



## Phylogenetic affinity of an enigmatic Rubiaceae from the Seychelles revealing a recent biogeographic link with Central Africa: gen. nov. *Seychellea* and trib. nov. Seychelleae

Sylvain G. Razafimandimbison<sup>a,\*</sup>, Kent Kainulainen<sup>b</sup>, Bruno Senterre<sup>c,d,e</sup>, Charles Morel<sup>f</sup>, Catarina Rydin<sup>g,h</sup>

<sup>a</sup> Department of Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

<sup>b</sup> Gothenburg Botanical Garden, Carl Skottbergs Gata 22A, SE-41319 Gothenburg, Sweden

<sup>c</sup> Plant Conservation Action Group, P.O. Box 392, Victoria, Mahé, Seychelles

<sup>d</sup> Island Biodiversity & Conservation Centre, Associated with the University of Seychelles, Anse Royale, Mahé P.O. Box 1348, Seychelles

<sup>e</sup> Evolutionary Biology & Ecology – CP 160/12, Université Libre de Bruxelles, 50 Av. F. Roosevelt, 1050 Bruxelles, Belgium

<sup>f</sup> Seychelles National Herbarium, Bel Etang Building, Mont Feuri, Seychelles

<sup>g</sup> The Bergius Foundation, The Royal Swedish Academy of Sciences, Box 50005, SE-104 05 Stockholm, Sweden

<sup>h</sup> Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden



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### ABSTRACT

The granitic islands of the Seychelles harbor about 268 native angiosperm species, with 28% being endemics there. The Seychelles biota contains a mix of ancient taxa with Gondwanan origins and young taxa that arrived there via dispersals. We investigate the phylogenetic position of an enigmatic, critically endangered, Seychellean endemic of the coffee family (Rubiaceae), *Psathura/Psychotria sechellarum*, and assess whether its presence on the granitic islands of the Seychelles is the result of vicariance or long-distance dispersal. Phylogenetic relationships of the family were reconstructed based on the Bayesian and maximum-likelihood phylogenetic analyses of sequence data from five plastid markers of 107 terminals. Divergence times were estimated using a Bayesian-based method. *Psathura/Psychotria sechellarum* is distantly related to *Psychotria* s.l. (including *Psathura*), and is strongly supported as sister to the Central African genus *Coltoecema*. Their striking morphological differences, coupled with their geographic separation and genetic distinctness, support the recognition of the new genus *Seychellea* and new tribe Seychelleae to accommodate the Seychellean species. The *Coltoecema-Seychellea* clade constitutes an early-divergent lineage in the subfamily Rubioideae, with an old stem and a young crown ages estimated to be in the Late Cretaceous and late Oligocene-early Pliocene, respectively. *Coltoecema* diverged from *Seychellea* in the late Oligocene-early Pliocene and their respective crown ages are inferred to be late Miocene-middle Pleistocene and Pleistocene, respectively. The ancestor of the two genera was likely present in Africa, and reached the Seychelles via avian dispersal. Unlike *Coltoecema* with three species, *Seychellea* is monospecific, with very few individuals left in the wild. The species should be a top candidate for conservation priority, as its extinction would cause loss of genetic diversity of this entire lineage.

### 1. Introduction

The Seychelles archipelago (widely known as the Seychelles) is situated about 1100 km northeast of Madagascar and 1600 km east of Africa, and is formed by granitic and coralline islands of various sizes and ages. The coralline islands of the Seychelles are of young volcanic origins, while the granite islands (hereafter called granitic Seychelles, encompassing 42 islands) and Madagascar are Gondwanan fragments of

the Indigascar landmass that were joined with India until about 90 Ma (e.g., Plummer and Belle, 1995; McLoughlin, 2001). East Gondwana, formed by the Indigascar, Antarctica, and Australia, split from Africa ca. 160 Ma (Royer and Coffin, 1992), and subsequently broke up 160–120 Ma (Storey, 1995; Storey et al., 1995; Reeves, 2014). India-Seychelles began to split from Madagascar 90–88 Ma and the separation of India and the Seychelles was estimated to have been completed about 65 Ma (e.g., Stephens, 1996). Like India and Madagascar, the present

\* Corresponding author.

E-mail address: [sylvain.razafimandimbison@nrm.se](mailto:sylvain.razafimandimbison@nrm.se) (S.G. Razafimandimbison).

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biota of the Seychelles harbors a mix of ancient taxa with Gondwanan origins [e.g., the Seychellean frog family Sooglossidae, Biju and Bossuyt, 2003; the Seychellean fern species of the genus *Nesolindsaea* Lehtonen & Christenh. (Lindsaeaceae), Lehtonen et al., 2010] and young taxa that arrived there via dispersals (e.g., Seychellean, monospecific genus *Paragenipa* Baill., Seychellean species of *Craterispermum* Benth. and *Psychotria* L., all Rubiaceae, Kainulainen et al., 2017; Razafimandimbison et al., 2017).

The granitic Seychelles are home to a great diversity of tropical forests (Senterre & Wagner 2014) with relatively low species diversity but high level of endemism (Friedmann, 1994; Kueffer, 2014). They harbor 268 native flowering plant species (Senterre et al., 2013) representing 216 genera. At least 13 genera are endemic to the granitic Seychelles and 12 of them are monospecific. All these endemic genera are listed among the most threatened plants of the Seychelles (Friedmann, 1994). Twenty-eight percent of the 268 species are endemic and about 35% are threatened, with two to five species reported to be extinct (e.g., Baider et al., 2010). Population fragmentation due to past habitat destruction and the spread of invasive alien species are the main threats for the plant diversity of the Seychelles (Fleischmann, 1997; Baider et al., 2010), with only about 12.5% of its natural habitats left (B. Senterre, unpubl. data). The enigmatic *Psathura sechellarum* Baker (Rubiaceae), endemic to the granitic islands of Mahé and Silhouette with unsettled taxonomic position, has been listed among the 10 most threatened angiosperm species in the Seychelles, with fewer than 50 individuals known (e.g., Ismail et al., 2011). The species has not previously been included in any phylogenetic analysis and molecular data have never been produced from it.

*Psathura sechellarum* (Fig. 1) was originally classified by Baker (1877) in the Western Indian Ocean genus *Psathura* Comm. ex Juss., and subsequently transferred to the pantropical genus *Nonatelia* Aubl., as *N. sechellarum* (Baker) Kuntze by Kuntze (1891), both based on its fleshy drupaceous fruits with five to six carpels (Fig. 1E and F). Summerhayes (1931) considered it to be part of the highly species-rich pantropical genus *Psychotria* L. on the basis of its fleshy fruits and pyrene number and texture. Despite its unsettled generic position, the species has always been classified in the tribe Psychotrieae of the subfamily Rubioideae. Recently, all the Mascarene and Malagasy *Psathura* species were transferred to *Psychotria* as a result of the molecular phylogenetic study by Razafimandimbison et al. (2014). These latter findings were seen as supporting the early transfer of *P. sechellarum* to *Psychotria* by Summerhayes (1931). In a subsequent study, the Seychellean species of *Psychotria* were inferred to have originated as the result of a single long-distance dispersal from Madagascar during the Miocene-Pliocene (Razafimandimbison et al., 2017). Given the current placement of *P. sechellarum* in *Psychotria* it would be reasonable to assume that this species is part of the Seychellean *Psychotria* lineage (cf. Razafimandimbison et al., 2014). However, material of *Psathura/Psychotria sechellarum* is scarce and the hypothesis has never been tested.

The main objectives of the present study are to rigorously assess the phylogenetic position of *P. sechellarum* based on new collections of the plant and investigate when and how its ancestor(s) reached the Seychelles. The conservation implications of our findings are discussed and taxonomic adjustments are presented.

## 2. Material and methods

### 2.1. Taxon sampling, molecular laboratory procedures, and morphological studies

A total of 107 terminals, including three newly collected specimens of *Psathura sechellarum* from the Mahé Island, were sampled for our study. All currently recognized tribes of the subfamily Rubioideae (except the monogeneric tribe Putorieae of the Spermaceae alliance) were represented and seven terminals from the other Gentianales families were selected to root the trees. All studied taxa are summarized in Appendix A. Additional material of *P. sechellarum* housed at the Herbaria P, S, and SEY

(see the additional specimens listed under “Taxonomic implications”) was studied morphologically, with particular emphasis on its general morphology (including the presence of raphides, stipule type and persistence, inflorescence position and type), the androecium and gynoecium of its flowers, and the pyrenes of its fruits.

DNA extraction and amplification were achieved following the protocols outlined in the following studies: Bremer and Manen (2000) for *atpB-rbcL* and *rbcL*; Oxelman et al. (1997) for *rps16*; Bremer et al. (1999) for *ndhF*; and Razafimandimbison and Bremer (2002) for *trnT-F*. The same primers as for PCRs were utilized for sequencing reactions. Samples were sent to Macrogen Europe (Amsterdam, the Netherlands) for sequencing.

### 2.2. Phylogenetic analyses

Sequences were aligned using Mafft v.7.402 (Katoh and Standley, 2013), and then manually adjusted in BioEdit (Hall, 1999). The protein-coding (*ndhF* and *rbcL*) and the noncoding plastid data (*atpB* spacer, the *rps16* intron, and *trnT-F* region) were treated as separated partitions. DNA substitution models were evaluated using MrAIC v.1.4.4 (Nylander, 2004; a script dependent on the program PHYML v.3.0; Guindon and Gascuel, 2003), and the GTR + I + G model was indicated as best-fit to the data for both partitions. Phylogenetic reconstructions were done by Bayesian Markov chain Monte Carlo inference (MCMC; Yang and Rannala, 1997), using the program MrBayes v.3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The combined data were analyzed with unlinked model parameter estimates for the two partitions (except for topology). The MCMC ran for  $20 \times 10^6$  generations (sampling every 1000th generation), of which the first 25% were excluded as burn-in. Corresponding analyses, using the same partitions and substitution models, were also done in a maximum likelihood (ML) framework using the program IQ-tree (Nguyen et al., 2015; Chernomor et al., 2016), with branch support assessed from results of 1000 standard bootstrap replicates.

### 2.3. Molecular dating analysis

Divergence times were estimated using BEAST 2.5.2 (Bouckaert et al., 2014), implementing the uncorrelated lognormal clock model and the birth-death tree prior (Gernhard, 2008). The root node was assigned a normally distributed age prior with a mean of 96 Ma and a standard deviation of 4.6 Ma; secondary calibration priors were similarly applied to the nodes representing the most recent common ancestor (mrca) of Rubiaceae ( $87 \pm 4.6$  Ma) and Rubioideae ( $75 \pm 4.6$  Ma), all strongly supported nodes. These age priors conform to the 95% highest posterior density (HPD) interval of corresponding nodes inferred in a study of Rubiaceae divergence times by Wikström et al. (2015). The BEAST analysis comprised six runs of  $50 \times 10^6$  generations sampled every 5000 generation. The first 25% of all samples were removed as burn-in, and Tracer 1.7.1 (Rambaut et al., 2018) was used to ensure that the effective sample sizes of the parameters were high ( $> 200$ ). Mean node ages and age density intervals were summarized on the sampled topology of the maximum product of clade credibilities. The MAFFT sequence alignment as well as the BEAST, IQ-tree, and MrBayes analyses were all performed on the CIPRES Science Gateway portal v.3.3 (Miller et al., 2010).

## 3. Results

### 3.1. Morphological studies

Below we report the results of our morphological investigations on *Psathura sechellarum* concerning the absence of raphides and its habit, stipule type and persistence, inflorescence position and type, the androecium and gynoecium of its flowers, and its fruit type and pyrenes. An updated, complete description of the Seychellean plant is presented



**Fig. 1.** *Psathura/Psychotria sechellarum* (= *Seychellea sechellarum*). A. Habit and its surrounding habitat. B. Fertile branch with red fleshy fruits. C. Fertile branch with floral buds and a single flower. D. Portion of an inflorescence with a longistylous flower. E and F. Infructescences with red fleshy fruits. Photos: A-B, D-F by Christopher Kaiser-Bunbury; C by Kent Kainulainen. (This figure is only shown in color in the online version of this article.)

below (under the section on “Taxonomic implications”).

*Psathura sechellarum* is a shrubby plant that does not contain raphides. The stipules are intrapetiolar, persistent, and are adaxially fused with the base of the petiole. The inflorescences are terminal, paniculate, biparous cymes, and are subtended by large, paired bracts at the top of the peduncle; the inflorescence axes are articulated, and composed of successive cyme units. The flowers are distylous, and bear five stamens, whose filaments are loosely attached to the corolla tube. The ovaries comprise five to six carpels and each locule contains a single, erect ovule. Finally, the fruits are globose drupes, red (when fully mature), and bear five to six, ribbed pyrenes.

### 3.2. Results of the molecular phylogenetic and dating analyses

Fig. 2 shows the 50% Bayesian majority consensus tree of Rubiaceae generated by MrBayes from the sequence data from *atpB-rbcL*, *ndhF*,

*rbcl*, *rps16* intron, and *trnT-F*, (the corresponding ML-topology from the IQ-tree analysis is shown in Appendix S1), while Fig. 3 depicts the maximum credibility (MCC) tree from the BEAST analysis. The overall topologies of these trees are similar to those found in previous studies of the family using an extensive sample of taxa (e.g., Rydin et al., 2009). The three samples of *Psathura sechellarum* formed a highly supported monophyletic group (BPP = 1, BS = 100%), which was strongly resolved as sister to the Central African genus *Colletocema* E.M.A Petit (Fig. 2, Appendix S1). The *Colletocema*–*Psathura sechellarum* clade was resolved as sister to a poorly supported large clade comprising the remaining Rubioideae (BPP = 0.94, Fig. 2; BS = 48%, Appendix S1). The estimated stem age of the *Colletocema*–*Psathura sechellarum* clade is 73.42 Ma (HPD: 80.26–66.31 Ma), corresponding to the Late Cretaceous. *Colletocema* diverged from *P. sechellarum* at 14.64 Ma (HPD: 27.15–5.09 Ma), corresponding to the late Oligocene–early Pliocene. The respective crown ages were inferred to be 3.2 Ma (HPD:

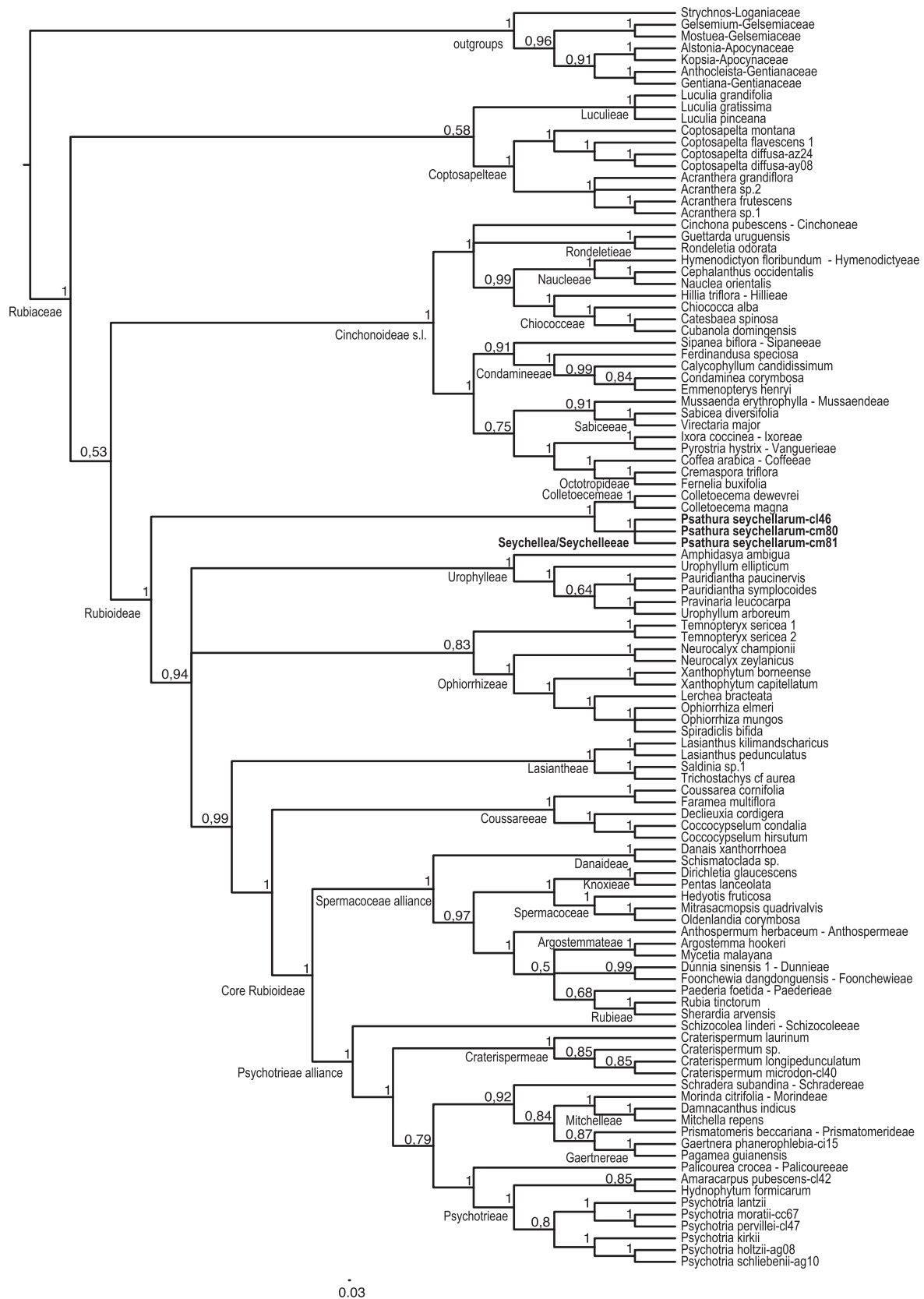
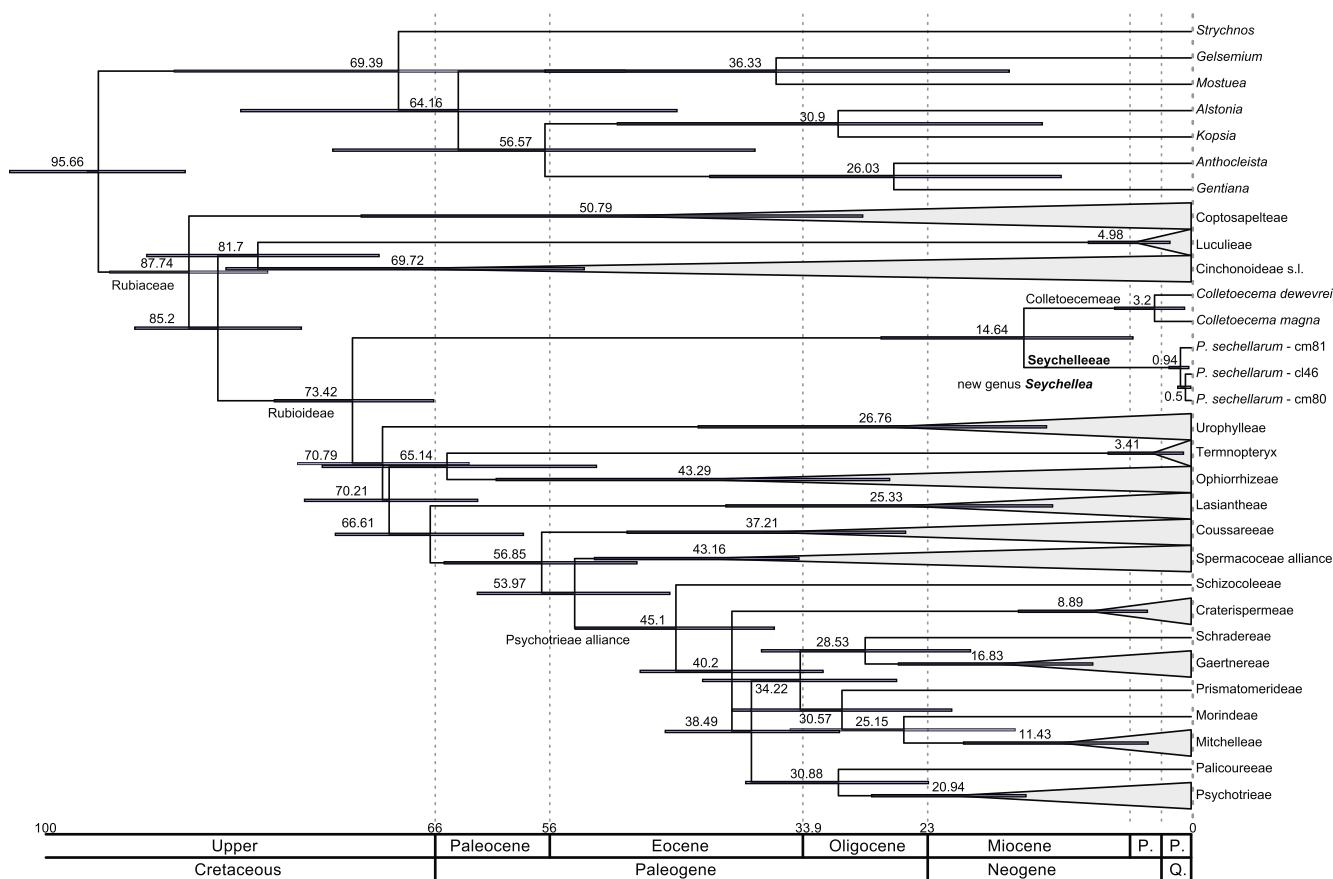


Fig. 2. Fifty-percent Bayesian majority-rule consensus tree of Rubiaceae (with focus on the subfamily Rubioideae) based on combined *atpB-rbcL/ndhF/rbcL/rps16/trnT-F* data from 107 samples. Values above nodes are Bayesian posterior probabilities.



**Fig. 3.** The maximum clade credibility (MCC) tree from the BEAST analysis of the combined Rubiaceae datasets. The tree is drawn as a chronogram calibrated against The Geologic Time Scale (Gradstein et al., 2012) and credibility intervals of the node age estimates are indicated by grey bars. Values above nodes are node ages (in million years).

6.7–0.57 Ma) for *Colletocecema* (corresponding to the late Miocene–middle Pleistocene) and 0.94 Ma (HPD: 1.94–0.2 Ma) for the three samples of *P. sechellarum* (corresponding to the Pleistocene) (Fig. 3).

#### 4. Discussion

##### 4.1. Phylogenetic position of the Seychellean plant and recognition of the new genus *Seychellea* and new tribe *Seychelleae*

The here detected clade comprising *Colletocecema*/Colletocemateae and the Seychellean endemic *Psathura*/*Psychotria sechellarum* is clearly among early-divergent lineages of the subfamily Rubioideae (Fig. 2), although precise phylogenetic relationships among the early-divergent groups of the subfamily remain unsettled (e.g., Manns et al., 2012; Rydin et al., 2017; the present study). The current inclusion of the Seychellean endemic in the tribe Psychotrieae [as member of the Western Indian Ocean genus *Psathura* (Baker, 1877), a genus now merged in *Psychotria* s.l. (Razafimandimbison et al., 2014), or specifically included in *Psychotria* as suggested by Summerhayes (1931)] is strongly rejected by the results of our study (Fig. 2, Appendix S1). This enigmatic Seychellean species has thus been erroneously classified in Psychotrieae for 142 years. The previous taxonomic decisions were based on the fact that this plant produces small, distylous flowers and drupaceous fruits, two characteristics of the tribe Psychotrieae (e.g., Andersson, 2002). However, distyly and fleshy fruits (including drupes) have evolved independently numerous times in Rubiaceae (e.g., Ferrero et al., 2012; Bremer and Eriksson, 1992, respectively). Further, *P. sechellarum* has a number of morphological features that markedly distinguish it from *Psychotria* s.l. sensu Razafimandimbison et al. (2014). In *Psychotria* s.l. and the other members of the Psychotrieae alliance

sensu Razafimandimbison et al. (2008, 2017) raphides are visible on vegetative parts, the stipules are interpetiolar and free, and stamens are borne on the corolla tube. In contrast, raphides appear absent in the Seychellean plant, its stipules are intrapetiolar and are fused adaxially with the base of the petiole, and stamens are loosely fused with the corolla tube. The paniculate, biparous cymes of the Seychellean plant have articulated nodes and persistent, paired bracteoles at the apex of each cyme unit, while in *Psychotria* s.l. inflorescences are not articulated and bracteoles are typically caducous. It is worth noting that intrapetiolar stipules are very rare in Rubiaceae (Robbrecht, 1988).

*Psathura*/*Psychotria sechellarum* differs markedly from *Colletocecema* by the absence of raphides, its intrapetiolar and persistent stipules fused with the base of the petiole; its terminal, paniculate, biparous cymes, its stamens whose filaments loosely fused with the corolla tube, its ovaries with five to six carpels, and its globose drupes containing five to six, ribbed pyrenes. In contrast, *Colletocecema* contains raphides, and has interpetiolar, free, and marcescent stipules, axillary, unbranched inflorescences paired at nodes, stamens with filaments borne on the corolla tube, bilocular ovaries, and elliptic drupes with two, ribbed pyrenes (see also Table 1 for a more complete comparison). Considering their striking morphological differences and their geographic separation, the sister-group relationship between the Seychellean endemic *Psathura*/*Psychotria sechellarum* and *Colletocecema*, revealed for the first time by our molecular phylogenetic study, is highly unexpected. Yet, the result is strongly supported and an exclusion of the Seychellean plant from *Psychotria* s.l. and the entire tribe Psychotrieae is thus necessary. One option could have been to merge it in *Colletocecema*, but that would have left *Colletocecema* morphologically highly heterogeneous and difficult to circumscribe (Table 1). We therefore chose to describe the new genus *Seychellea* Razafim., Kainul. & C.Rydin and the

**Table 1**  
Morphological and geographical differences between *Coltoecema* and *Seychellea*.

	<i>Coltoecema</i> (Piesschaert et al. (2000), Sonké et al. (2008), Dessein et al. (2011))	<i>Seychellea</i> (this study)
Distribution	Central Africa (Angola, Cameroun, Central Africa Republic, Congo, Democratic Republic of Congo & Gabon) = Congo basin	Seychelles (Mahé & Silhouette Islands)
Presence of raphides	Present	Absent
Stipule type	Interpetiolar, free from the petiole, and marcescent	Intrapetiolar, adaxially fused with the base of the petiole, and persistent
Stipule shape	Broadly triangular	Shallowly bifid
Inflorescence type	Paired at nodes	Paniculate, biparous cyme, articulated, bracteolate
Inflorescence position	Axillary	Terminal
Bracteoles	Absent	Paired, persistent bracts present at each node
Flower type	Distylous	Distylous
Number of locules	2	5–6
Shape of anthers	Appendiculate	Rounded
Position of stamens	Borne on the corolla tube	Loosely fused with the corolla tube
Fruit color	Violet or yellow	Red
Fruit shape	Elliptic	Globose
Number of pyrenes	2	5–6

new tribe Seychelleae Razafim., Kainul. & C.Rydin to accommodate the species (see Taxonomic implications below).

#### 4.2. Biogeographic implications

The sister relationship between the Central African genus *Coltoecema* and *Seychellea* reveals a biogeographic link between Central Africa and the Seychelles. The granitic Seychelles, to which *Seychellea* is currently restricted, were part of the Mesozoic Gondwana continent; nevertheless, Gondwanan vicariance is refuted by our results as explanation for the geographic distribution of the genera in the *Coltoecema-Seychellea* clade. The granitic Seychelles are fragments of the Indigascar landmass of East Gondwana, whereas Africa was part of West Gondwana (e.g., McLoughlin, 2001). The estimated divergence times of *Coltoecema* and *Seychellea* are between the late Oligocene and late Miocene (Fig. 3), which significantly post-date the sequential break-up of the major components of Gondwana in the Jurassic and Early Cretaceous (e.g., Royer and Coffin, 1992; McLoughlin, 2001; Reeves, 2014).

Instead, this late Cenozoic biogeographic link between Central Africa and the Seychelles is likely a result of long-distance dispersal. The direction of the dispersal route is difficult to establish with confidence, partly because of uncertainties regarding the deepest splits in the subfamily Rubioideae (see e.g., Fig. 2, and Rydin et al., 2017). However, there are indications on the presence of the common ancestor of *Coltoecema* and *Seychellea* in Africa. Eastward dispersals from Africa to islands of the Western Indian Ocean have been demonstrated from both animals and plants (e.g., Yoder and Nowak, 2006; Razafimandimbison et al., 2017; Kainulainen et al., 2017). Biogeographic studies of Rubiaceae have provided somewhat uncertain results but tentatively indicate Africa as part of the ancestral area of the subfamily Rubioideae (Antonelli et al., 2009; Manns et al., 2012), to which the *Coltoecema-Seychellea* clade belongs. While Asia too is indicated as a possible ancestral area of the subfamily in those studies, the Seychelles is a less likely ancestor area of the *Coltoecema-Seychellea* clade because no other early-divergent lineage of the subfamily Rubioideae is extant there. The remaining members of the Rubiaceae that are present in the Seychelles occupy derived positions in the subfamily Cincho-noideae s.l., and the Psychotriaceae and Spermaceae alliances of the subfamily Rubioideae.

It is unlikely that the hypothesized dispersal was aided by wind or sea currents. A prevailing eastward direction of wind and sea currents in the early Paleogene was replaced by a mostly westward direction in the Miocene (Ali and Huber, 2010), within which most of the confidence intervals of the estimated divergence times of *Coltoecema* and *Seychellea* fall (Fig. 3). Avian dispersal is a more likely process since,

like *Coltoecema* and *Seychellea*, their ancestor probably had small, fleshy, drupaceous fruits. Previous evidence of repeated Cenozoic dispersal eastward from Africa to the Western Indian Ocean region has mostly concerned dispersal to Madagascar (e.g., Yoder and Nowak, 2006; Kainulainen et al., 2017). Our study is, to our knowledge, the first that demonstrates a biogeographic connection between Central Africa and the Seychelles.

*Seychellea* is monospecific, like many plant genera in the Seychelles (e.g., Kueffer, 2014). The islands of the Seychelles have been considered to be too small to allow allopatric speciation and it has been argued that this observed pattern could be the result of anagenetic speciation (e.g., Kueffer, 2014; see also Takayama et al. (2003) for the Korean Ullung Island). On the other hand, the Seychelles were partly submerged during interglacial periods of the Pleistocene, causing some of their terrestrial biota to become wiped out (e.g., Fleischmann, 1997; Agnarsson and Kuntner, 2012). This is consistent with the majority of the Seychellean endemic species being found at intermediate and high elevations, with only two species confined to the coastal zone (e.g., Fleischmann et al., 2003). Therefore, it is possible that diversification subsequent to the range expansion in the Seychelles was followed by waves of extinction in the Quaternary (Maley, 1996). The current distribution of *Seychellea* in higher altitudes, i.e., the montane rainforests and inselbergs between 400 and 914 m above sea level on the Mahé and Silhouette Islands (Senterre et al., 2009; Senterre and Wagner, 2014), seems to lend some support for the latter (speciation followed by extinction) hypothesis. Based on these latter arguments *Seychellea* can be considered to be a sole potentially relict species.

*Coltoecema* is also species-poor but comprises at least three extant species with a most recent common ancestry dated from the late Miocene to middle Pleistocene. *Coltoecema dewevrei* (De Wild.) E.M. Petit is commonly found and restricted to the Congo basin (Sonké et al., 2008), which is part of the Lower Guinea and Congolia sensu White (1979). *Coltoecema gabonensis* Dessein & O. Lachenaud is endemic to the Ogooué basin in Gabon (Dessein et al., 2011), while *C. magna* Sonké & Dessein is only known from a single collection from the Ngovayang Massif in southern Cameroon (Sonké et al., 2008). These latter species are extremely rare, and are confined to the southern Lower Guinea sensu White (1979) (Sonké et al., 2008; Dessein et al., 2011). Like the Seychelles, ice ages have been considered dramatic periods of decline or extinction of the African flora (Robbrecht et al., 1996); the present species diversity and distribution of *Coltoecema* in the Lower Guinea-Congolia of Central Africa, in combination with the estimated node age, indicate that the group may well have been affected by the Pliocene-Pleistocene ice ages. The Congolia and Lower Guinea, together with the Upper Guinea and Kivu, are widely recognized as centers of biodiversity and endemism of the tropical African rainforests (White, 1979),

containing “refuge areas” that were fragmented as a result of the successive ice ages (e.g., Maley, 1996).

#### 4.3. Conservation implications

The new information about *Seychellea sechellarum* (Baker) Razafim., Kainul. & C.Rydin provided in our study is relevant to conservation biologists working to save the threatened endemic plants of the Seychelles. The monospecific *Seychellea* is member of one of the early-divergent lineages of the subfamily Rubioideae, a potentially relict lineage with a stem age here dated to the Late Cretaceous. The lineage is very species-poor in today’s biota, and extinction of *Seychellea* would cause loss of unique genetic diversity (see also Rydin et al., 2008). The conservation status of *S. sechellarum* (as *Psathura sechellarum*) was re-evaluated by Ismail et al. (2011), who changed its status from Endangered to Critically Endangered (IUCN, 2012) as a result of the destruction of its habitat natural and the spread of invasive alien species (Ismail et al., 2011). It is currently restricted to the Mahé and Silhouette Islands (Fig. 4), with most collections from the Morne Sechellois National Park of the Mahé Island. Its extent of occurrence (EOO) is less than 33 km<sup>2</sup> with fewer than 50 mature individuals left. According to Friedmann (2011), it is not yet in cultivation and both Ismail et al (2011) and Friedmann (2011) argue that an ex-situ conservation for the species is urgently needed.

#### 4.4. Taxonomic implications

Tribe Seychelleae Razafim., Kainul. & C.Rydin, trib. nov.

Type genus: *Seychellea* Razafim., Kainul. & C.Rydin.

Diagnosis: The new monogeneric tribe Seychelleae is characterized by a combination of the following characters: lack of raphides, intrapetiolar, persistent stipules adaxially fused with the base of the petioles, and stamens with filaments loosely fused with the corolla tube but easily separable from it.

Description (Fig. 1A–F, Friedmann, 2011)

Shrub 1–4 m tall, without raphides, stems terete. Leaves petiolate, 6–15 (–19.5) × 1.8–4.5 (5.5) cm, elliptic-obovate, coriaceous; margins

revolute; petioles 0.5–1.5 (–2) cm, terete, robust; stipules intrapetiolar, persistent, shallowly bifid, each adaxially fused with the base of the petiole; colleters elongate, abundant inside the stipules. Inflorescences terminal, biparous, paniculate cyme, subtended by large, narrowly triangular, paired bracts at the top of the peduncle, axes articulated, composed of successive cyme units, each cyme unit topped by one persistent, paired bracteoles and detached easily (in dried inflorescences), the youngest cyme units each bearing young floral buds completely enclosed by their paired bracteoles. Flowers subsessile, distylous; calyx tube ca. 2.5 mm long, lobes 5, deltoid, puberulous; corolla lobes 7–8 mm, white, tinged pink, glabrous inside and outside, throat hairy, lobes 5, thick, glabrous; stamens 5, included (brevistylous flowers) or exerted (longistylous flowers), anthers ca. 1 mm long, elliptic, dorsimedifixed, rounded at the apex, filaments loosely fused along the corolla tube; ovaries broadly obovoid, 5–6 locules, ovule 1 per locule, erect, styles ca. 2.5 mm (brevistylous flowers) or ca. 4.5 mm (longistylous flowers), with 5–6 stigmatic lobes. Fruits drupes, red, crown with persistent calyx lobes, 5–6 pyrenes, ribbed.

Habitat and distribution: This monogeneric tribe is exclusively restricted to the Mahé and Silhouette Islands of the Seychelles between 400 and 914 m, on Lower montane forests and inselberg fringes (Fig. 4).

Etymology: The genus name “*Seychellea*” refers to the micro-continent “Seychellea”, which is part of the granitic Seychelles currently submerged (Davies and Francis, 1964).

Included genus: *Seychellea* (1 species).

*Seychellea* Razafim., Kainul. & C.Rydin, gen. nov.,

Type: *Seychellea sechellarum* (Baker) Razafim., Kainul. & C.Rydin (= *Psathura sechellarum* Baker)

Diagnosis. This new monospecific genus is characterized by lack of raphides, intrapetiolar, persistent stipules adaxially fused with the base of the petioles, corolla tubes imperfectly fused, and stamens with filaments loosely fused with the corolla tube but easily separable from it.

Description. The description of Seychelleae is also valid for the genus *Seychellea*.

*Seychellea sechellarum* (Baker) Razafim., Kainul. & C.Rydin, comb. nov.

Basionym. *Psathura sechellarum* Baker, F.M.S.: 157 (1877); *Nonatelia sechellarum* (Baker) Kuntze, Revis. Gen. Pl. 1: 290 (1891); *Psychotria sechellarum* (Baker) Summerh., Bull. Misc. Inform. Kew 1928: 392 (1928). Type: Seychelles, Mahé, Sept. 1871 (fl.), *Horne 264* (lectotype here designated, K!).

Description. Same as the genus description (see also Friedmann, 1994, 2011).

Distribution. Same as the genus description

Vernacular name. Bwa kasan pti fey

Additional specimens. Seychelles. Mahé: geographic coordinate unknown, 1874, *J. Horne 565* (K!, K000412314); geographic coordinate and collecting date unknown, *Wright 120* (?); Forêt noire, 1876 (fl.), *G. De l’Isle s.n.* (P, P03796293!, P03796294!, P03796295!, P03796296!); Congo Rouge, 750 m alt., 4°38′38.3″S, 55°25′57.9″E, Janv. 1981, *F. Friedmann 3645* (P!, P01065297, SEY); près du chemin vers Congo Rouge, Mont Coton, Station de *Nepenthes*, Jul. 1985, *F. Friedmann 5300* (P!, P001065296); 720–750 m alt., 4°38′38.3″S, 55°25′57.9″E, 1970, *J. Procter 4084* (SEY), *J. Procter 4073* (SEY); 4°38′38.3″S, 55°25′57.9″E, 1991, *Evrard 11655* (SEY); 692 m alt., 4°38′43.3″S, 55°26′00.2″E, 2013, *C. Morel 57* (SEY); 731 m alt., 4°38′38.3″S, 55°25′57.9″E, 2012, *B. Bremer et al. 5402* (S, SEY); Glacis Sarcelle, 666 m alt., 4°38′19.6″S, 55°25′24.5″E, 2011, *L. Renguet s.n.* (SEY); Mont Sébert, 600–750 m alt., 4°38′37.9″S, 55°25′58.1″E, 1996, *A. l. Carlström s.n.*; Morne Sechellois, 500–914 m alt., 4°38′47.2″S, 55°26′24.9″E, 1996, *A. l. Carlström s.n.* (SEY); 820 m alt., 4°38′46.1″S, 55°26′12.8″E, 2011, *B. Senterre 5989* (SEY); Mont Seychellois, 790 m alt., 4°38′39.1″S, 55°26′24.7″E, 2011, *H. Elzein s.n.* (SEY); Péard, 790 m alt., 4°38′21.8″S, 55°26′17.8″E, 2011, *H. Elzein s.n.* (SEY); Péard, 821 m alt., 4°38′24.4″S, 55°26′10.2″E, 2013, *B. Senterre s.n.* (SEY); Péard, 845 m alt., 4°38′27.9″S, 55°26′12.7″E, 2011, *H. Elzein s.n.* (SEY); Péard, 826 m alt., 4°38′26.3″S, 55°26′11.4″E, 2013, *B. Senterre s.n.* Silhouette: Grand

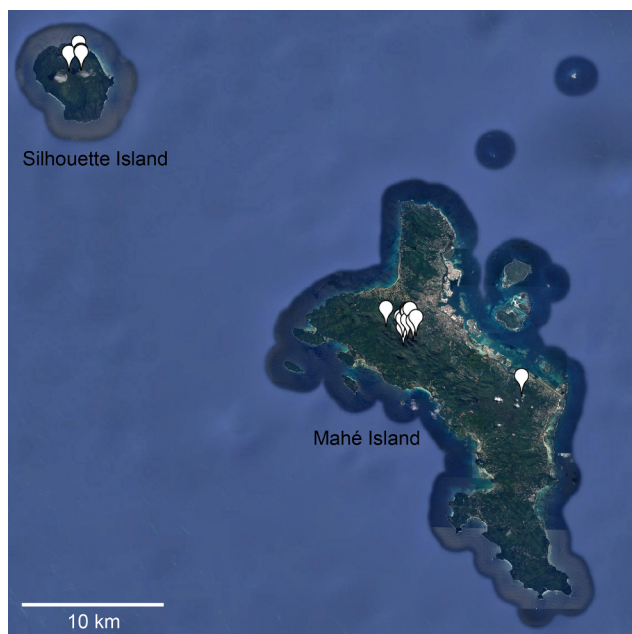


Fig. 4. Map showing the distribution of *Seychellea sechellarum* on the Mahé and Silhouette Islands of the Seychelles based on the collection information indicated on herbarium specimens studied from P, SEY, and S Herbaria. Google Earth Image © 2019 CNES/Airbus. Reproduced per attribution guidelines.

Congoman, 4°38'30.2"S, 55°14'00.1"E, Jan. 31, 1962, C. Jeffrey 800 (K1, 24474.000; P1, P01034049, SEY); Mt. Pot-à-Feu, 600 m alt., Nov. 1973 (fl.), Procter 4553 (P); Mont Pot-à-Feu, ca. 600 m alt., Nov. 04, 1973 (sterile), Luciano Bernardi 15,678 (P1, P01034050); Mont Pot-à-Eau, 500–620 m alt., 4°28'49.0"S, 55°14'05.1"E, 1996, L. A. Carlström s.n. (SEY); Mont Pot-à-Eau, 590 m alt., 4°28'51.2"S, 55°14'05.7"E, 2008, B. Senterre 5254 (SEY); Mont Dauban Est, 709 m alt., 4°38' 39.1"S, 55°26'24.7"E, 2012, B. Senterre s.n. (SEY).

Notes. Baker (1877) cited three syntypes (*Horne 264*, *Horne 565*, *Wright 120*) in the protologue of his *Psathura sechellarum*. We have seen scanned images of the two collections of Horne at Kew, and thus selected *Horne 264* as lectotype, because it is in good condition and has flowers and young fruits. Friedmann (2011) described the stipules of *Seychellea sechellarum* (as *Psathura sechellarum*) as interpetiolar, deeply bifid, with two halves of the paired stipule, i.e., one from one stipule and one from the other stipule, fused adaxially with the base of each petiole; when a petiole of a leaf blade is detached, it always comes off with the fused stipule (Friedmann, 2011: 574). We think that Friedmann's description of the stipules of *S. sechellarum* is erroneous, because our observation (S. Razafimandimbison, pers. obs.) shows that this Seychellean plant actually has intrapetiolar, shallowly bilobed stipules. In young, small branches the impression may be that the species has interpetiolar stipules that are deeply bilobed/bifid, as described by Friedmann (2011). The drawing on the Plate 177: 3 in Friedmann (2011) clearly shows one entire intrapetiolar stipule that is bilobed, and fused adaxially with the base of the petiole. The two halves of the paired stipules on the same side of a young branch look like they are fused but they are simply appressed. If one, on the other hand, looks at old branches, these so-called two halves of the paired stipules are completely separate, that is they are no longer appressed.

#### 4.5. Notes on the biogeographic origins of the Rubiaceae of the Seychelles

The Rubiaceae of the Seychelles contain about 40 species in 28 genera (Friedmann, 2011; S. Razafimandimbison, unpubl. data), of which 14 species or 35% are endemic (i.e., *Craterispermum microdon* Baker and two new undescribed *Craterispermum* species; *Glionnetia sericea* (Baker) Tirveng.; *Ixora pudica* Baker; *Paragenipa lancifolia* (Bojer ex Baker) Tirveng. & Robbr.; *Paracephaelis trichantha* (Baker) De Block; *Peponidium carinatum* (Baker) K.Kainul. & Razafim. and *P. celastroides* (Baker) K.Kainul. & Razafim.; *Psychotria pervillei* Baker and *P. silhouettae* Baker; *Rothmannia annae* (E.Wright) Keay, and *Seychellea sechellarum*. Eleven species (27.5%) are indigenous but not endemic (i.e., *Amaracarpus pubescens* Blume; *Empogona ovalifolia* (Hiern) Tosh & Robbr.; *Guettarda speciosa* L.; *Morinda citrifolia* L.; *Pentodon pentandrus* Vatke; *Polysphaeria multiflora* Hiern.; *Pyrostria bibracteata* Baker; *Tarenna sechellensis* (Baker) Summerh.; *Tarenna supra-axillaris* (Hemsl.) Bremek.; *Timonius flavescens* (Jack) Baker; and *Triainolepis africana* Hook.f.). An additional 16 species from eight genera have been introduced and some have become naturalized (*Coffea* L., *Euclinia* Salisb., *Gardenia* L., *Mitracarpus* Zucc., *Mussaenda* L., *Oldenlandia* L., *Rondeletia* L., and *Vanigeria* Juss.) (Friedmann, 2011).

Three monospecific rubiaceaceous genera (*Glionnetia* Tirveng., *Paragenipa*, and *Seychellea*) are endemic to the granitic Seychelles; the remaining genera are either pan- or paleotropical, and have species endemic to the Seychelles and/or indigenous species with wider distributions or introduced species.

Nine of the 14 Seychellean endemic species likely have Malagasy origins (*Craterispermum microdon* and two new undescribed ones,

*Paragenipa lancifolia*, *Paracephaelis trichantha*, *Peponidium carinatum* and *P. celastroides*, *Psychotria pervillei*, and *P. silhouettae*) (Kainulainen et al., 2017; Razafimandimbison et al., 2017). Two species are the result of two independent long-distance dispersal events from Asia (i.e., *Glionnetia sericea* and *Ixora pudica*), while *Rothmannia annae* has an East African origin (Kainulainen et al., 2017; Razafimandimbison et al., unpubl. data). *Seychellea sechellarum* is also likely to have an African origin. Among the 11 indigenous non-endemic species four species were descended from Malagasy ancestors (i.e., *Pyrostria bibracteata*, *Tarenna sechellensis*, *T. supra-axillaris*, and *Triainolepis africana*) (Kårehed and Bremer, 2007; Razafimandimbison et al., 2009; Kainulainen et al., 2017), three species with African origins (*Empogona ovalifolia*, *Pentodon pentandrus*, and *Polysphaeria multiflora*) (Tosh et al., 2009), and two species with Pacific and Asian origins (*Amaracarpus pubescens* and *Timonius flavescens*) (Razafimandimbison et al., 2017). The origins of the pantropical *Morinda citrifolia* (Razafimandimbison et al., 2010) and *Guettarda speciosa* are currently unknown. This information further confirms that Madagascar is the source of origin for the majority of Rubiaceae found on its neighboring archipelagos (e.g., Wikström et al., 2010; Kainulainen et al., 2017; Razafimandimbison et al., 2017).

## 5. Conclusions

In contrast with previous assumptions, this study demonstrates that *Psathura/Psychotria sechellarum* is distantly related to *Psychotria* s.l. and we described the new genus *Seychellea* and new tribe Seychelleae to accommodate this Seychellean plant. Its sister-group relationship with the Central African *Collettoecema* is surprising considering the morphological and geographic distinction of the two genera; yet it is highly supported and the monospecific *Seychellea* and its sister genus *Collettoecema* conceivably represent the very species-poor remnants of a relictual lineage, likely present in Africa, descending from a Late Cretaceous ancestor. The evolutionary split between *Seychellea* and *Collettoecema* reveals a more recent biogeographic connection between Central Africa and the Seychelles. Divergence time estimates of nodes in the *Collettoecema-Seychellea* clade indicate that the clade is too young for a range expansion to the Seychelles to be attributed to Gondwanan vicariance. *Collettoecema* and *Seychellea* diverged in the late Oligocene-early Pliocene and the ancestor of *Seychellea* probably reached the Seychelles via avian dispersal. *Seychellea sechellarum* is critically endangered and since its extinction would cause a loss of unique genetic diversity of a species-poor and relict lineage, it should be considered to be a top candidate for conservation priority. We strongly recommend urgent implementation of new in-situ and ex-situ conservation programs to ensure the continued survival of this species.

## Acknowledgements

We thank the Herbaria P, S, and SEY Herbaria for allowing access to their collections and images; the authorities of the Seychelles for issuing the research permit for SGR and KK to collect the Seychellean Rubiaceae in 2012; Dr. Christopher Kaiser-Bunbury for sharing his beautiful photos of *Seychellea sechellarum*; the anonymous reviewers for their constructive comments; and Anbar Khodabandeh for technical support. The project was funded by grants from the Knut & Alice Wallenberg Foundation Royal Swedish Academy of Sciences to cover field costs for KK, and from Stockholm University and the Royal Swedish Academy of Sciences to CR.

## Appendix A

See Table A1.



**Table A1**  
Vouchers and sequence accession information of the sampled taxa.

Taxa	Vouchers	<i>rbcl</i>	<i>rps16</i>	<i>ndhF</i>	<i>atpB-rbcl</i>	<i>trnT-F</i>
<i>Acranthera frutescens</i> Valetton	A. D. Poulsen 52 (AAU)	EU145449	EU145475	EU145398	EU145310	EU145525
<i>Acranthera grandiflora</i> Bedd.	J. Klackenberg & Lundin 541 (S)	EU145448	EU145474	EU145397	EU145309	EU145521
<i>Acranthera</i> Arn. ex Meisn. sp. 1	C. Ridsdale 2470 (L)	AM117198	EU145477	EU145400		AJ847408
<i>Acranthera</i> Arn. ex Meisn. sp. 2	Bremer 1731 (UPS)	AM117199	EU145478		EU145312	EU145524
<i>Alstonia scholaris</i> (L.) R.Br.	Fanning 212 (FTG)	X91760	AJ431032	AJ011982	DQ359161	AJ430907
<i>Amaracarpus pubescens</i> blume-cl42	Senterre 5380 (SEY)	KJ805582	KJ805187	KJ804988	KJ804402	KJ805382
<i>Amphidasya ambigua</i> (Standl.) Standl.)	Clark & Watt 736 (UPS)	Y11844	AF129271		EU145337	EU145576
<i>Anthocleista</i> Afzel. ex R.Br.		L4389		AJ235829	DQ131695	AJ490190
<i>Anthospermum herbaceum</i> L.f.	B. Bremer 3093 (UPS)	X83623	EU145496	AJ236284	AJ234028	EU145544
<i>Argostemma hookeri</i> King	Wanntorp s.n. (S)	Z68788	EU145497	AJ145419	AJ234032	EU145545
<i>Calycophyllum candidissimum</i> (Vahl) DC.	Sanders 1805 (FTG)	X83627	AF004030	AJ236285	DG131708	AF152646
<i>Dirichletia glaucescens</i> Hiern (as <i>Carphalea glaucescens</i> (Hiern) Verdc.)	S. Med. Plant project 215 (UPS)	Z68789	AM266817	AJ236287		AM266906
<i>Castesbaea spinosa</i> L.	Gillis 9569 (FTG)	X83628	AF004032	AM117343		AF152706
<i>Cephalanthus occidentalis</i> L.	Forbes s.n. (UC)	X83629	AF004033	AJ236288	DQ131710	AF152692
<i>Chiococca alba</i> (L.) Hitchc.	Bremer 2703 (S)	L14394	AF004034	AJ130835	DQ131711	AY763813
<i>Cinchona pubescens</i> Vahl	unknown collector s.n.	X83630	AF004035	AJ235843	AJ233990	AJ346963
<i>Coccocypselum condalia</i> Pers.	Pirani & Bremer 4891 (SPF)	AM117217	EU145499	EU145420	EU145324	EU145547
<i>Coccocypselum hirsutum</i> Bartl. ex DC.	B. Bremer 2700 (S)	X87145	EU145500	EU145421	EU145325	EU145548
<i>Coffea arabica</i> L.	Sanders 1803 (FTG)	X83631	AF004038	AJ236290	X70364	DQ153845
<i>Collettoecema dewevrei</i> (De Wild.) E.M.A Petit	S. Lisowski 47195 (K)	EU145457	AF129272	EU145409	DQ131713	EU145532
<i>Collettoecema magna</i> Sonké & Dessein	S. Dessein 1608 (BR)		KT218841		KT218712	KT218903
<i>Condaminea corymbosa</i> (Ruiz & Pav.) DC.	Bremer et al. 3387 (UPS)	Y18713	AF004039	AJ236291		AF102406
<i>Coptosapelta flavescens</i> Korth. (specimen 1)	Puff 950720-1/2 (WU)	Y18714	EU145484	AJ236292	EU145316	AM117354
<i>Coptosapelta montana</i> Korth. ex Valetton	Clemens & Clemens 40864 (K)	EU145451	EU145481	EU145402	EU145314	EU145526
<i>Coptosapelta diffusa</i> (Champ. ex Benth.) Steenis-az24	Bartholomew et al. 847 (AAU)	EU145452	EU145482	EU145403	EU145315	EU145527
<i>Coptosapelta diffusa</i> (Champ. ex Benth.) Steenis-ay08	Steward et al. 594 (S)	EU145453	EU145483	EU145404	AJ233987	DQ359166
<i>Coussarea hydrangeifolia</i> (Benth.) Benth. & Hook.f. ex Müll. Arg.	Fuentes 5504 (GB)	EU145460	EU145% = !	EU145422	EU145326	EU145549
<i>Craterispermum laurinum</i> (Poir.) Benth.	J. Kårehed et al. 303 (UPS)	AM945300	AM945325	AM945276	AM945243	AM945356
<i>Craterispermum longipedunculatum</i> Verdc.	Q. Luke 9196 (UPS)	KJ805650	KJ805256	LN680386	KJ804458	KJ805451
<i>Craterispermum microdon</i> Baker-cl40	Bremer et al. 5414 (S)	MF178767	MF178858	MF178682	MF178418	MF178943
<i>Craterispermum</i> sp. 2	Razafimandimbison & D. Ravelonarivo 656 (S)	AM945298	AM945313	AM945274	AM945242	AM945354
<i>Cremospora triflora</i> (Thonn.) K.Schum.	Andreasen 51 (UPS)	Z68856	AF200990		DQ131718	AF201040
<i>Cubanola domingensis</i> (Britton) Aiello	McDowell 4472 (JBSD)	X83632	AF004044	AM117345	DQ131720	AF152701
<i>Damnacanthus indicus</i> C.F.Gaertn.	Bremer 3107 (UPS)	Z68793	AF331647		AJ234015	
<i>Danais xanthorrhoea</i> (K.Schum.) Bremek.	Bremer 3079 (UPS)	Z68794	AM117297	AJ236293	AJ234019	DQ662138
<i>Declieuxia cordigera</i> Mart. & Zucc. Ex Schult. & Schult.f.	Pirani & Bremer 4893 (SPF)	AM117224	AM117298	EU145423	EU145327	EU145551
<i>Dunnia sinensis</i> Tutcher 1	Ge et al. 2002	EU145467	EU145515	EU145442	EU145339	EU145583
<i>Emmenopterys henryi</i> Oliv.	Robbrecht s.n. (UPS)	Y18715	AM117302	AJ236294	DQ131728	AF152637
<i>Faramea multiflora</i> A.Rich.	Bremer 3331 (UPS)	Z68796	AF004048	EU145424	EU145328	AF102422
<i>Ferdinandusa speciosa</i> Pohl	Malmé 2442 (UPS)	AM117226	AM117304	EU145412	DQ131735	EU145534
<i>Fernelia buxifolia</i> Lam.	De Block s.n. (BR)	AJ286704	AM117306		DQ131736	EU145540
<i>Foonchewia dangdongensis</i> R.J.Wang	R. Wang 1558 (IBSC)	JQ002642	JQ002638	JQ002646	JQ002650	
<i>Gaertnera phanerophlebia</i> Baker-cl15	Razafimandimbison et al. 1030 (S)	MF178790	MF178881	MF178705	MF178441	MF178965
<i>Gelsemium sempervirens</i> (L.) J.St.-Hil.	Bremer 3026 (UPS)	L14397	AJ431033	AJ011984	AJ233985	AJ430908
<i>Gentiana procera</i> Holm.	Struwe 1009 (S)	L14398	AJ431034	L36400	DQ398604	X77893
<i>Guettarda uruguensis</i> Cham. & Schldl.	X5-127, Gillis 9575 (FTG)	X83638	EU145489	AJ236297	DQ131739	EU145533
<i>Hedyotis fruticosa</i> L.	Lundqvist 11106 (UPS)	Z68799			AJ234026	AF381539
<i>Hillia triflora</i> (Oerst.) C.M.Taylor	Bremer 3101 (UPS)	X83642	AM117315	AJ236298	AJ233993	AM117362
<i>Hymenophyllum formicarum</i> Jack	Bremer 2701 (S)	X83645	AF001339		X76480	
<i>Hymenodictyon floribundum</i> (Hochst. & Steud.) Rob.	Puff 861109-3/1 (WU)	AJ347015	AF004058	EU145411	DQ131742	AY538454
<i>Ixora coccinea</i> L.	Bremer 2719 (UPS)	X83646	AM117321	AJ236299		AJ620117
<i>Kopsia fruticosa</i> (Roxb.) DC.	Bremer 3033 (UPS)	X91763	DQ660588	AJ235824		AM295091
<i>Lasianthus kilimandscharicus</i> K.Schum.	H. Lantz 119 (UPS)	AM117327	EU145426	EU145330	DQ662147	EU145366
<i>Lasianthus pedunculatus</i> (Griseb.) Urb.	C.M. Taylor 11719 (MO)	AM117238	AF004062		EU145331	EU145554
<i>Lerchea bracteata</i> Valetton	Axelius 343 (S)	AJ288610	EU145508	EU145433	AJ233997	EU145561
<i>Luculia pinceana</i> Hook.	N.N. Thin et al. 3061 (AAU)	EU145447	EU145472	145395	DQ131749	AM117371
<i>Luculia grandifolia</i> Ghose	Bremer 2713 (S)	X83648	AM900593	AM117346	AJ233986	AJ346929
<i>Luculia gratissima</i> (Wall.) Sweet	Cult. In Univ. Conn. Storres 870064 (no voucher =)	AM117243	AJ431036	AJ011987	EU145308	AJ430911
<i>Mitchella repens</i> L.	Breedlove et al. 32460 (MEXU)	JX412474	JX412453	AM945258	JX412412	JX412391
<i>Mitrasacmopsis quadrivalvis</i> Jovet	Kayombo et al. s.n. (UPS)	AJ616214	AM117329	EU145439	EU145336	EU145575
<i>Morinda citrifolia</i> L.		AJ318448	AJ320078	AJ236300	AJ234013	AF152616
<i>Mostuea brunonis</i> Didr.	Drozd & Molem 1998-11-08 (?)	L14404	HQ385186	AJ235828	DQ131697	HQ412964
<i>Mussaenda erythrophylla</i> Schumach. & Thonn.	Gillis 10838 (FTG)	X83652	EU145493	AJ130836	DQ131754	EU145535
<i>Mycetia malayana</i> (G. Don) Craib	Larsen 42486 (UPS)	Z68806	AF002771	FJ695310	AJ234033	AF152622
<i>Nauclea orientalis</i> (L.) L.	Bremer 3001 (UPS)	X83653	AJ320080	EU145410	EU145320	AJ346958
<i>Neurocalyx championii</i> Benth. ex Thwaites-ax37	Thor 601 (S)	EU145463	EU145509	EU145435		EU145563
<i>Neurocalyx zeylanicus</i> Hook.	B. & K. Bremer 937 (S)	Z68807	AM900594	EU145434	AJ233995	EU145562
<i>Oldenlandia corymbosa</i> L.	Bremer 3075 (UPS)	X83655	AF333381	AF381537		AY854053
<i>Ophiorrhiza elmeri</i> Merr.	Kjedsen & Poulsen 233 (AAU)	EU145464	EU145510	EU145436		EU145564
<i>Ophiorrhiza mungos</i> L.	Bremer 3301 (UPS)	X83656	AF004064	AJ30838		DQ662151
<i>Paederia foetida</i> L.	Ehrendorfer 930830-0801 (WU)	AF332373	AF004065		AJ234006	AF152619

(continued on next page)

Table A1 (continued)

Taxa	Vouchers	<i>rbcL</i>	<i>rps16</i>	<i>ndhF</i>	<i>atpB-rbcL</i>	<i>trnT-F</i>
<i>Pagamea guianensis</i> Aubl.	McDowell 5738 (ETSU)	AM945290	AF002744	AM945263	AM945229	AM945342
<i>Palicourea crocea</i> (SW.) Schult.	Cordio 2736 (SP)	AM117253	AF147510	AM945280	AM945247	AM945259
<i>Pauridiantha paucinervis</i> (Hiern) Bremek.	Bremer 3090 (UPS)	Z68811	AM900600	AJ236302	AJ233998	EU145578
<i>Pauridiantha symplocoides</i> (S. Moore) Bremek.	H. Lantz 123 (UPS)	AY538502	AF004068	UR145440	EU145338	EU145386
<i>Pentas lanceolata</i> (Forssk.) Deflers	Bremer 2702 (S)	X83659	AM266875	AJ236304	X76479	AM266963
<i>Pravinaria leucocarpa</i> Bremek.	Beaman 7950 (S)	AJ288617	AM900613	EU145441	AJ234001	EU145580
<i>Prismatomeris beccariana</i> (Baill. ex K.Schum.) J.T. Johanss.	C. Ridsdale 2461 (L)	AJ288618	AF331652	AM945271	AM945238	AM945352
<i>Psathura sechellarum</i> Baker-cl46	Bremer et al. 5402 (S), Mahé, Seychelles	MN437531	MN437540	MN437543	MN437534	MN437537
<i>Psathura sechellarum</i> Baker-cm80	C. Morel 57a (SEY), Mahé, Seychelles	MN437532	MN437541	MN437544	MN437535	MN437538
<i>Psathura sechellarum</i> Baker-cm81	C. Morel 57b (SEY), Mahé Seychelles	MN437533	MN437542	xxxx	MN437536	MN437539
<i>Psychotria holtzii</i> (K.Schum.) E.M.A.Petit-ag08	Luke 8342 (UPS)	AM945304	AM945330		AM945250	AM945362
<i>Psychotria kirkii</i> Hiern	B. Bremer 3102 (UPS)	AY538469	AM945327	AM945278	AM945246	AM945358
<i>Psychotria lantzii</i> (Bremek.) Razafim. & B.Bremer-am69	S. Razafimandimbison 517 (UPS)	KJ805780	KJ805379	KJ805184	KJ804592	KJ805579
<i>Psychotria moratii</i> Razafim. & B.Bremer-cc67	S. Razafimandimbison et al. 835 (S)	KJ805682	KJ805285	KJ805089	KJ804493	KJ805482
<i>Psychotria pervillei</i> Bakeri-cl47	Bremer et al. 5406 (S)	KJ805728	KJ805329	KJ805132	KJ804541	KJ805527
<i>Psychotria schliebenii</i> E.M.A.Petit-ag10	Q. Luke 8348 (UPS)	AM945303	AM945329	AM945282	AM945249	AM945361
<i>Pyrostria hystrix</i> (Bremek.) Bridson	Bremer 3791 (UPS)	AM117262	AM117338	EU145418	MN437545	AJ620168
<i>Rondeletia odorata</i> Jacq.	Bremer & Andreasen 3504 (UPS)	Y11857	EU145490	AJ235845	EU145321	AF152741
<i>Rubia tinctorum</i> L.	Bremer 3300 (UPS)	X83666		DQ359167	X76465	
<i>Sabicea diversifolia</i> Pers.	Bremer et al. 4018-BB18 (UPS)	EU145459	EU145494	EU145415	DQ131781	AJ847396
<i>Saldinia</i> A.Rich. ex DC. sp. 1	Bremer et al. 4038-BB38 (UPS)	AM117269	AF129275	EU145429	EU145332	EU145557
<i>Schismatoclada</i> Baker sp.	S. Razafimandimbison & D. Ravelonarivo 373 (MO)	AM117271	AM117341	EU145425	EU145329	EU145553
<i>Schizocolea linderi</i> (Hutch. & Dalziel) Bremek.	Adam 20116 (UPS)	AM117272	EU145498		EU145323	EU145546
<i>Schradera subandina</i> K.Krauss	Clark & Watt 878 (QCNE)	Y11859	AM945313	AM945264	AJ234014	AM945343
<i>Sherardia arvensis</i> L.	K. Andreasen 345 (SBT)	X81106	AF004082		X76458	EU145571
<i>Sipanea biflora</i> (L.f.) Cham. & Schldl.	Rova et al. 2005 (S)	AY538509	AF004085	EU145413	DQ131788	AF152675
<i>Spiradiclis bifida</i> Kurz	J. B. H. 55 (S)	EU145465	EU145511	EU145437		EU145565
<i>Strychnos nuxvomica</i>		L14410	AF004094	AJ235841	DQ131691	AF102484
<i>Temnopteryx sericea</i> Hook.f. 1	Dessein et al. 1768 (BR)	FJ209085			FJ226555	AM409175
<i>Temnopteryx sericea</i> Hook.f. 2	Tababe 99 (WAG)		AM900634			HM042590
<i>Trichostachys aurea</i> Hiern	Andersson & Nilsson 2304 (GB)	EU145462	EU145507	EU145431	EU145334	EU145559
<i>Urophyllum arboreum</i> (Reinw. ex Blume) Korth.	Boeca 7887 (S)		AM900617		DQ131793	EU145582
<i>Urophyllum ellipticum</i> (Wight) Thwaites	Lundqvist 11085 (UPS)	AJ288627	AM900619		AJ234002	EU145581
<i>Victectaria major</i> (K.Schum.) Verdc.	Reekmans 10916 (UPS)	Y11861	EU145495	EU145417	AJ233989	EU145537
<i>Xanthophyllum borneense</i> (Valeton) Axelius	Axelius 316 (UPS)	EU145466	EU145513	EU145438	EU145335	EU145567
<i>Xanthophyllum capitellatum</i> Ridl.	C. Ridsdale 2473 (L)	AJ288628	EU145412		AJ233996	EU145566

## Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ymp.2019.106685>.

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