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# *Costus maasiorum*: a new species of Neotropical *Costaceae* from western Ecuador

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**Key words**
*Costaceae*
*Costus*
Genome resequencing
Neotropics
SNP-based phylogeny
*Zingiberales*

**Abstract** We here describe *Costus maasiorum*, a new species from western Ecuador. This new species shares morphological similarities with *Costus macrostrobilus*, but differs in having plicate leaves, erect and triangular bract appendages, and semi-tubular elongate flowers. A phylogeny based on 5.9+ million single nucleotide polymorphisms (SNPs) strongly supports a sister relationship between *C. maasiorum* and *C. macrostrobilus*. Additional taxonomic sampling in subsequent analyses indicates a close relationship with *C. gibbosus* and *C. antioquiensis*. A comprehensive taxonomic description, including detailed photographs and information about the habitat and ecology of the new species are provided. A preliminary conservation status is recommended as Least Concern (LC).

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## INTRODUCTION

The genus *Costus* (*Costaceae*), a pantropical genus in the order *Zingiberales*, comprises just over 100 species, with a disjunct distribution consisting of a paraphyletic African grade and a more speciose neotropical clade resulting from a rapid radiation following a single long-distance dispersal event (Specht 2006, André et al. 2016). Neotropical *Costus* species are terrestrial rhizomatous herbs that range in vegetative height from 0.5 to over 3 m tall and can be recognized by their characteristic monistichous spiral phyllotaxy, tubular sheathing leaf bases each with a pronounced ligule, and terminal inflorescences with imbricate bracts arranged in several series of parastichies. Plants tend to grow abundantly in moist lowlands, wet thickets, clearings or streambeds at relatively low elevations (< 800 m), but some species have been collected up to 2000 m above sea level. The genus is a good model for investigating shifts between insect and hummingbird pollination syndromes (Maas 1972, Specht et al. 2001, Salzman et al. 2015), with several recent phylogenomic analyses (Valderrama et al. 2020, 2022), 17 newly described species (Maas et al. 2023), and a comprehensive monographic treatment for all neotropical species including photographic plates and dichotomous keys (Maas et al. 2026).

In this study we introduce a new species of *Costus*, *C. maasiorum*, that was initially collected in 1994 by author John L. Clark from the Bilsa Biological Station in Esmeraldas, Ecuador. The material collected by Clark and other botanists was long considered part of the large and morphologically confusing '*Costus guanaiensis* complex', which was recently revised as part of a monographic treatment of the neotropical *Costaceae* (Maas et al. 2026). In the process of making this revision, 12 forms pertaining to *C. guanaiensis* Rusby were described and a conclusion was made to recognize four species: *C. gibbosus* D.Skinner & Maas, *C. laevis* Ruiz & Pav., *C. macrostobilus* K.Schum., and *C. sinningiiflorus* Rusby, with plants previously considered to be part of *C. guanaiensis* var. *tarmicus* (Loes.) Maas being moved to the previously described *C. laevis* Ruiz & Pav. and the name *C. guanaiensis* being appropriately applied to a species restricted in distribution to Bolivia, Brazil (Acre), and Southeastern Peru. These decisions were the result of extensive collections-based herbarium research investigating the presence or absence of indument, colour of leaf undersides, and the shape of the flower with an emphasis on the labellum, all of which can be hard to interpret in herbarium-preserved specimens. At the end, collections belonging to this proposed new species were placed in *C. macrostrobilus* with the understanding that 'In NW Ecuador (near Bilsa and Lita) a form occurs with plicate leaves which are purplish on the lower side. This probably represents an undescribed species, but more material is needed' (see notes on *C. macrostrobilus*; Maas et al. 2026).

Based on the extensive revisionary work presented in Maas et al. (2026), we here present data that support the delimitation of a new species from within this complex. Morphological analyses and genome wide SNPs from genome resequencing

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data were used to confirm the status of the proposed *C. maasiorum* as a new species and to support the taxonomic treatment and phylogenetic placement of *C. maasiorum* within the neotropical species of *Costus*.

## MATERIAL AND METHODS

### *Morphological features*

The description of *C. maasiorum* is based on observations in the field, live material in cultivation, and from herbarium voucher specimens. As part of a recent monograph for all neotropical *Costaceae* (Maas et al. 2026), herbarium collections from 127 herbaria were analyzed to identify other individuals collected from this locality and/or that matched this description.

### *DNA extraction and sequencing*

Silica-dried vegetative tissue of *C. maasiorum* (*D.Skinner 3071*, BH) was used for DNA extraction using a modified SDS protocol (Edwards et al. 1991, Konieczny & Ausubel 1993) with the addition of a chloroform cleanup prior to DNA precipitation and tissue disruption with a mortar and pestle (De La Cerda et al. 2023). Quality and quantity of extracted DNA was assessed with a Qubit DNA BR Assay (Invitrogen, Waltham, MA, USA) and by gel electrophoresis with a 1.2% agarose gel. DNA was sent to Psomagen, Inc. (Rockville, MD, USA) for Illumina TruSeq DNA PCR-free library construction and sequencing on a NovaSeq6000 S4 sequencing targeting 15 Gb of 150 paired-end sequencing data.

### *SNP calling and phylogenetic inference*

Genome resequencing data for *C. maasiorum*, *C. asteranthus* Maas & H.Maas, *C. barbatus* Suess., *C. macrostrobilus* K.Schum., and *C. vinosus* Maas were obtained via Illumina sequencing at the Vincent J. Coates Genomics Sequencing Laboratory (UC Berkeley). Genome resequencing data were used to call SNPs (Single Nucleotide Polymorphisms) that were combined with the data set generated and presented in Valderrama et al. (2022) (see Table 1 for accession details). Raw sequencing data were cleaned using fastp v0.20.1 (Chen et al. 2018) with the following parameters: automatic detection of adapters, a minimum quality of 20, trimming poly-G strings, and a minimum read length of 75 bp. Cleaned reads for each species were mapped to the assembled *C. bracteatus* Rowlee genome (Valderrama et al. 2022) using bwa-mem2 v2.2.1 (Vasimuddin et al. 2019). Resulting SAM files were converted to BAM files and sorted with Samtools v1.14 (Li & Durbin 2009). Duplicates were marked using GATK v.4.1.4 (McKenna et al. 2010) prior to SNP calling. HaplotypeCaller was first used with the ERC flag to create GVCF (Genomic Variant Call Format) for each species individually. All resulting GVCFs were combined with GenomicsDBImport after creating five equal sized ranges of the genome to parallelize SNP calling followed by joint genotyping with GenoptypeGVCFs. The five generated VCF (Variant Call Format) files were combined into a single VCF using the GatherVcfs function.

Initial SNP calls were filtered in VCFtools v0.1.16 (Danecek et al. 2011) with the following parameters: retain only biallelic sites, a maximum missing of 0.9 for each site, minimum depth of 10, maximum depth of 200, minimum quality score of 30, minor

**Table 1** Accession numbers for samples used for whole genome resequencing and for calling SNPs

| Species | Collector, number and herbarium | Number of filtered SNPs | SRA genome Illumina |
|---|---|---|---|
| *Costus asteranthus* Maas & H.Maas | *D. Skinner 3435* (BH) | 5 757 262 | SRR28473661 |
| *Costus barbatus* Suess. | *D. Skinner 3213* (L & BH) | 5 813 261 | SRR28473660 |
| *Costus beckii* Maas & H.Maas | *D. Skinner 3394* (BH) | 5 719 805 | SRR18516558 |
| *Costus bracteatus* Rowlee | *D. Skinner 3030* (BH) | 5 854 260 | SRR18516557 |
| *Costus claviger* Benoist | *D. Skinner 3219* (UC) | 5 759 166 | SRR18516546 |
| *Costus comosus* (Jacq.) Roscoe | *D. Skinner 3031* (BH) | 5 742 257 | SRR18516540 |
| *Costus glaucus* Maas | *D. Skinner 3364* (BH) | 5 663 656 | SRR18516538 |
| *Costus juruanus* K.Schum | *D. Skinner 2693* (UC) | 5 711 212 | SRR18516537 |
| *Costus kuntzei* K.Schum | *D. Skinner 3086* (BH) | 5 734 997 | SRR18516536 |
| *Costus lasius* Loes | *D. Skinner 3127* (L & BH) | 5 739 301 | SRR18516535 |
| *Costus lima* K.Schum | *D. Skinner 3362* (BH) | 5 656 475 | SRR18516534 |
| *Costus maasiorum* sp. nov | *D. Skinner 3071* (BH) | 4 346 378 | SRR28473657 |
| *Costus macrostrobilus* K.Schum | *D. Skinner 3440* (BH) | 5 719 567 | SRR28473659 |
| *Costus malortieanus* H.Wendl | *D. Skinner 1562* (L) | 5 734 776 | SRR18516556 |
| *Costus pictus* D.Don | *D. Skinner 3172* (BH) | 5 820 310 | SRR18516555 |
| *Costus spicatus* (Jacq.) Sw | *D. Skinner 3385* (BH) | 5 796 382 | SRR18516553 |
| *Costus spiralis* (Jacq.) Roscoe | *D. Skinner 3218* (UC) | 5 763 657 | SRR18516552 |
| *Costus stenophyllus* Standl. & L.O.Williams | *D. Skinner 2613* (UC & BH) | 5 674 686 | SRR18516551 |
| *Costus villosissimus* Jacq | *D. Skinner 3074* (L) | 5 715 992 | SRR18516550 |
| *Costus vinosus* Maas | *D. Skinner 2952* (L) | 5 743 807 | SRR28473658 |
| *Costus whiskeycola* Maas & H.Maas | *D. Skinner 3026* (UC) | 5 733 459 | SRR18516539 |
| *Costus wilsonii* Maas | *D. Skinner 3092* (L & BH) | 5 741 338 | SRR18516548 |
| *Costus zingiberoides* J.F.Macbr | *D. Skinner 3406* (BH) | 5 757 122 | SRR18516547 |

allele frequency of 0.05, and minor allele count of 3. Based on previous results (Valderrama et al. 2022) samples were pruned for linkage disequilibrium (LD) in plink v1.90b6.21 (Purcell et al. 2007) using a $r^2$ of 0.2 in a 20 kb window with a 10 kb step size. The final pruned VCF file containing 5,885,804 SNPs was converted to a fasta and nexus format using vcf2phyllip (Ortiz 2019). A maximum-likelihood tree was inferred using raxml-ng v1.1.0 (Kozlov et al. 2019) using a GTR+G model of molecular evolution, 20 searches for the maximum likelihood tree, and 1000 bootstrap replicates. For comparison, a coalescence-based approach was also undertaken using the SVDquartets method for SNP-based coalescent analysis as implemented in PAUP v4a168 for an Ubuntu Linux machine (Swofford 2003, Chifman & Kubatko 2014, Chou et al. 2015) with 1000 bootstrap replicates.

Pairwise genetic difference, reported as a percentage, between each pair of taxa and overall mean genetic distance across all samples were calculated with Mega 11 (Tamura et al. 2021) with the following parameters: nucleotide data with a maximum composite likelihood model, a gamma distribution for rates among sites with a gamma parameter equal to 1, and pairwise deletion for missing data.

### *Distribution Map*

The species distribution map was generated using the software QGIS 3.34.6-Prizren (https://qgis.org/en/site/). Initially, the ‘world map’ and Google satellite map layers were loaded into the QGIS workspace and utilized to delineate the border of Ecuador and visualize the satellite imagery of its surrounding regions, respectively. The ‘world map’ layer was then clipped to display the geographic boundaries of Ecuador. Finally, verified and vouchered specimen observation sites were used to generate the layer containing the occurrence points, which was overlaid onto the clipped ‘world map’ layer to depict the distribution of *C. maasiorum* within Ecuador.

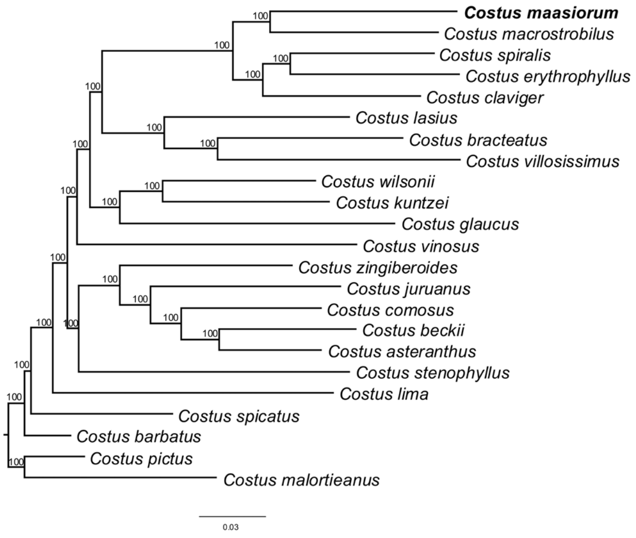


**Fig. 1** Maximum-likelihood SNP tree inferred with raxml-ng with 1000 bootstrap replicates. Based on this taxonomic sampling, *Costus maasiorum* (bold) is resolved as sister to *C. macrostrobilus* with 100% bootstrap support.

### *IUCN Assessment*

We assessed the extinction risk of *Costus maasiorum* following the IUCN Red List Categories and Criteria (2022) and updated criteria in the IUCN Standards and Petitions Committee (2024). We considered observations, collection localities, and population estimate from fieldwork. Species extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCAT (Bachman et al. 2011) with the default setting of 2 km, which corresponds to a 4 km² grid cell.

## RESULTS

Paired-end sequencing of *C. maasiorum* produced 22 Gb of raw data. Mean SNP coverage for *C. maasiorum* was 13x (compared to 29–62x for the other species, which were sequenced at a deeper depth) with 0.26 missing data (compared to 0.003–0.04 for the other species). The maximum likelihood tree from raxml-ng (Fig. 1) provided full resolution (100% bootstrap support) for the 23 sampled taxa, placing *C. maasiorum* as most closely related to *C. macrostrobilus* within the phylogeny. The coalescent tree produced a highly congruent topology, with the closest relative of *C. maasiorum* again resolved as *C. macrostrobilus* with full support (Fig. 2; 100% bootstrap support for every node).

The overall mean genetic distance across all samples is 25% as calculated with Mega11 (Table 2). The pairwise genetic distance between *C. maasiorum* and the sister taxon *C. macrostrobilus* is 18%. Pairwise distances between other sister species pairs across the genus are similar (e.g. 18% between *C. kuntzei* K.Schum. and *C. wilsonii* Maas; 0.10 between *C. asteranthus* Maas & H.Maas and *C. beckii* Maas & H.Maas; and 15% between *C. erythrophyllus* Loes., and *C. spiralis* (Jacq.) Roscoe) providing confidence in the recognition of *C. maasiorum* as a separate species from *C. macrostobilius*. The phylogenetic and pairwise distance results corroborate morphological data supporting the recognition of *C. maasiorum* as a distinct species.

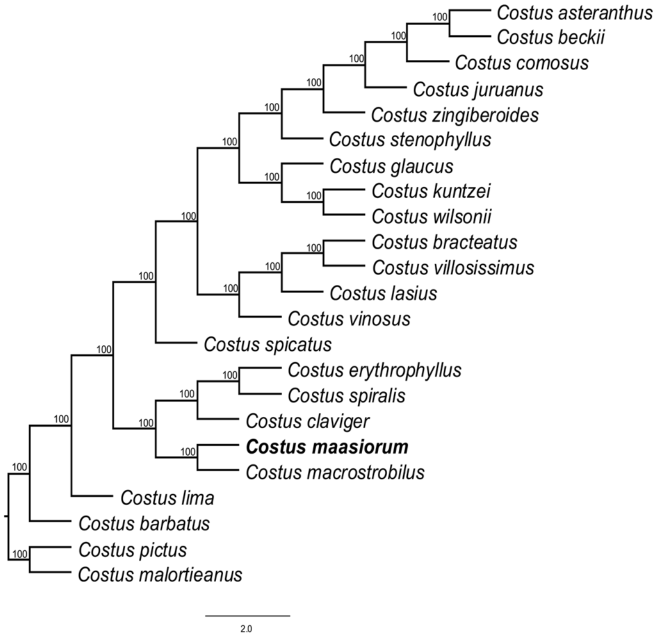


**Fig. 2** Coalescent SNP tree with 1000 bootstrap replicates. Based on this taxonomic sampling, *Costus maasiorum* sp. nov. (bold) is resolved as sister to *C. macrostrobilus* with 100% bootstrap support.

**Table 2** Pairwise distances (values given as percentages) between all accessions calculated with Mega11).

| | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **1. *C. asteranthus*** | - | | | | | | | | | | | | | | | | | | | | | | |
| **2. *C. barbatus*** | 13 | - | | | | | | | | | | | | | | | | | | | | | |
| **3. *C. beckii*** | 10 | 16 | - | | | | | | | | | | | | | | | | | | | | |
| **4. *C. bracteatus*** | 28 | 17 | 30 | - | | | | | | | | | | | | | | | | | | | |
| **5. *C. claviger*** | 28 | 19 | 30 | 32 | - | | | | | | | | | | | | | | | | | | |
| **6. *C. comosus*** | 12 | 14 | 14 | 28 | 28 | - | | | | | | | | | | | | | | | | | |
| **7. *C. glaucus*** | 29 | 17 | 31 | 31 | 32 | 29 | - | | | | | | | | | | | | | | | | |
| **8. *C. kuntzei*** | 24 | 14 | 27 | 26 | 27 | 24 | 22 | - | | | | | | | | | | | | | | | |
| **9. *C. lasius*** | 24 | 15 | 27 | 19 | 28 | 25 | 28 | 23 | - | | | | | | | | | | | | | | |
| **10. *C. lima*** | 27 | 13 | 29 | 31 | 32 | 27 | 30 | 26 | 28 | - | | | | | | | | | | | | | |
| **11. *C. maasiorum*** | 32 | 21 | 34 | 33 | 20 | 32 | 33 | 29 | 30 | 35 | - | | | | | | | | | | | | |
| **12. *C. macrostrobilus*** | 31 | 21 | 34 | 33 | 19 | 32 | 34 | 29 | 30 | 35 | 18 | - | | | | | | | | | | | |
| **13. *C. malortieanus*** | 25 | 11 | 27 | 30 | 31 | 25 | 28 | 25 | 27 | 26 | 34 | 34 | - | | | | | | | | | | |
| **14. *C. pictus*** | 17 | 05 | 19 | 22 | 23 | 17 | 21 | 17 | 19 | 19 | 26 | 25 | 10 | - | | | | | | | | | |
| **15. *C. juruanus*** | 16 | 15 | 18 | 29 | 29 | 17 | 30 | 26 | 26 | 28 | 33 | 33 | 26 | 18 | - | | | | | | | | |
| **16. *C. spicatus*** | 19 | 07 | 21 | 23 | 17 | 19 | 23 | 19 | 20 | 21 | 21 | 21 | 17 | 10 | 20 | - | | | | | | | |
| **17. *C. spiralis*** | 29 | 20 | 32 | 33 | 14 | 29 | 33 | 28 | 29 | 33 | 20 | 19 | 32 | 24 | 31 | 17 | - | | | | | | |
| **18. *C. stenophyllus*** | 24 | 15 | 27 | 29 | 31 | 25 | 30 | 26 | 27 | 28 | 34 | 33 | 27 | 19 | 26 | 21 | 32 | - | | | | | |
| **19. *C. villosissimus*** | 33 | 22 | 35 | 22 | 35 | 33 | 35 | 30 | 24 | 36 | 35 | 35 | 35 | 27 | 34 | 27 | 36 | 34 | - | | | | |
| **20. *C. vinosus*** | 27 | 16 | 29 | 29 | 32 | 27 | 31 | 27 | 27 | 30 | 34 | 34 | 29 | 21 | 29 | 23 | 34 | 28 | 35 | - | | | |
| **21. *C. erythrophyllus*** | 31 | 21 | 34 | 34 | 17 | 32 | 34 | 30 | 31 | 35 | 21 | 20 | 34 | 26 | 33 | 20 | 15 | 34 | 38 | 35 | - | | |
| **22. *C. wilsonii*** | 23 | 12 | 25 | 25 | 26 | 23 | 22 | 15 | 23 | 25 | 28 | 28 | 23 | 16 | 25 | 18 | 27 | 24 | 29 | 26 | 29 | - | |
| **23. *C. zingiberoides*** | 16 | 13 | 19 | 26 | 25 | 17 | 27 | 23 | 23 | 25 | 29 | 29 | 24 | 16 | 18 | 17 | 26 | 23 | 31 | 26 | 29 | 22 | - |

**Fig. 3** *Costus maasiorum* sp. nov.: **A.** Stem from *D.Skinner 3071* (BH) showing red striations; **B.** Close-up of lower side of leaf showing pubescence; **C.** Red lower side of leaf from a plant observed in Buenaventura in southern Ecuador; **D.** Close-up of upper side of leaf showing pubescence; **E.** Plant in habitat, Bilsa, Ecuador; **F.** Inflorescence from Bilsa, Ecuador. Photos A-F by Dave Skinner.

## TAXONOMY

***Costus maasiorum*** D.Skinner, J.L.Clark, & C.D.Specht, sp. nov.— Fig. 3–5

*Costus maasiorum* sp. nov. can be recognized by its plicate leaves, often dark purple underneath, the presence of appendaged bracts with the appendages being erect and triangular in shape, and the primarily yellow flower with the labellum presenting as a narrow, elongate floral tube. The overall morphology of the plant is similar to that of *Costus macrostrobilus*, but the species differs in having a more tubular labellum, plicate leaves (non-plicate or flat leaves in *C. macrostrobilus*) and in the shape of the bract appendages that are concave and somewhat pungent (ending in a stiff, sharp point in *C. macrostrobilus*). — Type: *Margot Bass, Laura Kueppers & Nigel Pitman 180* (holo U [U1213992]; iso MO [MO1439537]!, QCNE), Ecuador, Esmeraldas, Cantón Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabel, Bilsa road just SW of Station entrance, 500 m, 0º21' N, 79º44' W, 20 October 1994.

Herbs, 2–3 m tall. *Leaves* sheaths 15–25 mm diam, lower stems sparsely puberulous to glabrous with conspicuous reddish stripes; ligule slightly 2-lobed, 12–25 mm long, rather densely to sparsely puberulous; petiole 15–20 mm long, sparsely puberulous; lamina elliptic to narrowly elliptic, 45–65 by 10–25 cm, distinctly plicate, abaxially often dark purple in colour especially in young plants, adaxial surface glabrous, abaxial surface densely to sparsely puberulous to villose, base cuneate to slightly cordate, apex shortly acuminate, acumen c. 20 mm long. *Inflorescence* ovoid, 9–13 by 4.5–9 cm, terminating a leafy shoot; bracts glabrous; bracteoles, calyx, ovary, and capsule sparsely puberulous; bracts broadly ovate-triangular, 2.5–3 by 1.5–2.5 cm, red, coriaceous, callus dark green, present below the appendage, 4–5 mm long; appendages green, foliaceous, erect, broadly ovate-triangular, 1–2 by 1–1.5 cm, apex acute; bracteole boat-shaped, 20–25 mm long, red. *Flowers* abaxially oriented; calyx red, 10–12 mm long, lobes shallowly triangular, 1–2 mm long; corolla pale yellow, 60–70 mm long, glabrous, lobes narrowly elliptic, 45–55 mm long; labellum pale yellow, lateral lobes rolled inwards and forming a tube of 4–8 mm diam, oblong-elliptic when spread out, c. 60 by 25 mm, 3-lobed, lateral lobes strongly striped with red, middle lobe reflexed with yellow nectar guide, margin irregularly dentate to lobulate; stamen yellow, 30–35 by c. 12 mm, not exceeding the labellum, anther c. 10 mm long, apex red. *Capsule* ellipsoid, c. 12 mm long.

Distribution — Ecuador (Esmeraldas, El Oro, Imbabura) (Fig. 5).

Habitat & Ecology — At the type locality this species grows in grey clay soil in the shaded understory of primary forest.

Conservation Status — *Costus maasiorum* is endemic to the western Andean slopes of Ecuador. The first documented population of *C. maasiorum* was during preliminary floristic inventory work in the 1990s during the establishment of the Bilsa Biological Station in the Esmeraldas Province inside the Reserva Ecologica Mache-Chindul. The Bilsa Biological Station is a private reserve of more than 4000 hectares in the eastern portion of the Mache-Chindul Mountains managed by the Jatun Sacha Foundation. This area was inventoried during the 1990s (Clark et al. 2006), including an expedition with Dr. Paul Maas in 1997. Other populations are likely equally as abundant but not reflected by the number of specimens in herbaria due to insufficient collecting and confusing taxonomic boundaries. A second population is from the Jocotoco Conservation Foundation's Reserva Biologica Buenaventura in the El Oro province along the western Andean slopes in southern Ecuador. The population from Buenaventura is represented in Fig. 4) and included in the assessment based on an iNaturalist observation (https://www.inaturalist.org/observations/4057898). There are no known herbarium specimens corresponding to the population from Buenaventura. A third population is from near Lita, along the road towards San Lorenzo in the western Andean slopes of northern Ecuador. A fourth population is from Centinela, near the outskirts of Santo Domingo de los Tsáchilas along the western Andean slopes of northern Ecuador. The calculated AOO = 24 km$^2$ and the EOO = 32 550+ km$^2$. Based on the available information and according to the IUCN Red List criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022), *C. maasiorum* does not meet any of the criteria for endangered or Near Threatened. The preliminary IUCN assessment for *C. maasiorum* is Least Concern (LC).

*Etymology* — *Costus maasiorum* is named in honour of the botanical couple Professor Paul J.M. Maas and Hiltje Maas-van de Kamer and the contribution of this couple to systematic and taxonomic work within the *Costaceae*. It was Dr. Paul Maas who visited Bilsa in 1997 and first noted this species as undescribed. Paul began working on *Costaceae* during his PhD in which he completed two monographs on New World *Costoideae* for Flora Neotropica, establishing himself as the expert on this and other families of Neotropical *Zingiberales*. The two Flora Neotropica volumes, which included revisions of the *Costoideae*, provided species level descriptions and detailed understanding of taxonomic limits, biogeographic distributions, morphological variation, and relationships among species of *Costaceae* that still stand today, often being confirmed by subsequent DNA-based phylogenetic studies. Paul's observations of differences between closely related species and awareness of variation noted in living plants and in herbarium specimens enabled and inspired decades of research on this interesting and charismatic tropical family. While his career shifted to working on *Annonaceae*, a large piece of Paul's botanical vision and passion stayed with *Costaceae* and the *Zingiberales*, and Paul joined forces with Hiltje Maas-van de Kamer to serve as a colleague, collaborator and mentor to new students interested in learning from and contributing to his taxonomic legacy. Together as partners in botany and in life, Paul and Hiltje maintained their presence as preeminent researchers of *Costaceae* until today, having completed a monograph of African *Costaceae* in 2016 (Maas-van de Kamer et al. 2016), described 18 new species of Neotropical *Costaceae* in 2023 (Maas et al. 2023), and completed a massive monograph of Neotropical *Costaceae* now submitted for publication here published in Blumea. The prolific botanical couple has also made significant contributions to our current knowledge of *Cannaceae* (Maas van de Kamer & Maas 2008), *Zingiberaceae* (in particular *Renealmia*; Maas 1977), and neotropical mycoheterotrophic plant lineages, including a 1988 revision of the Colombian species of *Triuridaceae* and *Burmanniaceae* (Maas 1988), as well as studies on mycoheterotrophic *Gentianaceae* (Merckx et al. 2013) and *Burmanniaceae* (Merckx et al. 2006). Paul and Hiltje Maas are also well-known, admired and loved throughout the neotropics

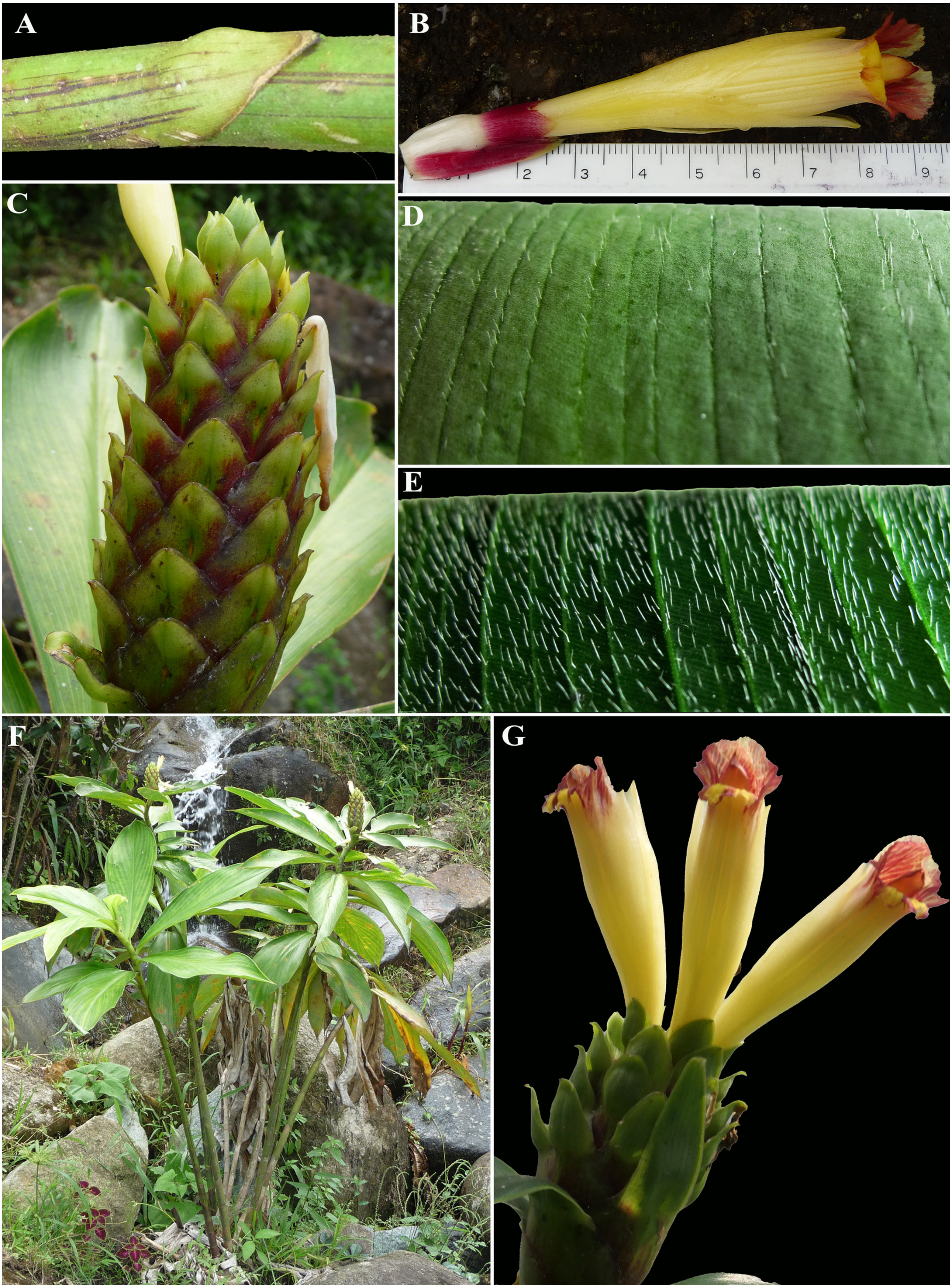


**Fig. 4** *Costus maasiorum* sp. nov. specimen *D.Skinner 3202*: **A.** Stem and ligule with red striations. **B**. Flower with attached immature fruit and bracteole. **C.** Inflorescence close-up of same plant showing appendaged bracts. **D-E**. Upper (D) and lower (E) side of leaves showing variation in indument and red coloration as compared with Fig. 3. **F.** Plant in habitat at Siete Cataratas, Ecuador. **G.** Close up of young inflorescence showing sequential flowering with spiromonistichous phyllotaxy. Photos A-G by Dave Skinner.

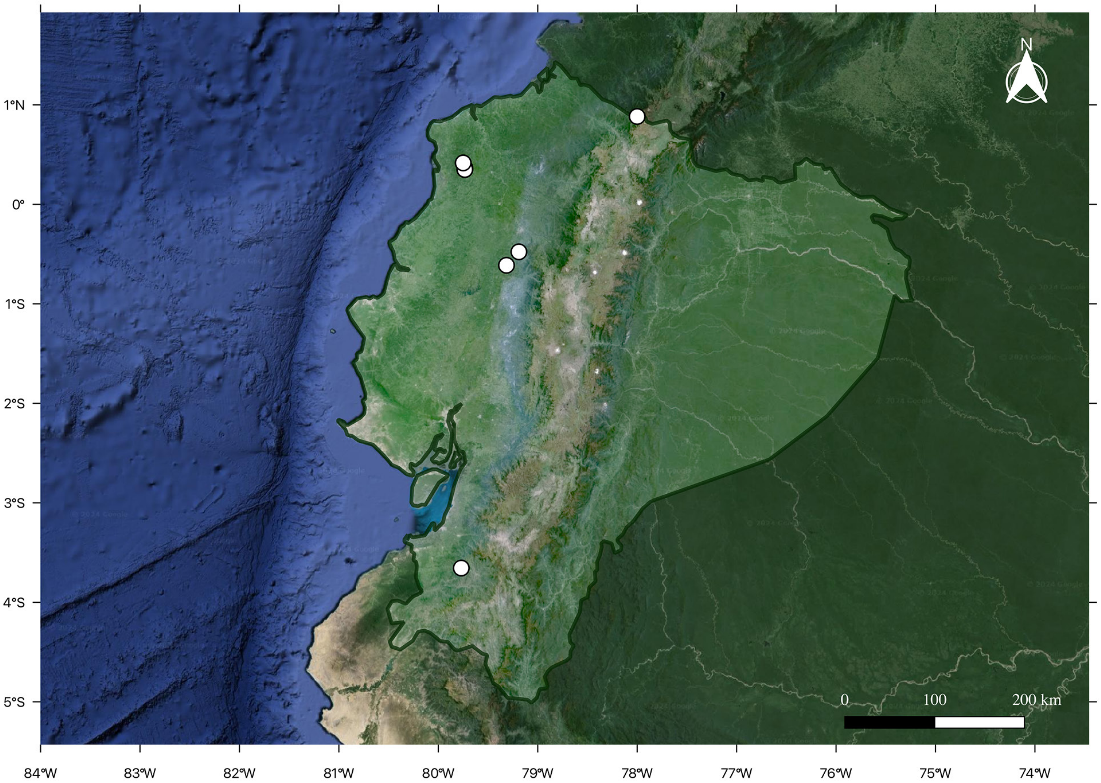
for their delivery of dynamic, passionate, engaged and witty lectures on Neotropical plant families and on stories from their 60+ years of botanical exploration – many of which include the escapades of the ‘familia Maas’ in Brazil, Suriname, Colombia, Ecuador, and Bolivia. A great number of Neotropical botanists have been the recipient of the generous hospitality of Paul and Hiltje – whether in Manaus (Brazil) or in Bunnik (the Netherlands). There are no other persons more deserving of the honour of having a species of Neotropical *Costus* named after them - as a couple and as a team - than Paul and Hiltje Maas, and the only thing that took so long was finding a new *Costus* that they had not yet discovered and named themselves.

*Other specimens examined.* — Ecuador. Esmeraldas: canton Quinindé, Cordillera Mache-Chindul, Reserva Ecological Mache-Chindul, X. *Cornejo 10029* (GUAY); road between El Descanso and Herrera, 400–600 m, 0º21’ N, 79º44’ W, 17 Jan 1997, *J.L. Clark et al. 3820* (MO, QCNE); Bilsa Biological Station, Loma de los Guerrilleros, 650 m, 0º21’ N, 79º44’ W, 20 Feb 1997, permament plot #2, *J.L. Clark 3967* (MO, QCNE); parroquia Viche, Reserva Ecológica Mache-Chindul, Comunidad Caña Braval, Cabaceras de Río Viche, estero Sabaleta, 250 m, 0º25’ N, 79º45’ W, 11 Mar 1998, *J.L. Clark, C. Pallis & J. West 4606* (MO, QCNE); Bilsa Biological Station, along old road to Mono, 400-600 m, 0º21’ N, 79º44’ W, 10 Oct 1994, *N. Pittman 829* (MO, QCNE). Imbabura, Lita area, Las Siete Cascadas, 900 m, 0°52’58.8” N, 78°31’1.994” W, *D. Skinner 3202* (L). Santo Domingo de los Tsáchilas: canton Santo Domingo, parroquia Polanco, sector Bolo Alto, Bosque y Cascadas Las Rocas, propiedad de Eduardo Díaz, waterfalls in the Bolo watershed, 500-600 m, 0º28’38.1” S, 79°11’22.4” W, 12 Jul 2022 *J.L. Clark et al. 16784* (QCA, SEL); cultivated specimen from Fairchild Botanical Garden, wild collection unknown, *D. Skinner 3540* (BH). (For herbarium abbreviations see Thiers continuously updated).

Notes — Plants of this species were previously included in *Costus guanaiensis* Rusby var. *tarmicus* (Loes.) Maas and most recently considered as conspecific with *C. laevis* Ruiz & Pav. (as a ‘hairy form’) or *C. macrostrobilus* based on the shape of the bract appendages. This new species shares characteristics with both *C. laevis* and *C. macrostrobilus*. It is easily recognized vegetatively by the presence of plicate leaves, often deep purple on the undersides in young plants. The differences in the shape of the labellum between *C. maasiorum* and *C. macrostrobilus* are remarkable. The species described here presents a tubular flower (associated with ornithophilous pollination), while the latter has a horizontally spreading labellum (associated with mellitophilous pollination). These differences suggest that different pollinators may be visiting the flowers of these two taxa, potentially limiting gene flow. Other characters of the inflorescence are discordant with hummingbird pollination (overall green inflorescence, labellum stripes and nectar guide), and reproductive isolation of these lineages has yet to be tested and floral visitors to be documented. However, given the phylogenetic importance of floral shape in pollination syndromes within the genus (Valderrama et al. 2022), the contrasting flower forms support the idea of independent evolutionary trajectories for *C. maasiorum* and *C. macrostrobilus*.

The new species differs from *Costus gibbosus* found in western Ecuador by lacking the characteristic gibbous lower sheaths, and instead having smooth sheaths with distinctive red longitudinal markings. In addition, the bract appendages of *C. maasiorum* are always upright, but in *C. gibbosus* are horizontal in orientation, often with a distinctly incurved apex. In phylogenetic analyses using hyb-seq data (data not shown), exemplars of *C. maasiorum* are recovered as sister to *C. gibbosus* together in a clade with *C. macrostrobilus*, confirming a close relationship with both taxa.

**Fig. 5** Distribution of *Costus maasiorum*. White circles represent verified localities.



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