!; isotype, UC!). Figure 19.

Plants possibly dioecious, robust, glabrous; stem internodes 3-8 cm, terete. Leaves to 10×4.5 cm, ovate, shiny when dry, apex attenuate, base obtuse, venation pinnate, even the minor venation evident, midvein running into apex, with 4 basal lateral veins running at least halfway down the blade; petiole 1 cm, distinct. Fruit-bearing inflorescence ca. 4 cm, subtended by 2 or more small, blunt, partly caducous scale leaves, axis angular; peduncle 4-6 mm, followed by ca. 4 pairs of triads and 1 to 3 pairs of monads and a single terminal flower; triads and flowers sessile, at least the lower bracts broad, with obtuse apex, caducous. Flowers hexamerous, not sunken in nodal cups, flower bud 3.5 mm; ovary ca. 1 mm; anthers extremely small, ovate, essentially sessile; style perhaps twice as long as the petals, tightly contorted even after anthesis; stigma large, capitate. Fruit (immature) ovoid, apex blunt, calyculus irregularly dentate.

Distribution. Peristethium tortistylum is so far known only from its type, collected in Ecuador (Pastaza).

Discussion. The protologue of Struthanthus tortistylus (Kuijt, 2003a) described the plant as dioecious, but I now regard that as insufficiently established, and the possibility of bisexual flowers cannot be excluded. A single petal with a normal, minute anther has been observed on the UC isotype, suggesting bisexual flowers, but this aspect needs better documentation.

Peristethium tortistylum is morphologically similar to both P. aequatoris and P. polystachyum. From both latter taxa, P. tortistylum is distinguished by its one to several pairs of subterminal monads and an evident terminal flower that is raised on a short length of inflorescence axis, exceeding the sessile triads. From P. aeguatoris, it differs in the fact that the branches are terete (vs. slightly quadrangular to carinate). Peristethium polystachyum, being dioecious, has twisted styles in its female flowers, and male flowers generally have no styles; another difference is the crowded condition of its most distal flowers, where a pair of monads is rarely found. Once plants of P. polystachyum develop fruits, the most striking characteristic of that species is the dramatic swelling of the inflorescence nodes, giving the axis a somewhat beaded aspect, the fruits placed in nodal cups. This aspect is clearly visible in the type photograph of P. polystachyum (F neg. 29465). Peristethium tortistylum does not exhibit this feature.

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