A new species of Paranecepsia (Euphorbiaceae-Acalyphoideae) from Madagascar and its relationships among the ‘alchorneoids clade’

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Abstract. The formerly monotypic genus Paranecepsia Radcl.-Sm. is expanded with the description and illustration of a second species, Paranecepsia andrafiabensis Barberá & O. Lachenaud sp. nov. Molecular phylogenetic analyses of plastid rbcL and trnL-F data confirm a sister relationship between the new species and P. alchorneifolia Radcl.-Sm., as members of the alchorneoids clade. Paranecepsia andrafiabensis sp. nov. is notable for expanding the character states for the genus (now including both 2- and 3-locular ovary species) and broadening the geographic range of the genus from continental Africa to Madagascar. The new species adds to the diverse karst limestone endemics of northwestern Madagascar, where it has a very restricted distribution at the base of the western wall of the Ankarana tsingy. An amended generic description of Paranecepsia and a key to the species are also presented. Paranecepsia andrafiabensis sp. nov. is provisionally assessed as VU D1 based on the IUCN Red List criteria.

Keywords. Alchorneeae, Ankarana, Africa, Madagascar, tsingy.


Introduction

Euphorbiaceae Juss. in the strict sense (excluding Phyllanthaceae Martinov, Picrodendraceae Small, Putranjivaceae Meisn. and Peraceae Klotzsch) is a highly diverse family with about 230 genera and more than 6300 species. It includes some of the largest genera of flowering plants like Euphorbia L. and Croton L., but most genera have only few species, including more than 120 genera with 1 to 3 species. These small genera are often poorly understood and, in most cases, known from sparse and/or incomplete collections. An example of one such genus is Paranecepsia Radcl.-Sm. (Radcliffe-
This African genus was described based on specimens with staminate flowers and fruit (Radcliffe-Smith 1975) as a monotypic, dioecious group characterized by its conspicuous leaf stipels, staminate flowers with an accrescent calyx and apiculate anthers, and 3-lobed fruits (Radcliffe-Smith 2001). The type species, *Paranecepsia alchorneifolia* Radcl.-Sm., is a small tree of riverine forests occurring in northeastern Mozambique and southern Tanzania. The pistillate flowers of *Paranecepsia* were originally unknown, causing subsequent misinterpretation of floral details inferred from the fruits (i.e., 5–7 unequal sepals and no petals indicated in Radcliffe-Smith 1987, 2001), which were later amended by Vorontsova & Hoffmann (2007) based on a petaliferous flowering pistillate specimen from Tanzania collected in 2001. As its name suggests, *Paranecepsia* has morphological similarities with *Necepsia* Prain, with both genera included in tribe Bernardieae G.L.Webster (Webster 1994; Radcliffe-Smith 2001) or Pycnocomeae subtribe Necepsinae G.L.Webster (Webster 2014). Previous molecular phylogenetic analyses of Euphorbiaceae using a comprehensive sampling of genera (Wurdack et al. 2005; Tokuoka 2007) have shown that *Paranecepsia alchorneifolia* is part of the informally recognized ‘alchorneoids’ clade, a group partially supported by morphological data (Wurdack et al. 2005). *Paranecepsia alchorneifolia* was included by Wurdack et al. (2005) in the *rbcL* analysis, where it was recovered sister to *Pseudagrostistachys* Pax & K.Hoffm. In the combined analysis (*rbcL + trnL-F*), the authors excluded *Paranecepsia*, but *Pseudagrostistachys* was recovered at the most basal node of the alchorneoids (Wurdack et al. 2005).

Madagascar is a major hotspot of diversity and endemism for plants in general and for Euphorbiaceae in particular. Approximately 44 genera and 478 species of Euphorbiaceae s. str. (Madagascar Catalogue 2022) have been recorded from this country, and new species from different genera continue to be described every year (e.g., Kainulainen et al. 2017; McPherson 2017, 2019; Castillon & Castillon 2018; Montero-Muñoz et al. 2020, 2022; Haevermans & Hetterscheid 2021). The family occurs all over Madagascar but is especially well represented in dry areas, and especially in the limestone karsts formations named ‘tsingys’ that form large massifs in the west of the island and harbour many endemic species.

While studying unidentified Euphorbiaceae specimens from Madagascar in 2018, the second author discovered two fruiting collections that did not match any genus recorded from the island, and reminded him of the East African *Paranecepsia*, although their fruits were bilocular (instead of trilocular). Both collections were made in 1969 at the base of the Ankarana tsingy wall by R. Capuron and P. Morat, and their discovery spurred a recent expedition in November 2019 to the western part of Ankarana National Park to search for flowering material of this plant. Morphological features of the resulting new collections confirmed that they represented an undescribed species of *Paranecepsia*, which clearly broadened the generic concept for that genus (notably for locule ovary number) and extended its distribution from continental Africa to Madagascar. We describe this new species herein and present an expanded description of genus *Paranecepsia*. In addition, we generated sequence data from the plastid *rbcL* and *trnL-F* regions for the new species to verify its generic placement and provide a phylogenetic framework, further refining relationships within the alchorneoids clade.

**Material and methods**

The work is based on a study of herbarium material from BR, COI, DSM, K, MA, MO, NHT, P, TAN and TEF, flowers preserved in spirit, and field observations. Acronyms of herbaria follow Index Herbariorum (Thiers continuously updated). Most of the specimens have been seen.

For the phylogenetic analysis, silica gel dried leaf samples of the new *Paranecepsia* were extracted following the CTAB protocol (Doyle 1991). The *trnL-F* region was amplified using the same primers as in Silva et al. (2020). The *rbcL* region was sequenced using the following sets of primers: rbcLaf (ATG-
The three accessions of the new species of Paranecepsia have identical sequences within each locus. The trnL-F sequences were most similar to Necepsia afzelii Prain (97.88% identity, 100% of query cover) and the rbcL sequences to Paranecepsia alchorneifolia (99.71% identity, 100% of query cover). In the phylogenetic analysis, the sequences of the new species were recovered monophyletic with high posterior probability (PP = 1), and sister in turn to Paranecepsia alchorneifolia (PP = 0.94) (Fig. 1). This clade was sister to the Necepsia-Pseudagrostistachys clade (PP = 9.98); both clades form the two main lineages, clades A and B (Fig. 1), of the alchorneoids (PP = 1). Alchorneeae s. str. excluding Mareyopsis Pax & K.Hoffm. formed a strongly supported (PP = 1) monophyletic group that was nested in a polytomy with other members of the alchorneoids (Fig. 1).
**Taxonomic treatment**

Class Magnoliopsida Brongn.
Order Malpighiales Mart.
Family Euphorbiaceae Juss.

Genus *Paranecepsia* Radcl.-Sm.

*Kew Bulletin* 30: 684 (Radcliffe-Smith 1975 publ. 1976), **here amended**.

**Type species**
Description

Dioecious shrubs to medium-sized trees up to 15 m high, very ramose with *Terminalia*-like branching (Aubréville’s model); bark greyish. Indumentum of simple trichomes. Buds perulate. Stipules subulate, tardily caducous. Leaves deciduous, alternate, spirally arranged, clustered near apices of twigs and interspersed with bud scales, simple, petiolate, stipellate or not; vernation involute; leaf blade oblanceolate to elliptic, shallowly serrate or crenate-serrate with glandular teeth; venation pinnate, midrib prominent above, lateral veins 10–16 pairs, tertiary veins scalariform to reticulate; domatia present as hairy tufts in the axils of the secondary veins; basilaminar glands present or absent. Inflorescences racemose (strongly reduced in *P. andrafiabensis* sp. nov.), axillary, solitary; the staminate ones with 1–5 flowers per bract; the pistillate ones with 1–2 flowers; bracts small, subulate. Staminate flowers with pedicel articulate; calyx closed in bud, later splitting into 3–5 valvate lobes which become reflexed; petals absent; stamens 20–40, glabrous, with filaments free, anthers 2-loccular, dorsifixed, introrse, thecae pendulous and longitudinally dehiscent, connective not enlarged; receptacle subglobose; disk glands free, interstaminal, numerous, forming a raspberry-like structure; pistillode absent. Pistillate flowers long-pedicellate; pedicels articulate; sepals 5, free, slightly unequal, elliptic to obovate, entire, foliaceous and prominently veined, green, persistent and slightly accrescent in fruit; petals 5, free, alternisepalous, linear to oblanceolate, entire, glabrous, similar in colour and texture to the sepals but much smaller and with hardly prominent venation; staminodes 1–10, sometimes absent; disc annular to slightly undulate, glabrous; ovary sessile, 2 or 3 locular, with strigose indumentum; ovules 1 per locule; styles bidentate, connate at base, persistent; stigmas shortly frimbriate. Fruits capsular, 2 or 3 lobed, pubescent, dehiscent in 2 or 3 bivalved mericarps (coccii); endocarp thinly woody; columella persistent. Seeds globose, smooth, ecarunculate and exarillate, testa plain brown or mottled, hilum ellipsoid to narrowly oblong.

Key to the species of *Paranecepsia*

1. Leaves with petioles 0.2–0.8 cm long and stipels 2.5–5 mm long; staminate inflorescences up to 9 cm long; pistillate flowers with sepals 5–9 mm long; ovary 3-locular; fruits 5–6 × 10 mm; seed coat plain brown ................................................................. *Paranecepsia alchorneifolia* Radcl.-Sm.
   – Leaves with petioles 0.6–2.6 cm long and stipels (if present) 1–2.2 mm long; staminate inflorescences up to 1.3 cm long; pistillate flowers with sepals 9–15 mm long; ovary 2-locular; fruits 7–8 × 13 mm; seed coat mottled ........................................ *Paranecepsia andrafiabensis* Barberá & O.Lachenaud sp. nov.

*Paranecepsia alchorneifolia* Radcl.-Sm.


Material examined

Type

MOZAMBIQUE – *Niassa Province* • into a forest gallery of a dried stream, at side of the road Negomano-Mueda, ca 30 km N of Chomba; 11°20′ S, 38°30′ E; 11 Nov. 1959; staminate fl.; *A. Gomes e Sousa* 4514; holotype: K[K000425585], K[K000425586] (image!); isotypes: COI[COI00077121], COI[COI00077122] (image!), EA n.v., LISC[011861], PRE[PRE0659451-0] (image!), SRGH[SRGH0106464-0] (image!).

Note: the holotype consists of two sheets with cross labelling as “sheet 1” and “sheet 2”, both with a “holotype” annotation in A. Radcliffe-Smith’s handwriting, and they should be taken to constitute a single specimen according Turland et al. (2018, Art. 8.3). There are several variations of the type collection label, the most specific of which is typewritten in Portuguese on COI[COI00077121] and indicates “À beira de um rio seco, a poucos metros da ponte da estrada Mueda-Negomano, cerca de 30 kms oeste de Chomba [On the edge of a dry river, a few meters from the Mueda-Negomano highway
Fig. 2. Distribution of the genus *Paranecepsia* Radcl.-Sm. in east Africa and Madagascar. *Paranecepsia alchorneifolia* Radcl.-Sm. (circles), *Paranecepsia andrafiabensis* Barberá & O.Lachenaud sp. nov. (square).
bridge, about 30 kms west of Chomba], 11°20’ S, 38°30’ E. The label coordinates are clearly very inaccurate (in Tanzania, ca 100 km from Chomba) but from Google Earth imagery the closest match to this bridge locality is 36 km NNW of Chomba at 11°15’49.54″ S, 39°10’55.09″ E, in an area presently very degraded by agricultural activity.

Other material
MOZAMBIQUE – no locality; 4 Apr. 1960; sterile; A. Gomes e Sousa 4514A; COI, K, LISC[011862].

– Maputo Province • gallery of the river Ridi, westwards Porto Amélia town; 12°55’ S, 40°15’ E; alt. 15 m; 1 Oct. 1964; sterile; A. Gomes e Sousa 4831; BR, COI, K. – Cabo Delgado Province • Macondes, andados 30 km de Chomba para Negomano, ao longo do rio Matiu; alt. 300 m; 13 Apr. 1964; sterile; A.R. Torre & J. Paiva 11880; LISC.

TANZANIA – Lindi Region • Nanjilinji Division, Likawage Ward, ca 6 km E of Liwiti Village, Dagano ya Kiyenje na Mavunji [Junction of Ndagano and Mavuji Rivers]; 9°7’ S, 39°10’ E; alt. 60 m; 14 Nov. 2005; staminate fl.; C.J. Kayombo, P. Ezrom, H. Makelele and A. Mabruki 5203; MO[5940755] • Namatimbili Forest; alt. 250 m; 26 Nov. 2001; pistillate fl.; F. Mbago and B. Mpanda 2244; K. – Morogoro Region • Kilombero Game Control Area; alt. 300 m; 2 Nov. 1998; fruit; A.S. Mkeya and P. Metele 1062; MO[5677723].

– Maputo Province • Ambilobe, Andrafiabe village, at the base of the wall of Ankaranatsingy; 12°55’40” S, 49°03’41” E; alt. 66 m; 21 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2770; holotype: MO-6956134; isotypes: BR, P, TAN.
Paratypes

MADAGASCAR – Diana Region • Andreaiba, PM 200 from the camp, on the circuit to Grotte de Andreaiba; 12°55′55″ S, 49°03′29″ E; alt. 72 m; 21 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2764; BR, MA, MO, P, TAN • ibid.; staminate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2765; BR, MO, P, TAN • ibid.; offshoot; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2767; BR, MO, P, TAN • Andreaiba, at the base of the wall of Ankarana; 12°55′40″ S, 49°03′41″ E; alt. 66 m; 21 Nov. 2019; staminate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2769; BR, MA, MO, P, TAN • ibid.; 12°55′38″ S, 49°03′45″ E; alt. 49 m; 21 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2771; BR, MO, P, TAN • ibid.; 12°55′51″ S, 49°03′32″ E; alt. 48 m; 21 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2772; BR, MO, P, TAN • ibid., 12°56′08″ S, 49°03′22″ E; alt. 37 m; 23 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2797; BR, MO, P, TAN • ibid., 12°56′08″ S, 49°03′20″ E; alt. 38 m; 23 Nov. 2019; pistillate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2798; BR, MA, MO, P, TAN • ibid.; 12°56′05″ S, 49°03′23″ E; alt. 62 m; 23 Nov. 2019; staminate fl.; P. Barberá, P. Antilahimena, J. Razanatsoa and S. Andriazafy 2799; BR, MO, P, TAN • à la base du mur de l’Ankarana; 16–28 Jan. 1969; fr.; Service Forestier (R. Capuron) 28711_SF; BR[0000025668131V], G, K, MO[6911563], P[05570467], TEF • forêt au pied de la falaise de l’Ankarana; Jan. 1969; fr.; P. Morat 3054; MO[5990069], P[05570468], P[05570469], P[05570470], P[05570471], TAN.

Description

Medium sized tree, 5–15 m high, 14–40 cm DBH; bark smooth when young, with numerous warty lenticels, gray; older bark scaly forming small or medium-sized loosely attached plates; twigs cylindrical, glabrous, soon woody with pale buff-grey bark. Bud scales triangular to ovate, 2–5.5 × 0.7–2 mm, apex acuminate to very long acuminate, glabrous to densely pubescent on both faces. Staminate flowers and 1–3(–5) bractes up to 1.3 cm long, greenish, anthers 0.4–0.7 mm long, yellowish, thecae elliptic, connective minutely apiculate; disk glands outside at least towards apex, glabrous inside, yellowish to greenish; stamens 20–33, 3–5, ovate-lanceolate, 2.7–4.8 × 0.4–2.5 mm, acute to shortly acuminate, papyraceous, appressed-pubescent outside at least towards apex, glabrous inside, yellowish to greenish; stamens 20–33, filaments 2–3.5 mm long, greenish, anthers 0.4–0.7 mm long, yellowish, thecae elliptic, connective minutely apiculate; disk glands elongated, glabrous, greenish. Pistillate inflorescences 1(–2)-flowered, axis glabrous; bract very narrowly lanceolate, 1.1–3 × 0.2–0.3 mm, acute, pubescent. Pistillate flowers with pedicel 0.6–1.6 cm long, articulate (0.1–)0.4–1 cm from the bract; sepals 4–5, separate from each other, slightly unequal in size, narrowly elliptic or elliptic to oblanceolate, sometimes oblong, 7–15 × 2–6(–7) mm, papyraceous, glabrous inside, sparsely pilose on the central part outside, hairy apically, conspicuously veined, apex acute to acuminate,
Fig. 3. Illustration of *Paranecepsia andrafiabensis* Barberá & O.Lachenaud sp. nov. a. Branch with pistillate flower. b. Bud. c. Leaf base with stipels. d. Detail of the lower leaf surface with domatia. e. Leaf margin. f. Staminate inflorescence. g. Staminate flower. h. Stamen. i. Pistillate flower. j. Petal of pistillate flower. k. Ovary and stigmas, lateral view. l. Fruit with persistent calyx, lateral view. m. Fruit, top view. n. Seed, lateral view. From Barberá et al. 2797 (a–b), Capuron SF-28711 (c–e, l–n), Barberá 2799 (f), Barberá et al. 2765 (g–h), Barberá et al. 2771 (i), Barberá et al. 2798 (j), Barberá et al. 2764 (k). Drawn by O.Lachenaud.
rarely rounded, margins entire; petals (1–)2–5, unequal, linear or narrowly elliptic to narrowly oblanceolate, (0.2–)0.6–5(–5.4) × (0.05–)0.1–0.8(–1.2) mm, acute, glabrous, yellowish to greenish; staminodes 1 or absent, extending to the same length as the disc, basally terete, apically enlarged; disc 1.8–2.6 mm wide, yellowish to greenish, glabrous; ovary 2-locular, 2–4.2 × 3.5–7.3(–8.3) mm, greenish-yellowish; styles 2, 2.5–3.2 mm long, connate, pilose, greenish, stigmas bifid, shortly fimbriate. Fruits strongly bilobed, 7–8 × 13 × 7.5 mm,

Fig. 4. Field photographs of *Paranecepsia andrafiabensis* Barberá & O. Lachenaud sp. nov. a. Forest of *Paranecepsia andrafiabensis*. b. Old trunk. c. Seedlings. d. Detail of old tree trunk. e. Detail of young tree trunk. From Barberá et al. 2769 (b, d), Barberá et al. 2767 (c), Barberá et al. 2798 (e). Photos by P. Barberá.
minutely tuberculate, covered with a dense rufous puberulous indumentum, and with sparse longer whitish trichomes ca 0.2 mm long (one at the top of each tubercle), brownish when dry; pedicel 1.4–1.9 cm long; calyx and petals persistent; columella ca 5 mm long; seeds globose, ca 6 × 6 mm, testa mottled with dark and pale brown, hilum broadly ellipsoid, ca 2.2 × 2 mm.

**Distribution, habitat, and phenology**

*Paranecepsia andrąfiabensis* sp. nov. is only known from the dry, deciduous forest on karstic limestone (‘tsingy’) that surrounds part of the base of the western wall of the Ankarana tsingy, in northwestern Madagascar, at elevations between 37 and 72 m. The flowering material of this species was collected in November and the fruiting one in January.

![Fig. 5. Field photographs of *Paranecepsia andrąfiabensis* Barberá & O.Lachenaud sp. nov. a. Bud. b. Domatia hair tufts at primary-secondary vein junctions. c. Leaf base and stipule. d. Stipels. From Barberá et al. 2767 (a, c–d), Barberá et al. 2765 (b). Photos by P. Barberá.](image-url)
Preliminary conservation assessment

Paranecepsia andrafiabensis sp. nov. is endemic to northwestern Madagascar where it grows at the base of the western wall of the Ankarana tsingy. It is presently known from 11 herbarium specimens, two of them collected in fruit by Morat and Capuron in 1969, and recently (in 2019) several collections with

Fig. 6. Field photographs of Paranecepsia andrafiabensis Barberá & O.Lachenaud sp. nov. a. Staminate inflorescence. b. Pistillate inflorescence. c. Detail of the bract of the pistillate flower. d. Pistillate flower, lateral view. e. Pistillate flower, top view. From Barberá et al. 2799 (a), Barberá et al. 2765 (b–c), Barberá et al. 2771 (d), Barberá et al. 2772 (e). Photos by P. Antilahimena (a) and P. Barberá (b–e).
flowers and fruits were made at east of Andrafiabe village. All the collections represent seven occurrences and only one subpopulation of the species. We have verified that the species is abundant at this site with many seedlings and mature trees. Based on a 2 × 2 km cell size, the AOO is estimated as 4 km², which is less than the upper threshold for “Critically Endangered” status under Criterion B2. The EOO is the same as the AOO. All known occurrences are located at the limits of a protected area (Ankarana National Park), and no specific threats have been identified at the present time. However, we estimate that the population size is less than 1000 mature individuals, and that the species presumably has a low dispersal ability. For these reasons, Paranecepsia andrafiabensis is assigned a preliminary status of VU D1.

Notes
The stipels at the base of the leaf blade are present on some specimens and absent in others, even on very young leaves; this appears to be individual variation.

Discussion
The addition of Paranecepsia brings the number of native Malagasy genera of Euphorbiaceae to 40 (5 alchorneoids), which contain over 450 species (14+ alchorneoids) (Madagascar Catalogue 2022). The other genera of alchorneoids in Madagascar include Alchornea Sw., Amyrea Leandri, Orfleia Baill., and Necepsia.

Our phylogenetic reconstruction verifies the placement of the new species within the genus Paranecepsia and, as expected, shows similar relationships within the alchorneoids and related lineages as in Wurdack et al. (2005), including the paraphyletic position of the two Alchornea species sampled. The alchorneoids consist of 12–15 genera and ca 120 species that are currently classified in tribes Alchorneae (Hurus.) Hutch., Agrostistachydeae (Müll.Arg.) G.L.Webster, Caryodendraceae G.L.Webster, and Pycnocomeae Hutch. (Webster 2014). As suggested by Wurdack et al. (2005), the supported nodes of sister taxa indicate that Alchorneae s. str. might be expanded to include the members of the alchorneoid clade. Potential synapomorphies in wood anatomy (Hayden & Hayden 2000; Wurdack et al. 2005) and in pollen (Nowicke & Takahashi 2002; Wurdack et al. 2005) have been indicated by previous authors supporting Alchorneae s. str. within the alchorneoids. Further morphological studies and phylogenetic analyses need to be done, using more phylogenetically informative genetic regions and a broader taxon sampling within this clade, including a larger representation of its largest genus (Alchornea), needed to better understand the phylogenetic structure within the alchorneoids. However, our analysis expands the generic members of this clade confirming Paranecepsia, which, although previously sampled in Wurdack et al. (2005), was only represented by a single rbcL sequence of Paranecepsia alchorneifolia.

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References


**Appendix 1.** GenBank accession numbers for the *rbcL*, *trnL-F* sequences used in the phylogenetic analysis. Voucher information is provided for the new generated sequences of *Paranecepsia andrafiabensis* Barberá & O.Lachenaud sp. nov.