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Shuaria (Gesneriaceae), an Arborescent New Genus from the Cordillera del Cóndor and Amazonian Ecuador

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Abstract—A new neotropical genus, ***Shuaria***, with a single species, ***S. ecuadorica***, is described from the Cordillera del Cóndor and Amazonian regions of southeastern Ecuador and is placed in the family Gesneriaceae, tribe Beslerieae. The placement of ***Shuaria*** in the tribe Beslerieae is strongly supported by molecular sequence data generated from analyses of nuclear ribosomal DNA internal transcribed spacer region (ITS), and the chloroplast DNA *trnL* intron, *trnL-trnF* intergenic spacer region. Sequence data were generated for 33 species representing most of the generic diversity from the tribes Beslerieae and Napeantheae. ***Shuaria*** is characterized by the following unique combination of relatively uncommon characters in the Gesneriaceae: arborescent habit; opposite leaf arrangement sometimes interrupted by alternate leaves; lepidote trichomes on vegetative and floral structures; small white flowers with a dorsal gibbosity at the base of the corolla tube; and a bivalved septicidally dehiscent capsule. The suite of uncommon characters initially made ***Shuaria*** difficult to place in the Gesneriaceae and within a known tribe. ***Shuaria*** is restricted to the Ecuadorian provinces of Pastaza, Morona-Santiago, and Zamora-Chinchipe in lowland Amazonian tropical wet forest and in lower montane cloud forest on the western slopes of the Cordillera del Cóndor. A key and a table are presented for differentiating ***Shuaria*** from other related genera.

Resumen—Se describe ***Shuaria***, un nuevo género neotropical de la Cordillera del Cóndor y la región amazónica del suroriente del Ecuador, con una sola especie, ***S. ecuadorica***, y se le incluye en la tribu Beslerieae de la famlia Gesneriaceae. La ubicación de ***Shuaria*** en la tribu Beslerieae se basa en las secuencias de ADN generadas por los análisis de la región ITS del ADN ribosomal nuclear, y de la región intergénica *trnL* intron, *trnL-trnF* del ADN del cloroplasto. Se secuenciaron 33 especies, representando la mayor parte de de la diversidad genérica de las tribus Besleriaceae y Napeantheae. ***Shuaria*** se caracteriza por la siguiente combinación única de caracteres que no son comunes en la familia Gesneriaceae: el hábito arborescente; hojas opuestas algunas veces intercaladas con hojas alternas; tricomas lepidotos en las estructuras vegetativas y florales; pequeñas flores blancas con una gibosidad dorsal en la base del tubo de la corola; y una cápsula septicida bivalvada. Este conjunto de caracteres inusuales inicialmente hizo difícil colocar ***Shuaria*** en Gesneriaceae y en sus tribus conocidas. ***Shuaria*** se restringe a las provincias ecuatorianas de Pastaza, Morona-Santiago, y Zamora-Chinchipe en el bosque húmedo tropical de las tierras bajas amazónicas, y en bosque nublado montano bajo en las vertientes occidentales de la Cordillera del Cóndor. Se presenta una clave y una tabla para distinguir entre ***Shuaria*** y otros géneros estrechamente vinculados.

Keywords—Beslerieae, Ecuador, Gesneriaceae, Napeantheae, phylogenetics, taxonomy.

The Cordillera del Cóndor is an eastern outlier of the Andean mountains that extends about 150 km from north to south in southeastern Ecuador and adjacent northern Peru. The Cóndor forms part of the discontinuous chain of sub-Andean cordilleras that are situated between the Eastern Cordillera of the Andes and the Amazon lowlands, parallel to the main Andean chain but attaining lower elevations and separated from the main Eastern Cordillera by lower elevation valleys. Besides the Cóndor, some other sub-Andean cordilleras include the Galeras and Cutucú ranges in Ecuador and the Cordillera Azul and Yanachaga ranges in Peru. Whereas the main Eastern Cordillera is comprised mostly of metamorphic and volcanic rocks, the sub-Andean cordilleras are made up principally of Mesozoic and early Tertiary sediments, sandstone and limestone, deposited at the western margin of South America prior to the rise of the Andes and uplifted concurrently with the main Andes, largely in the past million years. Intrusive igneous formations, often bearing deposits of gold, copper, and other minerals also form part of the Cóndor and the other sub-Andean cordilleras.

Botanical exploration of the Cordillera del Cóndor region in Ecuador was initiated in 1990, but further fieldwork during the 1990s was limited due to an ongoing dispute between Ecuador and Peru over the location of the international border, culminating in an armed conflict between the two countries in 1995. A treaty signed in 1998 established the precise location of the border and restrictions in access to the region were lifted. Thus, botanical inventories in the region have continued during the past decade. These floristic inventories have revealed a number of taxonomic novelties, and most of the newly described taxa are locally endemic and edaphically restricted to the oligotrophic sandstone plateaus and adjacent areas of the Cóndor region (Neill 2005). The recently described flowering plant taxa from the Cóndor region include several species within genera that were previously considered endemic to the sandstone plateaus or tepuis of the Guayana Shield in southern Venezuela and adjacent areas. Examples include *Stenopadus andicola* Pruski in the Asteraceae (Pruski 1998) and *Phainantha shuariorum* C. Ulloa & D. A. Neill in the Melastomataceae (Ulloa Ulloa and Neill 2006).

Among the collections made in the Cordillera del Cóndor region on several occasions is a small understory tree with opposite (occasionally alternate), exstipulate leaves, branched inflorescences with rather small, white, gamopetalous, hypogynous flowers, and dry capsular fruit. This taxon was initially recognized as a member of the Lamiales, but could not readily be assigned to an extant genus or family of that order. This enigmatic taxon seemed to the collectors and other botanists who examined the material to be similar in overall appearance to two monotypic genera that occur in the same general region of eastern Ecuador: *Sanango racemosum* (Ruiz & Pav.) Barringer and *Peltanthera floribunda* Benth. In fact, some collections were erroneously determined as *Peltanthera* Benth & Hook. Both *Sanango* G. S. Bunting & J. A. Duke and *Peltanthera* have traditionally been placed in Buddlejaceae, but *Sanango* was transferred to Gesneriaceae by Wiehler (1994) following morphological and anatomical studies by Norman (1994) and Dickison (1994); whereas *Peltanthera* has been retained in Buddlejaceae (Norman 2000). Molecular systematic studies (Oxelman et al. 1999; Bremer et al. 2002; Wang et al. 2004) strongly support *Peltanthera* as closely related to the Gesneriaceae.

Additional specimens of this undetermined taxon from localities farther north in lowland Amazonian Ecuador also turned up in the "mystery plant cabinets" at the Missouri Botanical Garden (MO) and the National Herbarium of Ecuador (QCNE). Recent collections of this small understory tree included leaf material for DNA extraction and sequencing to help resolve its placement. We describe this taxon herein as a new genus and species, *Shuaria ecuadorica* D. A. Neill & J. L. Clark, placed in Gesneriaceae, tribe Beslerieae, and present a discussion of its phylogenetic placement, ecology, and distribution.

Materials and Methods

Taxon Sampling and Outgroup Selection—Thirty-three species are included in the analyses (Appendix 1). Twenty-seven taxa representing twenty-six species were sequenced for the internal transcribed spacer (ITS) region of 18S-26S nuclear ribosomal DNA (nrDNA) and the *trnL* intron as well as the *trnL-trnF* intergenic spacer region of chloroplast DNA (cpDNA). Sequence data obtained from GenBank for six species were selected from Zimmer et al. (2002) so that all major tribes from the New World and two species from the Old World were represented in the analyses. Most species were photographed in the field and determinations were verified with herbarium voucher specimens, photographs, and the literature. All taxa have fertile voucher specimens archived at the Smithsonian Institution's U. S. National Herbarium (US), Marie Selby Botanical Gardens (SEL), or the Alabama Museum of Natural History (UNA). Two separate collections representing two populations of *Shuaria ecuadorica* were included in the analyses. All other species in the analyses are represented by only one accession.

Previous studies strongly support monophyly of Beslerieae and Napeantheae (Smith 2000; Zimmer et al. 2002; Roalson and Clark 2006; Roalson et al. 2008) and taxon sampling therefore emphasized members of these two tribes. Taxon sampling for this study includes a recent field-collected leaf sample dried in silica gel of *Anetanthus* Hiern ex Benth. (*J. L. Clark 10003*) whereas Smith (2000) utilized DNA extracted from a herbarium collection from 1966 (*Irwin et al. 14055*).

Peltanthera floribunda and *Sanango racemosum* were selected as outgroups. Molecular phylogenetic studies (Smith et al. 1997; Oxelman et al. 1999; Bremer et al. 2002) strongly support *Peltanthera* and *Sanango* as closely related to the Gesneriaceae. The close relationship of *Sanango* and Gesneriacerae is supported by vegetative and floral anatomy (Dickison 1994), chemotaxonomy (Jensen 1994), morphology, and distribution (Norman 1994). It is equivocal whether *Sanango* and *Peltanthera* are recognized as sister-taxa to the Gesneriaceae or basal members of the Gesneriaceae, but they are clearly not closely related to Buddlejaceae or Loganiaceae. The phylogenetic analyses are rooted with *Peltanthera* based on Wang et al. (2004), which unequivocally supports the sister-group relationship of *Peltanthera* to the rest of Gesneriaceae.

DNA Extraction, Amplification, and Sequencing—All tissue samples included in the analysis were collected in the field and dried in silica gel. Leaf samples were ground using a ThermSavant FastPrep FP120 cell disrupter (Qbiogene, Carlsbad, California). DNA was isolated using the Qiagen DNeasy™ DNA isolation kit (Qiagen, Valencia, California).

Templates of the nrDNA internal transcribed spacer region (ITS) were prepared using the primers ITS5HP (Suh et al. 1993) and ITS4 (White et al. 1990). The cpDNA *trnL* intron and *trnL-trnF* intergenic spacer were amplified using the primers trnLc and trnLf (Taberlet et al. 1991). The reverse and forward of the internal primers ITS2 and ITS3 (White et al. 1990) were used in cycle sequencing to obtain independent and overlapping sequence reads for the entire ITS region.

Polymerase chain reaction (PCR) amplifications followed the procedures described by Baldwin et al. (1995) utilizing Taq DNA polymerase (Promega, Madison, Wisconsin). To reduce within-strand base pairing that can result in interference with Taq polymerase activity, we found it essential to use 5% DMSO and 5% BSA in PCR reactions for ITS. The PCR products were electrophoresed using a 1.0% agarose gel in 1 × TBE (pH 8.3) buffer, stained with ethidium bromide to confirm a single product, and purified using PEG 8000 (polyethylene glycol) in 2.5 M NaCl under the conditions described in Johnson and Soltis (1995). Direct cycle sequencing of purified template DNAs followed the manufacturer's specifications, using the ABI Prism® BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems, Foster City, California). Cycle sequencing was carried out with the two initial PCR primers and the internal primers, ITS3 and ITS2 (White et al. 1990). Sequencing was performed using an Applied Biosystems Model 377 Automated DNA Sequencing System (PE Biosystems).

DNA chromatograms were edited and contigs were assembled using Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, Michigan). The sequences were truncated to include only ITS1, 5.8S, and ITS2 regions. Identification of the ends of ITS1 and ITS2 were determined by comparisons with other Gesneriaceae sequences (Zimmer et al. 2002). All sequences are deposited in GenBank (Appendix 1).

Alignment and Phylogenetic Analyses—All sequences were initially aligned using ClustalW (Larkin et al. 2007) under the multiple alignment mode. The resulting sequences were then imported into the program SeAl version 1.0a1 (Rambaut 1996) multiple sequence editor for the final alignment. Because the sequences were not highly divergent, it was possible to make minor adjustments so that overlapping gaps were minimized. Phylogenetic data matrices are available in Nexus format from TreeBASE (study number S2572).

The parsimony analysis was performed to completion using a two stage heuristic search in PAUP* 4.0b10 (Swofford 2002). The first stage of the analysis was done using the following settings: 1,000 random additions, holding 10 trees at each step; tree bisection-reconstruction (TBR) branch swapping with no more than 10 trees saved for each rep; MULTREES option not in effect. The second stage of the analysis was performed on all most parsimonious trees in memory with the same settings, but with the MULTREES option in effect. Other searches were conducted, but did not find shorter trees using the settings above with the following changes: 10 random addition cycles limited to 1,000 trees of equal length for each of the replicates; 1,000 random addition cycles limited to 100 trees of equal length for each of the replicates.

Additional tree searches were done using the parsimony ratchet analysis of WinClada (Nixon 2002) and NONA (Goloboff 1994) with NONA acting as the parsimony search engine and WinClada as the tree and data editor. Ten separate tree searches were done using the parsimony ratchet analysis in WinClada using the following settings: 400 iterations per search, one tree held for each iteration, 160 characters sampled (10% of the total), amb = poly- (only uses characters that can be defined as unambiguous to support a clade), and a random constraint level of 10. Separate tree searches were performed in WinClada as suggested by Nixon (1999) since the ratchet option can sometimes get stuck on suboptimal "islands" and it is therefore better to perform many separate searches with fewer iterations than one larger search with more iterations.

Clade robustness for the parsimony analysis was evaluated in PAUP* using the bootstrap (Felsenstein 1985) and Bremer support (Bremer 1988; Donoghue et al. 1992). The bootstrap analysis was based on 10,000 replicates with the full heuristic search option in effect with the following settings for each search: 10 random addition cycles, holding 10 trees at each step; tree bisection-reconstruction (TBR) branch swapping, saving a maximum of 10 trees for 1,000 replicates. Bremer support was used to examine branches that collapsed as tree length was increased by one step in conjunction with the heuristic search option in PAUP*. Each successive increase in tree length resulted in an increased number of corresponding trees. A strict consensus tree was obtained for each set of trees until all branches collapsed. The parsimony analyses and clade support were evaluated for the individual ITS and *trnL-F* regions (data not shown). Conflict between datasets was evaluated by comparing incongruence of strongly supported clades from individual datasets. There were no well-supported clades (bootstrap values ≥ 70%) between the two topologies that were in conflict. The two genic regions were therefore combined in a total evidence analysis.

For the Bayesian analysis MrModeltest 2.2 (Nylander 2004) was used to determine the model of sequence evolution that best fit the individual nrDNA and cpDNA datasets. MrModeltest 2.2 is a modified version of Modeltest 3.6 (Posada and Crandall 1998) that uses the Aikaike Information Criterion to assess the significance of adding parameters to the 24 different models of sequence evolution that can be used in MrBayes 3.1 (Ronquist and Huelsenbeck 2003). The ITS and *trnL-F* matrices were evaluated separately to determine the model of sequence evolution that best fit the data. The final Bayesian analysis had two data partitions with corresponding models for each region. The incongruence length difference test (ILD; Farris et al. 1994) was performed in the program PAUP* (Swofford 2002) to determine whether the ITS and *trnL-F* data sets are significantly different from random partitions of the combined data.

The Bayesian phylogenetic analysis was implemented using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). Four chains were run for 1,000,000 generations with a tree sampled every 50 generations. The burn-in period was determined by constructing a XY scatter plot of tree maximum likelihood values in a MS-Excel spreadsheet. The point where these values stabilize and randomly hover around a mean was taken as the point in which sampling within the posterior probability distribution began. Posterior probability values were determined by computing the 50% majority-rule consensus tree of all compatible trees, excluding trees sampled during the "burn-in period".

Results

***DNA Sequencing and Alignment*—**The four ITS sequencing primers produced overlapping fragments that collectively covered the entire spacer and 5.8S rDNA regions along both strands. The aligned ITS data matrix was 699 base pairs (bp) long with 430 (62%) variable sites, of which 319 (46%) were parsimony informative. The length of the unaligned sequences varied from 607–647 bp. The two outgroups of the analysis contributed 15 of the 319 parsimony informative characters. There were no ambiguously aligned sites excluded from the analysis. The mean pairwise divergence for the ITS region was 18.8% (with a range of 8–37.8%).

The two *trnL-F* sequencing primers produced overlapping fragments that collectively covered the entire *trnL* intron and the *trnL-trnF* intergenic spacer regions along both strands. The aligned *trnL-F* data matrix was 912 bp long with 252 variable sites (28%). The length of the unaligned complete sequences varied from 745–890 bp. The number of parsimony informative characters was 100 (11%). The two outgroups of the analysis contributed 11 of the 100 parsimony informative characters. There were no ambiguously aligned sites excluded from the analysis. The mean pairwise divergence for the entire *trnL-F* region was 3.7%. (with a range of 0.20–10%).

The two samples of *Shuaria* represented two distinct populations. The ITS sequences of the two samples differed by 7 bp and the *trnL-F* sequences differed by 8 bp.

***Parsimony Analysis*—**The parsimony analysis of the combined ITS and *trnL-F* data resulted in nine most parsimonious trees (length = 1,579 steps, consistency index [CI] = 0.68, retention index [RI] = 0.72, rescaled consistency index [RC] = 0.49). Figure 1 shows the strict consensus of these trees.

The tribes Beslerieae and Napeantheae are strongly supported with respective bootstrap values of 99% and 100% (Fig. 1). Monophyly for all genera with two or more species is also strongly supported with bootstrap values ranging from the lowest of 87% (*Besleria*) to 100%. *Shuaria* is strongly supported (BS = 99%; Bremer support = 14) as a member of the tribe Beslerieae (Fig. 1).

The individual analysis of the *trnL-F* data did not result in a well-resolved phylogeny (results not presented here). The combined analysis of the two datasets provided significantly more resolution over the analysis of individual datasets. Thus, a total evidence approach was followed (Kluge 1989; Bruneau et al. 1995; Nixon and Carpenter 1996; Graham et al. 1998).

***Bayesian Analysis*—**The ILD test suggests that the ITS and *trnL-F* data sets are significantly different ($p = 0.01$). The model selection implemented in the program Modeltest 2.2 (Posada and Crandall 1998) resulted in GTR + G for *trnL-F* and GTR + G + I for ITS. The Bayesian analysis presented here partitioned the two datasets, which allowed for each marker to be modeled under different parameter values. The first 20% of trees were excluded as burn-in and the analysis achieved stationarity after 5,550 generations. Figure 2 shows the majority rule consensus tree resulting from the partitioned Bayesian analysis of the combined ITS and *trnL-F* data with posterior probability (PP) values and mean branch lengths.

The tribes Beslerieae and Napeantheae are strongly supported with respective PP values of 1.00 and 0.99 (Fig. 1). Monophyly for all genera with two or more species is also strongly supported with posterior probability values of 1.00. *Shuaria* is strongly supported (PP = 0.99) as a member of the tribe Beslerieae and as the sister genus (PP = 0.99) to a clade of *Anetanthus* sp. + *Tylopsacas cuneatum* (Fig. 2).

Discussion

Shuaria was initially difficult to place in a known family and genus because it does not present characters that would make it readily identifiable to currently recognized families in the order Lamiales, despite its similarity in overall appearance to *Peltanthera* and *Sanango* (Table 1). Norman (2000), who included *Peltanthera* in her monograph of Buddlejaceae, examined some of the collections and remarked that *Shuaria* seemed to belong in the Gesneriaceae (pers. comm. 2007). Other specialists who studied the material (e.g. L. E. Skog, R. Liesner, and the present authors) were suspect of its placement in that family. Even with molecular results strongly supporting the placement of *Shuaria* in the family Gesneriaceae, it was not easy to place it in a known tribe based on morphological characters alone.

Phylogenetic Placement of Shuaria*—Shuaria* is strongly supported as belonging to the tribe Beslerieae by our molecular data (Figs. 1, 2). The parsimony and Bayesian analyses suggests that *Shuaria* is the sister taxon to *Tylopsacas* and *Anetanthus* (Figs. 1, 2). This relationship was initially surprising because *Shuaria* is a tree, 3–5 m tall, while *Anetanthus* is a prostrate herb with elongate stems and *Tylopsacas* is a small herb with a basal rosette of leaves. The remaining four genera in the Beslerieae are small herbs to subshrubs (Table 1).

In the flower characters and the type of inflorescence (pair-flowered cyme) *Shuaria* can be unambiguously referred to the Gesneriaceae. However, there are a number of uncommon characters such as arborescent habit, presence of both opposite and alternate leaves, and lepidote trichomes found on vegetative and floral parts. At the least, the latter two characters are autapomorphies at the family level.

***Phyllotaxy*—**The leaf arrangement in *Shuaria* is usually opposite but it is common to find shoots with opposite leaf arrangement interrupted by alternate leaves (Fig. 3E). Some herbarium collections of *Shuaria* have only alternate leaves and no opposite leaves (e.g. *W. Palacios 12109* and *E. Freire & L. Santi 3352*). Field observations made by two of the authors have confirmed that alternate leaves are present in most individuals. The presence of both opposite and alternate leaves (Fig. 3E) in *Shuaria* represents a unique pattern of phyllotaxy for the Gesneriaceae.

***Indumentum*—**The indumentum of *Shuaria ecuadorica* is composed of three types of trichomes: (1) lepidote, (2) glandular (restricted to the inner corolla surface near the anthers), and (3) unicellular–unbranched trichomes. The multicellular stellate-lepidote or dentate-lepidote trichomes are unique among all known Gesneriaceae, but strikingly similar to those of *Croton* L. (Euphorbiaceae) as described and illustrated by Webster et al. (1996). According to the terminology of Webster et al. (1996) the stellate-lepidote shield lies close to the epidermis on a short stalk and is stellate by the presence of 15–20 lobes that give it a star-like appearance (Fig. 3) and those with a shallower sinus between the lobes are "dentate-lepidote". The peltate shield is ca. 100–120 μm in diameter and the stalk

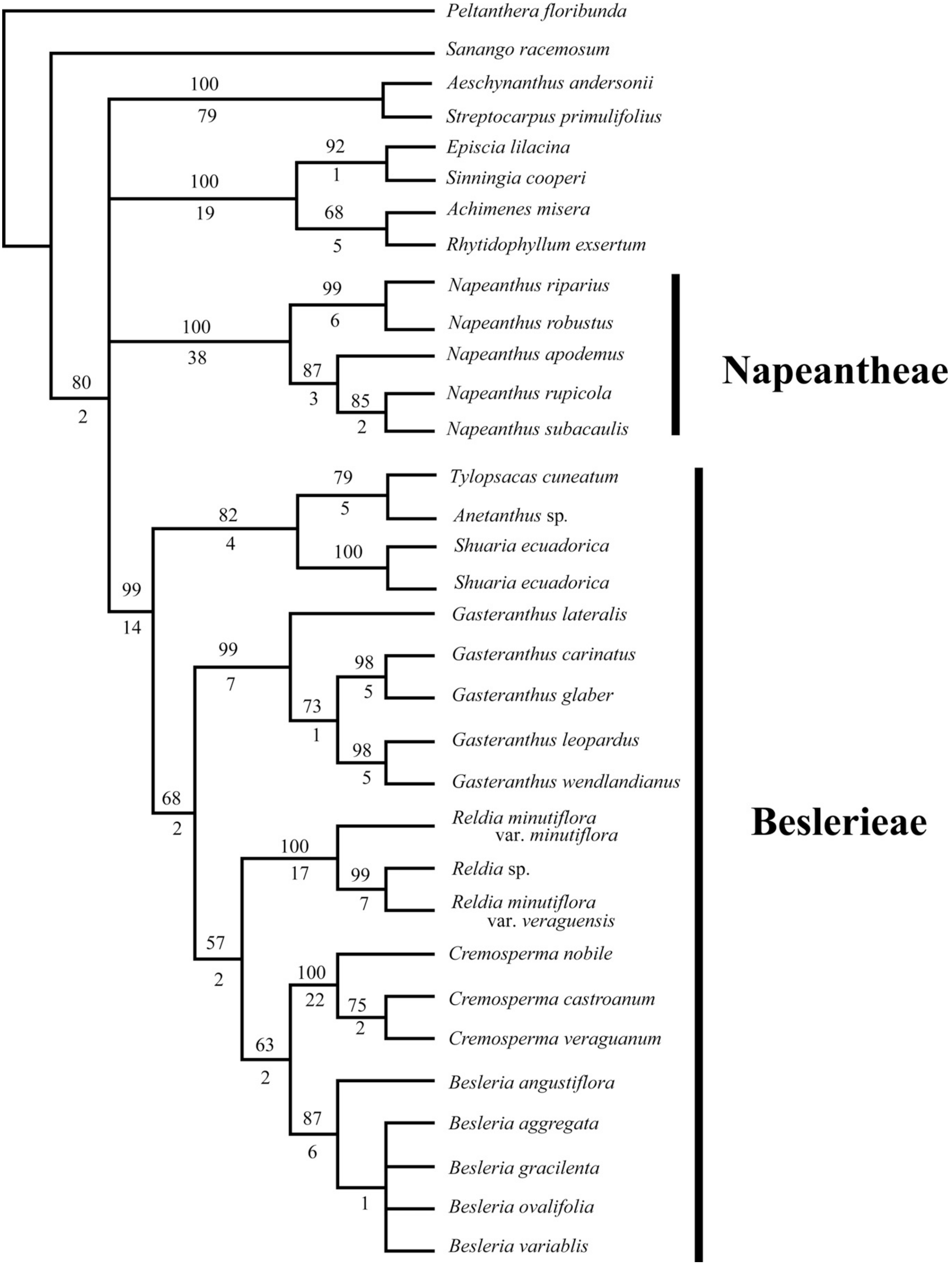

FIG. 1. Strict consensus of nine most parsimonious trees (length = 1,579 steps) from parsimony analysis of nrDNA ITS and cpDNA *trnL-F* data sets (CI = 0.68, RI = 0.72). Tree rooted with *Peltanthera floribunda*. Numbers above branches are bootstrap values (>50%) and numbers below branches are Bremer support values.

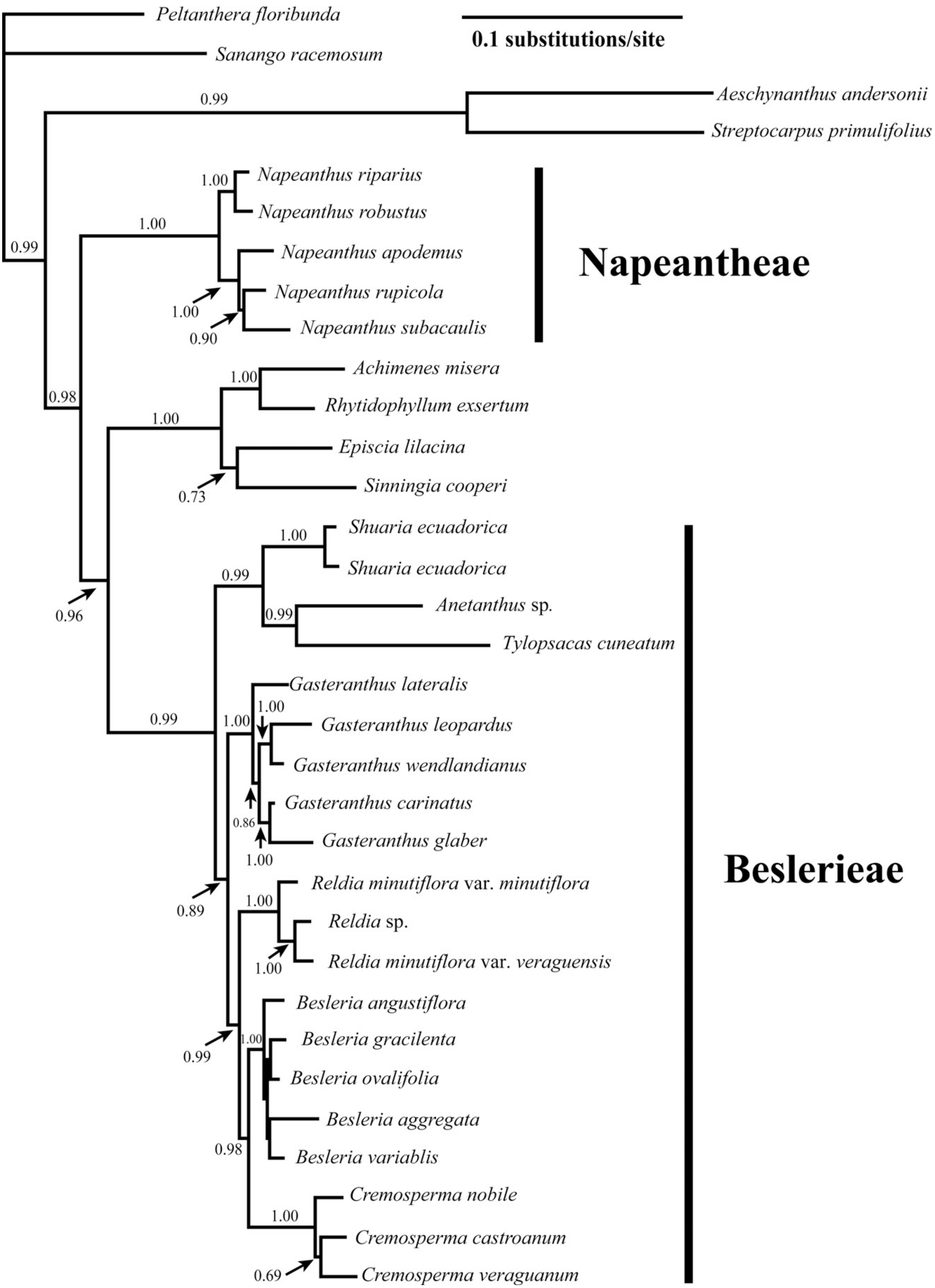

FIG. 2. Majority rule consensus tree (excluding burn-in trees) with mean branch lengths from the partitioned Bayesian analysis of the combined *trnL-F* and ITS data. Branch lengths are proportional to the mean number of substitutions per site as measured by the scale bar. Numbers on branches indicate Bayesian posterior probability (PP) values.

TABLE 1. Morphological characters of *Shuaria* compared to other genera in the tribes Beslerieae and Napeantheae as well as genera in unassigned tribes (*Resia*, *Cremospermopsis*, *Peltanthera* and *Sanango*).

Character	*Shuaria*	*Besleria*	*Anetanthus*	*Cremosperma*	*Gasteranthus*	*Reldia*	*Tylopsacas*	*Cremospermopsis*	*Napeanthus*	*Resia*	*Peltanthera*	*Sanango*
Habit	Tree or shrub	Herb or shrub	Herb	Herb	Herb	Herb	Herb	Herb or subshrub	Herb	Herb	Tree	Tree
Leaf arrangement	Opposite & alternate	Opposite	Opposite	Opposite	Opposite	Alternate	Congested	Opposite	Congested	Congested	Opposite	Opposite
Fruit type	Capsule	Berry	Capsule	Capsule	Capsule	Capsule	Capsule	Capsule	Capsule	Capsule	Capsule	Capsule
Placentation	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal	Parietal
Style persistence in fruit	Persistent	Caducous	Persistent	Caducous	Caducous	Persistent	Not observed	Not observed	Not observed	Not observed	Not observed	Not observed
Inflorescence bracts	Absent	Absent	Present or absent	Absent	Absent	Absent	Absent	Present	Present	Present or absent	Absent	Absent
Peduncle (=hypopodium)	Present	Absent	Absent	Present	Usually present, rarely absent	Present	Present	Present	Present	Present	Present	Present
Calyx lobe connation	Basal only	Basal only	Basal only	2/3 to full	Basal only	Basal only	Basal only	1/3–2/3	Basal only	Basal to 1/3	Basal only	Basal only
Calyx lobe equality	Equal	Equal	Equal	Equal	Equal	Equal	Equal	Unequal to equal	Equal	Equal	Equal	Equal
Corolla symmetry	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Slightly zygomorphic	Zygomorphic	Actinomorphic	Slightly zygomorphic
Gibbosity [‘spur’]	Present	Present	Present	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent
Nectary	Absent	Present	Present	Present	Present	Present	Present	Present	Absent	Present	Present	Present
Stamen number	Four	Four	Four	Four	Four	Four	Four	Four	Four	Four	Five	Four
Seed surface	Reticulate	Striate	Striate	Striate	Papillate or striate	Striate	Not observed	Papillate	Striate	Striate	Reticulate/honey-combed	Reticulate-striate

width is 10–15 µm. These trichomes are visible under a dissecting scope, due to their flat and glistening surface. The trichome stalks are persistent, but the shield is often absent and may fall off with minor abrasion. The peltate trichomes can be observed on most floral and vegetative parts of *Shuaria*. Their density is highest on the abaxial leaf surface where they form a matted indumentum.

Inflorescence Structure—The inflorescence structure in *Shuaria* is in general agreement with Gesneriaceae (pair-flowered cymes), but uncommon in the tribe Beslerieae for having a well-developed peduncle and a noncondensed dichasial branching of the cyme. Most species in the Beslerieae have inflorescences in which the flowers are strongly congested. The dense flower clusters may be positioned on elongate peduncles (e.g. *Gasteranthus corallinus* (Fritsch) Wiehler, bearing a cluster of 4–6 (-16) flowers on a long peduncle) or, by extreme shortening of the peduncle, be sessile in the leaf axils (e.g. *Besleria lutea* L.). Other species of *Gasteranthus* and *Besleria* have single axillary flowers (in a phylogenetic context, these single flowers are derived from pair-flowered cymes by reduction).

The greatest resemblance of the inflorescences of *Shuaria* is perhaps with *Anetanthus gracilis* Hiern, in which the axillary inflorescences have also an elongate peduncle and are not condensed. However, here only the first branching seems to be dichasial, while the subsequent ones are monochasial (the inflorescences thus representing “double cincinni” in contrast to the compound dichasia of *Shuaria*). In one undescribed species of *Anetanthus* from Ecuador the cyme is reduced to a single axillary flower (Clark, in prep.).

Shuaria and *Tylopsacas* inflorescences are superficially similar because the cyme units are not strongly condensed. However, in *Tylopsacas* the pair-flowered cymes are unilateral (many flowered cincinni, in contrast to dichasial cymes in *Shuaria*) and their development may be similar as in *Monophyllaea* R. Br. and *Epithema* Blume (described by Weber 1975, 1988, 1995), with a permanent apical meristem producing unit primordia (from which flower pairs develop) in an alternate manner. The inflorescence structure of *Shuaria* is more typical of other Gesneriaceae and the presence of an elongate peduncle and noncondensed lateral cyme units is symplesiomorphic.

A conspicuous character that differentiates the inflorescence of *Shuaria* from that of *Sanango* and *Peltanthera*, is the absence of bracteoles (prophylls, often simply referred to as bracts) within the cyme. The absence of bracteoles has been regarded as a defining character for the tribe Beslerieae (Wiehler 1983; Weber 1995, 2004), but its importance at tribal level was questioned by Skog and Kvist (2002) in their description of *Cremospermopsis*. This genus appears much like *Cremosperma*, but has bracteoles within the cyme. Skog and Kvist (2002), therefore, refrained from assigning *Cremospermopsis* to the Beslerieae because it would be the only genus with bracteoles, but they also emphasized that tribal boundaries for Beslerieae based primarily on the absence or presence of bracteoles was conjectural. Recent classifications have included *Cremospermopsis* as a member of the tribe Napeantheae (Skog and Boggan 2006). The phylogeny presented here strongly supports ebracteate inflorescences as a synapomorphy for the Beslerieae.

Fruit Morphology—Despite extreme differences in habit between *Shuaria*, *Tylopsacas*, and *Anetanthus*, these three genera share a fruit character that is rare in the New World members of the Gesneriaceae. All three genera have a dry capsular fruit with septicidal dehiscence (Fig. 4F). It is ambiguous

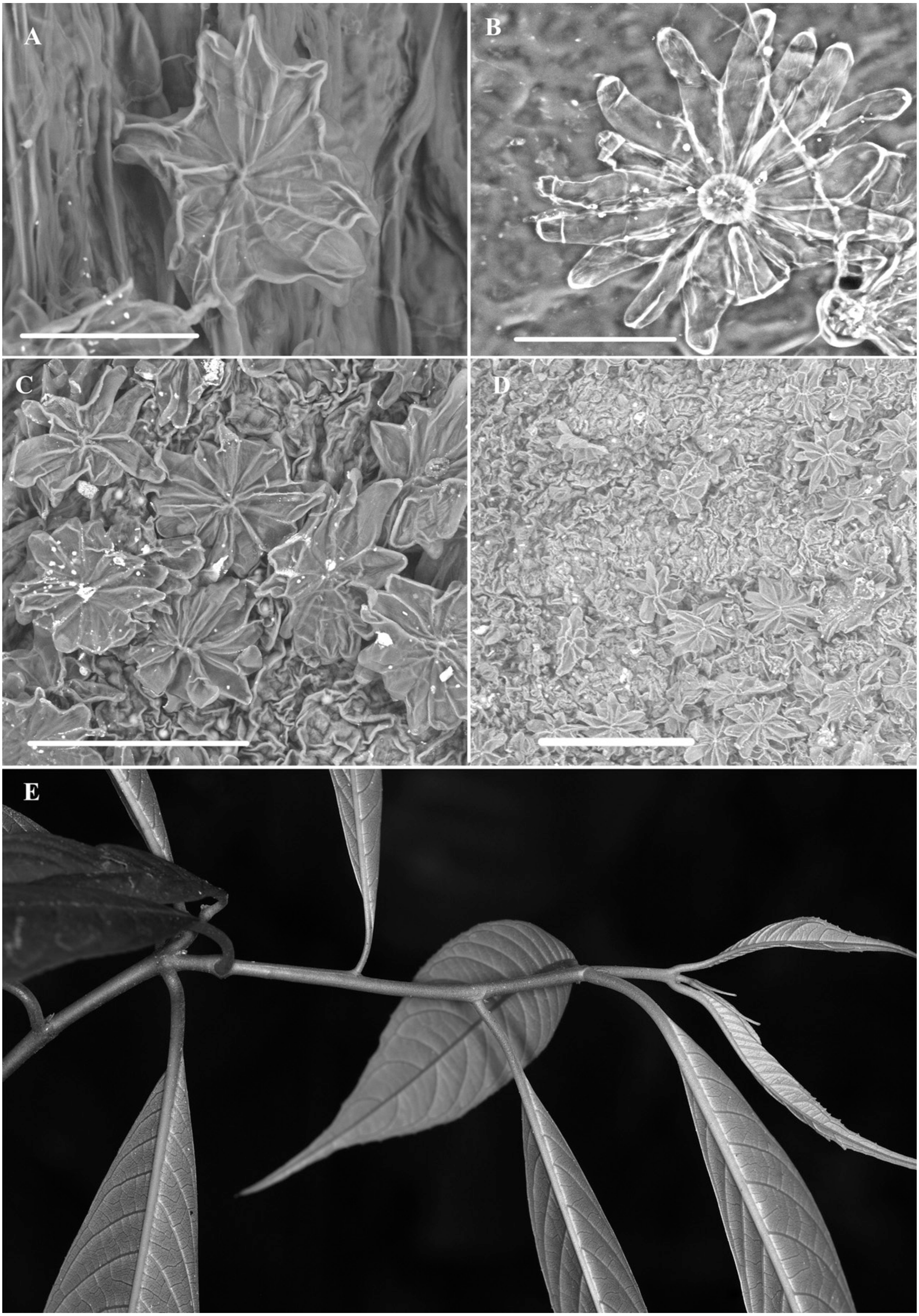

Fig. 3. SEM photographs of trichomes and phyllotaxy of *Shuaria*. A. Trichome on pedicel of immature fruit (*D. A. Neill 15912*); B. Trichome on adaxial leaf surface (*H. van der Werff 21704*); C. Outer surface of lower sepal (*D. A. Neill 15912*); D. Outer surface of median petal (*D. A. Neill 15912*); E. Apex of leafy branching shoot showing phyllotaxy changing from alternate at base then opposite then alternate then opposite near apex (*J. L. Clark et al. 10825*). Scale bars for A & B = 50 µm, scale bar for C = 100 µm, scale bar for D = 150 µm.

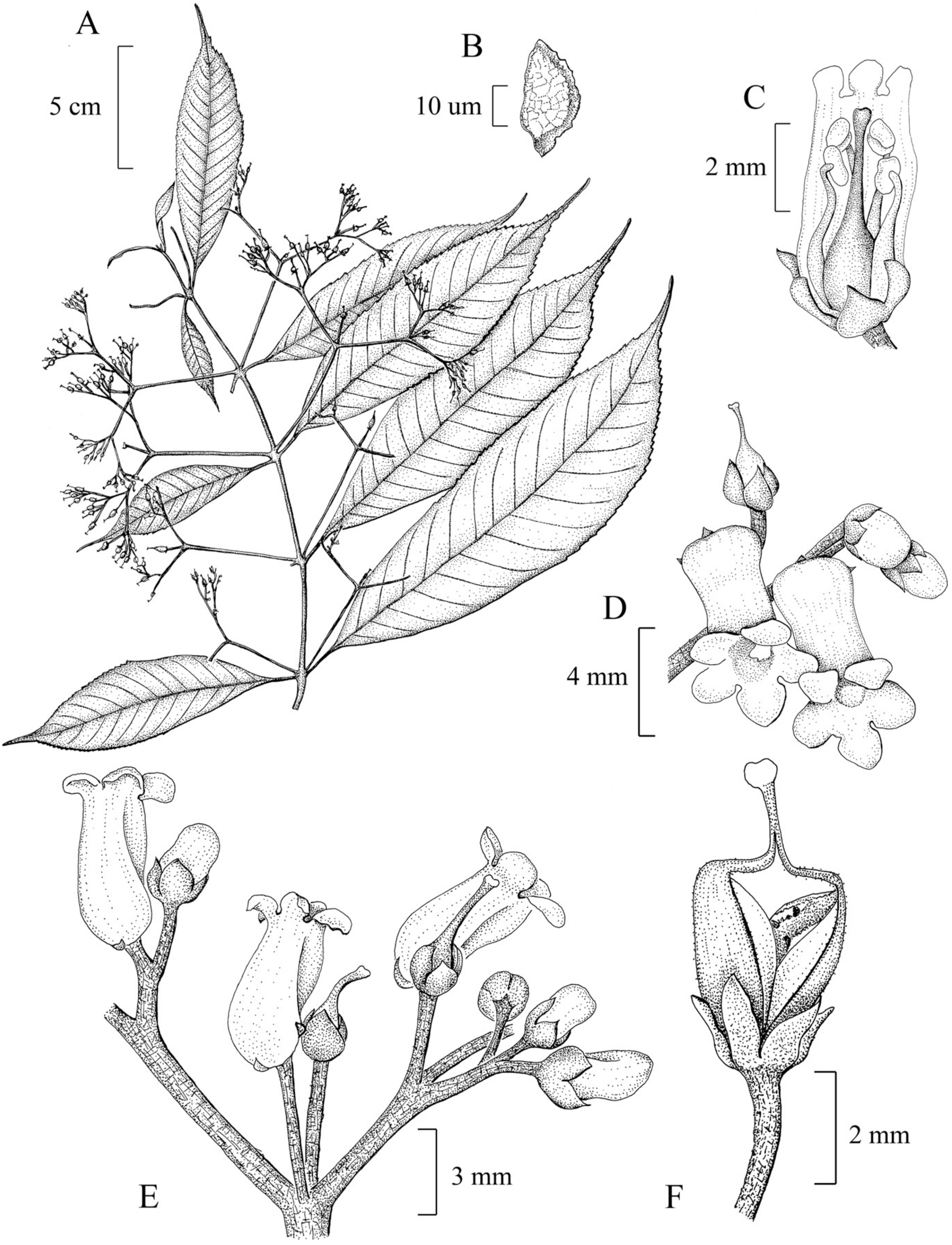

FIG. 4. *Shuaria ecuadorica.* A. Flowering branch showing axillary inflorescences with repeated dichasial branching; B. Seed with reticulate surface; C. Opened flower showing stamens and pistil; D. Portion of cyme with open flowers; E. Portion of cyme showing dichasial and subsequently monochasial branching with paired flowers; F. Mature capsule (lateral view) showing septicidal dehiscence and persistent style (A: *Morales 1922*; B & C: *Neill 13180*; D & F: *Fuentes 1171*; E: *Palacios 12109*).

whether septicidal dehiscence is plesiomorphic (relictual) or derived in this group. In the Didymocarpoid Gesneriaceae septicidally dehiscent capsules are only found in some clades of the "Basal Asiatic and European genera" (*Corallodiscus* Batalin, *Haberlea* Friv., *Ramonda* Rich., etc.) and are thought to be plesiomorphic (Weber 2004). Other genera in the Beslerieae have either indehiscent fleshy berries (*Besleria* L.) or semifleshy to fleshy capsules that split loculicidally. Apart from indehiscent fleshy berries in *Besleria*, the standard fruit type in the tribe Beslerieae is a laterally compressed capsule that dehisces loculicidally with two reflexing valves. In some cases, fruits split loculicidally and then secondarily septicidally with four valves as seen in *Gasteranthus calcaratus* subsp. *oncogastrus* (Hanst.) L. E. Skog & L. P. Kvist (Skog and Kvist 2000). A third type of fruit dehiscence in the Beslerieae is a capsule that splits irregularly (e.g. *Cremosperma muscicola* L. P. Kvist & L. E. Skog). Field observations and photographs of *Cremosperma muscicola* (*J. L. Clark 6328*) from northwestern Ecuador suggest that in some individuals the capsule is actually four-valved instead of splitting irregularly as reported by Kvist and Skog (1988). Careful field observations documented by photographs suggest that other species of *Cremosperma* Benth. also have four-valved capsules. It is likely that the fruits of *Cremosperma* are similar to those of some *Gasteranthus* species where the fruits first split loculicidally and then secondarily septicidally (Skog and Kvist 2000). The fruit dehiscence in *Reldia* Wiehler is a dry bivalved capsule that splits loculicidally (Kvist and Skog 1989). The fruit dehiscence in *Napeanthus* Gardn. is two-valved and loculicidal and when four-valved it is loculicidal and septicidal (Leeuwenberg 1958). An interesting note regarding four- and two-valved capsules was given by Wiehler (1976) where he documented that the fruit dehiscence in *Anetanthus* is definitely septicidal, but occasionally a small tear or slit is produced at the apex of the capsule. These small tears in the apex of the capsule will occasionally further develop and give the capsule the appearance of dehiscing loculicidally. Whether or not this occurs in species of *Napeanthus*, *Gasteranthus*, and *Cremosperma*, which are said to have capsules with irregular or four-valved dehiscence, will need to be carefully evaluated in future studies.

Seed Morphology—An interesting character shared by *Anetanthus* and *Tylopsacas* is the presence of winged seeds. The round and flat seed with developed wings is unique in the Gesneriaceae. Wiehler (1976), therefore, suggested a close relationship of the two genera. The distinctive winged seed with pustulate surface of *Tylopsacas cuneatum* was illustrated by Ivanina (1965) and SEM images were presented by Beaufort-Murphy (1983). The winged seeds of *Anetanthus gracilis* were illustrated by Wiehler (1976) and similar seeds of *A. rubra* L. E. Skog were illustrated by Skog (1982).

The seeds of *Shuaria* are not winged and of the usual small size and form. The surface is reticulate whereas most seed surfaces in the New World Gesneriaceae are striate, with long and narrow, slightly or tightly spirally arranged cells. Reticulate seed surfaces frequently occur in the paleotropical Gesneriaceae, especially in the basal clades, but also in *Streptocarpus* Lindl. subg. *Streptocarpus* and *Didymocarpus* Wall. In the New World a reticulate seed surface is uncommon, but documented in some species of *Cremosperma* (Beaufort-Murphy 1983).

Shuaria, Peltanthera, and Sanango—One feature that is superficially similar in *Shuaria* and *Peltanthera* is the anther that, upon dehiscence, appears peltate (from whence the generic name *Peltanthera*). But otherwise the reproductive structures of these two genera are rather different: the inflorescence of *Peltanthera* is a many-flowered compound panicle, distinct from the thryse made up of pair-flowered cymes in *Shuaria*. Moreover, *Peltanthera* has five rather than four stamens and a loculicidally, not septicidally dehiscent capsule. Norman (2000) suggested that morphological evidence is equivocal as to whether *Peltanthera*, like *Sanango*, should be transferred to Gesneriaceae, or remain in Buddlejaceae even though this is not consistent with other studies that support a close relationship with the Gesneriaceae (Oxelman et al. 1999; Bremer et al. 2002; Wang et al. 2004).

Future Taxon Sampling—Absent from the current molecular analyses are *Resia* H. E. Moore and *Cremospermopsis* L. E. Skog & L. P. Kvsit. *Resia* is a poorly known and rarely collected genus of two species from Colombia and Venezuela (Skog and de Jesús 1997). *Cremospermopsis* (Skog and Kvist 2002) is a genus of two species restricted to the humid forests in the Colombian departments of Antioquia and adjacent Bolívar. A third species of *Cremospermopsis* was recently discovered in the lowlands of northern Peru (I. Salinas, Pers. Comm.). Both of these genera have species with bracteate inflorescences and including them in future studies will allow for a more accurate assessment of the Beslerieae and Napeantheae. More taxon sampling is essential for *Anetanthus* because some species have bracteoles (e.g. *A. gracilis*) and others lack bracteoles (e.g. *Anetanthus* sp. used for this study).

Phylogenetic Relationship of Napeantheae and Beslerieae—One important result of the phylogeny presented here is the lack of support (Fig. 2; Bayesian inference) or unresolved relationship (Fig. 1; parsimony) for a sister group relationship between the tribes Napeantheae and Beslerieae. Phylogenetic studies that included taxa from these two tribes consistently supported them as sister-groups. Smith (2000) included fourteen species from the Beslerieae, four species from the Napeantheae, and representatives from all tribes within the Gesnerioideae using the cpDNA marker *ndhF*. Smith (2000) strongly supported a sister-group relationship between Napeantheaee and Beslerieae (Bremer support of 10 and bootstrap value of 95). Other phylogenetic studies using the same three samples of Beslerieae and a single species of Napeantheae (Zimmer et al. 2002; Roalson et al. 2005, 2008) suggest a sister-group relationship between Napeantheae and Beslerieae with bootstrap values ranging from 68–70. Smith et al. (2004) did not recover a sister-group relationship using two species for each tribe based on a phylogeny using the floral symmetry gene *CYCLOIDEA*. The relationship of the Napeantheae and Beslerieae will need to be assessed more carefully as many of these studies lack sufficient taxon sampling (Zimmer et al. 2002; Roalson et al. 2005, 2008) or they were based on genes (e.g. *ndhF*) with limited variability (Smith 2000).

Taxonomic Treatment

Shuaria ecuadorica D. A. Neill & J. L. Clark, gen. et sp. nov.—TYPE: ECUADOR. Zamora-Chinchipe, Cantón El Pangui, Cordillera del Cóndor region, Río Wawaime watershed, tributary of Río Quimi, below site of proposed EcuaCorriente copper mine, on ridge near 1-ha forest inventory "Wawaime Plot", tall cloud forest on ridge, on substrate of mixed sand and clay soil, below sandstone plateau, 1,130 m, 3°34′18″S 78°26′46″W, 22 Sep 2007 (fl, fr), *D. A. Neill, C. Davidson & S. Christoph*

15912 (holotype: QCNE!; isotypes: AAU!, F!, GB!, HA!, K!, LOJA!, NY!, MO!, P!, QCA!, UNA!, US!, USM!).

Hoc genus et species a ceteris Gesneriaceis combinatione characterum sequentium distinguitur: habitu arborescente, foliis oppositis interdum cum foliis alternis mixtis, partibus floralibus vegetativisque trichomatibus lepidotis vestitis, capsulis septicide dehiscentibus atque cymis pedunculatis et dichasialibus.

Small tree 3–5 (-8) m tall, with trunk to 6 cm DBH, frequently with multiple trunks arising from the tree base; young stems puberulent. Leaves opposite and decussate, sometimes mixed with alternate leaves, nearly isophyllous when opposite; petiole 5–15 mm long, shallowly sulcate, glabrous; blade (6.0-) 9.5–19.0 cm long, (1.0-) 1.5–5.0 cm wide, narrowly oblong to elliptic, sometimes slightly falcate, base acute and often oblique, apex acuminate, margins serrulate to serrate with glandular teeth separated at intervals of ± 4–5 mm; abaxially with sparse, unbranched single-celled trichomes; abaxially and adaxially with stellate trichomes with radii that are connected by webbing forming a shield-like scale, lateral veins 9–14 per side. Inflorescences emerging from the upper foliage leaves, pair-flowered dichasial cymes with 2–4 orders of branches, bracteoles (bracts within the cyme) lacking, flower number per inflorescence from 6–16; peduncle 3–6 cm long; axes of lateral cyme units 1.0–2.5 cm long; pedicels 3–5 mm long. Calyx uniformly light green, of five equal lobes, 1.5–2.5 mm long, 0.4–0.5 mm wide at base, broadly triangular, slightly connate at the base and attenuate at apex. Corolla uniformly white, tubular, gibbous at the base and shallowly pouched on the ventral side, corolla posture perpendicular relative to the calyx at anthesis, tube 4–7 mm long, to 2 mm wide, limb of five equal, rounded lobes, lobes to 1 mm long and 1 mm wide, reflexed at anthesis, inner corolla tube on upper half with gland-tipped unbranched trichomes. Androecium with four fertile subequal to didynamous stamens, filaments broad and flattened near the base, adnate to the base of the corolla tube for 1–2 mm, staminode present, half as long as the fertile filaments; anthers included, the 4 anthers connate prior to anthesis and separating at anthesis, appearing peltate after anthesis. Nectary absent. Gynoecium unilocular, ovoid with a broad base and a tapering apex, transgressing into the style, the style extending to near the mouth of the corolla tube, even with the anthers, stigma bilobed. Fruit a bivalved dry capsule, septicidally dehiscent, with a long persistent style and often tearing from the base by the splitting of the valves. Seeds numerous, minute, elliptic, surface reticulate, less than 1 mm long.

Additional Specimens Examined—ECUADOR. Morona-Santiago: Cantón San Juan Bosco, Cordillera del Cóndor, valle del Río Coangos, Río Tsurim entre los centros Shuar de Numpatkain y Banderas, 1,100 m, 3°20′44″S 78°14′08″W, 21 Oct 1999 (fl, fr), *P. Fuente et al. 1171* (MO, QCNE, UNA); Cantón Limon Indanza, Cordillera de Huaracayo, east of Cordillera del Cóndor and Río Changos, forest on sandstone ridge, east of Shuar village of Tinkimints, 1,600 m, 3°15′51″S 78°11′30″W, 24 Mar 2001 (fl, fr), *D. A. Neill & J. Manzanares 13180* (MO, QCNE, UNA, US); Cordillera del Cóndor, cumbre del Cerro Chikichiki Naint a 4 km al sureste del centro Shuar Warints, 1220 m, 3°10′13″S 78°14′33″W, 9 Oct 2002 (fr), *G. Toasa 8955* (MO, QCNE, UNA). Pastaza: Cantón Arajuno, campamentos temporales 9, 22 y 25, línea propuesta del oleoducto Villano-CPF por ARCO, km 25 noroeste del pozo Villano 2, 700 m, 1°27′S 77°36′W, 3–14 Sep 1988 (fl, fr), *E. Freire & L. Santi 3352* (MO, QCNE, US); Cantón Pastaza, Pambayacu, Río Lliquino, 420 m, 1°29′S 77°22′ W, 7–10 May 1992 (fl), *W. Palacios 10144* (MO, QCNE, US); km 17 del propuesto oleoducto ARCO Villano-El Triunfo, 600 m, 1°31′S 77°30′W, 25 Feb 1994 (fr), *W. Palacios 12109* (MO, QCNE, US); Los Vencedores, Estación Experimental Pastaza ESPOCH, 800–1000 m, 1°30′S, 77°56′W, 1 Sep 1995 (fl), *R. Pinus et al. RBS-0017* (CHEP, QCNE). Zamora-Chinchipe: Cantón El Pangui, parroquia Tundayme, Cordillera del Cóndor region, Terreno de Ecuacorriente S. A. copper mine development, trail Piloto, 6–8 km S of mine headquarters, 1,291 m, 3°35′51″S 78°25′57″W, 15 May 2009 (fl), *J. L. Clark et al. 10825* (AAU, F, K, MO, NY, QCNE, SEL, UNA, US, W); Cantón El Pangui, Cordillera del Cóndor region, vicinity of EcuaCorriente copper mine development, valley of Río Wawaime, 8.1 km S of mine headquarters on road to mine site, 1,291 m, 3°35′51″S 78°25′57″W, 7 Apr 2006 (fr), *T. B. Croat et al. 96736* (MO, QCNE, UNA); vicinity of Río Zamora and village of Quimi, along road from military post to Cóndor Mirador military outpost, ca. 3.5 km S of junction in road to Tundayme, San Marcos and EcuaCorriente copper mine headquarters, 1,135 m, 3°26′21″S 78°28′17″W, 12 Apr 2006 (fl, fr), *T.B. Croat 96979* (MO, QCNE, UNA); Parroquia Tundayme, valle del Río Quimi, 970 m, 3°33′07″S 78°26′59″W, 6 Oct 2006 (fl, fr), *C. Morales & D. Reyes 1922* (MO, QCNE); *C. Morales & D. Reyes 1951* (MO, QCNE); cuenca del Río Wawaime, propiedad de la empresa EcuaCorriente, 970 m, 3°33′07″S 78°26′59″W, 6 Oct 2006 (fr), *D. Reyes & C. Morales 1191* (MO, QCNE, UNA); *D. Reyes & C. Morales 1197* (MO, QCNE, UNA); Río Wawaime watershed, tributary of Río Quimi, along road above EcuaCorriente mine camp, 1,300 m, 3°34′43″S 78°26′07″W, 26 Oct 2006 (fl), *H. van der Werff et al. 21704* (LOJA, MO, QCNE, UNA); Río Wawaime watershed, tributary of Río Quimi, tall forest on ridge, with mixed sand/clay soil, above "Wawaime Plot", 1-hectare forest inventory plot on same ridge, EcuaCorriente copper mine concession, 1,230 m, 3°34′27″S 78°26′40″W, 1 May 2008 (fl, fr) *D. Neill et al. 16363* (LOJA, MO, QCNE, UNA); Cantón Nangaritza, Parroquia Guayzimi, Cordillera del Cóndor, camino al hito de Pachicutza desde el campamento militar, 1,050–1,100 m, 4°07′S 78°37′W, 17 Oct 1991, *C. Cerón et al. 16759* (MO, QCNE, UNA); Río Nangaritza, Pachicutza, camino al hito de Pachicutza, 900–1,000 m, 4°07′S 78°37′W, 18 Oct 1991 (fr), *W. Palacios & Exp. Tratado Cooperación Amazónica 8192* (MO, QCNE, UNA, US); Miazi, sendero hacia el hito, 900–1,200 m, 16 Oct 1991, *J. Jaramillo 13947* (MO, QCA); cuenca alta del Río Nangaritza, Centro Shuar Shaime, por la unión de los Ríos Nangaritza y Numpatakaime, sitio La Wantza, 900 m, 4°18′49″S 78°40′56″W, 15 Oct 2002 (fl), *W. Quizhpe et al. 413* (LOJA, MO, QCNE, UNA).

Etymology—The generic name is based on the name of the Shuar indigenous ethnic group of Amazonian Ecuador, who now comprise a population of about 110,000. The ancestral Shuar territory in Pastaza, Morona-Santiago and Zamora-Chinchipe provinces corresponds quite closely to the known range of *Shuaria ecuadorica*, and several of the collections were made in forests owned by rural Shuar communities. The specific epithet refers to the country of origin, Ecuador, to which the species is endemic, as far as its geographical distribution is presently known.

Distribution and Habitat—*Shuaria ecuadorica* is known from the provinces of Pastaza, Morona-Santiago, and Zamora-Chinchipe, Ecuador, in lowland Amazonian tropical wet forest, and in lower montane cloud forest on the western slopes of the Cordillera del Cóndor, with an elevation range for all known populations from 420 m to 1,600 m. In the western Amazonian peneplain of Pastaza province, *Shuaria ecuadorica* occurs on dissected, hilly terrain, mostly along well-drained ridge tops. Soil types were not included in the collection labels on the specimens from lowland Amazonia at 420–700 m in Pastaza province. On the slopes of the Cordillera del Cóndor in Morona-Santiago and Zamora-Chinchipe provinces, it occurs at 900–1,600 m elevation on mixed sand and clay soil, derived in part from the nutrient-poor Hollín sandstone formation, but primarily on slopes below the sandstone plateau where the sand is eroded from above, rather than on pure crystalline sandstone substrate. The species grows as a small tree in the shaded understory of primary forest. It sometimes occurs in rather dense understory populations, as at the type locality in the Río Quimi watershed, of 30 or more individuals in an area of about 0.1 ha (1,000 m^2) with most mature trees in the population in flower simultaneously. It has not yet been recorded from the eastern slopes of the Cordillera del Cóndor in the department of Amazonas, Peru, but several of the Ecuadorian localities are less than 10 km from the

Ecuador-Peru border that follows the crest of that sub-Andean mountain range.

Phenology—Collected in flower in March, May, September, and October. Collected in fruit in February, March, April, September, and October.

Conservation and IUCN Red List category—This species has not been found in any formally protected area in Ecuador. It occurs in dense local populations of 30 or more reproductive adults, but these populations are widely scattered, and in large areas of the Cordillera del Cóndor region with appropriate habitat where intensive botanical inventories have been conducted, *Shuaria ecuadorica* has not been found. Deforestation in the region continues for the establishment of cattle pastures and subsistence crops by colonists who have migrated from more populated areas of Ecuador. In general, this species is better protected in lands within its geographical distribution owned by indigenous Shuar communities that maintain most of their territory as undisturbed forest. Some of the populations, including the type locality, may be eliminated by future mining operations, but the transnational mining companies that are beginning to operate in the region are developing plans to mitigate their environmental impacts, including set-asides and support for conservation of areas of similar habitat near the mining sites. More long-term impacts such as future climate change could threaten these small, scattered populations. According to the IUCN Red List criteria for estimated range, area of occupancy and population size (IUCN 2001), and considering the uncertain future of habitat conservation in most of its range *Shuaria ecuadorica* should be listed in the category NT (Nearly Threatened).

Key to the Genera Traditionally Recognized in the Tribes Napeantheae and Beslerieae, and Neotropical Genera not Currently Recognized in Assigned Tribes

1\. Trees, more than 3 m tall 2
2\. Bracts within the inflorescence absent. Corolla at anthesis perpendicular relative to the calyx; corolla zygomorphic . . . . *Shuaria*
2\. Bracts within the inflorescence partly present. Corolla at anthesis erect relative to the calyx; corolla nearly actinomorphic 3
3\. Stamens 5, exserted; anthers basifixed, 2-celled, after pollen shed walls recurving, the anthers thus becoming seemingly peltate and 4-celled; seed surface reticulate with narrow honey-comb-like wings . . . . *Peltanthera*
3\. Stamens 4, included; anthers basifixed, 2-celled, after pollen shed retaining their basifixed and 2-celled appearance; seed surface smooth and not winged . . . . *Sanango*
1\. Herbs to subshrubs, less than 3 m tall 4
4\. Leaves alternate, not in a basal rosette . . . . *Reldia*
4\. Leaves opposite, occasionally clustered in a basal rosette 5
5\. Fruit a berry . . . . *Besleria*
5\. Fruit a capsule 6
6\. Leaves congested in a basal rosette 7
7\. Petiole 5 cm or longer . . . . *Tylopsacas*
7\. Petioles less than 2 cm or blade sessile 8
8\. Peduncles elongate with sessile or reduced pedicels, inflorescence bracts present and well developed . . . . *Resia*
8\. Peduncles elongate with well-developed pedicels; inflorescence bracts reduced or absent . . . . *Napeanthus*
6\. Leaves evenly spaced on an elongate stem 9
9\. Conspicuous stomatal clusters present on the lower leaf surfaces . . . . *Gasteranthus*
9\. Conspicuous stomatal clusters absent on the lower leaf surfaces 10
10\. Inflorescence bracts present . . . . *Cremospermopsis*
10\. Inflorescence bracts absent 11
11\. Prostrate herb; seeds winged and flattened . . . . *Anetanthus*
11\. Erect herb; seeds not winged and narrowly elliptic . . . . *Cremosperma*

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APPENDIX 1. Taxa, GenBank accession numbers, (ITS, *trnL-F*; — = sequence not obtained), collection locality, and voucher specimen information with herbarium acronym in parentheses.

Ingroup. *Achimenes misera* Lindl., AY047067, AY047126, Cultivated (Central America), *L. E. Skog 7903* (US); *Aeschynanthus andersonii* C. B. Clarke, AY047040, AY047099, Cultivated (China, Myanmar, Thailand), *L. E. Skog 7777* (US); *Anetanthus* sp., GQ119595, —, Ecuador, *J. L. Clark 10003* (US); *Besleria aggregata* (Mart.) Hanst., GQ119596, GQ166796, Bolivia, *J. L. Clark 6790* (US); *Besleria angustiflora* Fritsch, GQ119597, GQ166797, Ecuador, *J. L. Clark 4575* (US); *Besleria gracilenta* C. V. Morton, GQ119598, GQ166798, Peru, *J. L. Clark 8202* (US); *Besleria ovalifolia* Rusby, GQ119599, GQ166799, Bolivia, *J. L. Clark 6852* (US); *Besleria variabilis* C. V. Morton, GQ119600, GQ166800, Ecuador, *J. L. Clark 5629* (US); *Cremosperma castroanum* C. V. Morton, GQ119601, GQ166801, Ecuador, *J. L. Clark 7104* (US); *Cremosperma nobile* C. V. Morton, GQ119602, GQ166802, Ecuador, *J. L. Clark 7143* (US); *Cremospsperma veraguanum* Wiehler, GQ119603, GQ166803, Panama, *J. L. Clark 8618* (US); *Episcia lilacina* Hanst., AY047091, AY047150, Cultivated (Colombia, Costa Rica, Nicaragua, Panama), *L. E. Skog 8132* (US); *Gasteranthus carinatus* Wiehler, GQ119604, GQ166804, Ecuador, *J. L. Clark 7502* (US); *Gasteranthus glaber* L. E. Skog & L. P. Kvist, GQ119605, GQ166805, Ecuador, *J. L. Clark 6130* (US); *Gasteranthus lateralis* (C. V. Morton) Wiehler, GQ119606, GQ166806, Ecuador, *J. L. Clark 7619* (US); *Gasteranthus leopardus* M. Freiberg, GQ119607, GQ166807, Ecuador, *J. L.*

Clark 6331 (US); *Gasteranthus wendlandianus* (Hanst.) Wiehler, GQ119608, GQ166808, Ecuador, *J. L. Clark 6421* (US); *Napeanthus apodemus* Donn. Sm., GQ119587, GQ166791, Panama, *J. L. Clark 8565* (US); *Napeanthus riparius* Philipson, GQ119588, GQ166792, Ecuador, *J. L. Clark 9157* (US); *Napeanthus robustus* Fritsch, GQ119589, GQ166793, Ecuador, *J. L. Clark 5651* (US); *Napeanthus rupicola* Feuillet & L. E. Skog, GQ119590, GQ166794, Guyana, *H. D. Clarke 10351* (US); *Napeanthus subacaulis* (Griseb.) Benth & Hook. f. ex Kuntze, GQ119591, GQ166795, Venezuela, *J. L. Clark 6898* (US); *Reldia* sp., GQ119609, GQ166809, Ecuador, *J. L. Clark 8835* (US); *Reldia minutiflora* (L. E. Skog) L. P. Kvist & L. E. Skog var. *minutiflora,* GQ119610, GQ166810, Ecuador, *J. L. Clark 8017* (US); *Reldia minutiflora* var. *veraguensis* (Wiehler) L. P. Kvist & L. E. Skog, GQ119611, GQ166811, Panama, *J. L. Clark 8619* (US); *Rhytidophyllum exsertum* Griseb., AY047055, AY047114, Cultivated (Cuba), *L. E. Skog 8050* (US); *Sinningia cooperi* (Paxt.) Wiehler, AY047082, AY047141, Cultivated (Brazil), *L. E. Skog 7808* (US); *Streptocarpus primulifolius* Gand., AY047039, AY047098, Cultivated (South Africa), *L. E. Skog 7868* (US); *Tylopsacas cuneatum* (Gleason) Leeuwenb., GQ119592, GQ166814, Guyana, *K. M. Redden 1460* (US); *Shuaria ecuadorica* D. A. Neill & J. L. Clark, GQ119593, GQ166812, Ecuador, *D. A. Neill 15912* (MO); *Shuaria ecuadorica* D. A. Neill & J. L. Clark, GQ119594, GQ166813, Ecuador, *D. A. Neill 13180* (MO).

Outgroups. *Peltanthera floribunda* Benth., GQ119585, GQ166789, Costa Rica, *B. Hammel 24426* (MO); *Sanango racemosum* (Ruiz & Pav.) Barringer, GQ119586, GQ166790, Cultivated (Ecuador), *J. L. Clark 8863* (US).