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Monograph

Monograph of the western Indian Ocean genus *Paracephaelis* (Rubiaceae – Pavetteae), with description of thirteen new species

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Abstract. The western Indian Ocean genus *Paracephaelis* is revised. Sixteen species are endemic to Madagascar, 12 of which are new for science: *P. aristata* sp. nov., *P. bardotiae* sp. nov., *P. capitulifera* sp. nov., *P. gautieri* sp. nov., *P. grandifructa* sp. nov., *P. longipedicellata* sp. nov., *P. orientalis* sp. nov., *P. pauciflora* sp. nov., *P. ranirisonii* sp. nov., *P. russata* sp. nov., *P. sambavensis* sp. nov., and *P. seyrigii* sp. nov. *Paracephaelis trichantha* occurs on the east coast of continental Africa and on the islands of the Aldabra Group. One other species is newly described from the Comoros, *P. comorensis* sp. nov. *Paracephaelis* is characterized by sessile inflorescences, pubescent inflorescence and flower parts, ovules arranged at the periphery of the placenta, laterally flattened seeds with entire endosperm and a shallow elongate hilum, and pollen with supratectal elements. Of the Malagasy endemics, five species are assessed as Critically Endangered with *P. sambavensis* sp. nov. possibly Extinct in the Wild, three are Endangered, four are Vulnerable, one is Near Threatened, and three are Least Concern. Outside Madagascar, *P. trichantha* and *P. comorensis* sp. nov. are assessed as Vulnerable.

Keywords. Aldabra, Comoros, East-Africa, Madagascar, taxonomy.

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Introduction

Madagascar is known for its unique biodiversity and high levels of endemism. Recently, revisions of several Malagasy taxa have resulted in an extraordinary increase of recognized species. This is the case for animals from all different orders such as mammals (e.g., mouse lemurs; Olivieri *et al.* 2007), freshwater fishes (Benstead *et al.* 2003), amphibians (e.g., frogs; Rakotoarison *et al.* 2017), insects (e.g., assassin bugs, mayflies; Benstead *et al.* 2003; Forthman *et al.* 2016), but also for plants from different families such as Burseraceae Kunth (*Canarium* L., from 3 to 33 species; Daly *et al.* 2015), Oleaceae Hoffmanns. & Link (*Noronhia* Stadtm. ex Thouars, from 47 to 83 species; Hong-Wa 2016), Rhamnaceae Juss. (*Gouania* Jacq., from 7 to 16 species; Buerki *et al.* 2011), and Sapindaceae Juss. (*Beguea* Capuron, from 1 to 10 species; Schatz *et al.* 2017). The same trend occurs in the Rubiaceae Juss., with ca 800 species one of the largest plant families in Madagascar. Recent taxonomic studies considerably raising species numbers took place for genera such as *Astiella* Jovet (from 1 to 12 species; Groeninckx *et al.* 2017), *Flagenium* Baill. (from 3 to 6 species; Ruhsam & Davis 2007), *Gaertnera* Lam. (from 26 to 42 species; Taylor *et al.* 2014), and *Ixora* L. (from 17 to 32 species; De Block 2007, 2008, 2014a, 2014b).

Paracephaelis Baill. is another genus of Rubiaceae of which the species number rises spectacularly. Until recently, *Paracephaelis* was known from three species in Madagascar (*P. cinerea* (A.Rich. ex DC.) De Block, *P. saxatilis* (Scott Elliot) De Block, and *P. tiliacea* Baill.), and a single species from the Seychelles and the east coast of mainland Africa, *P. trichantha* (Baker) De Block. The three Malagasy species occur in dry forests in western, northern and southern Madagascar while *P. trichantha* is a coastal species found in dry forests and thickets. Recently, however, a molecular phylogenetic study of the tribe Pavetteae showed that the monospecific genus *Homolliella* Arènes is nested within *Paracephaelis* (De Block *et al.* 2015). Unlike the other species of *Paracephaelis*, *P. sericea* (Arènes) De Block (*Homolliella sericea* Arènes) occurs in humid evergreen forest in the High Plateau region in Madagascar. The species is more robust in all aspects, e.g., stipules, leaves, flowers, and fruits, and differs further by the calyx tube which is much longer than the calyx lobes (vs a short calyx tube and calyx lobes longer than or equal in length to the tube in the other four species of *Paracephaelis*). Despite these ecological and morphological differences, molecular evidence clearly places *P. sericea* in *Paracephaelis* (De Block *et al.* 2015).

Species of *Paracephaelis* (Fig. 1) have terminal, usually sessile inflorescences, all parts of which are densely pubescent. Flowers (ovaries, calyces, and corollas) are also densely pubescent and fruits are at least moderately pubescent. Most species have pubescent stems, stipules, and leaves, and the calyces are well-developed, either with the calyx tube longer than the calyx lobes or vice versa. They are further characterized by laterally flattened seeds with a shallow, linear or elongate hilum and entire endosperm, ovules that are positioned at the periphery of the placenta, and pollen with supratectal microgemmae (De Block & Robbrecht 1998; De Block 2003).

In this revision, thirteen new species of *Paracephaelis* are presented. All species of *Paracephaelis* are described in detail and illustrated. A distribution map, provisional conservation assessment, and list of exsiccatae are given. The range of variation in the characters of the genus is discussed and a determination key is provided.

Material and methods

Methods follow normal practice of herbarium taxonomy (De Vogel 1987). Vegetative characters are described based on herbarium material. Description and sizes of flowers and fruits cover the range of dried and alcohol-preserved material and their colours are given for living material. In the absence of flowers, certain characters such as size and shape of the ovary, calyx tube and calyx lobes were scored on young or aborted fruits. Flowering and fruiting periods are based on dates given on the labels of the herbarium material. Terminology generally follows Robbrecht (1988) but leaf shape is described according to the terminology of simple symmetrical plane shapes (Anonymous 1962). Following Robbrecht (1988: 74), the calyx is considered restricted to the structures above the ovary/hypanthium. The calyx tube then corresponds to the unlobed, basal, tubular portion of the calyx. The characters of the ovary (hypanthium) are given separately in the descriptions.

Herbarium specimens of the following institutions were studied: BR, G, K, MO, P, S, TAN, TEF, and WAG; herbarium acronyms follow Index Herbariorum (Thiers continuously updated). All material cited was seen, except when stated otherwise (n.v. = material not seen; online = seen at a virtual herbarium site; scan = scan of specimen received). Material collected by staff of the Malagasy Service des Eaux et Forêts was given consecutive numbers in the series SEFM (suffix -SF) and CRNPNM (suffix -RN). When possible, the names of the individual collectors were retrieved from Dorr (1997). Plant material studied is listed per province, with provinces listed from north to south and from east to west. Within each province, regions are listed alphabetically, as are districts. Within each district, specimens are listed alphabetically per collector. Localities are cited as given by the collectors on the specimen labels, but regions and districts have been added in order to reflect the new administrative division of the country. If no GPS coordinates were available on the label, coordinates of localities were determined using

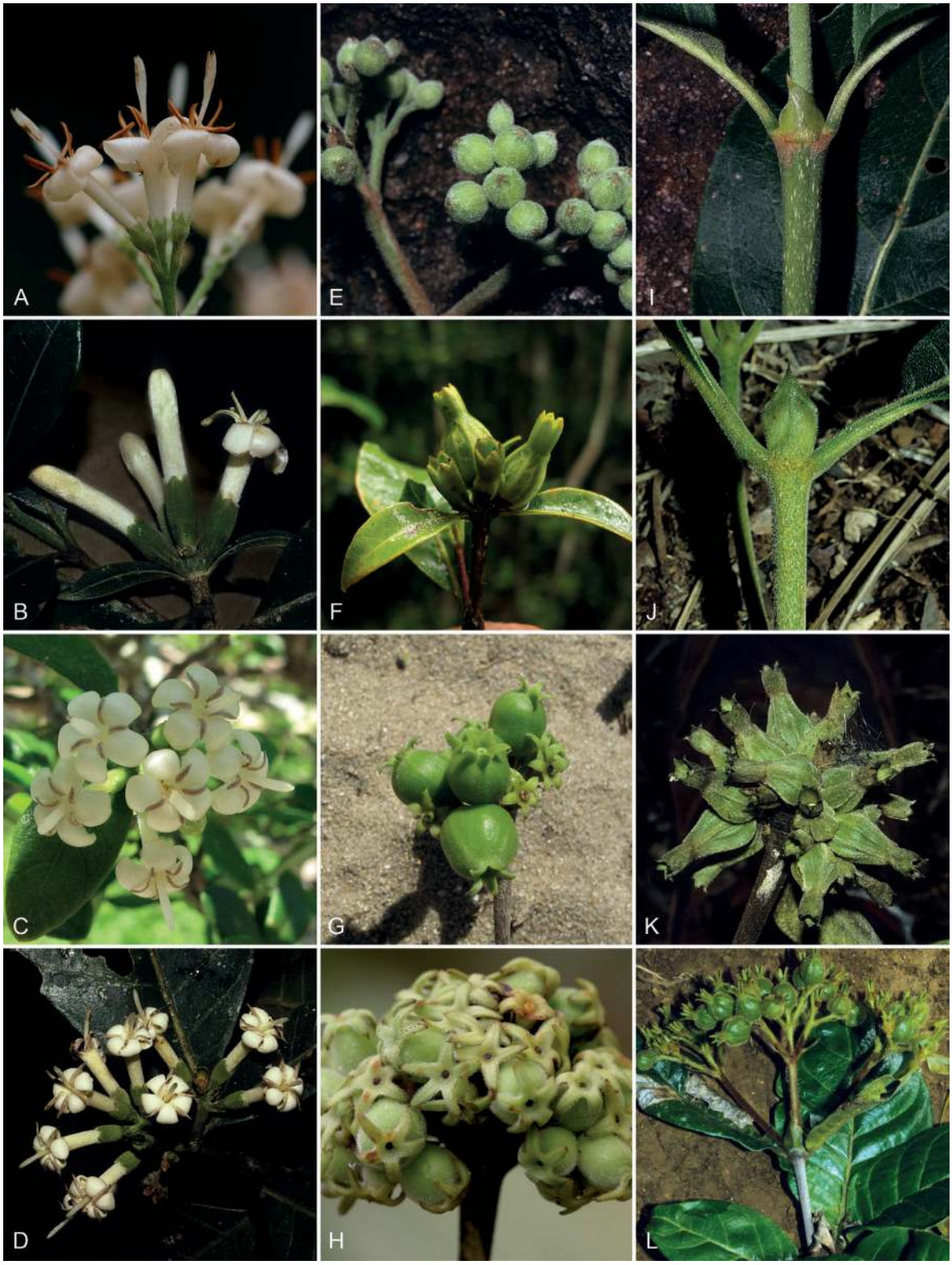

Fig. 1. Flowers, fruits and stipules of *Paracephaelis* Baill. **A–D**. Inflorescences. **E–H**. Fruits. **I–J**. Stipules. **K–L**. Infrutescences. **A, E, I**. *P. cinerea* (A.Rich. ex DC.) De Block. **B**. *P. pauciflora* De Block sp. nov. **C, G**. *P. saxatilis* (Scott Elliot) De Block. **D**. *P. sericea* (Arènes) De Block. **F**. *P. ranirisonii* De Block sp. nov. **H**. *P. tiliacea* Baill. **J–K**. *P. capitulifera* De Block sp. nov. **L**. *P. russata* De Block sp. nov. Photographs: P. De Block (B–E, G, I–L); S. Dessein (A, H); L. Gautier (F).

the online Gazetteer to Malagasy Botanical Collecting Localities (Schatz *et al.* 2003). Also, 1:500 000 maps from the Malagasy Institut National de Géodésie et Cartographie were used. Distribution maps were drawn using QGIS Desktop ver. 3.4.11 (QGIS Development Team 2020) or GeoCAT (Geospatial Conservation Assessment tool; Bachman *et al.* 2011). The conservation status was assessed by applying the IUCN Red List Category criteria (IUCN 2017) using GeoCAT. Cell size has been chosen at 2 × 2 km as suggested by IUCN.

Abbreviations

coll. ignot.	=	collector unknown
fir.	=	firaisana (canton)
fkt.	=	fokotany (smallest territorial subdivision recognized in Madagascar, consisting of one or more villages)
fl	=	flowering
fr	=	fruiting
PK	=	point kilométrique
PN	=	Parc National
RN	=	Route Nationale
RNI	=	Réserve Naturelle Intégrale
RS	=	Réserve Spéciale
s.dat.	=	without date
s.loc.	=	without locality
st	=	sterile

Results

Taxonomic history

Paracephaelis was described based on a single collection, *Pervillé 633*, from Ambongo (Mahajanga, Madagascar), which was "malheureusement fortement incomplète" (Baillon 1879: 315). As a result, Baillon's description of the characters of *Paracephaelis* and its type species, *P. tiliacea*, was quite sketchy. Furthermore, he wrongly interpreted the aestivation of the corolla lobes as valvate. Some eighty years later, Arènes (1960) was able to complement the description of the genus after more herbarium material came at his disposal. He noted the overall pubescence of the inflorescence parts but wrongly described the corolla aestivation as imbricate, the stigma as bilobed, and the seeds as winged. Arènes (1960) also published the monospecific genus *Homolliella*, which is now considered to be part of *Paracephaelis* (De Block *et al.* 2015). At the same time, he described *Homollea* Arènes, comprising three species. Both genera were dedicated to Homolle who had previously identified them but had not published them. Arènes commented upon the close relationship between *Homolliella* and *Paracephaelis*, providing characters to distinguish them. Most of these were based on wrong observations (e.g., stamens and style included in the corolla tube, stigma bilobed, and seeds winged in *Paracephaelis* vs stamens and style excluded, stigma undivided, and seeds not winged in *Homolliella*).

When describing *Paracephaelis*, Baillon (1879, 1880) expressed doubt as to its exact position within the Rubiaceae, but, because of its capitate inflorescences and 'valvate' aestivation, placed the genus near *Nauclea* L. and *Sarcocephalus* Afzel. ex R.Br. in the tribe Naucleeae. Arènes (1960) transferred *Paracephaelis* to the tribe Gardenieae and placed *Homollea* and *Homolliella* in the same tribe. Later on, Ridsdale (1978), a specialist of the tribe Naucleeae, confirmed that *Paracephaelis* was not a member of the Naucleeae as suggested by Baillon. Capuron (1973), in his unpublished treatment of the Rubiaceae of Madagascar and the Comores, sank *Paracephaelis*, *Homollea*, and *Homolliella* in the tribe Ixoreae. His tribal concept was wide, the tribe Ixoreae including genera of the current tribes Pavetteae, Coffeeae, Gardenieae, Octotropideae, and Ixoreae. Capuron's Ixoreae s. lat. (correct name Coffeeae s. lat.:

Robbrecht 1984) coincided with the Gardenieae s. lat. of earlier authors (Hooker 1873; Schumann 1891). Robbrecht (1984) segregated from this large complex the tribe Pavetteae comprising genera with terminal inflorescences, 3- or 4-colporate tectate pollen grains, small bilocular drupes with one to many seeds freely surrounding the placenta and having a hilar cavity surrounded by an annulus and exotestal cells either parenchymatic or with thickenings along the outer tangential wall. Bridson & Robbrecht (1985) tentatively included *Homollea*, *Homolliella*, and *Paracephaelis* in the Pavetteae, a position which was confirmed later by molecular studies (De Block *et al.* 2015). Bridson & Robbrecht (1985) noted that the three genera have laterally flattened seeds with entire endosperm and an elongate to linear, shallow hilum.

Within the modern concept of the tribe Pavetteae, Homolle (1938) and Capuron (1973) recognized only two genera in Madagascar: *Enterospermum* Hiern (current name *Coptosperma* Hook.f.; De Block *et al.* 2001), characterized by seeds with ruminate endosperm, and *Tarenna* Gaertn., characterized by seeds with entire endosperm. Within the genus *Tarenna*, Homolle (1938) recognized a separate section "*Cinerescens*" comprising species characterized by a reduced placenta and seeds with an elongate shallow hilum ("graines non ombiliquées"). In this section she included *Paracephaelis cinerea* (as *Tarenna cinerea* (A.Rich.) Homolle) and *Paracephaelis comorensis* sp. nov. (as *Enterospermum comorense* Homolle). However, because of the lack of a Latin diagnosis or description, the name was not validly published (see Note 1 of genus *Paracephaelis*). Like Homolle, Capuron in his unpublished revision of the Rubiaceae of Madagascar and the Comores (1973) was well aware of the great variation in *Tarenna* and recognized five sections, three of which (section "*Cinereae*", section "*Homollea*", and section "*Paracephaelis*") consisted of species characterized by laterally flattened seeds with a shallow elongated hilum. Capuron (1973) mainly used placentation characters to separate these three sections. He characterized section *Cinereae* by placentas attached to the top of the septum with (1–)2–4 ovules pendulous from its lower margins. This section comprised a single species, which is now named *Paracephaelis cinerea*. Section *Paracephaelis* was characterized by large placentas attached to the middle of the septum, with (2–)4–7(–10) ovules positioned at the periphery of the placenta. Capuron included five species in this section, including the type species of *Homolliella.* All five species belong to *Paracephaelis* as circumscribed in the current paper. Section *Homollea* was characterized by placentas attached to the base of the septum with 2–3 collateral ovules ascending from their superior margin. This section corresponds to Arènes' genus *Homollea* and according to Capuron included three species. Recently, De Block (2018) described two further species in *Homollea* and amended the placentation data: placentas attached to the middle or somewhat below the middle of the septum, with 2–7 ovules arising from the superior margin.

As "a practical way to deal with a poorly known group including different elements pending an in-depth study", Bridson (1979: 377; 1988) also included species with ruminate endosperm (*Enterospermum*) in *Tarenna*. She recognized six informal infrageneric groups for the continental African representatives of *Tarenna*, mainly based on differences in placentation and seed structure. Since her study did not take into account Malagasy taxa, the genera *Homollea* and *Homolliella* were not mentioned. However, Bridson's infrageneric group VI, characterized by pubescent corollas, seeds with a shallow elongated hilar groove, and 2–3 ovules pendulous from a small placenta, consisted of a single species *Tarenna trichantha*, which is now known as *Paracephaelis trichantha*.

While often included in *Tarenna*, some botanists considered *Homollea*, *Homolliella*, and *Paracephaelis* to be separate genera closely allied to *Tarenna*. Capuron (1973) left open the possibility that, based on seed and placentation characters, these three groups might merit recognition at generic level. Bridson & Robbrecht (1985) accepted *Homollea*, *Homolliella*, and *Paracephaelis* as distinct genera, closely allied to *Tarenna*. This was also the case for De Block (De Block 1997, 2003; De Block & Robbrecht 1998), who considered the three genera to be closely related because of the typical placentation with ovules at the periphery of the placenta, the laterally flattened seeds with entire endosperm and shallow elongate hilum, and the pollen with supratectal elements.

A recent molecular phylogenetic study (De Block *et al.* 2015), showed the close relationship between *Homolliella* and *Paracephaelis* which formed a well-supported monophyletic clade. With *Homolliella sericea* nested within *Paracephaelis*, the genus was placed in synonymy with the latter. *Homollea* was also retrieved as a monophyletic lineage but its relationship with the *Paracephaelis*-*Homolliella* clade remained unresolved. A molecular study focusing on the Afro-Malagasy species of the Pavetteae (De Block *et al.* 2018) showed that, despite the morphological characters they have in common, *Paracephaelis* and *Homollea* are not sisters. In fact, *Paracephaelis* was poorly supported as sister to a clade consisting of two strongly supported subclades, the first one comprising the genus *Homollea* and three newly described genera *Exallosperma* De Block, *Helictosperma* De Block, and *Pseudocoptosperma* De Block and the second subclade comprising a number of species of *Coptosperma* including the type C. *nigrescens* Hook.f. and the newly described genus *Tulearia* De Block. While these four recently described genera do not share seed and pollen characters with *Homollea* and *Paracephaelis*, three of them (with the exception of *Pseudocoptosperma*) have similar placentation with the ovules arranged at the periphery of the placenta (De Block *et al.* 2018).

Baillon (1879) recognized a single species at the time of publication of the genus *Paracephaelis*. During the 1960's and 70's, Leroy from the Muséum national d'histoire naturelle in Paris worked on the Rubiaceae of Madagascar. He was of the opinion that *Paracephaelis* was larger than the single species hitherto described and that it consisted of at least four species. He marked the names *P. recurva*, *P. diegoensis*, and *P. calyptroides* on specimens in P but did not formally publish the new species. In 2003, based on morphological characters, De Block (2003) transferred two Malagasy species and one species from East Africa and the Seychelles from *Tarenna* to *Paracephaelis*, formally bringing the species number of the genus up to four (*P. cinerea*, *P. saxatilis* and *P. trichantha*). In 2015, *Homolliella sericea* was transferred to *Paracephaelis* based on molecular data (De Block *et al.* 2015). In the current paper, 13 new species are described bringing the species number of *Paracephaelis* up to 18.

Characters of Paracephaelis

Habit

Paracephaelis comprises small to large shrubs and trees. In dry vegetation types, the height of the plants usually ranges between one and eight meters. Some species, occurring in more humid vegetation types, are trees of greater height. Trees up to 20 m tall and a dbh (diameter at breast height) of 35 cm are found in *P. capitulifera* sp. nov., *P. pauciflora* sp. nov., *P. sericea*, and *P. grandifructa* sp. nov. from high plateau or mid-elevation humid forest, and in *P. orientalis* sp. nov. and *P. sambavensis* sp. nov. from littoral or lowland humid forest. *Paracephaelis tiliacea* (Fig. 21A) is the only species within the genus to show a *Terminalia*-branching pattern. Branches are sympodial and plagiotropic by apposition. Growth is episodical. Branch modules consist of a long first internode, horizontal in orientation. Distally, the internodes become progressively shorter and the apical meristem is reoriented, producing an erect short-shoot. A lateral meristem takes over the further extension of the branch, while the apical meristem of the short-shoot forms an inflorescence. This growth model agrees with the Fagerlind model of Hallé *et al.* (1978). In *P. tiliacea*, two lateral meristems sometimes take over the growth after the short-shoot produces an inflorescence (Fig. 21B). *Terminalia*-branching occurs in several Malagasy Pavetteae from dry deciduous or semi-deciduous forests, e.g., in *Schizenterospermum* Homolle ex Arènes, *Exallosperma*, and *Helictosperma*. According to Hallé *et al.* (1978), trees of this architecture are usually relatively small, restricted to the understory of the forest and designed to produce small numbers of seeds at frequent intervals.

Pubescence

All species of *Paracephaelis* have densely pubescent inflorescence and flower parts. Most also have densely pubescent vegetative parts. The pubescence varies from short appressed to long erect hairs. The

colour of the pubescence is white, reddish or tawny. The pubescence of both vegetative and reproductive parts yields good identifying characters at species level.

Shoots and branches

Young shoots are somewhat flattened, often bisulcate and usually densely pubescent. They are glabrous in *P. comorensis* sp. nov. and *P. gautieri* sp. nov., usually glabrous in *P. orientalis* sp. nov., and sometimes glabrous in *P. cinerea* and *P. trichantha*. Older branches are usually terete, glabrescent to glabrous, with the bark greyish, fawnish, greyish brown, reddish brown or brown and often somewhat flaking. Internodes are short (0.3–2.5 cm long) in branches of *P. aristata* sp. nov. and *P. gautieri* sp. nov. as well as in flowering branches of *P. saxatilis* and *P. tiliacea* (<1 cm long) and *P. seyrigii* sp. nov. (<2 cm long).

Leaves

In *P. saxatilis*, *P. seyrigii* sp. nov., and *P. tiliacea*, the leaves are grouped at the end of lateral shoots. Leaves may be deciduous in *P. cinerea* and *P. tiliacea*. Sometimes leaves are anisophyllous. This is the case in specimens of *P. cinerea* and *P. grandifructa* sp. nov.

Petiole length varies between 2 and 30 mm with some species consistently having short petioles. This is the case for *P. aristata* sp. nov., *P. bardotiae* sp. nov., *P. gautieri* sp. nov., *P. longipedicellata* sp. nov., *P. ranirisonii* sp. nov., and *P. saxatilis*, the petioles of which range between 2 and 6 mm in length. The petioles are canaliculate above and usually variously pubescent. In rare cases, the petioles are glabrous (e.g., in *P. gautieri* sp. nov., *P. orientalis* sp. nov., or rarely in *P. cinerea*).

Leaf shape and size is variable. Leaves vary in length between 1 and 23 cm and between 0.5 and 13 cm in width. In *P. aristata* sp. nov. and *P. gautieri* sp. nov., the leaves are consistently narrowly obovate or narrowly elliptic and leaf width does not exceed 1.7 cm. In *P. saxatilis*, the leaves are ≤4 cm long (size 1–4 × 0.7–2.8 cm), an easy differentiating character. Leaves are broadly elliptic, broadly ovate or orbicular with bases (strongly) cordate or unequally truncate in *P. tiliacea* (size: 7–20 × 5–15 cm). Orbicular or suborbicular leaves are also sporadically found in *P. cinerea*, *P. saxatilis*, *P. seyrigii* sp. nov., and *P. trichantha*, but in most species leaves are elliptic, obovate, ovate, more rarely narrowly elliptic, narrowly obovate or narrowly ovate. Leaf bases can be attenuate, cuneate, acute, obtuse, unequal, rounded, truncate or cordate. Leaf tips are almost exclusively acuminate with the acumen 3–20 mm long in ten of the 18 species. But the leaf tips are rounded to obtuse, and often mucronulate, or retuse in *P. bardotiae* sp. nov., *P. gautieri* sp. nov., *P. ranirisonii* sp. nov., *P. saxatilis*, and *P. trichantha*. *Paracephaelis aristata* sp. nov. is named for the aristate leaf tip. In *P. cinerea* and *P. seyrigii* sp. nov., the leaf tips are variable. Leaf margins are revolute in dry specimens and sparsely ciliate in some species, e.g., in *P. bardotiae* sp. nov., *P. cinerea*, *P. pauciflora* sp. nov., and *P. trichantha*.

The leaves of most species of *Paracephaelis* are coriaceous. They are papyraceous to subcoriaceous in *P. comorensis* sp. nov., *P. longipedicellata* sp. nov., *P. russata* sp. nov., and *P. tiliacea*, and, subcoriaceous in *P. cinerea*. Leaves are often somewhat bullate (in dried state) in *P. capitulifera* sp. nov. Generally, the leaves of *Paracephaelis* are pubescent. Usually, the upper leaf surface is sparsely to densely covered with minute to short erect hairs, the lower leaf surface moderately to densely covered with minute, short or long erect hairs. But some species have different pubescence and this can be a good differentiating character at species level. As regards the pubescence on the lower leaf surface, this is sericeous in *P. ranirisonii* sp. nov. and lanate in *P. longipedicellata* sp. nov. These are the only two species in which the lower leaf surface is not visible in between the pubescence. In several species, both leaf surfaces are consistently glabrous. This is the case for *P. gautieri* sp. nov., *P. bardotiae* sp. nov., *P. comorensis* sp. nov. and, usually, *P. orientalis* sp. nov., although the midrib and secondary veins may be sparsely pubescent. *Paracephaelis aristata* sp. nov. combines a glabrous upper leaf surface with a lower leaf surface that is densely covered with long erect or spreading hairs. In *P. longipedicellata* sp. nov., *P. pauciflora* sp. nov., *P. sericea*, and

P. saxatilis, the upper leaf surface is usually variously pubescent but rarely glabrous (with hairs on midrib and secondary veins), but the lower leaf surface is always pubescent. Two species are variable in their leaf pubescence: *P. cinerea* and *P. trichantha*. In these species, the variation shows a geographical pattern (see Notes of *P. cinerea* and *P. trichantha* for further details).

The midrib is usually impressed above, over the whole leaf surface or at least in the basal half. In *P. sambavensis* sp. nov. and *P. sericea*, the midrib is raised with a central groove above. In all species, the midrib is prominently raised on the lower leaf surface. Secondary veins vary in number between 3 and 16 on each side of the midrib, depending on the size of the leaf. In *P. saxatilis*, the species with the smallest leaves, the number of secondary veins is the lowest (3–7). The secondary veins are sometimes impressed on the upper surface and usually raised on the lower surface. Pubescence of the midrib and secondary veins often differs somewhat from that on the leaf blade, e.g., hairs more appressed. Midrib and secondary veins may be sparsely to moderately pubescent on an otherwise glabrous leaf surface. Higher order venation is often obscured by the pubescence on the leaf blade or inconspicuous on both leaf surfaces, more rarely easily visible. In some species, the higher order venation may be somewhat impressed above and somewhat raised below (e.g., *P. seyrigii* sp. nov.). In *P. comorensis* sp. nov. and *P. trichantha* it is often discolorous below and somewhat paler than the lower leaf surface.

Domatia are absent in *P. aristata* sp. nov., *P. capitulifera* sp. nov., *P. longipedicellata* sp. nov., *P. ranirisonii* sp. nov., *P. russata* sp. nov., *P. saxatilis*, *P. seyrigii* sp. nov., and *P. tiliacea*, which are mostly species with densely pubescent lower leaf surfaces. In the other species, domatia are present in some leaves. Ciliate pit domatia occur in *P. bardotiae* sp. nov. and *P. gautieri* sp. nov. (lower leaf surfaces glabrous). In *P. trichantha* both ciliate pit (lower leaf surface glabrous) and hair tuft domatia (lower leaf surface pubescent) occur. The other species have hair tuft domatia in those specimens with at least some pubescence on the lower leaf surface (even if just on the midrib and secondary veins). In *P. sambavensis* sp. nov., hair tuft domatia are sometimes present in reduced form in the axils of higher order venation.

Stipules

The stipules are sheath-like, their bases fused into a cone that surrounds the stem, their upper parts free. The sheaths are triangular or ovate in shape, keeled or not, and, usually variously pubescent outside. In some species, the sheaths gradually taper into an acute or obtuse tip, e.g., in *P. pauciflora* sp. nov., or tips are acute to shortly acuminate, e.g., in *P. sericea*. In such cases, the awn is considerably shorter than the sheath and not exceeding a length of 2.5 mm. In other species, the sheaths are topped by a needle-like awn, reaching a length of up to 4 mm (e.g., *P. aristata* sp. nov., *P. bardotiae* sp. nov., *P. comorensis* sp. nov.) or even 6 mm (*P. russata* sp. nov.), but often shorter. In these species, the length of the awn may be equal to (e.g., *P. comorensis* sp. nov.) or longer than that of the sheath (e.g., *P. aristata* sp. nov., *P. bardotiae* sp. nov.), but this is somewhat variable at species level. In *Paracephaelis*, the stipular sheaths vary in length between 1 and 30 mm, the awns between 0 and 6 mm. The largest stipules are found in *P. sericea* (9–32 mm long).

In most species the inner surface of the stipules is glabrous. At the base, a single or several rows of colleters are present. In some species, the colleters are interspaced with sparse long hairs. Two species deviate from this typical pattern. Above the basal row of colleters, a sparse covering with appressed hairs occurs over the whole inner surface in *P. russata* sp. nov. but is restricted to the upper half in *P. longipedicellata* sp. nov.

In some species, only the youngest stipule pairs show the typical outer pubescence while the older ones become corky, greyish, and glabrous, e.g., in *P. seyrigii* sp. nov. and *P. tiliacea*. In these two species, but also in *P. ranirisonii* sp. nov., *P. gautieri* sp. nov., and *P. orientalis* sp. nov., the stipules are caducous, although stipular remnants remain visible on the branches.

In *P. sericea* and *P. capitulifera* sp. nov., yellow, orange-red or brown mucus (produced by the colleters inside the stipules) may be visible on the youngest stipule pair, and sometimes also covers the young inflorescences.

Inflorescences

In *Paracephaelis*, inflorescences are terminal on lateral shoots. In *P. tiliacea* and *P. seyrigii* sp. nov., they are terminal on lateral short-shoots. These short-shoots have short internodes and are covered by remnants of the caducous stipules, while the leaves have fallen. In *P. tiliacea*, terminal inflorescences become pseudo-axillary later on. Because of the *Terminalia*-branching pattern, a lateral meristem takes over the growth of the short-shoot on which an inflorescence develops, thereby placing the inflorescence into a lateral (pseudo-axillary) position. Inflorescences in *Paracephaelis* are sessile. When terminal on lateral short-shoots with the leaves fallen, the inflorescences may seem shortly pedunculate (e.g., *P. tiliacea* and *P. seyrigii* sp. nov.). However, the only truly pedunculate inflorescences occur in *P. longipedicellata* sp. nov. While sessile inflorescences are common, certain specimens of this species have peduncles up to 3 cm long. In these pedunculate inflorescences, the first order bracts are differently shaped from the first order bracts in sessile inflorescences. They are not similar to a vegetative leaf pair and stipules but strongly reduced in size, the foliar parts linear (instead of leaf-like) and less than 5 mm long.

The inflorescences in *Paracephaelis* are trichotomously branched and bracteate. Rarely, metatopic displacements can be observed. In *P. longipedicellata* sp. nov., a displacement of the first order branching 1–5 mm above the first order bracts may be observed (concaulescence: Endress 2010). In *P. cinerea* and *P. russata* sp. nov. on the other hand, the higher order bracts are sometimes displaced 1–4 mm above the branching point of the axes (recaulescence: Endress 2010). Usually, either the inflorescence as a whole or the partial inflorescences are compact. This trend culminates in the capitate inflorescences of *P. capitulifera* sp. nov. and *P. grandifructa* sp. nov. The only exception is *P. longipedicellata* sp. nov., which has lax inflorescences. Inflorescence size varies between 0.5 and 10 cm in length and 1 and 13 cm in width (measured without flowers or fruits). First order axes are between 0.2 and 7 cm long. Most species have numerous flowers per inflorescence. Lower flower numbers occur in *P. aristata* sp. nov., *P. bardotiae* sp. nov., and *P. pauciflora* sp. nov. (3–15 flowers), *P. gautieri* sp. nov., *P. grandifructa* sp. nov., *P. longipedicellata* sp. nov., *P. ranirisonii* sp. nov., *P. saxatilis*, and *P. orientalis* sp. nov. (5–60 flowers). Uniflorous inflorescences are rarely encountered in *P. longipedicellata* sp. nov. Flowers are sessile (*P. capitulifera* sp. nov., *P. grandifructa* sp. nov., *P. orientalis* sp. nov., *P. ranirisonii* sp. nov., and *P. seyrigii* sp. nov.) or shortly pedicellate (0–3(–6) mm long in flowering stage), except in *P. longipedicellata* sp. nov. which has pedicels 8–20 mm long. In some species, the pedicels elongate considerably in fruiting stage. This is the case in *P. sambavensis* sp. nov. (pedicels 1–2 mm long when flowering, up to 5(–8) mm long when fruiting), *P. bardotiae* sp. nov. (0.5–3 mm vs 0.5–7 mm long), and *P. russata* sp. nov. (0–5 mm vs 0–12 mm long). All inflorescence axes, including pedicels, are densely pubescent. This is also the case for the outer surface of higher order bracts and bracteoles and the outer surface of all flower parts (ovary, calyx, and corolla). Axes, pedicels, bracts, and bracteoles are green in living condition.

Bracts and bracteoles are here described as consisting of stipular and foliar parts, i.e., the parts that are in the same position as the stipules and the leaves on a vegetative node, respectively. With the exception of the pedunculate inflorescences in *P. longipedicellata* sp. nov., the first order bracts (the pair of bracts supporting the entire inflorescence) are similar to a vegetative leaf pair and stipules. The foliar parts resemble the vegetative leaves in shape. They may be similar in size or somewhat to considerably smaller (e.g., *P. russata* sp. nov.: leaves of first order bracts 3–12 cm long, vegetative leaves 11.5–21 cm long). Second order bracts may be identical to the first order bracts but with smaller leaves and reduced stipular parts, which is often the case for the bract pair on the central axis. Alternatively, they resemble the higher order bracts, with reduced or absent stipular parts and foliar parts triangular and vaulted, trilobed or linear, 1–10 mm long, or, more rarely, linear and leaf-like, up to 15 mm long. The inner surface of the second

and higher order bracts is usually moderately to densely covered with appressed hairs. Colleters are present in a basal row (basally in the inflorescence) or as 2 basal marginal clusters of 1 to few colleters (higher up in the inflorescence).

Flowers

The flowers of *Paracephaelis* are actinomorphic and 5-merous. Aestivation is contorted to the left.

Calyx

In some species, the calyx tube is much longer than, or, more rarely, equal in length to the lobes, which are triangular, ovate or quadrangular to somewhat oblong. This is the case for a number of Malagasy species, mostly occurring in East and Central Madagascar (exception *P. longipedicellata* sp. nov. from northern Madagascar). Calyx tubes are 3–12 mm long in *P. capitulifera* sp. nov., *P. grandifructa* sp. nov., and *P. pauciflora* sp. nov., and, 2–5 mm long in *P. sericea*, with the calyx lobes 0.5–2.5 mm long. In *P. orientalis* sp. nov. and *P. ranirisonii* sp. nov., the calyx tube ranges between 1.5 and 2.5 mm with the lobes 1–2 mm long. In *P. sambavensis* sp. nov. and *P. longipedicellata* sp. nov., the calyx tube is only slightly longer than or equal in length to the lobes (0.7–1.5 mm long). With the exception of *P. ranirisonii* sp. nov., all these species grow in humid vegetation types. The other species of *Paracephaelis* have calyx tubes that are (much) shorter than the lobes, which are narrowly triangular or oblong. Calyx lobes 1.5–4 mm long are found in *P. aristata* sp. nov., *P. bardotiae* sp. nov., *P. russata* sp. nov., and *P. tiliacea* with the calyx tube up to 1.5 mm long. In *P. gautieri* sp. nov., *P. saxatilis*, and *P. seyrigii* sp. nov., the calyx tube is up to 1 mm and the calyx lobes up to 2 mm long. The smallest calyces are found in *P. cinerea*, *P. comorensis* sp. nov., and *P. trichantha* (tubes 0.2–0.6 mm and lobes 0.25–1 mm long). All these species with short calyx tubes and narrow calyx lobes grow in dry deciduous or semi-deciduous vegetation types. They occur mostly in northern, southern or western Madagascar. The two non-Malagasy species of *Paracephaelis* also belong to this group. In some species, accrescent calyces were observed. The calyx lobes grow in fruiting stage in *P. seyrigii* sp. nov., while the calyx tube is accrescent in *P. orientalis* sp. nov. and *P. ranirisonii* sp. nov. In *P. aristata* sp. nov., both calyx tube and lobes grow in fruiting stage. The calyx is densely pubescent outside, with the hairs varying from short and appressed to long and erect. The inner surface of the calyx tube and lobes is rarely glabrous, e.g., in *P. aristata* sp. nov. (tube and lobes glabrous) and *P. sambavensis* sp. nov. (lobes glabrous). In most species, however, the inner surface is densely covered with minute to long appressed hairs. Colleters are absent from the calyx tube, although single colleters are sometimes present in the sinuses of the calyx lobes in *P. bardotiae* sp. nov. Calyx lobes are closely joined but do not overlap at their bases. The calyx is green in living plants.

Corolla

The corolla tube is narrowly cylindrical and its outer surface is densely covered with ± long appressed hairs. The inner surface of the corolla tube is at least partly pubescent, usually in its upper half, with long, erect or spreading hairs. The pubescence is not visible in the throat and the inner surface of the corolla lobes is glabrous. The corolla tube varies in length between 3.5 and 33 mm. The smallest flowers are found in *P. trichantha* (tube 3.5–6 mm and lobes 1.2–2 mm long), the largest ones in *P. sericea* (tube 6–17 mm and lobes 5–8 mm long) and *P. pauciflora* sp. nov. (tube 11–33 mm and lobes 5–9 mm long). The corolla tube is always longer than the corolla lobes, which are oblong with a blunt tip. The corolla is greenish white in bud, white at anthesis and turns yellowish with age.

The stamens are inserted in the sinuses of the corolla lobes at the level of the throat, except in *P. longipedicellata* sp. nov., where they are inserted ca 1 mm below the level of the throat. The anthers are linear, sagittate at the base, basifixed or basimedifixed and the connective continues into a short sterile apical appendix (up to 0.5 mm long). Anther length varies between 1.5 and 8 mm. The smallest anthers are found in *P. trichantha* (1.5–2 mm long), the longest ones in *P. longipedicellata* sp. nov.

(ca 8 mm long), *P. pauciflora* sp. nov., and *P. sericea* (5–7 mm long). Usually, the anthers are completely exserted at anthesis, or their bases (ca 1 mm) remain included in the corolla tube. The one exception is *P. longipedicellata* sp. nov., the anthers of which are included in the corolla tube for 2–2.5 mm at their bases. The exserted part (5.5–6 mm long) is spirally twisted, a feature absent from all other species in the genus. The anthers are (sub)sessile or have short filaments, usually 0.1–1(–1.5) mm long. The exception is *P. orientalis* sp. nov. with filaments 2–2.5 mm long. This is the only species in the genus in which the connective (but not the filament) is sparsely covered with appressed hairs. In *P. cinerea* and *P. trichantha*, the connective often dries reddish brown.

The ovary is cupular, bilocular, 0.75–3 mm long, green in living condition and densely pubescent with the same variation in pubescence type as the calyx. In certain species, the ovary is longitudinally ribbed when dried, e.g., in *P. gautieri* sp. nov., *P. grandifructa* sp. nov., *P. pauciflora* sp. nov., *P. saxatilis*, and *P. sericea*. The axile placentas are attached to the middle or the upper half of the septum and the ovule number per locule varies from 1 to 14. Two placentation types can be distinguished. In *P. cinerea*, *P. comorensis* sp. nov., and *P. trichantha*, 1–5 ovules are pendulous from the base of a small placenta (Fig. 2I–K). In the other species, the number of ovules per locule usually is higher and the ovules are distributed around the periphery of the placenta (Fig. 2A–E, A'). Rarely, some ovules occur on the abaxial surface of the placenta (e.g., in *P. tiliacea*). The highest ovule numbers are found in *P. aristata* sp. nov. (6–10), *P. grandifructa* sp. nov. (7–14), *P. pauciflora* sp. nov. (6–9), and *P. tiliacea* (4–10). Low ovule numbers occur in, e.g., *P. gautieri* sp. nov., *P. sambavensis* sp. nov. (3–4), and *P. russata* sp. nov. (1–4). In case of few ovules, these may be restricted to the top of the placenta (Fig. 2F–H), similar to the placentation in the genus *Homollea* (De Block 2018).

Style and stigma are exserted from the corolla tube for 2–17 mm at anthesis. The style is slender and moderately to densely covered with ascending or erect hairs from below the level of the papillae to somewhat above the base. The stigma is bilobed but the lobes are permanently fused over their entire length, with only the very tips free. Papillae are present in the longitudinal grooves along the lines of fusion of the stigmatic lobes. In most species, the fused stigmatic lobes are not conspicuously thickened. In *P. cinerea*, *P. comorensis* sp. nov., *P. trichantha*, *P. saxatilis* and *P. seyrigii* sp. nov., the upper 1.5–3 mm of the stigma is fusiform. In the first three species, the papillate grooves run along the thickened part of the stigma and further down along the thin 'style' for ca 1–2 mm. In *P. saxatilis* and *P. seyrigii* sp. nov., however, the papillate zone only starts below the thickened part of the stigma. In *Paracephaelis*, the papillate zones are between 2.5 and 16 mm long. A considerable part of the receptive zone is situated below the thickened part of the stigma or included within the corolla tube at anthesis. Inclusion of papillate zones in the corolla tube occurs especially in species with long stigmatic lobes, e.g., in *P. pauciflora* sp. nov. In this species, style and stigma are exserted for 2–6 mm at anthesis and the papillate zone is 7–15 mm long, meaning that papillate grooves are included in the corolla tube for 5–10 mm. The papillate grooves often become wider further down, and, at their bases, almost the entire circumference of the stigma is receptive. As a result, an insect with a long, pollen-covered proboscis reaching into the corolla tube would always come into contact with the receptive zone.

Fruits

The fruits are bilocular drupes, spherical or ovoid in shape, and crowned by the persistent calyx. Certain species possess small, spherical fruits, ca 0.5 cm in diameter (e.g., *P. cinerea*, *P. comorensis* sp. nov., *P. saxatilis*), while others have larger ovoid fruits up to 2 cm long (measured without the persistent calyx; e.g., *P. sericea*: 10–12 × 8–11 mm; *P. grandifructa* sp. nov.: 15–20 × 10–15 mm).

The exocarp is moderately to densely pubescent. The somewhat larger fruits are often longitudinally ribbed (when dried). Fruits are recorded as green by collectors for most species of *Paracephaelis*. They are reported as black when mature in *P. saxatilis* (1 record) and *P. trichantha* (3 records). When the fruits are

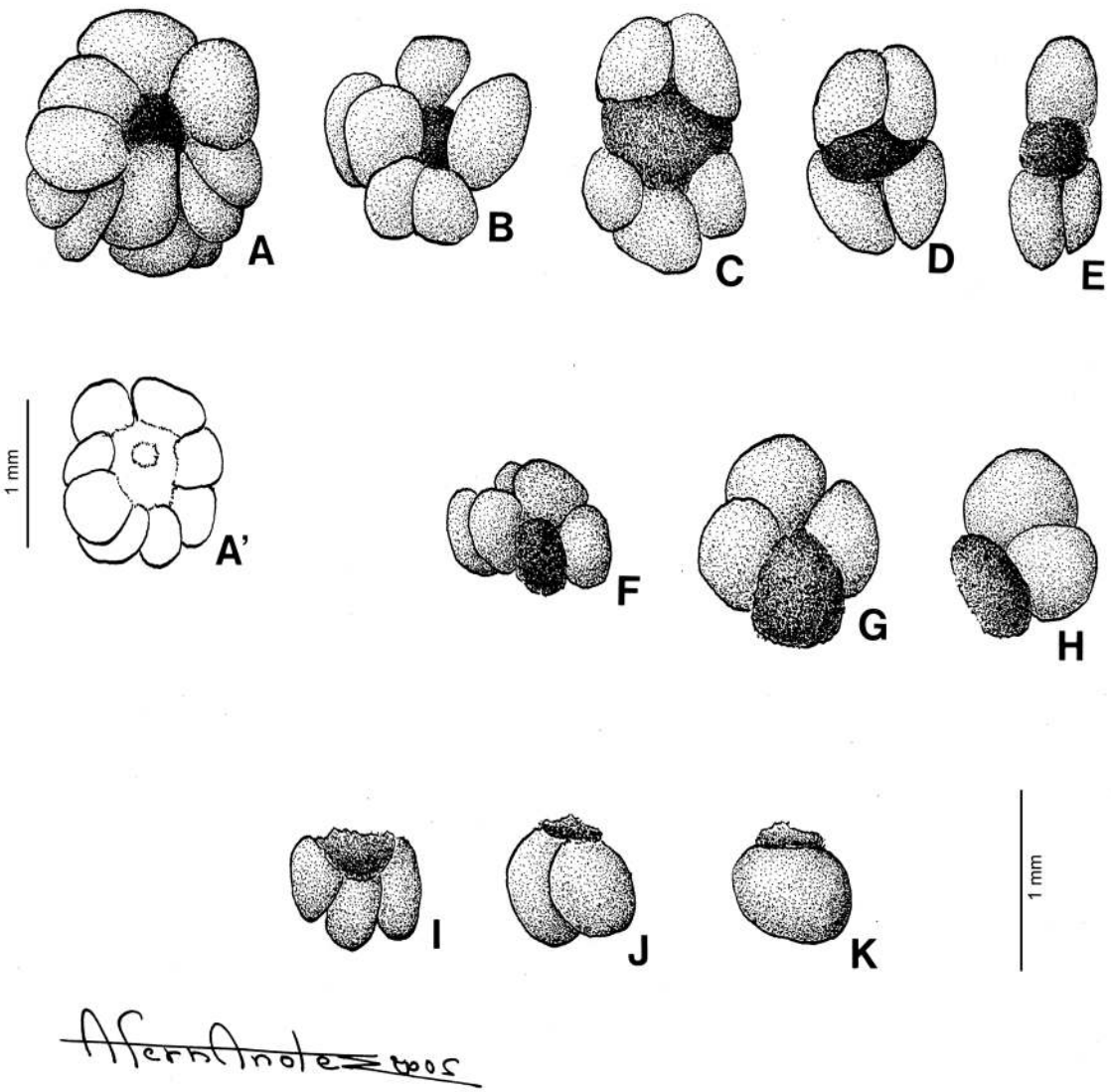

Fig. 2. Overview of the placentation in *Paracephaelis* Baill. **A–K**. Abaxial views of placenta and ovules. **A'**. Adaxial view of placenta and ovules with zone of attachment of the placenta indicated. **A–C**. Typical placentation type of *Paracephaelis*, with many ovules arranged at the periphery of the placenta. **D–E**. Idem, with fewer ovules. **F–H**. Idem, but ovules restricted to the top of the placenta. **I**. Typical placentation type in *P. cinerea* (A.Rich. ex DC.) De Block, *P. comorensis* De Block sp. nov. and *P. trichantha* (Baker) De Block. **J–K**. Idem, with fewer ovules. Drawn by Mr A. Fernandez. From *Perrier de la Bâthie 13452* (*P. tiliacea* Baill., A, A'); *Pervillé 633* (*P. tiliacea* Baill., B); *Capuron 23451-SF* (*P. longipedicellata* De Block sp. nov., C); *McPherson et al. 14875A* (*P. saxatilis* (Scott Elliot) De Block, D); *Gautier et al. 4188* (*P. gautieri* De Block sp. nov., E); *De Block et al. 1280* (*P. bardotiae* De Block sp. nov., F); *De Block et al. 1048* (*P. russata* De Block sp. nov., G–H); *Capuron 23073-SF* (*P. cinerea* (A.Rich. ex DC.) De Block, I); *Barthelat et al. 732* (*P. comorensis* De Block sp. nov., J); and *Labat & Pascal 2887* (*P. comorensis* De Block sp. nov., K).

ripe, the vascular bundles in the mesocarp are sclerified. The mesocarp is relatively thin in, e.g., *P. cinerea*, *P. comorensis* sp. nov., and *P. longipedicellata* sp. nov., but in others the mesocarp is well-developed, consisting of a multi-layered anastomosing network of sclerified vascular bundles. This is the case in the humid forest species *P. pauciflora* sp. nov., *P. sericea*, *P. grandifructa* sp. nov., and *P. capitulifera* sp. nov.

Each fruit contains two pyrenes, each comprising one to several seeds. The pyrenes are hemispherical or hemi-ovoid in shape, with a flat adaxial and a convex abaxial side, papyraceous to thinly crustaceous adaxially and crustaceous to somewhat stony abaxially. The pyrenes vary in shape and size (3–10 mm long) depending on the species and the size of the fruit. The base of the pyrene is rounded to truncate. The apex can be acuminate (e.g., *P. capitulifera* sp. nov.: Fig. 7F; *P. russata* sp. nov.: Fig. 16F), apiculate (e.g., *P. comorensis* sp. nov.: Fig. 9H; *P. longipedicellata* sp. nov.), acute (e.g., *P. ranirisonii* sp. nov.) or rounded (e.g., *P. pauciflora* sp. nov.; *P. grandifructa* sp. nov.). The adaxial side of the pyrene shows a small opening, which varies in position between species: somewhat below the middle (e.g., *P. grandifructa* sp. nov.; *P. bardotiae* sp. nov.), somewhat above the middle (e.g., *P. sambavensis* sp. nov.: Fig. 17E), in the upper half (e.g., *P. capitulifera* sp. nov.: Fig. 7F) or close to the apex of the pyrene (e.g., *P. comorensis* sp. nov.: Fig. 9H). From the apex of the pyrene to the top of the opening, a thin longitudinal ridge may be present. This ridge can be outspoken (e.g., *P. sericea*), weakly developed (e.g., *P. russata* sp. nov.: Fig. 16F), or absent (e.g., *P. comorensis* sp. nov.: Fig. 9H; *P. longipedicellata* sp. nov.). Below the opening in the pyrene, the longitudinal ridge may continue into a longitudinal depression (e.g., *P. capitulifera* sp. nov.: Fig. 7F). Robust pyrenes open along this longitudinal ridge and depression whereas soft pyrenes have no opening mechanism.

Seeds

The seeds in *Paracephaelis* are laterally flattened with a convex dorsal and a straight or somewhat concave ventral side (Fig. 3A–C). They are dark to reddish brown, smooth, and glossy. Ventrally, a shallow, narrowly elongate or linear hilar cavity is present, caused by the local absence of the seed-coat. The size of the seeds is 2–5 × 2–4 mm and depends partly on the number of seeds per locule, which generally varies between one and four.

The seed-coat consists of a single-layered exotesta and a multi-layered endotesta (Fig. 3E–F). The cells of the endotesta are thin-walled, not filled with tannins and usually only visible in young seeds or around the hilum of the seed. In mature seeds, the endotesta is crushed into an amorphous layer, sometimes including calcium oxalate crystals, by the growth of the endosperm (Fig. 3E–F). The exotesta cells are polygonal and isodiametrical to somewhat elongate in surface view and have straight walls (Fig. 3D). The cell lumen is filled with tannins. In most species, the thickenings of the exotestal cells are restricted to the outer tangential wall and the upper parts of the radial walls, as e.g., in *P. tiliacea* and *P. trichantha* (Bridson & Robbrecht 1985: fig. 8). But in, e.g., *P. sericea*, *P. pauciflora* sp. nov., and *P. grandifructa* sp. nov., the thickenings continue along the radial walls over practically the whole cell height (Fig. 3E). The thickenings of the exotesta cells are plate-like and continuous but in each cell a circular interruption of the thickenings occurs. This is a narrow ring-shaped intrusion from the cell lumen. In a longitudinal section the ring-like intrusion is visible as two narrow canals running to the outer edges of the cells (Fig. 3E–F). At the abaxial side of the seed the exotesta cells are between 50 and 150 µm high, depending on the species. Around the hilum the exotesta cells are elongated but, in contrast to the situation in other Pavetteae (e.g., *Leptactina* Hook.f. or *Pavetta* L.: Robbrecht 1984: figs 3–5), the thickenings do not take part in this elongation (Fig. 3F).

Pollen

The pollen grains of *Paracephaelis* are 3-zonocolporate (Fig. 4A, C). They are small, with the polar and equatorial axes 13–27 µm long. Their shape is circular to subtriangular in polar view (Fig. 4A, C). The ectocolpi are sharply demarcated, 0.5–3.3 µm wide at the equator, and have obtuse to acute ends. The

membrane is only slightly sunken and covered with granules (Fig. 4J–K). The ectocolpi are relatively long (Fig. 4A, C) with the apocolpium index 0.29–0.37. The mesoapertures are lolongate pori (Fig. 4K) or pori (Fig. 4J), 1.1–2.3 × 1.0–1.7 µm. The endoapertures are colpi (Fig. 4L), usually diverging into terminal

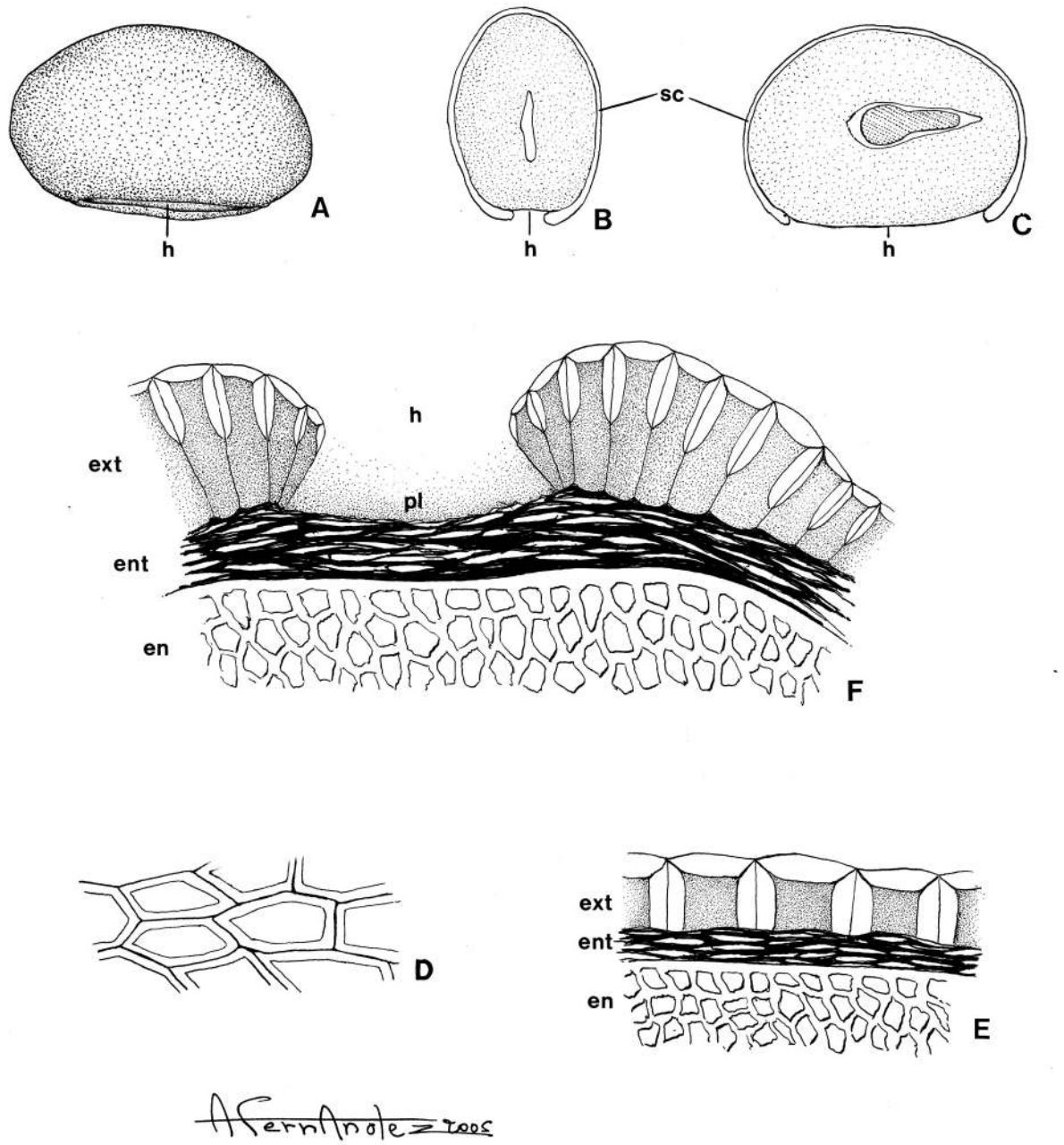

Fig. 3. Seed and seed-coat of *Paracephaelis grandifructa* De Block sp. nov. **A**. Lateral view of seed, showing the elongate, shallow hilum. **B**. Transverse section through seed, showing embryo sac. **C**. Longitudinal section through seed, showing embryo sac and embryo. **D**. Seed-coat in surface view. **E**. Section through seed-coat on the abaxial side of the seed, showing plate-like thickenings along outer tangential and lateral walls of the exotesta cells. **F**. Section through seed-coat in the region of the hilum, showing elongation of the exotesta cells. Drawn by Mr A. Fernandez. From *Solo & Randrianasolo 25*. Abbreviations: en = endosperm; ent = endotesta; ext = exotesta; h = hilum; pl = placenta; sc = seed-coat.

horns (Fig. 4M) or, more rarely, with acute ends. Sometimes, an endocingulum occurs with or without horns along its lateral sides. A prominent annular costa (Fig. 4L) is present. The sexine is usually perforate at apo- and mesocolpium (Fig. 4A–C, E–G), more rarely, it is microreticulate at the mesocolpium, e.g., in *P. saxatilis* (Fig. 4D, H–I). Supratectal elements are present in the shape of microgemmae 0.1–0.2 µm large (Fig. 4A–O; Bridson & Robbrecht 1985: fig. 7; De Block & Robbrecht 1998: fig. 3). The pollen wall (exine) varies in thickness between 0.85 and 1.3 µm. Nexine and tectum are of similar thickness or the nexine is somewhat thinner than the tectum (nexine 0.29–0.47 µm; tectum 0.37–0.47 µm). The

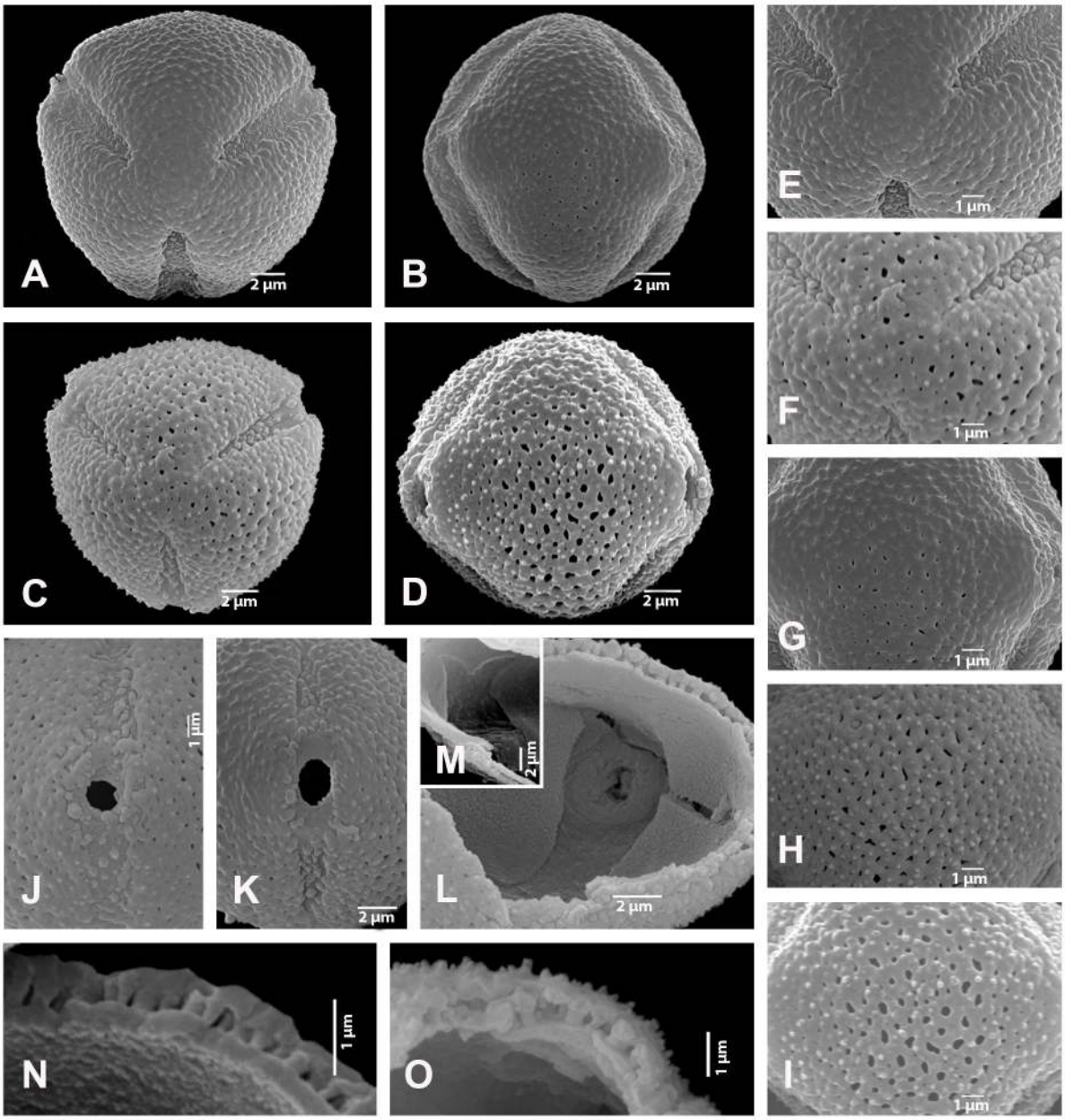

Fig. 4. Pollen of *Paracephaelis* Baill.; SEM images. **A, C**. Polar view. **B, D**. Equatorial view. **E–F**. Apocolpium. **G–I**. Mesocolpium. **J–K**. Ectocolp and mesoaperture. **L**. Endocolp with annulus. **M**. End of endocolp, diverging into terminal horns. **N–O**. Pollen wall. From *Lebosaka 9397-RN* (*P. longipedicellata* De Block sp. nov., A–B, E, G, M–N); *Dumetz 1230* (*P. saxatilis* (Scott Elliot) De Block, C–D, F, I, K); and *Capuron 20419-SF* (*P. seyrigii* De Block sp. nov., H, J, L, O).

collumelleae are shorter than the tectum and nexine or equal in height to these layers (0.14–0.47 µm long). The nexine is granular on the inside (Fig. 4L, N).

Reproductive biology

Flowering is seasonal for all species. Peaking in January and February, 90 % of all flowering takes place from November to March, even in widespread species such as *P. cinerea*. Earlier or later flowering is rare. In *P. longipedicellata* sp. nov. from northern and northwestern Madagascar, anthesis takes place in March and April, somewhat later than in the majority of the species. In *P. pauciflora* sp. nov., flowering starts in January and continues into March and even April (*Labat et al. 3079*). Later flowering takes place sporadically in, e.g., *P. seyrigii* sp. nov. (Bekily District: *Seyrig 425*: April), *P. orientalis* sp. nov. (Taolagnaro District: *Rajoharison et al. 207*: May), *P. saxatilis* (Taolagnaro District: *d'Arcy & Rakotozafy 15412*: May; *Decary 4207*: June), *P. sericea* (Taolagnaro District: *Eboroke 1043*: June), and *P. trichantha* (Aldabra Atoll: *Friedmann 4550 & 4733*: May; *Friedmann 4823*: June; *Hnatiuk 732028*: July; Kenya: *Marquis s.n.*: July). All late-flowering Malagasy specimens are from southern (Bekily) or southeastern (Taolagnaro) Madagascar, where the wet season extends from November to May and the dry season is not well-defined, with some amount of rain falling each month (Vincelette *et al.* 2007). Flowering earlier than November is equally rare as late flowering, with a few specimens of *P. saxatilis* and *P. sericea* flowering in September and October. It should be noted, though, that the accuracy of the phenological data are strongly dependant on the collecting periods, which are often restricted to the wet season.

The flowers of *Paracephaelis* are sweetly scented (e.g., *P. cinerea*: *Dorr et al. 4554*; *P. comorensis* sp. nov.: *Mouly 554*; *P. gautieri* sp. nov.: *Gautier et al. 4188*; *P. grandifructa* sp. nov.: *Messmer et al. 748*; *P. pauciflora* sp. nov.: *Schatz et al. 1941*; *P. trichantha*: *Fosberg 49388*), and flowers turn from white to yellowish with age. These two factors indicate pollination by animal vectors. Flowering is diurnal, but flowers may also be open at night (no observations). No mention of pollinators is made on collector labels and no pollinators were observed during the author's collecting activities. Flower scent, structure (3.5–33 mm long, narrowly cylindrical corolla tubes, spreading or reflexed corolla lobes, exserted style and stigma, at least partly exserted and often reflexed anthers) and colour (whitish) suggest that pollinators can be bees, butterflies or moths depending on corolla tube length and whether flowers are open at night.

Most of the Pavetteae show secondary pollen presentation (De Block *et al.* 2018). Secondary pollen presentation was noted for *P. comorensis* sp. nov. (*Mouly 554*) and observed for *P. sericea* (pers. obs.). Species showing secondary pollen presentation have proterandrous flowers: the anthers open in mature bud stage, depositing the pollen on the receptaculum pollinis, i.e., the unreceptive stigma. At anthesis, the pollen is presented to flower visitors (functionally male stage). Only later, after the self-pollen is gone, the receptive zones on the stigma become active (functionally female stage). In *P. saxatilis* and *P. seyrigii* sp. nov., the thickened part of the stigma acts as pollen presenter. Since the lines of fusion of the lobes are only papillate below the thickened part, there is spatial separation between the pollen receptive and pollen presenting surfaces of the stigma. This trend was also observed in other species of Pavetteae (De Block & Igersheim 2001).

Paracephaelis has small, fleshy, indehiscent fruits. Dispersal is probably endozoochorous as small, fleshy drupes are eaten and dispersed by frugivorous birds and small mammals. Animals are attracted by brightly coloured fruits. But fruit colours in *Paracephaelis* are not well known. They are probably greenish or brownish in several species, although black shiny fruits were observed in *P. saxatilis* and *P. trichantha*. Seed dispersal by animals and especially by birds with large home-ranges is considered highly efficient. Eriksson & Bremer (1991) showed that in the Rubiaceae the possession of drupes, which invariably means dispersal by animals, combined with the possession of a shrub habit was an extremely successful strategy. Snow (1981) indicated rubiaceous fruits as an important food source for frugivorous birds in the

tropics, especially for smaller, ± unspecialized frugivores foraging in the lower levels of the vegetation. The genus *Paracephaelis*, which consists mostly of shrubs or small trees, clearly has adopted this strategy.

Habitat, distribution, conservation

Paracephaelis occurs throughout Madagascar, along the east coast of continental Africa, and on the islands of the Comoros and the Aldabra Atoll. The genus grows in both humid and dry vegetation types over a large range of elevations.

Several species of *Paracephaelis* are under collected, with three species known from less than ten collections (*P. grandifructa* sp. nov., *P. orientalis* sp. nov., *P. russata* sp. nov.) and five known from three or less collections: *P. aristata* sp. nov., *P. bardotiae* sp. nov., *P. gautieri* sp. nov., *P. ranirisonii* sp. nov., and *P. sambavensis* sp. nov. Of these last five species, four were recently collected for the first time (from 1997 onwards) showing that the collection of plant material is still extremely relevant in Madagascar. Despite the fact that some species of *Paracephaelis* are known from only a few specimens, the IUCN category Data Deficient (DD) was avoided since it tends to underestimate the number of threatened species (Callmander *et al.* 2005, 2007).

Madagascar is known for its rich biodiversity and its high level of endemicity. The preservation of this biodiversity is a priority. However, the remaining natural habitats in Madagascar are severely fragmented and under high anthropogenic pressure (e.g., Harper *et al.* 2007). The level of poverty in the country is high, with most of the population dependent on subsistence farming for their livelihood. The main threat to the natural vegetation in Madagascar is clearing for slash-and-burn agriculture (Styger *et al.* 2007). Energy demand is also an important driver of degradation of natural vegetation with most people using firewood or charcoal as domestic energy sources. Other threats are yearly bushfires to renew grazing lands, illegal logging of hardwood, industrial and artisanal mining, hunting, sourcing of subsistence, medicinal or ornamental plant material, the spread of invasive species, and cyclones (Cardiff & Andriamanalina 2007; USAID 2014; Waeber *et al.* 2019). Because of Madagascar's high population growth, pressure on the remaining natural habitats will only increase (Nicoll 2003). With the exception of the Aldabra Atoll, which is a well-protected World Heritage site, the threats to *Paracephaelis* in the other parts of its distribution (coastal East Africa, the Comoros) are similar to those in Madagascar.

Most species of *Paracephaelis* occur in at least one protected area, which gives them a certain level of protection but is by no means a guarantee for their survival. Nearly all protected areas in Madagascar suffer encroachment by anthropogenic actions such as slash-and-burn agriculture, bushfires, grazing, logging, traditional mining, hunting, etc. (Nicoll & Langrand 1989; Hartley *et al.* 2007; Goodman *et al.* 2008; Draper 2010; Innes 2010). With little financial means and few staff and resources, the protected areas are unable to control and halt this encroachment (Nicoll & Langrand 1989; Hannah *et al.* 2008; Wingen 2011).

Of the 18 species of *Paracephaelis*, five Malagasy species are assessed as Critically Endangered: *P. bardotiae* sp. nov., *P. gautieri* sp. nov., *P. ranirisonii* sp. nov., and *P. sambavensis* sp. nov. from northern Madagascar, and *P. aristata* sp. nov. from south-eastern Madagascar. Of these, the most threatened are *P. sambavensis* sp. nov., which was not collected for more than 50 years and is probably extinct, and *P. aristata* sp. nov., which is only known from a single location outside of a protected area. Three Malagasy species, *P. capitulifera* sp. nov., *P. russata* sp. nov., and *P. tiliacea* are assessed as Endangered. Of these, *P. tiliacea*, occurring in the dry deciduous forests of western Madagascar, is certainly most threatened. Four Malagasy species (*P. grandifructa* sp. nov., *P. longipedicellata* sp. nov., *P. orientalis* sp. nov., and *P. seyrigii* sp. nov.) are listed as Vulnerable as are the two non-Malagasy species, *P. comorensis* sp. nov. and *P. trichantha*. The four remaining Malagasy species are assessed as Near Threatened (*P. pauciflora* sp. nov.) or Least Concern (*P. cinerea*, *P. saxatilis*, and *P. sericea*).

Related taxa

Species of *Paracephaelis* are easily recognized at the genus level by the often pubescent vegetative parts, the pubescent inflorescences, the often well-developed calyces, the densely pubescent corollas, the ovules positioned at the periphery of the placenta, the pollen with supratectal microgemmae, and the laterally flattened seeds with entire endosperm and a shallow elongate hilum.

This seed type is exclusive to *Paracephaelis* and the genus *Homollea*, which also shares well-developed calyces, ovules that are positioned at the periphery of the placenta, and pollen with supratectal microgemmae. *Homollea* differs from *Paracephaelis* by the fact that its inflorescences are pseudo-axillary and pedunculate. Only *P. longipedicellata* sp. nov. has pedunculate inflorescences and this species differs from all species of *Homollea* in that its calyx tube and lobes are more or less equal in length whereas *Homollea* has calyx lobes that are much longer than the tube. Furthermore, three out of five species of *Homollea* have glabrous vegetative and reproductive parts (De Block 2018).

Flowers with well-developed calyces and pubescent corollas also occur in other Malagasy Pavetteae from dry vegetation types. In *Exallosperma longiflora* De Block and *Helictosperma malacophylla* (Drake) De Block, the corolla is densely covered with erect hairs (vs densely covered with ± long appressed hairs in *Paracephaelis*). In both genera, the calyx lobes are much longer than the calyx tube as is also the case in many species of *Paracephaelis*. But *Exallosperma* De Block and *Helictosperma* De Block have *Terminalia*-branching (only present in *P. tiliacea*), a different placentation type (3–4 ovules arising on top of a small placenta attached to the lower half of the septum), pollen without supratectal micro-elements and very different fruit and seed structures and therefore cannot be confused with *Paracephaelis* (De Block *et al.* 2018).

Most similar to *Paracephaelis* are the two species belonging to *Tulearia* De Block. Both have large flowers, the corolla of which is densely covered with ± long appressed hairs as in *Paracephaelis*, and well-developed calyces. In *T. splendida* De Block, the calyx lobes are much longer than the calyx tube. *Tulearia capsaintemariensis* De Block exhibits the typical '*Homolliella*' calyx type, with short, rounded calyx lobes and a long calyx tube. *Tulearia* has the same placentation type as *Paracephaelis* but the pollen have no supratectal micro-elements and the fruit and seed structure is different (fruits with 2 pyrenes, each containing 1(–2) ruminate seeds; De Block *et al.* 2018).

'*Homolliella*' type calyces are also present in the two species of *Robbrechtia* De Block. The central Malagasy *Robbrechtia grandifolia* De Block occurs together with *P. sericea* and *P. pauciflora* sp. nov., whereas the northern Malagasy *R. milleri* De Block also shares its distribution area with *P. sericea*. The four species share well-developed stipules, pubescent vegetative parts, pubescent inflorescences, well-developed calyces with long calyx tubes and shorter lobes. *Robbrechtia* can be distinguished from *Paracephaelis* by the different placentation type (1–4 ovules impressed in and not arranged at the periphery of the placental tissue), fruit and seed type (fruit with a single pyrene containing a single ruminate seed), and pollen without supratectal micro-elements. Furthermore, the corolla tube is either glabrous outside or only its upper third is sparsely to densely covered with short erect hairs in *Robbrechtia*.

Taxonomic treatment

Class Equisetopsida C.Agardh
Subclass Magnoliidae Novák ex Takht.
Superorder Asteranae Takht.
Order Gentianales Juss. ex Bercht. & J.Presl
Family Rubiaceae Juss.

Genus ***Paracephaelis*** Baill.

Adansonia 12: 316 (Baillon 1879); *Histoire des Plantes* 7: 496 (Baillon 1880); *Natürliche Pflanzenfamilien* 4 (4): 60 (Schumann 1891); *Notulae Systematicae* 16: 7, fig. 1, 1–7 (Arènes 1960); *Systematics and Geography of Plants* 73: 100 (De Block 2003): *Flora Zambesiaca, Rubiaceae* 5 (3): 619 (Bridson 2003); *Taxon* 64: 91 (De Block *et al.* 2015). – Type species: *P. tiliacea* Baill.

Homolliella Arènes, *Notulae Systematicae* 16: 16, fig. 4, 19–25 (Arénes 1960); *Taxon* 64: 91 (De Block *et al.* 2015). – Type species: *Homolliella sericea* Arènes.

Description

Shrubs, 1–6 m tall, or small to large trees, 4–20 m tall, dbh up to 30 cm. Pubescence whitish, tawny or reddish brown. Young shoots somewhat flattened, often bisulcate, variously pubescent or, more rarely, glabrous; older branches usually terete, glabrous or glabrescent, bark often corky, flaking or not, greyish, pale brown, fawn, brown or reddish brown. Leaves rarely deciduous, petiolate; petioles canaliculate above, 0.2–3 cm long, variously pubescent or, more rarely, glabrous; blades variously shaped, from narrowly elliptic/ovate/obovate to orbicular, (sub)coriaceous or, more rarely, papyraceous, both surfaces variously pubescent or, more rarely, glabrous; base attenuate to strongly cordate; tip acuminate with acumen 0.2–2.5 cm long, retuse, rounded, obtuse, acute and often mucronulate, or aristate; margin revolute (when dried); domatia present or absent; venation brochidodromous; midrib usually impressed (at least in the basal leaf half) or raised with a central groove (e.g., *P. sambavensis* sp. nov., *P. sericea*) above, prominently raised below; secondary veins 3–14 on each side of midrib. Stipules interpetiolar, basally fused into a cone with upper parts free, outer surface moderately to densely pubescent, more rarely sparsely pubescent or glabrous, inner surface usually glabrous, with 1–3 rows of colleters, sometimes interspaced with long hairs, at the base; sheath triangular or, more rarely, ovate, 0.1–3 cm long, often keeled; tip acute or obtuse, or, more often, with needle-like awn up to 6 mm long. Inflorescences terminal on lateral shoots or lateral short-shoots, sometimes becoming pseudo-axillary later on (*P. tiliacea*), usually sessile but rarely shortly pedunculate (*P. longipedicellata* sp. nov.), cymose, compact to lax, consisting of (1–)3 to numerous flowers; all inflorescence parts (peduncle, axes, pedicels, bracts, and bracteoles) densely pubescent with short to long, erect, spreading or appressed hairs (hairs more appressed on bracts and bracteoles when dried); in sessile inflorescences, first order bracts identical to vegetative leaf pair and stipules, with leaves identical in size to vegetative leaves, somewhat to conspicuously smaller or always fallen (resulting in a seemingly shortly pedunculate inflorescence; e.g., *P. tiliacea*); central second order bracts sometimes identical to first order bracts but with reduced stipular parts and smaller leaves, or, identical to higher order bracts; higher order bracts with stipular parts reduced or absent and foliar parts triangular and vaulted, trilobed or linear, 1–10 mm long, or, more rarely, linear and leaf-like, up to 15 mm long; bracts and bracteoles moderately to densely, or rarely sparsely, covered with short appressed hairs and with a basal row of colleters or 2 basal marginal groups of 1 to few colleters inside. Flowers fragrant, sessile or pedicellate, 5-merous, hermaphrodite. Calyx usually well-developed with tube longer than lobes in species from humid vegetation types, lobes longer than tube in species from dry vegetation types, rarely tube and lobes of ± equal length, green in living condition, densely covered with short to long, erect, spreading or appressed hairs outside, inner surface often covered with appressed hairs but without colleters; tube cylindrical, 0.2–12 mm long; lobes 0.25–4(–5 in fruiting stage) mm long,

narrowly triangular, triangular, ovate, quadrangular or somewhat oblong in shape, bases not overlapping, tips acute, obtuse, rounded or acuminate; tube and/or lobes sometimes accrescent in fruiting stage. Corolla white, turning yellowish with age, densely covered with ± long appressed (or rarely somewhat spreading) hairs outside, at least partly pubescent inside, throat glabrous; tube narrowly cylindrical, 3.5–33 mm long, longer than or, more rarely, equal to lobes in length; lobes contorted to the left in bud and spreading at anthesis, oblong, 1.2–9 mm long, inner surface glabrous, tips blunt. Stamens inserted in the sinuses of the corolla lobes at or, rarely, somewhat below the level of the throat (*P. longipedicellata* sp. nov.); anthers completely exserted or basalmost 1–2.5 mm included in corolla tube at anthesis, linear, 1.2–8 mm long, basi- or basimedifixed, sagittate, with short sterile apical appendix to ca 0.5 mm long; filaments 0–2.5 mm long. Disc annular, fleshy, glabrous. Ovary cupular, bilocular, 0.7–3 mm long, green in living condition, often longitudinally ribbed when dried, densely pubescent. Placentation axile; placenta attached to middle or upper half of septum; (1–)3–14 ovules arranged at periphery of large placenta, or, 1–5 ovules pendulous from small placenta. Style and stigma white; style slender, moderately to densely covered with erect or ascending hairs on its upper half; stigma at least partly exserted at anthesis, stigmatic lobes fused over their entire length, usually not much thickened or at most (upper part) slenderly fusiform, only the very tips spreading, papillae located in the lines of fusion of the stigmatic lobes, papillate grooves 2.5–16 mm long. Fruits drupaceous, spherical to ovoid, longitudinally ribbed or not (when dried), moderately to densely covered with short to long, erect, spreading or appressed hairs; calyx persistent; mesocarp thin or well-developed, vascular bundles sclerified; pyrenes 2, hemi-ovoid or hemispherical, usually crustaceous, with rounded or truncate base, rounded, acute or acuminate tip, and small adaxial opening; larger pyrenes with longitudinal central ridge running from the apex to the top of the adaxial opening, sometimes continuing into a longitudinal depression below it and pyrene opening along this longitudinal ridge and depression; smaller pyrenes without longitudinal ridge and depression, without opening mechanism; seeds laterally compressed, (1–)2–10/fruit, reddish brown or dark brown, hilar cavity shallow, elongate to linear; endosperm entire; embryo with foliaceous cotyledons, radicle inferior. Pollen grains 3-zonocolporate; exine perforate at apocolpium, perforate or rarely microreticulate at mesocolpium: supratectal microgemmae present.

Distribution and habitat

A genus with 18 species, centred in Madagascar (16 endemic species), with one species (*P. comorensis* sp. nov.) endemic to the Comoros and another species (*P. trichantha*) occurring along the coast in eastern Africa and on the islands of the Aldabra Group. Occurring in both humid and dry vegetation types: humid littoral, sublittoral, low-elevation to montane forest, high plateau forest, gallery forest, dry littoral forest and dune vegetation, scrub, semi-deciduous or deciduous dry forest; on sandy (white or laterite) soil or on rocky substrate, also on limestone or limestone covered with sand; 0–1700 m a.s.l.

Notes

1. Homolle (1938: 608) published a separate section within the genus *Tarenna*, comprising species characterized by a reduced placenta and seeds with an elongate shallow hilum ("graines non ombiliquées") and cited *P. cinerea* and *P. comorensis* sp. nov. as members. Unfortunately, section "*Cinerescens*" was only accompanied by a short French description, which does not constitute valid publication according to art. 39.1 of the International Code of Nomenclature for algae, fungi, and plants (Turland *et al.* 2018).

2. In his unpublished *Révision des Rubiacées de Madagascar et des Comores*, Capuron recognized the sections "*Cinereae*" (1973: 169) and "*Paracephaelis*" (1973: 174) in his broadly circumscribed genus *Tarenna*. Both sections correspond to *Paracephaelis* as delimited here. See Taxonomic history for further information.

3. Bridson (1979: 400, 1988: 585) used the informal name *Tarenna* "group VI" to indicate the only continental African species of *Paracephaelis*, *P. trichantha*.

Key to the species of *Paracephaelis*

1. Pedicels 8–20 mm long in flowering stage; bracteoles on pedicel 1–10 mm below the ovary, not opposite; anthers ca 8 mm long, part exserted from corolla tube spirally twisted (when dried); calyx tube and lobes of ± equal length, lobes quadrangular or shortly oblong, 0.7–1.2 mm long, with rounded tips ..... ***P. longipedicellata*** De Block sp. nov.
– Pedicels 0–3(–6) mm long in flowering stage; bracteoles at base of ovary or on pedicel just below ovary, (sub)opposite; anthers (1.5–)3–5(–7) mm long, not spirally twisted; calyx lobes much longer than calyx tube or vice versa, or, if of equal length, then either lobes (narrowly) triangular or pedicels much shorter 2

2. Leaves 1–4 × 0.7–2.8 cm, grouped at the end of lateral shoots; blades elliptic, ovate, rarely obovate or orbiculate; inflorescences 0.6–1.5 × 1–2 cm; calyx tube (0.2–)0.4–0.7 mm long, lobes triangular, 0.8–1.5 mm long ..... ***P. saxatilis*** (Scott Elliot) De Block
– Leaves up to 23×12 cm, not consistently < 4 cm long, only rarely grouped at the end of lateral shoots; blades of different shape, if as narrow as above, then > 4 cm long and/or shape narrowly obovate or narrowly elliptic; inflorescences 1–10 × 1–13 cm; usually, either calyx tube (1–12 mm) or lobes (1.5–4 mm) longer, or, if of similar length, then inflorescences much larger 3

3. Ovary + calyx ≤ 2.5 mm long (flowering stage); calyx tube + lobes ≤ 1.5 mm long; per locule 1–5 ovules pendulous from the base of a small placenta; fruits spherical, 0.3–0.6 mm in diameter..... 4
– Ovary + calyx 3–17 mm long (flowering stage); calyx tube + lobes 2–14 mm long; per locule (1–)2–14 ovules at the periphery of a large placenta, rarely ovules restricted to top of placenta; fruits often ovoid, if spherical, then usually larger 6

4. Leaves 6–23 × (2.5–)4–13 cm, papyraceous or subcoriaceous, both leaf surfaces glabrous or with sparse long appressed hairs on midrib and secondary veins, tip acuminate, acumen 5–25 mm long; young shoots glabrous ..... ***P. comorensis*** De Block sp. nov.
– Leaves 2–13 × 1–8.5 cm, subcoriaceous or coriaceous, both leaf surfaces variously pubescent or glabrous, tip only rarely acuminate; young shoots rarely glabrous but usually pubescent 5

5. Petioles 7–22 mm long; calyx lobes 0.25–0.5 mm long; corolla tubes 3.5–5.5(–6) mm long; corolla lobes 1.2–2 mm long; anthers 1.5–2 mm long, filaments 0.1–0.2 mm long .... ***P. trichantha*** (Baker) De Block
– Petioles 4–10(–15) mm long; calyx lobes 0.5–1 mm long; corolla tubes 5–7.5 mm long; corolla lobes 3–4.5 mm long; anthers 3–4 mm long, filaments ca 1 mm long .... ***P. cinerea*** (A.Rich. ex DC.) De Block

6. Upper leaf surface glabrous, sometimes with some pubescence on margin, midrib and secondary veins 7
– Upper leaf surface variously pubescent (pubescence not restricted to margin, midrib and secondary veins) 13

7. Calyx tube (much) longer than calyx lobes, tube 1–10 mm long, lobes 0.5–2 mm long, quadrangular, broadly ovate or triangular; tree 8–20 m tall, more rarely shrub to 5 m tall; inflorescences with numerous flowers, more rarely with 12–60 flowers 8
– Calyx lobes (much) longer than calyx lobes, tube 1–1.5(–2 in fruiting stage) mm long, lobes 1.2–3(–5 in fruiting stage) mm long, oblong or triangular; shrub or small tree to 6 m tall; inflorescences with 3–35 flowers 11

8. Inflorescences with 3–12 flowers; calyx tube 4–10 mm long; corolla tube 1.1–3.3 cm long .... ***P. pauciflora*** De Block sp. nov. (upper leaf surface glabrous)
– Inflorescences with 12 to numerous flowers; calyx tube 1–5 mm long; corolla tube 0.6–1.7 cm long 9

9. Stipules 0.8–3 cm long; calyx tube 2–5 mm long .... ***P. sericea*** (Arènes) De Block (upper leaf surface glabrous)
– Stipules 0.25–0.8 cm long; calyx tube 1–2 (–3 in fruiting stage) mm long 10

10. Leaves 4.5–10.5 × 1–4 cm; inflorescences 1.5–4 × 2–5 cm; flowers sessile; bracteoles 1.5–2 mm long; calyx tube 1.5–2 mm long in flowering stage, ca 3 mm long in fruiting stage; connective sparsely covered with appressed hairs ..... ***P. orientalis*** De Block sp. nov.
– Leaves 13–18 × 5.5–8.5 cm; inflorescences 4–8 × 4–8 cm; pedicels 1–2 mm long in flowering stage, up to 5(–8) mm long in fruiting stage; bracteoles ca 1 mm long; calyx tube 1–1.5 mm long; connective unknown ..... ***P. sambavensis*** De Block sp. nov.

11. Lower leaf surface densely covered with long, erect or spreading hairs .... ***P. aristata*** De Block sp. nov.
– Lower leaf surface glabrous, either completely or with some hairs on margin, midrib and secondary veins 12

12. Young shoots and petioles glabrous; stipular awn 1–1.5 mm long; both leaf surfaces completely glabrous; bracteoles 0.7–1.2 mm long; calyx lobes 1.2–1.5 mm long .... ***P. gautieri*** De Block sp. nov.
– Young shoots and petioles densely covered with spreading or appressed hairs; stipular awn 2–4.5 mm long; margin, midrib and sometimes secondary veins sparsely to moderately pubescent on both leaf surfaces; bracteoles 2–3 mm long; calyx lobes 2.5–3 mm long ..... ***P. bardotiae*** De Block sp. nov.

13. Calyx lobes longer than calyx tube; young shoots, petioles, inflorescence axes and pedicels densely covered with long erect or spreading hairs 14
– Calyx tube longer than calyx lobes; young shoots, petioles, inflorescence axes and pedicels densely covered with short erect hairs 16

14. Leaves not clustered at the end of lateral shoots; stipules 1–2.5 cm long; bracteoles 3–5 mm long; pedicels 0–5 mm long in flowering stage, 0–12 mm long in fruiting stage .... ***P. russata*** De Block sp. nov.
– Leaves clustered at the end of lateral shoots; stipules 3–7 mm long; bracteoles 1.5–3 mm long; pedicels 0–2 mm long 15

15. *Terminalia*-branching present; pubescence reddish brown, tawny or whitish; leaves probably deciduous, 7–20 × 5–15 cm, papyraceous or subcoriaceous; inflorescences terminal, becoming pseudo-axillary; calyx lobes (1.5–)2–3.5 mm long ..... ***P. tiliacea*** Baill.
– *Terminalia*-branching absent; pubescence tawny or, more rarely, whitish; leaves not deciduous, 2–8.5 × 1.5–5 cm, coriaceous; inflorescences terminal; calyx lobes 1.5–2 mm long in flowering stage, up to 3.5 mm long in fruiting stage ..... ***P. seyrigii*** De Block sp. nov.

16. Leaves with lower surface sericeous, tips obtuse to retuse; ovary and calyx densely covered with long, spreading or erect hairs outside ..... ***P. ranirisonii*** De Block sp. nov.
– Leaves with lower surface densely covered with erect hairs, tips acuminate with acumen 0.3–2 cm long; ovary and calyx densely covered with short erect hairs outside 17

17. Inflorescences capitate; flowers sessile 18
– Inflorescences not capitate; flowers sessile or shortly pedicellate, pedicels 0–2(–5) mm long 19

18. Leaves often drying somewhat bullate; bracteoles 1.5–2.5 mm long, tips acute; calyx lobes with obtuse to rounded tips, not reflexed; fruits 15–20 × 10–15 mm ..... ***P. grandifructa*** De Block sp. nov.
– Leaves not drying bullate; bracteoles 3–3.5 mm long, tips acuminate; calyx lobes with acuminate and reflexed tips; fruits 10–13 × 8–10 mm ..... ***P. capitulifera*** De Block sp. nov.

19. Inflorescences with 3–12 flowers; stipules 0.4–0.9 cm long; calyx tubes 4–10 mm long; corolla tubes 1.1–3.3 cm long ..... ***P. pauciflora*** De Block sp. nov.
– Inflorescences with 12 to numerous flowers; stipules 0.8–3 cm long; calyx tubes 2–5 mm long; corolla tubes 0.6–1.7 cm long ..... ***P. sericea*** (Arènes) De Block

Paracephaelis aristata De Block sp. nov.
urn:lsid:ipni.org:names:77260704-1
Fig. 5

Diagnosis

Differing from *Paracephaelis saxatilis* by having narrowly obovate leaves (vs elliptic, ovate, rarely obovate or orbiculate), longer and oblong calyx lobes in flowering stage (2.5–5 mm vs 0.8–1.5 mm long and triangular), and glabrous inner calyx surfaces (vs densely covered with long appressed hairs).

Etymology

The specific epithet refers to the aristate leaf apex.

Type material

MADAGASCAR – **Toliara Province, Anosy Region, Taolagnaro District** • Ambatorongorongo, Amboavola, Sarisambo; 297 m a.s.l.; 7–10 Jun. 1999; fr; *Rabenantoandro, Randrihasipara & Ramisy 115*; holotype: MO scan; isotypes: BR[BR000000906218], K n.v., P[P00274306] n.v., TAN n.v.

Description

Shrub, ca 2 m tall; pubescence tawny. Young shoots brownish, densely covered with ± short appressed hairs; older branches pale greyish or fawnish, glabrous; internodes short, 0.3–2 cm long. Petioles 2–6 mm long, densely covered with ± short appressed hairs. Leaf blades narrowly obovate, (1.2–)1.5–5.5 × 0.5–1.5 cm, thickly coriaceous, drying brown and not discolorous, upper surface glossy and glabrous, lower surface densely covered with long erect or spreading hairs (but ± appressed on midrib); base attenuate; tip shortly aristate; domatia absent; 4–7 secondary veins on each side of midrib, inconspicuous above, raised below; higher order venation inconspicuous on both surfaces. Stipules triangular with needle-like awn, outer surface densely covered with ± short appressed hairs, inner surface glabrous with row of colleters at the base; sheath 1–2 mm long; awn 2–4 mm long. Inflorescences sessile, 1–2 × 1.5–3 cm, with (3–)5–15 flowers; inflorescence parts densely covered with ± short appressed hairs; first order axes 0.2–1.5 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted, 5–10 mm long, or, linear leaf-like, up to 15 mm long; bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts narrowly triangular, 3–5 mm long, tips acute. Flowers sessile or shortly pedicellate, pedicels 0–3 mm long (in fruiting stage). Calyx densely covered with appressed to spreading hairs outside, inner surface glabrous; tube ca 1 mm long in flowering stage, ca 2 mm long in fruiting stage; lobes oblong, often somewhat unequal in length, 2.5–3 mm long in flowering stage, 4–5 mm long in fruiting stage, tips rounded with small acumen. Mature corolla, stamens, style and stigma

unknown. Ovary 1.5–2 mm long, densely covered with spreading hairs; per locule 6–10 ovules arranged at periphery of placenta attached to upper half of septum. Fruits spherical, ca 1 cm in diam., glossy (when dried), densely covered with spreading hairs. Mature pyrenes and seeds unknown.

Distribution

Only known from Ambatorongorongo Mountain in Taolagnaro District, Anosy Region (Toliara Province) (Fig. 23A).

Habitat and phenology

Low-elevation forest; elev. ca 300 m. Flowers: unknown; Fruits: June.

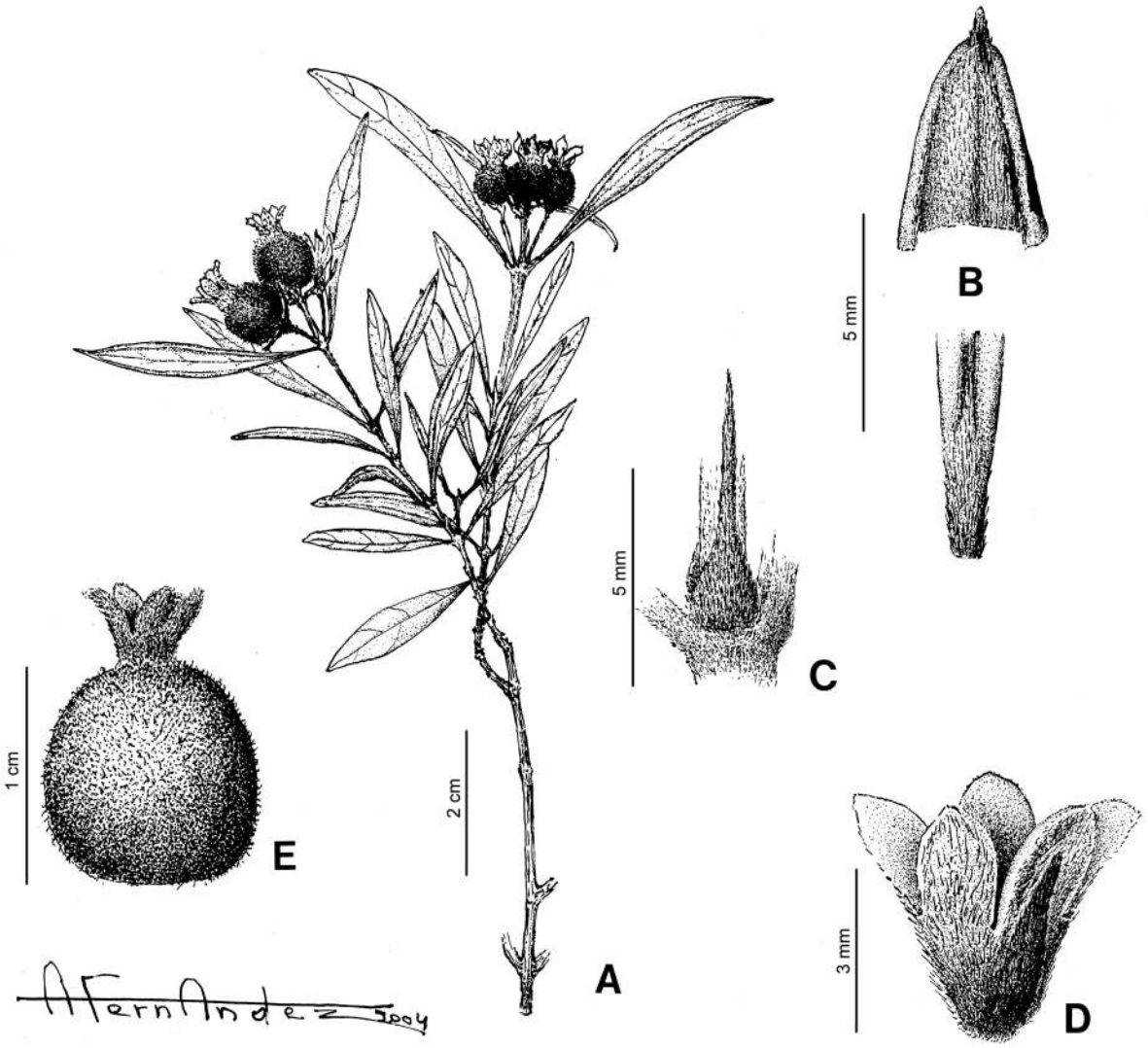

Fig. 5. *Paracephaelis aristata* De Block sp. nov. **A**. Fruiting branch. **B**. Leaf base and tip. **C**. Stipule. **D**. Bracteole, ovary and calyx. **E**. Fruit. Drawn by Mr A. Fernandez. From *Rabenantoandro et al. 115.*

Vernacular name

Mantsaka (*Rabenantoandro et al. 115*).

Provisional IUCN assessment

Critically Endangered: CR B2ab(iii). *Paracephaelis aristata* sp. nov. is only known from a single collection, which means that the extent of occurrence (EOO) cannot be calculated. The area of occupancy (AOO) is 4 km^2, which complies with the Critically Endangered category under criterion B2. The species occurs in a single location, which complies with the Critically Endangered category under subcriterion 'a' of criterion B2. The only material was collected in 1999 on Ambatorongorongo Mountain, located ca 25 km W-SW of Taolagnaro. This isolated mountain close to Ranopiso can be viewed as the southernmost extension of the Anosyennes Mountains (Nussbaum & Raxworthy 1994). In south-eastern Madagascar, littoral, lowland, and montane humid, as well as dry forest come together (Goodman *et al.* 1997). In between those different forest types, transitional forests with intermediate characteristics exist. These forests have a high conservation priority (Nicoll & Langrand 1989; Ganzhorn *et al.* 1997). The Ranopiso region hosts many endemic species of reptiles and amphibians (Ganzhorn *et al.* 1997) and the forest on Ambatorongorongo Mountain is known for its high species richness and local endemism for lemurs, amphibians, and reptiles (Ramanamanjato *et al.* 2002). It is highly likely that the same is true for plant species. At least one other species of Rubiaceae is only known from Ambatorongorongo, notably *Flagenium pedunculatum* Ruhsam & A.P.Davis (Ruhsam & Davis 2007). Ambatorongorongo Mountain and surrounding regions were once completely forested but the ever-increasing human pressure resulted in destruction and degradation of the forests to a point where now only isolated forest patches remain in between rice paddies, fields, and lands used for pasturage (Ramanamanjato *et al.* 2002). The forests on Ambatorongorongo Mountain are not protected but are of a high conservation priority (Ramanamanjato *et al.* 2002). Since *Paracephaelis aristata* sp. nov. is only known from this one location outside of a protected area in a region where deforestation continues even now, the species is assessed as Critically Endangered.

Note

This species is only known from the type. Flowers have not been collected. Label information on *Rabenantoandro et al. 115* indicates the habitat as "forêt de transition".

Paracephaelis bardotiae De Block sp. nov.
urn:lsid:ipni.org:names:77260705-1
Figs 2F, 6

Diagnosis

Differing from *Paracephaelis aristata* sp. nov. by having reddish brown bark (vs pale greyish or fawnish), glabrous lower leaf surfaces (vs densely covered with long erect or spreading hairs), and densely pubescent inner calyx surfaces (vs glabrous).

Etymology

The species is named in honour of Ms Martine Bardot-Vaucoulon, who collected extensively in the tsingy of Ankarana.

Type material

MADAGASCAR – **Antsiranana Province, Diana Region, Antsiranana II District** • Anivorano Nord, Ankarana RS, Mahoro; 7 Nov. 1997; fr; *Bardot-Vaucoulon & Andrianantoinina 933*; holotype: P; isotypes: P.

Other material studied

MADAGASCAR – **Antsiranana Province, Diana Region, Antsiranana II District** • Ankarana, sentier botanique, ca 17 km NE of Mahamasina; 17 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1280*; BR, K, MO, P, TAN.

Description

Small tree, 2.5–5 m tall; pubescence tawny. Young shoots brown, densely covered with spreading or appressed hairs; older branches reddish brown, flaking, glabrous. Petioles 2–6 mm long, moderately to densely covered with appressed to spreading hairs. Leaf blades narrowly elliptic, narrowly obovate, elliptic, obovate or ovate, 3–8 × 1–2.5 cm, coriaceous, drying brown or blackish brown and not discolorous, upper surface glossy, both surfaces glabrous except for sparsely ciliate margin, midrib and sometimes secondary veins; base cuneate, obtuse or rounded; tip rounded and mucronate; ciliate pit domatia present; midrib moderately to densely covered with appressed hairs on both surfaces; 6–10 secondary veins on each side of midrib, inconspicuous on both surfaces, rarely sparsely covered with appressed hairs below; higher order venation inconspicuous on both surfaces. Stipules triangular with needle-like awn, outer surface moderately to densely covered with spreading or appressed hairs, inner surface glabrous with row of colleters interspaced with long appressed hairs at the base; sheath 1.5–2 mm long; awn 2–4.5 mm long. Inflorescences sessile, 1–2.5 × 1–2.5 cm, with 5–15 flowers; inflorescence parts densely covered with appressed or spreading hairs; first order axes 0.3–1.5 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted, 3–5 mm long, or, linear leaf-like,

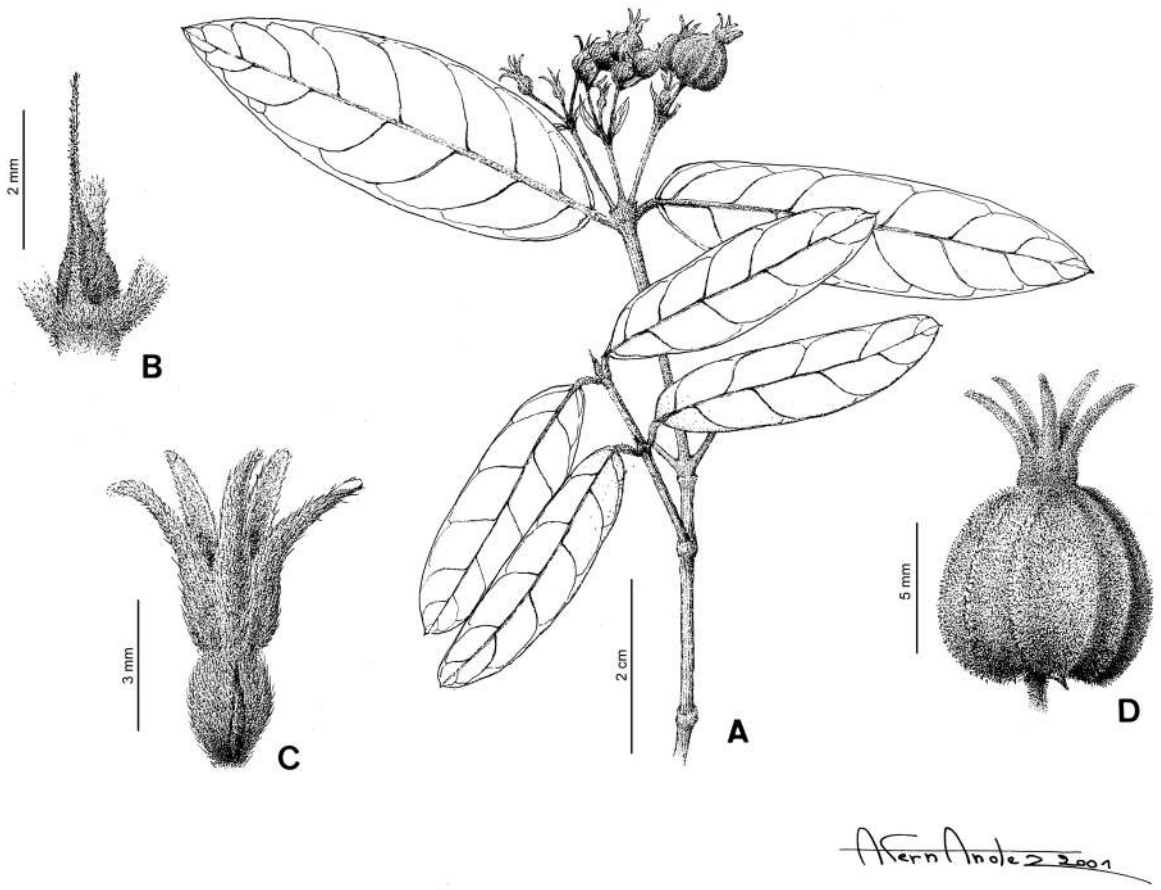

Fig. 6. *Paracephaelis bardotiae* De Block sp. nov. **A**. Fruiting branch. **B**. Stipule. **C**. Bracteole, ovary and calyx. **D**. Fruit. Drawn by Mr A. Fernandez. From *Bardot-Vaucoulon & Andrianantoinina 933*.

up to 10 mm long; bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts narrowly triangular, 2–3 mm long, tips acute. Flowers shortly pedicellate, pedicels 0.5–3 mm long when flowering, 0.5–7 mm long when fruiting. Calyx densely covered with appressed hairs outside (lobes less densely pubescent than tube), inner surface densely covered with long appressed hairs all over but most dense at the base; tube 1.2–1.5 mm long; lobes oblong or triangular, 2.5–3 mm long, tips obtuse. Mature corolla, stamens, style and stigma unknown. Ovary 1.5–2 mm long, faintly ribbed longitudinally (when dried), densely covered with appressed or spreading hairs (more densely pubescent than calyx); per locule 3–8 ovules arranged at periphery of placenta attached to middle of septum. Fruits ovoid or spherical, at least 0.6–0.8 cm in diam., faintly ribbed longitudinally and glossy (when dried), densely covered with appressed to spreading hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical or hemi-ovoid, 5–6.5 × 4–5.5 mm, crustaceous, with rounded base, shortly acuminate tip, small adaxial opening somewhat below the middle and longitudinal central ridge running from the apex to the top of the adaxial opening. Seeds (1–)2–6(–10) per fruit, 3–4 × 2.5–3 mm.

Distribution

Only known from Ankarana National Park in Antsiranana II District, Diana Region (Antsiranana Province) (Fig. 23A).

Habitat and phenology

Low-elevation dry, deciduous or semi-deciduous forest; on limestone covered by sand or clay. Flowers: January; Fruits: November.

Provisional IUCN assessment

Critically Endangered: CR B2ab(iii). Since *P. bardotiae* sp. nov. is known from only two collections, it is impossible to estimate the EOO. The AOO of the species is estimated to be 8 km^2, which complies with the Critically Endangered category under criterion B2. The two specimens were collected in Ankarana Special Reserve in 1999 and 2002. The species thus occurs in a single location, which complies with the Critically Endangered category under sub criterion 'a' of criterion B2. The Ankarana Special Reserve was instated in 1956 and, legally, protection is complete (Nicoll & Langrand 1989). In reality, however, infringements into the reserve are common (Nicoll & Langrand 1989; Cardiff & Befourouack 2008). Forests in the Ankarana Special Reserve are destroyed by bushfires and are cleared for slash-and-burn agriculture. In the last 25 years, the reserve has experienced an enormous influx of migrant miners hunting for sapphires. The miners undercut the forest soil and set up semi-permanent camps inside the reserve. Furthermore, forests in the Ankarana Special Reserve are threatened by illegal logging for hardwood, firewood, and wood for the production of charcoal, by hunting, and by the selective collection of plant species for medicinal or subsistence use (Nicoll & Langrand 1989; Cardiff & Befourouack 2008; Fondation pour les Aires Protégées et la Biodiversité de Madagascar 2020). Because of these facts, a reduction in the extent and quality of the habitat of *P. bardotiae* sp. nov. is inferred. This threat, in combination with the low AOO and the single location, qualifies the species for Critically Endangered status.

Note

This species is only known from two collections. Mature flowers and fruits are still to be collected.

Paracephaelis capitulifera De Block sp. nov.
urn:lsid:ipni.org:names:77260706-1
Figs 1J–K, 7

Diagnosis

Differing from *Paracephaelis sericea* by having shorter stipular sheaths and longer awns (sheaths 8–13 mm and awns 1.5–4 mm vs sheaths 8–30 mm and awns 1–2 mm long), more secondary veins

on each side of the midrib (10–15 vs 8–10), capitate inflorescences (vs not capitate), longer bracteoles (3–3.5 mm vs 1–2 mm long), and longer calyx tubes and lobes (tube 3–8 mm and lobes 1–2.5 mm vs tube 2–5 mm and lobes 0.5–1.5 mm long).

Etymology

The species epithet is based on the capitate inflorescences.

Type material

MADAGASCAR – **Antananarivo Province, Analamanga Region, Ankazobe District** • forêt d'Ambohitantely, jardin botanique; 1464 m a.s.l.; 6 Feb. 1999; fr; *De Block & Rakotonasolo 736*; holotype: BR[BR0000022757661]; isotypes: BR[BR0000022757616], BR[BR0000022757623], G, K, MO, P, TAN, TEF, WAG.

Other material studied

MADAGASCAR – **Antananarivo Province, Analamanga Region, Ankazobe District** • forêt d'Ambohitantely, sur le Tampoketsa d'Ankazobe; 1600 m a.s.l.; 27 Feb. 1966; fr; *Capuron 24569 bis-SF*; P, TEF • ibid.; 25 Nov. 1968; fl; *Capuron 28271-SF*; BR, P, TEF • Manankazo, along RN 4; 1574 m a.s.l.; 17 Feb. 1999; fr; *De Block & Rakotonasolo 831*; BR, G, K, MO, P, TAN • forêt d'Ambohitantely; 24 Feb. 1945; fr; *Homolle & Boiteau D3*; BR, P • Ambohitantely Reserve, along south limit of reserve; 1603 m a.s.l.; 13 Feb. 2018; fr; *Razafimandimbison, Razafindrahaja, Atalahy & Swenson 2139*; BR, MO n.v., P online, S n.v., TAN n.v. – **Renivohitra District** • parc botanique et zoologique de Tsimbazaza, arboretum; 1200 m a.s.l.; 19 Jan. 1975; fl; *Croat 28780*; K, MO. – **Vakinankaratra Region, Antanifotsy District** • Ambatotsipihina, Tsinjoarivo, Ambatolampy; 1300 m a.s.l.; 21 Nov. 1949; fl; *coll. ignot. 1035-SF*; P, TEF. – **Fianarantsoa Province, Amoron'i Mania Region, Ambatofinandrahana District** • commune Itremo, forêt gallerie d'Antsirakambiaty; 1594 m a.s.l.; 12 Dec. 2004; fl; *Andriamihajarivo 267*; MO n.v., P online • Itremo massif, near Itremo, 213 km SW of Antananarivo; 1650 m a.s.l.; 30 Oct. 1997; fl, fr; *Davis, Andriantiana, Gower & Malcomber 1018*; BR, K, P, TAN • montagnes W d'Itremo, W de Betsileo; 1500–1700 m a.s.l.; 18–22 Apr. 1955; fr; *Humbert 28298*; BR, P • Itremo, Antsirakambiaty; 18 May 2005; st; *Rakotonasolo & Rakotoarinivo 1014*; BR, K, TAN • Itremo, 40 km en voiture W d'Ambatofinandrahana, Ianasana, dans une grande vallée (N-S) 25 km (vol d'oiseau) W du pont d'Ianasana; 1500–1610 m a.s.l.; 8 Apr. 1998; fl; *Randrianaivo, Birkinshaw, Rakotomamonjy, Andriantiana & Randrianasolo 171*; BR, K, MO. – **Ambositra District** • forêt de Kijole, Mangatanaboampy; 14 Feb. 1952; fr; *coll. ignot. 5218-SF*; P, TEF.

Description

Shrub to 5 m tall or tree to 10 m tall with dbh to 20 cm; pubescence tawny. Young shoots brown or reddish brown, densely covered with short erect hairs; older branches brown to greyish brown, flaking, glabrescent but pubescence remaining for a long time. Petioles 5–15 mm long, densely covered with short erect hairs. Leaf blades elliptic, ovate or rarely obovate, 6–14 × 2.5–7 cm, coriaceous and often somewhat bullate (when dried), drying brown to dark or blackish brown above and somewhat paler below, upper surface glossy, both surfaces densely covered with short erect hairs but pubescence on midrib and secondary veins often more appressed; base cuneate to attenuate; tip acuminate with acumen 0.3–1.5 cm long; domatia absent; 10–15 secondary veins on each side of midrib, often somewhat impressed above, raised below; higher order venation visible on both surfaces, often somewhat impressed above (especially towards the tip or the margin of the leaf), somewhat raised below. Stipules ovate to triangular with needle-like awn, keeled, outer surface densely covered with short erect hairs, inner surface glabrous with 2–3 rows of colleters at the base; sheath 8–13 mm long; awn 1.5–4 mm long; brown or orange-reddish mucus often present on youngest stipule pair, sometimes extending onto young inflorescences. Inflorescences sessile, capitate, 2–7.5 × 1–4.5 cm, with 12 to numerous flowers; inflorescence parts densely covered with short

erect hairs; first order axes 0.2–2 cm long; second order bracts with stipular parts broadly triangular, < 1 cm long, foliar parts broadly triangular and vaulted, or, more rarely, trilobed (with lateral lobes much smaller than central lobes), single or central lobe up to 1 cm long, tips acuminate; higher order bracts identical but stipular parts reduced or absent, foliar parts 4–7 mm long; bracteoles at base of ovary, opposite, stipular parts absent, foliar parts broadly triangular, 3–3.5 mm long, tips acuminate. Flowers sessile. Calyx densely covered with short erect hairs outside, inner surface densely covered with minute appressed hairs all over but most dense at the base; tube 3–8 mm long, with faint longitudinal ribs (when dried); lobes ovate or triangular, 1–2.5 mm long, keeled, margins ciliate, tips acuminate and often reflexed. Corolla tube ca 13 mm long, inner surface unknown; lobes ca 5 mm long. Stamens, style and stigma unknown. Ovary 1.5–2 mm long, longitudinally ribbed (when dried), densely covered with short erect hairs; placentation

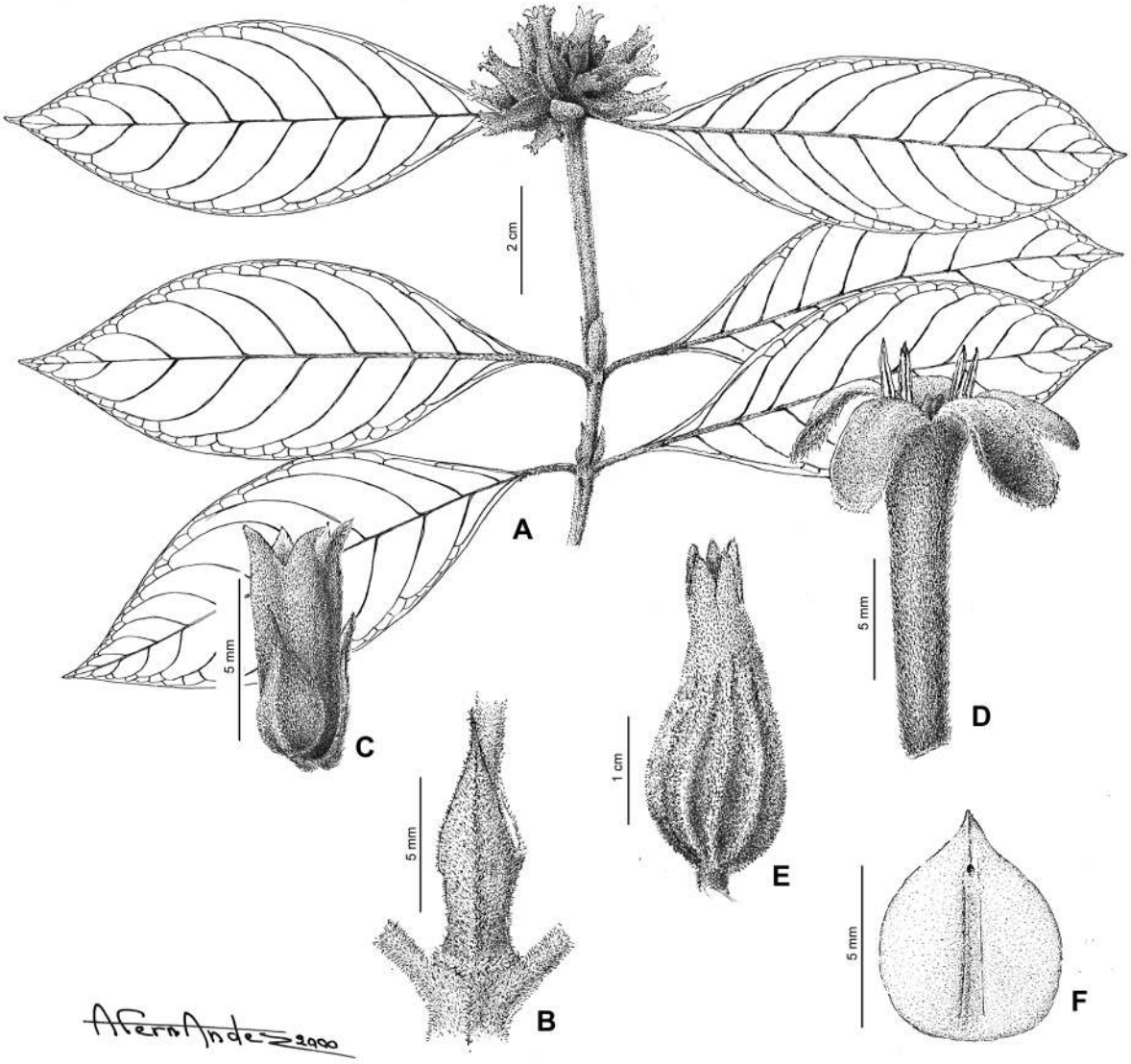

Fig. 7. *Paracephaelis capitulifera* De Block sp. nov. **A**. Fruiting branch. **B**. Stipules. **C**. Bracteoles, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. **F**. Pyrene, adaxial view. Drawn by Mr A. Fernandez. From *De Block & Rakotonasolo 831* (A), *De Block & Rakotonasolo 736* (B, E–F) and *coll. ignot. 1035-SF* (C–D).

unknown. Fruits ovoid, 10–13 × 8–10 mm, strongly ribbed longitudinally (when dried), densely covered with short erect hairs; fruit wall well-developed, with multi-layered anastomosing network of sclerified vascular bundles; pyrenes hemi-ovoid, ca 6.5 × 5 mm, crustaceous, with rounded base, acuminate tip, small adaxial opening in upper ⅓rd and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it; pyrene opening along this longitudinal ridge and depression. Seeds 4–8 per fruit, 3–5 × 2–3.5 mm.

Distribution

Restricted to the Central Highlands. Present in: Ankazobe and Renivohitra Districts, Analamanga Region, and Antanifotsy District, Vakinankaratra Region (Antananarivo Province); Ambatofinandrahana and Ambositra Districts, Amoron'i Mania Region (Fianarantsoa Province) (Fig. 23A).

Habitat and phenology

High plateau forest, gallery forest; elev. 1200–1700 m. Flowers: November–January; Fruits: February–November.

Vernacular name

Tsitola (*coll. ignot. 5218-SF*).

Provisional IUCN assessment

Endangered: EN B2ab(iii). This assessment is based on 15 herbarium collections with detailed locality data, collected between 1945 and 2018. A 16th specimen was collected in the arboretum of the Parc botanique et zoologique de Tsimbazaza in 1975 (*Croat 28780*). No information was found on whether this tree had been planted or whether it occurred naturally in the arboretum. During searches in 2010, this tree was not found (Franck Rakotonasolo: pers. com.). As a result, this location is not taken into account for this assessment. The EOO of *P. capitulifera* sp. nov. is estimated to be 19 843 km^2, which complies with the Vulnerable category under criterion B1. The AOO is 36 km^2, which complies with the Endangered category under criterion B2. The species occurs in 5 locations, which is the upper limit for the Endangered category under subcriterion 'a' of criterion B2. *Paracephaelis capitulifera* sp. nov. is restricted to the Central Highlands, which are densely populated and house several large cities. Human impact is high, consisting of subsistence agriculture (rice, manioc, sweet potatoes, …) and extensive cattle grazing, for which yearly burning of the grasslands is affected (McConnell *et al.* 2015). Throughout the Central Highlands, most forest cover has been destroyed (Gade 1996), with only small patches remaining. *Paracephaelis capitulifera* sp. nov. occurs in Ambohitantely Special Reserve and Itremo New Protected Area, both of which are threatened by bushfires and cattle grazing. Also, logging for construction wood, firewood and, wood for charcoal production, collection of plants for medicinal, subsistence or ornamental use, and hunting take place (Nicoll & Langrand 1989; Langrand 2003; La Maison de Madagascar 2020). Additional threats to the natural vegetation in Itremo are artisanal mining and invasive species (*Pinus* L.; La Maison de Madagascar 2020). Because of the above-mentioned facts, a reduction in the extent and quality of the habitat of *P. capitulifera* sp. nov. is inferred. This threat, in combination with the low AOO and the low number of locations, qualifies *P. capitulifera* sp. nov. as Endangered.

Notes

1. One specimen with mature flowers was seen online (P). In *coll. ignot. 1035-SF*, the corolla tube is ca 13 mm long and the corolla lobes ca 5 mm long. The flowers could not be studied.

2. Prior to the synonymization of *Homollliella* with *Paracephaelis* (De Block *et al.* 2015), herbarium specimens were annotated by the author as "*Homolliella capitulifera*", a name which was never published.

Paracephaelis cinerea (A.Rich.) De Block
Figs 1A, E, I, 2I, 8

Systematics and Geography of Plants 73: 100 (De Block 2003).

Basionym

Pavetta cinerea A.Rich. in DC., *Prodromus Systematis Naturalis Regni Vegetabilis* 4: 492 (De Candolle 1830); *Mémoire sur la Famille des Rubiacées*: 101 (Richard 1830); *Mémoires de la Société d'Histoire naturelle de Paris* 5: 181 (Richard 1834). **Type:** MADAGASCAR – **Antananarivo Province, Analamanga Region, Antananarivo Renivohitra District** • in monte Tananarivo; s.dat.; fl; *A. Richard in Drake s.n.*; holotype: P[P00115278].

Homotypic synonyms

Ixora cinerea (A.Rich) Drake, *Histoire physique, naturelle, et politique de Madagascar* 36: pl. 421 (Drake del Castillo 1897); *Bulletin mensuel de la Société linnéenne de Paris* 2: 1308 (Drake del Castillo 1898); *Annuaire du Conservatoire et du Jardin botaniques de Genève* 11–12: 107, fig. 14 (Hochreutiner 1908). – *Chomelia cinerea* (A.Rich.) Dubard & Dop, *Journal de Botanique (Morot)*, sér. 2, 3: 11 (Dubard & Dop 1925). – *Tarenna cinerea* (A.Rich.) Bremek., nom. illeg., *Repertorium Novarum Specierum Regni Vegetabilis* 37: 7, 189 (Bremekamp 1934; see Note 2); *Bulletin de la Société botanique de France* 85: 607 (Homolle 1938); *Révision des Rubiacées de Madagascar et des Comores*: 170 (Capuron 1973). – *Tarenna spodia* Bremek., *Repertorium Novarum Specierum Regni Vegetabilis* 47: 96 (Bremekamp 1939).

Heterotypic synonym

Webera hispidula Baker, *Journal of Botany (London)* 20: 137 (Baker 1882). **Type**: MADAGASCAR – **Fianarantsoa Province** • chiefly in Betsileo land; s.dat.; fl; *Baron 150*; holotype: K, isotype: P.

Other collections examined

MADAGASCAR – **Antsiranana Province, Diana Region, Antsiranana II District** • montagne des Français, 4 km from the junction of the main road to Ramena; 78 m a.s.l.; 21 Jul. 2007; fr; *Andriamahay & Rakotoarisoa 1794*; K • Analamera RS, 80 km S d'Antsiranana par route et 2.5 km E du village d'Ambery (Antranonaomby); 507 m a.s.l.; 17 Jun. 1994; fr; *Andrianantoanina & Rabeharinosy 705*; BR, MO • montagne Andrao à Lingvatou [Lanivato]; s.dat.; fl; *Bernier 319*; BR, P • forêt d'Orangea, E de Diego-Suarez; 22 Feb. 1962; fl; *Capuron 20942-SF*; BR, P, TEF • forêt de Sahafary, bassin de la Saharaina; 200 m a.s.l.; 20 Feb. 1962; fl; *Capuron 20969-SF*; BR, P, TEF • lisière supérieure de la forêt d'Andranomadiro, rebord S du plateau de Sahafary, entre les bassins de la Saharenana et de l'Irodo; 300 m a.s.l.; 27 Dec. 1963; fl, fr; *Capuron 23073-SF*; P, TEF • environs d'Antsoha, S du mont Raynaud, piste de la baie de Rigny; 28 Feb. 1964; fl; *Capuron 23293-SF*; BR, P, TEF • rebord S du plateau de Sahafary, haut de la forêt d'Andranomadiro; 26 Feb. 1964; fr; *Capuron 23309-SF*; BR, P, TEF • Analamera, along Ambtabe river; 40 m a.s.l.; 7 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1111*; BR, MO, P, TAN, WAG • Analamera, bank of Irodo river, close to Irodo camp; 40 m a.s.l.; 8 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1133*; BR, G, MO, TAN, UPS • ibid.; 10 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1174*; BR, K, MO, P, TAN • baie de Sakalava; 0–100 m a.s.l.; 19 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1291*; BR, K, MO, P, TAN, WAG • forêt d'Orangea, side closest to Ramena; 0–100 m a.s.l.; 24 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1384*; BR, G, K, MO, TAN • commune Mahavanona, fkt. Andranomanitra, Antafiankoroka, massif forestier de la montagne des Français; 204 m a.s.l.; 4 Feb. 2005; fl; *Rabefarihy 52*; BR, MO, P, TAN • montagne des Français; 12 Feb. 2003; fr; *Rakotonasolo & Rogers 582*; P, K • montagne des Français, road to Ivovona; 12 Feb. 2003; fr; *Rakotonasolo & Rogers 585*; BR, K • Andrafiabe, Ambolobozokely, Anosy, 4 km NE du village d'Ambolobozokely; 22 m a.s.l.; 30 Mar. 2007; fr;

Rakotondrafara 497; BR, CNARP n.v., MO, P, TAN • commune Sadjoavato, fkt. Saharenana, forêt d'Andranomadiro, SW of Sahafary, S-facing watershed draining plateau; 300 m a.s.l.; 14 Feb. 2005; fr; *Schatz, Ratovoson & Riri Guittou 4274*; BR, CNARP n.v., MO, P, TAN • commune Sadjoavato, fkt. Saharenana, forêt de Sahafary; 210 m a.s.l.; 15 Feb. 2005; fl; *Schatz, Ratovoson & Guittou 4299*; CNARP n.v., MO n.v., P online, TAN n.v. – **Nossi-Be District** • Nossi-Be, bords de la mer entre Amponbilava et Djabul; Feb. 1851; fl; *Boivin s.n.*; P • Nossi-Komba; Dec. 1879; fl; *Hildebrandt* 3227; BM, G, K, P. – **Sava Region, Vohemar District** • Port Leven; 1849; fl, fr; *Boivin 2430*; P • commune Daraina, Daraina, Bekaraoka-Sud; 9 Apr. 2008; fr; *Bremer, Mouly, Ravelonarivo & Kainulainen 5122*; S • commune Daraina, Daraina, forêt de Solaniampilana-Maroadabo; 12 Apr. 2008; fr; *Bremer, Mouly, Kainulainen & Mariano 5161*; S • forêt d'Andaingo, S de la rivière d'Andripatra, N de Vohemar; 16 Mar. 1967; fl; *Capuron 27443-SF*; BR, P, TEF • vestige forestier d'Ambatrabe, S de Maintialaka, N de Vohemar; 15 Mar. 1967; fl; *Capuron 27458-SF*; BR, P, TEF • S de Vohemar; Mar. 1967; fl; *Capuron* 27477-SF; P, TEF • commune Daraina, Daraina, forêt d'Ankaramy, à 910 m du point côté 361, au 203°; 200 m a.s.l.; 22 Feb. 2004; fl; *Nusbaumer & Ranirison 1201*; BR, G n.v. • commune Nosibe, lieu de campement au lac Sahaka, près de la forêt d'Analabe; 22 Feb. 2003; fl; *Rabevohitra, Rabenantoandro & Razakamalala 4479*; MO, P • commune Nosibe, Anjiabe, forêt littorale d'Analabe; 24 Feb. 2003; fl; *Rabevohitra, Rabenantoandro & Razakamalala 4531*; MO, P • Maromikotro-Iloky, road to Daraina; 21 Feb. 2013; fl; *Rakotonasolo, Randriamboavonjy, Letsara, Bone & Andriantiana 2143*; BR, K, MO, P, TAN • commune Daraina, Daraina, forêt de Bekaroaka, partie nord, à 420 m du point côté 96, au 133°; 180 m a.s.l.; 10 Feb. 2004; fl; *Ranirison & Nusbaumer 401*; BR, G n.v. • commune Daraina, Daraina, forêt d'Ankaramy, à 1160 m du point côté 361, au 171°; 27 Feb. 2004; fl; *Ranirison & Nusbaumer 491*; BR, G n.v. • commune Daraina, Daraina, forêt d'Antsaharaingy, à 1080 m du point côté 41, au 303°; 42 m a.s.l.; 18 Apr. 2004; fr; *Ranirison 685*; BR, G n.v. • commune Nosibe, forêt littorale d'Analabe près du village d'Anaborano et du lac Sahaka; 21 m a.s.l.; 12 Jul. 2003; fr; *Razakamalala, Rabevehitra & Rakotomamonjy 577*; MO n.v., P online • fir. Tsarabaria, fkt. Manakana, forêt sublittorale E du village d'Ambondrobe; 13 Mar. 2004; fl; *Razakamalala, Rabevohitra & Faralahy 993*; BR, K, MO • fir. Tsarabaria, fkt. Manakana, forêt littorale d'Ambondrobe; 20 May 2004; fr; *Razakamalala 1317*; MO n.v., P online • Vohemar; 1840; fr; *Richard s.n.*; P • Vohemar; s.dat.; fr; *Richard in Drake 47*; P • aux environs de Vohemar; s.dat.; fr; *Richard 83*; L, P • Vohemar; 1840; fr; *Richard 649*; P • Port Leven; 1850; fl, fr; *Vesco s.n.*; P. – **Toamasina Province, Alaotra-Mangoro Region, Ambatondrazaka District** • lac Alaotra; s.dat.; fr; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *3832* (*MEN-75*); P • lac Alaotra; s.dat.; fl; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *3878* (*ANK-206*); P • lac Alaotra; s.dat.; fl; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *3923* (*MEN-6*); P • forêt d'Analamihilana; 850 m a.s.l.; 27 Dec. 1944; fl; *Cours 1996*; BR, P • Antandrokomby; Jun. 1957; fl; *Peltier J. & M. 964*; P, TAN. – **Andilamena District** • fkt. Ampamoho, forêt d'Analalava, 10 km S d'Andilamena; 1006 m a.s.l.; 8 Dec. 2001; fl; *Randrianaivo, Ratodimana, Razafindrabeaza, Razanatsoa, Rakotozanahary, Rabeabimanana & Tolozafy 814*; K, MO, P. – **Moramanga District** • on the left of Mangoro river; 920 m a.s.l.; 13 Jan. 2001; fl; *Rakotonasolo 285*; BR, K. – **Mahajanga Province, Betsiboka Region, Maevatanana District** • Ampanibe, près du confluent de l'Ikopa et du Betsiboka; Feb. 1899; fl; *Perrier de la Bâthie 828*; P. – **Tsaratanana District** • bord N du sentier vers Antaminbaribe, forêt d'Ampasindava, village le plus proche Ampasindava; 28 Apr. 1958; fr; *Razafinarivo 19142-SF*; BR, P, TEF. – **Boeny Region, Ambato-Boeni District** • RNI 7, Ankarafantsika, Bevasaka; 100 m a.s.l.; Mar. 1933; fl; *coll. ignot. 144-SF*; P • forêt de Maroabolay, village le plus proche Antafia, fir. Sitampiky; 8 Mar. 1957; fr; *coll. ignot. 17762-SF*; P, TEF • Ampijoroa forestry station, forest across from lake Ravelobe; 14 Feb. 1999; fl; *De Block & Rakotonasolo 813*; BR, MO, P, TAN • forêt d'Ankarokaroka, village le plus proche Antafia, fir. Sitampiky; 21 Jan. 1958; fl; *Tefamilia 19322-SF*; TEF • RNI 7, Ankarafantsika, Tsaramandroso; 28 Sep. 1951; fr; *Tsilizy 2974-RN*; BR, P, TEF. – **Mahajanga I District** • environs de Majunga; 2–15 m a.s.l.; Dec. 1924; fl; *Humbert 4048*; BR, P • dunes de Majunga; Jan. 1921; fl; *Perrier de la Bâthie 13459*; BR, P. – **Mahajanga II District** • Mariarano, Ankatsabe, forêt d'Ankatsabe; 16 m a.s.l.; 20 Apr. 2007; fr; *Rakotoarivelo, Miandrimanana, Randrianarivelo, Razakamalala & Beby 88*; MO n.v., P online, TAN n.v. – **Mitsinjo District** • Tsiombikibo; 24 m a.s.l.;

6 May 2005; fr; *Andriamahay & Rakotoarisoa 1055*; K. – **Soalala District** • RNI 8, Namoroka, ca 38.5 km S of Soalala; 130 m a.s.l.; 3 Feb. 2000; fl; *Davis, Rakotonasolo & Wilkin 2534*; BR, K, P, TAN • ca 3 km S of Soalala; 5 m a.s.l.; 8 Feb. 2000; fl; *Davis & Rakotonasolo 2546*; BR, K, P, TAN • Soalala; 12 Jul. 1977; fr; *Rakotozafy 1925*; TAN • fir. Andranomavo; 24 Feb. 1956; fl; *Randriamiero 8646-RN*; BR, P, TAN, TEF (as *coll. ignot. 17476-SF*). – **Melaky Region, Antsalova District** • Bemaraha; Aug. 1943; fr; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *6191*; P. – **Maintirano District** • forêt Analalava, 1600 m NE du campement Mokotra, fir. Maintirano; 24 Feb. 1955; fr; *coll. ignot. 14803-SF*; P, TEF • forêt d'Amboloando, village le plus proche Amboloando, fir. Maintirano; 30 May 1956; fr; *coll. ignot. 16391-SF*; BR, P, TEF. – **Sofia Region, Antsohihy District** • Anjimangirana, 3 km W of Anjimangirana (Analananbe) village; 290 m a.s.l.; 30 May 2000; fr; *Rakotonasolo 172*; BR, K, P, TAN • Anjimangirana, Analananbe, Andrafiborizina; 285 m a.s.l.; 30 May 2000; fr; *Rakotonasolo 186*; BR, K, TAN • Ankerika, Andohanakerika; 200 m a.s.l.; 3 Jun. 2000; fr; *Rakotonasolo 199*; BR, K, TAN. – **Boriziny-Vaovao District** • N of Port Bergé; 70 m a.s.l.; 18 Jan. 1988; fl; *Bisset M52*; K • Mandritsara; Apr. 1974; fr; *Morat 4469*; P. – **Mampikony District** • Bongolava, Ampombimanangy, Bongolava forest, 6 km W of Ampombimanangy; 221 m a.s.l.; 14 Jun. 2008; fr; *Andriamahay & Rakotoarisoa 2047*; K. – **Mandritsara District** • Ambalafarihy, village le plus proche Ambalafarihy, fir. Antsirabe; 14 Mar. 1966; fr; *Sajy 25847-SF*; P, TEF. – **Antananarivo Province, Analamanga Region, Andramasina District** • Andramasina, Ambatolampy; Dec. 1958; fl; *Bosser 12461*; TAN. – **Anjozorobe District** • Analabe, N d'Antananarivo; Mar. 1953; fr; *Bosser 5111*; P • Analabe centre; Mar. 1953; fr; *Bosser* 5229; TAN • Anjozorobe, by the side of Mananara river; 23 Dec. 1999; fl; *Rakotonasolo 119*; BR, K, TAN. – **Ankazobe District** • Tampoketsa d'Ankazobe; 29 Apr. 1943; fr; *Decary 19311*; BR, P • 30 km N of Ankazobe, Tampoketsa d'Ankazobe; 1600 m a.s.l.; 18 May 1974; fr; *Gentry 11822*; MO, P, TAN • plateau du Tampoketsa entre la Mahazemba et le Bemarivo; Jun. 1905; fr; *Perrier de la Bâthie 3626*; P • Tampoketsa d'Ankazobe; 1500 m a.s.l.; s.dat.; fr; *Perrier de la Bâthie 17315*; P. – **Antananarivo Renivohitra District** • Antananarivo; s.dat.; fl; *Hilsenberg & Bojer s.n.*; BM • in monte Tananarivo; s. dat.; fl; *Richard in Drake s.n.*; P. – **Manjakandriana District** • forêt de la Mandraka; s.dat.; fl; *d'Alleizette 10*; P. – **Itasy Region, Arivonimamo District** • Antongona, environs d'Antananarivo; Jan. 1956; fl; *Bosser 8946*; TAN • Antongona; Jan. 1960; fl; *Bosser 13460*; TAN • Antongona, rochers à 40 km W d'Antananarivo; 1500 m a.s.l.; 16 Jan. 1960; fl; *Leandri 2591*; P • Antongona; 16 Jan. 1960; fl; *Peltier J. & M. 1752*; P, TAN. – **Miarinarivo District** • lac Itasy; Feb. 1964; fl, fr; Bosser 19183; P. – **Vakinankaratra Region, Ambatolampy District** • PK 35 at stream-crossing S of Behenjy on road from Antananarivo to Antsirabe (RN 7); 1300–1400 m a.s.l.; 12 Jan. 1986; fl; *Dorr, Barnett & Rakotozafy 4554*; K, MO, P. – **Antanifotsy District** • Ambohimandroso, près d'Ambatolampy, bords de l'Onive; 1500 m a.s.l.; Dec. 1955; fl; *Bosser 8781*; P, TAN. – **Antsirabe II District** • Antsirabe; 1600 m a.s.l.; Jan. 1914; fl; *Perrier de la Bâthie 3508*; BR, P. – **Betafo District** • Mandoto; 6 Dec. 1939; fl; *Decary 15245*; BR, P. – **Faratsiho District** • Ramainandro, Ankaratra; Jan. 1955; fl; *Bosser 7587*; P, TAN. – **Fianarantsoa Province, Ihorombe Region, Ihosy District** • entrée d'Ihosy, face à la piste d'aviation; 570–631 m a.s.l.; 3 Jan. 1999; fl; *Allorge 2236*; P • bassin de la Sahambana, SE d'Ihosy, PK 21 de la route Ihosy-Ivohibe; 9 Feb. 1963; fr; *Capuron 22606-SF*; BR, K, P, TEF • Isalo PN, canyon des makis; 9 Jan. 1999; fl; *De Block, Rakotonasolo & Randriamboavonjy 586A*; BR, K, MO, P, TAN • Isalo PN, beyond canyon des makis; 9 Jan. 1999; fr; *De Block, Rakotonasolo & Randriamboavonjy 586B*; BR, K, MO, TAN • road from Ihosy to Farafangana, 9 km before Ihosy, PK 26; 745 m a.s.l.; 30 Jan. 2006; fl; *De Block, Tosh & Rakotonasolo 1942*; BR, K, MO, TAN, UPS • environs d'Ihosy; 1 Feb. 1957; fl; *Descoings 2191*; P, TAN • inselberg on RN 7 to Tulear; 22°10′12.9″ S, 46°22′39.4″ E; 812 m a.s.l.; 30 Jan. 2007; fl; *Groeninckx, Rakotonasolo, Dessein & De Block 162*; BR, MO, P, TAN, UPS • Ranohira; s.dat.; fr; *Homolle 1463*; K, P • environs d'Ihosy; 800–900 m a.s.l.; Mar. 1934; fr; *Humbert 14471*; P • haute vallée de la Menarahaka, E d'Ihosy; 700–800 m a.s.l.; 28 Jan.–10 Apr. 1955; fl; *Humbert 28554*; BR, P • Ranohira, E d'Isalo; 750–800 m a.s.l.; Feb. 1955; fr; *Humbert 28795*; P. – **Amoron'i Mania Region, Ambatofinandrahana District** • Analandratehina, route vers Ambatomenaloha; 1615 m a.s.l.; 27 Apr. 2012; fr; *Andrianaivoravelona, Ravaoarisoa, Lazasoa, Ralaivao & Manampisoa 613*; BR, K, MO, P, TAN • environs d'Ambatofinandrahana

(Betsileo); 1400–1500 m a.s.l.; 16 Jan. 1955; fr; *Humbert & Capuron 28091*; P • Itremo, gallery forest in Analamaizina; 31 Nov. 2009; fl; *Rakotonasolo, Moat, Rakotoarinivo, Rakotoarisoa, Bachman & Couch 1520*; BR, K, P, TAN • Analabe, ca 1 km SE of Analabebiby; 16 Dec. 2011; fl; *Randriamboavonjy, Rajaovelona & Andriamilanto 1011*; BR, K, MO, P, TAN. – **Ambositra District** • Faliarivo, W d'Ambositra; 1600 m a.s.l.; 15 Jan. 1955; fl; *Humbert & Capuron 28023*; P. – **Haute Matsiatra Region, Ambalavao District** • RNI 5, Andringitra, Sendrisoa; 19 Dec. 1952; fl; *Rakoto 4823-RN*; P, TAN, TEF. – **Toliara Province, Anosy Region, Amboasary-Atsimo District** • forêt d'Ankirikirika (Ankiritry); 25 Jan. 1945; fl; *Homolle E1*; P. – **Betroka District** • vallée de la Manambolo, bassin du Mandrare, au confluent de la Sakamalio, mont Morahariva; 1000–1200 m a.s.l.; Dec. 1933; fl; *Humbert 13145*; BR, P. – **Taolagnaro District** • RN 10, 16 km W of Manambaro; 110 m a.s.l.; 21 Feb. 1975; fr; *Croat 31950*; K, MO, P, TAN • RNI 11, Andohahela, Fort-Dauphin, parcelle 3, Ankazofotsy; 100–250 m a.s.l.; 21–23 Jun. 1994; fr; *Eboroke 823*; BR, K, MO, P • Ambatoabo, Mahamavo, Ankazomena, subhumid forest of Andohahela; 660 m a.s.l.; 25 Apr. 2009; fr; *Rakotonasolo, Ratovoson, Iso Fiadana, Rasolondrainy & Constant Mbola 1244*; BR, MO, P • RNI 11, Andohahela, parcelle 3; 100–300 m a.s.l.; 18 Feb. 1993; fr; *Randriamampionona 124*; BR, K, MO, P, WAG • RNI 11, Andohahela, parcelle 3; 100–300 m a.s.l.; 8–10 Apr. 1993; fr; *Randriamampionona 269*; BR, K, MO, P, UPS, WAG • Andohahela, parcelle 3, Ankazofotsy; 15 May 2001; fr; *Randriamampionona 1001*; BR, CNARP n.v., MO, P, TAN. – **Atsimo-Andrefana Region, Beroroha District** • fkt. Beronono-Makay, déviation canyon vers le plateau Behetaheta; 531 m a.s.l.; 16 Jan. 2010; fl; *Rakotovao, Razakamalala & Andriantiana 5105*; MO n.v., P online, TAN n.v. • fkt. Antsoa, village le plus proche Antanamary, Androsy; 254 m a.s.l.; 9 Jan. 2011; fl; *Razakamalala 5892*; BR, MO, P, TAN. – **Betioky District** • Manasoa Tanosy; 14 Jan. 1913; fl; *Afzelius s.n.*; P, S • Manasoa Tanosy; 14 Jan. 1913; fl; *Afzelius 258*; S • Manasoa Tanosy; 14 Jan. 1913; fl; *Afzelius 264*; S • road from Betioky to Ampanihy; 27 km from Betioky; 335 m a.s.l.; 6 Feb. 2007; fl; *De Block, Dessein, Groeninckx & Rakotonasolo 2317*; BR, MO, BR, TAN. – **Morombe District** • N of Toliara, forêt de Mikea, 23–25 road-km W of Vorehy; 50 m a.s.l.; 12 Feb. 1998; fr; *McPherson & Razafimandimbison 17411*; K, MO • forêt de Mikea axe Ankilimihavotse-Ankindranoke, Basibasy; 0–50 m a.s.l.; 1 Feb. 2000; fl; *Ranaivojaona et al. 308*; MO n.v., P online, TAN n.v. – **Sakaraha District** • Mahaboboka, Marotsiraka, forêt proche du village d'Ambinanitelo; 447 m a.s.l.; 20 Dec. 2010; fl; *Andriamihajarivo, Razanatsima & Fagnarena Miandry 1828*; P online • Mahaboboka, Marotsiraka, partie NW de la forêt d'Analavelona, près de la source, W de la rivière de Manasay; 1293 m a.s.l.; 16 Jan. 2012; fl; *Andriamihajarivo & Fagnarea 1833*; BR, MO, P, TAN • Mahaboboka, Marotsiraka Betsileo, village le plus proche Andombiry, forêt d'Analavelona le long de la rivière Manasay; 997 m a.s.l.; 1 Dec. 2016; fl; *Andriamihajarivo, Rehary & Bruno 1992*; MO n.v., P online, TAN n.v. • Sakaraha; Feb. 1956; fr; *Bosser 9138*; BR, P, TAN • bassin de la Mananadabo dans le massif de l'Analavelona, N du Fiherenana; 1000–1300 m a.s.l.; 13–15 Dec. 1962; fl; *Capuron 22200-SF*; BR, P, TEF • Lambomakandro; 3 Mar. 1943; fl, fr; *Decary 18896*; BR, P • Zombitse-Isoky, Zombitse PN; 612 m a.s.l.; 1 Feb. 2007; fr; *Groeninckx, Rakotonasolo, Dessein & De Block 177*; BR, G, MO, P, TAN • Mahaboboka, fkt. Marotsiraka Betsileo, forêt de Marokobay NE du village d'Ambinanintelo; 462 m a.s.l.; 20 Feb. 2011; fr; *Randrianarivony, Rakotoarivony, Helison, Heriman & Rehary 245*; MO n.v., P online, TAN n.v. • commune Mahaboboka, fkt. Marotsiraka Betsileo, Analavelona, forêt de Manasay; 1335 m a.s.l.; 18 Jan. 2012; fl; *Randrianarivony, Ramarosandratana, Andriamihajarivo & Makabe 411*; MO n.v., P online, TAN n.v. • Mahaboboka, Ambinanintelo, forêt d'Analavelona, forêt d'Andohaniankokoky au bord de la rivière Ankokoky; 970 m a.s.l.; 5 Dec. 2015; fl; *Randrianarivony, Rakotoarivony, Helison, Heriman, Rehary & Rebesa 801*; MO n.v., P online, TAN n.v. – **Menabe Region, Morondava District** • Kirindy forest, Andranomena RS; 17 m a.s.l.; 21 Feb. 2018; fl; *Atalahy, Razafindrahaja, Swenson & Razafimandimbison 115*; P online, S n.v. • forêt de Kirindi, CFPF Morondava (forêt d'Andalandahalo), jardin botanique 2, ca 45 km NE of Morondava; 15 m a.s.l.; 20 Feb. 2000; fr; *Davis, Rakotonasolo & Wilkin 2570*; BR, K, P, TAN • Andranomena forest, ca 17 km before turn-off to Kirindi; 16 m a.s.l.; 18 Jan. 2007; fl; *De Block, Rakotonasolo, Groeninckx & Dessein 2168*; BR, MO, TAN • Kirindy forest, N part - Conoco 7; 16 m a.s.l.; 19 Jan. 2007; fl; *De Block, Rakotonasolo, Groeninckx & Dessein 2193*; BR, G, MO, P, TAN • RN 35 at Antsehase bridge/river;

197 m a.s.l.; 23 Jan. 2007; fr; *De Block, Dessein, Groeninckx & Rakotonasolo 2244*; BR, MO, P, TAN, UPS, WAG • Lamboukily, 14 km from camp de base in Kirindi; 42 m a.s.l.; 20 Jan. 2007; fl; *Groeninckx, Rakotonasolo, Dessein & De Block 105*; BR, G, MO, P, TAN, WAG • RN 35, ca 22 km from Morondava on road to Antananarivo, dunes des Belges; 19 m a.s.l.; 24 Jan. 2007; fl; *Groeninckx, Rakotonasolo, Dessein & De Block 149*; BR MO, P, TAN, WAG • commune Bemanonga, Andranomena Reserve; 18 Mar. 2011; fl, fr; *Kainulainen, Razafimandimbison, Razafindraibe & Wikström 170*; BR, S • commune Bemanonga, fkt. Marofandilia, village le plus proche Kirindy, forêt de Kirindy; 57 m a.s.l.; 12 Apr. 2013; fr; *Razakamalala, Randrianaivo & Rakotondrasaona 7404*; MO n.v., P online, TAN n.v. • commune Bemanonga, fkt. Marofandilia, village le plus proche Kirindy, forêt de Kirindy; 59 m a.s.l.; 21 Apr. 2013; fr; *Razakamalala, Randrianaivo & Rakotondrasaona 7505*; MO n.v., P online, TAN n.v. – **Without locality** • chiefly in Betsileo land; 1890; fl; *Baron 150*; K, P • s.dat.; fl; *Baron 4596*; BM, K, P • 1840; fl; *Bernier s.n.*; K • N de Madagascar; 1835; fl; *Bernier in Guillemin 319*; P • côte orientale; 1853; fl, fr; *Boivin in Barbey-Boissier s.n.*; G • s.dat.; fr; *Boivin in Cosson 2430*; P • s.dat.; fl; *d'Alleizette s.n.*; P • s.dat.; fr; *Homolle 1419*; BR, K, P.

Description

Shrub or small tree, 1–5(–7) m tall; pubescence whitish to tawny; leaves sometimes caducous. Young shoots brown or dark brown but rapidly becoming corky and then fawnish or orange brown, rarely glabrous but usually sparsely to densely covered with appressed or erect hairs; older branches corky, grey, greyish brown or reddish brown, somewhat flaking, glabrescent or glabrous. Petioles 4–10(–15) mm long, rarely glabrous, usually sparsely to densely covered with appressed or erect hairs. Leaf blades broadly obovate, broadly elliptic, orbicular, obovate, elliptic, ovate, rarely narrowly elliptic, 2–12 × 1–8.5 cm, subcoriaceous, drying dark or blackish brown above, somewhat paler below or not discolorous, upper surface glossy, moderately to densely covered with minute to short erect hairs sometimes combined with sparse long appressed hairs associated with higher order venation, or, glabrous but then usually at least midrib or midrib and secondary veins pubescent, lower surface moderately to densely covered with long erect hairs to woolly or glabrous except for midrib and secondary veins; margin ciliate; base cuneate, obtuse, rounded, rarely truncate, subcordate or somewhat unequal; tip rounded, obtuse, acute, more rarely acuminate or retuse; hair tuft domatia often present; 5–10 secondary veins on each side of midrib, impressed above and raised below; midrib and secondary veins densely to sparsely covered with long appressed hairs on both surfaces or rarely glabrous; higher order venation visible on both surfaces. Stipules triangular with needle-like awn, often somewhat keeled, outer surface rarely glabrous but usually with at least a few appressed hairs along the base and/or along the midrib, or, moderately to densely covered with appressed hairs all over, inner surface glabrous with row of colleters at the base; sheath 1.5–4 mm long; awn 0.5–3 mm long. Inflorescences sessile but leaves of first order bracts often fallen (giving the impression of short peduncle), 1.5–5 × 2–8 cm, with (15–)25–numerous flowers; inflorescence parts densely covered with ± long appressed, spreading or erect hairs; first order axes 0.3–3 cm long; higher order bracts often displaced 1–4 mm above branching point, with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted or more rarely ovate, 2–4 mm long; bracteoles at base of ovary and opposite or on pedicel somewhat below ovary and subopposite, stipular parts absent, foliar parts narrowly triangular to linear, ca 1(–1.5) mm long, tips acute. Flowers sessile to shortly pedicellate, pedicels 0–2 mm long. Calyx densely covered with appressed, spreading or erect hairs outside, inner surface densely covered with appressed hairs; tube 0.2–0.5 mm long; lobes triangular, 0.5–1 mm long, tips acute. Corolla tube 5–7.5 mm long, inner surface moderately covered with long erect hairs in upper half; lobes 3–4.5 mm long. Anthers 3–4 mm long, completely exserted from corolla tube at anthesis; filaments ca 1 mm long; connective often drying reddish brown. Ovary ca 1 mm long, densely covered with appressed, spreading or erect hairs; per locule 1–4 ovules pendulous from small placenta attached to upper half of septum. Style and stigma 11–13 mm long, exserted for 5–7 mm; style densely covered with long erect hairs in upper half (pubescence visible at anthesis); stigmatic lobes 4.5–5 mm long, upper 2.5–3 mm fusiform; papillate grooves along fusiform part and running further down for ca 2 mm. Fruits

Fig. 8. *Paracephaelis cinerea* (A.Rich. ex DC.) De Block. **A**. Flowering and fruiting branches. **B**. Flower. **C**. Flower bud. **D**. Longitudinal section through ovary and calyx. **E**. Bracteole, ovary and calyx. **F**. Longitudinally opened flower with style and stigma. **G**. Anther. **H**. Fruit. **I**. Seed. Adapted from Drake del Castillo (1897: pl. 421).

spherical, 3.5–6 mm in diam., wrinkled when dried, moderately to densely covered with appressed, spreading or erect hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical, 3–5 mm in diam., papyraceous, with rounded base and tip and small opening in upper half adaxially. Seeds (1–)2–6 per fruit, 2.5–4 × 2–3.5 mm.

Distribution

Known throughout Madagascar. Present in: Antsiranana II and Nossi-Be Districts, Diana Region, and Vohemar District, Sava Region (Antsiranana Province); Ambatondrazaka, Andilamena and Moramanga Districts, Alaotra-Mangoro Region (Toamasina Province); Maevatanana and Tsaratanana Districts, Betsiboka Region, Ambato-Boeni, Mahajanga I, Mahajanga II, Mitsinjo and Soalala Districts, Boeny Region, Antsalova and Maintirano Districts, Melaky Region, and, Antsohihy, Boriziny-Vaovao, Mampikony and Mandritsara Districts, Sofia Region (Mahajanaga Province); Andramasina, Anjozorobe, Ankazobe, Antananarivo Renivohitra and Manjakandriana Districts, Analamanga Region, Arivonimamo and Miarinarivo Districts, Itasy Region, and, Ambatolampy, Antanifotsy, Antsirabe II, Betafo and Faratsiho Districts, Vakinankaratra Region (Antananarivo Province); Ihosy District, Ihorombe Region, Ambatofinandrahana and Ambositra Districts, Amoron'i Mania Region, and, Ambalavao District, Haute Matsiatra Region (Fianarantsoa Province); Amboasary-Atsimo, Betroka and Taolagnaro Districts, Anosy Region, Beroroha, Betioky, Morombe and Sakaraha Districts, Atsimo-Andrefana Region, and, Morondava district, Menabe Region (Toliara Province) (Fig. 23B).

Habitat and phenology

Dry deciduous or semi-deciduous forest or forest remnants, dry littoral forest, dry scrub, more rarely subhumid forest; on sandy soil (laterite or white sand) or on rocks; elev. 0–1650 m. Flowers: (November–) December–March; Fruits: February–September.

Vernacular names and uses

Lengohazo (*Humbert 14471*); tarety (*coll. ignot. 14803-SF*); voatoana (*Randriamiero 8646-RN*). The species is used for firewood (*coll. ignot. 14803-SF*) and wood for construction (*coll. ignot. 14803-SF*, *coll. ignot. 17762-SF*, *Razafinarivo 19142-SF*).

Provisional IUCN assessment

Least Concern. This assessment is based on 153 herbarium collections collected between 1840 and 2018. The species occurs throughout Madagascar and the EOO is estimated to be 504 911 km^2, far exceeding the upper limit of any threat category under criterion B1. The AOO is estimated to be 456 km^2, which complies with the Endangered category under criterion B2. The number of locations far exceeds 20, which is higher than the upper limit for any threat category under subcriterion 'a' of criterion B2. The species is present in several protected areas, notably: Andohahela (parcelle 3); Ankarafantsika; Andringitra, Analamerana, Bemaraha, Isalo, Kirindi, Loky-Manambato, montagne des Français, and Zombitse-Vohibasia. Throughout Madagascar natural vegetation is impacted by anthropogenic action, e.g., slash-and-burn agriculture, burning for grazing, logging for construction wood, firewood, and wood for the production of charcoal, resulting in a decrease in the quantity and quality of the habitat of *P. cinerea*. However, the species is very widespread and, while certainly threatened locally by destruction of its habitat, its large distribution area covers many other localities with more intact natural vegetation. Because of the above-mentioned facts, the species is assessed as Least Concern.

Notes

1. *Paracephaelis cinerea* is very variable in leaf shape, size and pubescence. Specimens with densely pubescent lower leaf surfaces are found mostly in the Central Highlands and in northern Madagascar (Analamera, forêt d'Orangea, Daraina), much less along the west coast. Specimens with less pubescent

leaves have the same distribution range but were also frequently collected along the west coast and in south-eastern Madagascar (Andohahela). A number of specimens have (almost) completely glabrous leaves (with at most a few hairs on the midrib on upper and/or lower leaf surfaces). They are restricted to the Diana and Sava Regions. Examples are *Vesco s.n.*, *Capuron 27477-SF*, *Richard 83*, and *Razakamalala et al. 993*. Other specimens have large, densely pubescent, almost orbicular leaves and relatively large inflorescences. They are most common in the Diana, Sava, and Boeny Regions and differ strikingly from *P. cinerea* specimens with smaller, less pubescent leaves. Leroy annotated one of these specimens (*Capuron 24670-SF*) as "*Paracephaelis diegoensis*". Other examples of this large-leafed form are *Andrianantoanina & Rabeharinosy 705*, *Rakotonasolo et al. 2143*, *Ranirison & Nusbaumer 491*, and *Capuron 23073-SF*. But except for the large, orbicular leaves, no characters differentiate these specimens from other *P. cinerea* representatives. The morphological diversity of *P. cinerea* is the largest in the Diana and Sava Regions in northern Madagascar, where one may encounter all forms described above. It is also there that caducous specimens were collected (e.g., *De Block et al. 1174* from Analamera; *De Block et al. 1291* from baie de Sakalava).

2. Bremekamp (1934) transferred *Pavetta cinerea* to the genus *Tarenna*, giving it the name *Tarenna cinerea*. However, this name was already in use for a species from Thailand (Craib 1932); therefore, the new combination was illegitimate. Bremekamp (1939) renamed the species *Tarenna spodia*.

3. Capuron (1973) erroneously used the name "*Tarenna sericea*" when referring to *Tarenna cinerea* (A.Rich.) Bremek in his unpublished *Révision des Rubiacées de Madagascar et des Comores*. He placed this species in the monospecific section *Cinereae* within *Tarenna*.

4. In the past, specimens of *P. cinerea* were annotated by different authors. Leroy annotated *Capuron 24670-SF as* "*Paracephaelis diegoensis*" and *Sajy 25847-SF* as "*Paracephaelis calyptroides*". Homolle annotated *Humbert 4048* and *Perrier de la Bâthie 13459* as "*Tarenna cinerea* var. *majungensis*". Baker annotated *Baron 4596* as "*Tarenna heterophylla*". Attempting to classify the morphological variation within *P. cinerea* in an early phase of this revision, De Block annotated *Capuron 23309-SF* as "*Paracephaelis cinerea* subsp. *diegoensis*". None of these names were validly published.

5. Bojer invalidly published the name "*Pavetta glauca*" for *Pavetta cinerea* (Bojer 1837: 172).

6. The specimen *Baron 4596* is present in BM, K and P. All duplicates contain a mixture of material from *P. cinerea* and *Helictosperma malacophylla*.

7. One specimen, *Boivin s.n.*, from Île Sainte Marie, collected in 1849 with hardly any label data, is discarded for the provisional IUCN assessment. It is the only specimen of *P. cinerea* from the Analanjirofo Region and may be wrongly localized.

Paracephaelis comorensis De Block sp. nov.
urn:lsid:ipni.org:names:77260707-1
Figs 2J–K, 9

Diagnosis

Differing from *Paracephaelis trichantha* by having thinner (papyraceous or subcoriaceous vs coriaceous) and larger leaves (6–23 × (2.5–)4–13 cm vs 2.5–13 × 2.5–8 cm), acuminate leaf tips (vs rounded, obtuse or retuse and mucronate), longer stipular awns (2–4 mm vs 0.5–2 mm long), longer corolla lobes (3–4.5 mm vs 1.2–2 mm long), longer anthers (3–3.5 mm vs 1.5–2.5 mm long), and longer filaments (0.75–1 mm vs 0.1–0.2 mm long).

Etymology

The species epithet is based on the geographic distribution of the species.

Type material

COMORO ISLANDS – **Mayotte** • Grande Terre, Handrema, Pointe Handrema; 200 m a.s.l.; 7 Dec. 1996; fl; *Labat & Pascal 2887*; holotype: P[P00078874]; isotypes: K, MAO n.v., MO, WAG [WAG.1466458].

Other material studied

COMORO ISLANDS – **Anjouan** • face NW du mont Tingui, village Hambo, canton Ouani; 10 Mar. 1957; fr; *coll. ignot. 16655-SF*; P online • s.loc.; s.dat.; fl; *Lavanchie 22*; P. – **Mayotte** • Bandrélé, Choungui Kely, Hauts de M'tsamoudou; 7 Feb. 2001; fl; *Barthelat, M'Changama & Sifary 288*; G n.v., K, MAO n.v., MO n.v., P • Ilot Bouzi, Mamoudzou; 4 Mar. 2002; fl; *Barthelat, Gomel & Sifari 732*; BR, K, MAO n.v., P • Tsararano, Ironi Bé; 15 Jul. 2006; fr; *Barthelat, Mchangama & Ali Sifari 1654*; G n.v., K, MAO n.v., MO n.v., P • Grande Terre, Longoni; 20 Jul. 2006; fr; *Barthelat, Mchangama & Ali Sifari 1656*; MAO n.v., MO n.v., P online • s.loc.; 1840; fr; *Boivin s.n.*; K • s.loc.; 1840; fr; *Boivin in Drake s.n.*; P • bord de la mer à Pamanzi, côte ouest; 1850; fr; *Boivin 3179*; K, P • s.loc.; 1850; fr; *Boivin 3180*; P • centre NE, près du sommet du mont Sapéré; 550 m a.s.l.; 23 Feb. 1975; fl; *Floret 1188*; K, P • Saziley crête; 1 Jun. 1999; fr; *Mas 224*; K, P • Petite Terre, Moya, rocher intermédiaire entre les deux Moyas; 0–60 m a.s.l.; 5 Feb 2007; fl; *Mouly 554*; BR, K n.v., MAO n.v., P, TAN n.v. • Grande Terre, Combani, Mt. Combani, bordure de Réserve du Mlima Combani, le long du Grande Randonnée; 200–300 m a.s.l.; 8 Feb. 2007; fl; *Mouly 580*; BR, K n.v., MAO n.v., P • Grande Terre, Sohoa littoral à la base du plateau de Sohon, versant ouest; 0–30 m a.s.l.; 12 Feb. 2007; fl; *Mouly 616*; BR, MAO n.v., P • Chissioua Mtsamboro, près du sommet; 221 m a.s.l.; 15 Apr. 1999; fr; *Pignal & Pibot 1166*; BR, MO, P. – **Mohéli** • Hamavouno, lac de Boundouni; 87 m a.s.l.; 26 May 2006; fr; *Labat, Yahaya & Abdou 3704*; K, P online.

Description

Shrub or tree, to 8 m tall, dbh to 20 cm; pubescence whitish or more rarely tawny. Young shoots brown or dark brown, glabrous; older branches corky, greyish or pale brown, glabrous. Petioles 10–25 mm long, moderately to sparsely covered with long appressed or spreading hairs. Leaf blades ovate or, more rarely, elliptic or broadly obovate, 6–23 × (2.5–)4–13 cm, papyraceous to subcoriaceous, drying brown or more rarely greenish and hardly discolorous, upper surface somewhat glossy, glabrous or with midrib and, more rarely, secondary veins sparsely covered with long appressed hairs, lower surface glabrous or with midrib sparsely to moderately and secondary veins sparsely covered with long appressed hairs; margin sometimes sparsely ciliate; base cuneate or, more rarely, obtuse, rounded or truncate; tip acuminate, acumen 5–15(–25) mm long; hair tuft domatia present; midrib and secondary veins often somewhat paler than blade on the lower surface; (6–)8–12 secondary veins on each side of midrib, somewhat raised below; higher order venation often somewhat discolorous below. Stipules triangular with needle-like awn, keeled, outer surface moderately to sparsely covered with long appressed or spreading hairs at the base or along the keel, inner surface glabrous with row of colleters interspaced with sparse hairs at the base; sheath 2.5–4 mm long; awn 2–4 mm long. Inflorescences sessile, compact, 2–4.5 × 3.5–7 cm, with numerous flowers; inflorescence parts densely covered with appressed or spreading hairs; first order axes 0.3–1.3(–2.5) cm long; higher order bracts with stipular parts reduced or absent, foliar parts triangular and vaulted, 2–6 mm long; bracteoles present or absent, if present then on pedicel somewhat below ovary, usually not opposite, stipular parts absent, foliar parts linear, 0.75–1 mm long, tips acute. Flowers shortly pedicellate or rarely subsessile, pedicels (0–)1–3(–5) mm long. Calyx densely covered with appressed hairs outside; tube 0.4–0.6 mm long, inner surface with ring of long appressed hairs; lobes triangular, 0.4–0.6 mm long, inner surface glabrous or sparsely covered with short appressed hairs, margins ciliate, tips acute. Corolla tube 5–7 mm long, inner surface densely covered with long erect hairs in upper half or upper ⅔; lobes 3–4.5 mm long, margins ciliate. Anthers 3–3.5 mm long, completely exserted from

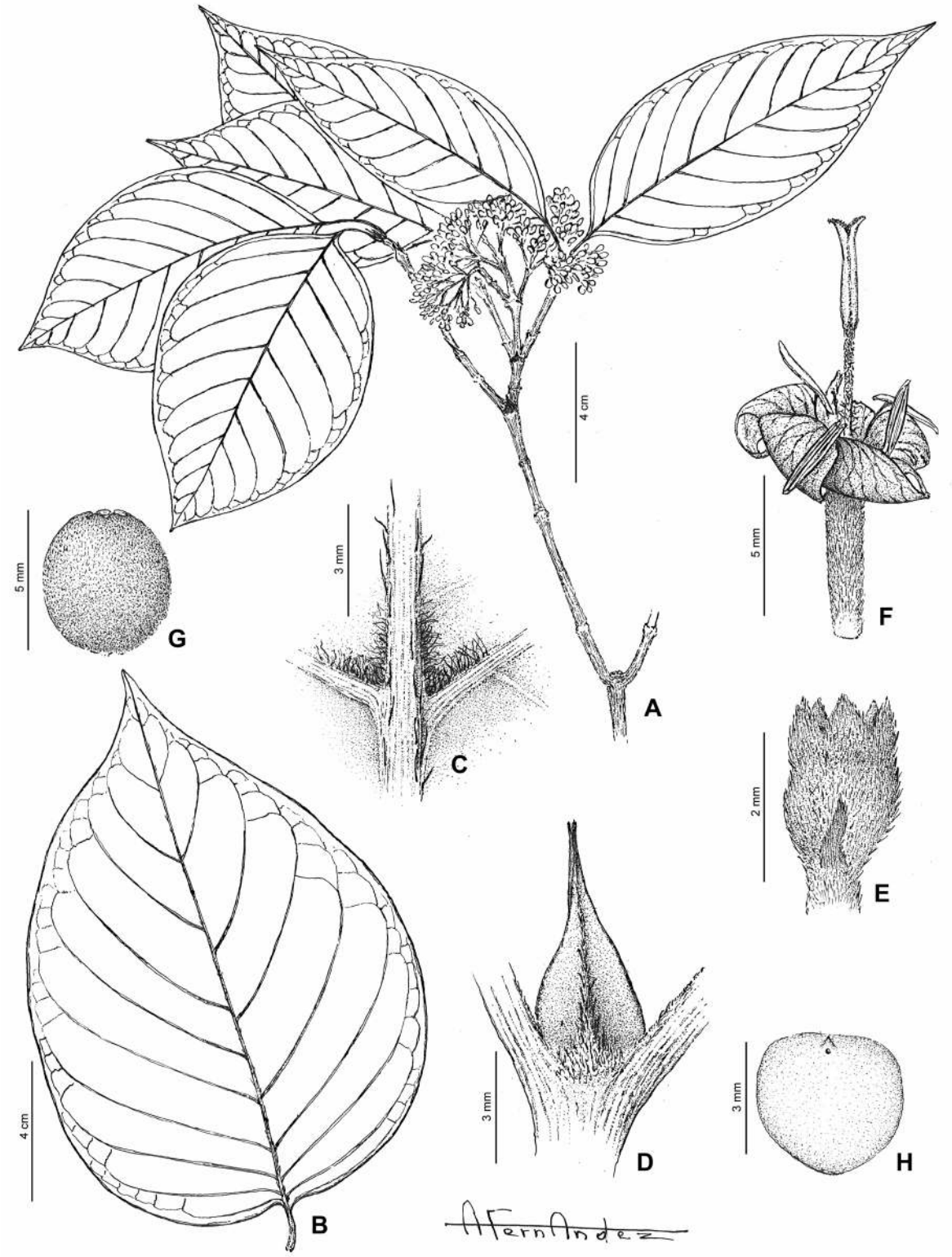

Fig. 9. *Paracephaelis comorensis* De Block sp. nov. **A**. Flowering branch. **B**. Leaf. **C**. Domatia and pubescence on midrib. **D**. Stipule. **E**. Bracteole, ovary and calyx. **F**. Corolla, stamens, style and stigma. **G**. Fruit. **H**. Pyrene, adaxial view. Drawn by Mr A. Fernandez. From *Labat & Pascal 2287* (A), *Mouly 580* (B–D), *Mouly 616* (E–F) and *Pignal & Pibot 1166* (G–H).

corolla tube at anthesis; filaments 0.75–1 mm long. Ovary 0.75–1.2 mm long, densely covered with ± short appressed hairs; per locule (1–)3–5 ovules pendulous from small placenta attached to upper half of septum. Style and stigma 9–14 mm long, exserted for 4–6.5 mm; style densely covered with long erect hairs from 2–4 mm above base to somewhat below papillate zone; stigmatic lobes 4–4.5 mm long, upper 2–2.5 mm fusiform; papillate grooves running along fusiform part and further down for ca 2 mm. Fruits spherical, 0.4–0.5 cm in diam., wrinkled when dried, moderately to densely covered with short appressed hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical, 3.5–4 mm in diam., membranous adaxially, thinly crustaceous abaxially, with rounded base, shortly acuminate tip and small adaxial opening somewhat below the apex. Seeds (1–)2–4 per fruit, 2–2.5 × 2.5–3 mm.

Distribution

Mostly collected from Mayotte, but also occurring on Mohéli and Anjouan (Comoro Islands) (Fig. 24).

Habitat and phenology

Dry forest or thicket, mesophyllous (intermediate) forest; on rocks; elev. 0–550 m. Flowers: December–March; Fruits: March–July. According to Barthelat (2019), flowering continues until May, but this was not observed by the author.

Vernacular names

Botinati (*coll. ignot. 16655-SF*); mora folaka malandy (*Barthelat et al. 732*); mora folaka tamtam (*Barthelat et al. 288*).

Provisional IUCN assessment

Vulnerable: VU B1ab(iii) B2ab(iii). This assessment is based on 14 herbarium collections with detailed locality data, collected between 1850 and 2007. The EOO of *P. comorensis* sp. nov. is estimated to be below 1009 km^2 (the sum of the surface areas of Mayotte, Anjouan, and Moheli), which complies with the Endangered category under criterion B1. The AOO is estimated to be 56 km^2, which also complies with the Endangered category under criterion B2. The species is known from 10 locations, which is the upper limit for the Vulnerable category under subcriterion 'a' of criterion B2. In 8 of these 10 locations, the presence of the species was confirmed relatively recently (between 1999 and 2007). The species is present in the Réserve Forestière de Majimbini and was also collected near the border of the Réserve Forestière de Combani. In the Comoros, 80–90% of the natural vegetation has been destroyed and replaced by fields for subsistence farming, secondary forests of which the understory is planted with, e.g., bananas, as well as plantations, grassland, and very degraded uncultivable areas known as padza (Stafford 2001). The Comoro islands, e.g., Anjouan, are densely populated and population densities continue to rise, with ca 90% of the inhabitants depending on subsistence farming for their livelihood (Doulton *et al.* 2015). The islands' deforestation has been the highest in the world between 2000 and 2010 (Doulton *et al.* 2015). Remaining forests are cleared for subsistence farming and the grazing of livestock, targeted for construction wood, firewood, wood for the production of charcoal, and other resources such as, e.g., medicinal plants, with secondary damaging factors being volcanic eruptions, cyclones, and invasive exotic species (Louette 2004). Because of these facts, a reduction in the extent and quality of the habitat of *P. comorensis* sp. nov. is inferred. This threat, in combination with the low AOO and the 10 locations, qualifies *P. comorensis* sp. nov. as Vulnerable.

Notes

1. The three specimens *Boivin 3180* (P) bear the name "*Tarenna comorensis*" and are placed in a type folder in P. But this species name was never published. This historical material is not chosen as type of *P. comorensis* sp. nov. because the material is only present in P and one of the three sheaths is a

mixture of material (the second specimen belongs to *Coptosperma mitochondrioides* Mouly & De Block). Furthermore, no flowers and only few fruits are available.

2. The *Paracephaelis* specimens from the Comoro Islands have historically been placed with *P. trichantha* (usually as *Tarenna trichantha*; Fosberg 1979; Fosberg & Renvoize 1980; Bridson 1979, 1988, 2003). The material from the Comoros is similar to *P. trichantha* by the densely pubescent, compact inflorescences, the small corolla and calyx, and similar to its glabrous form as regards the pubescence of the vegetative parts. But there are many differences, such as larger, less coriaceous leaves with acuminate tip and longer stipular awns, corolla tubes, corolla lobes, anthers and filaments.

3. In *Mouly 554*, the dense pubescence on the outer surface of the corolla lobes is restricted to the basal halves while the upper halves are glabrous.

4. This species was recognized as new by several botanists who annotated specimens in the P herbarium. Boivin annotated *Boivin 3179* as "*Lamprospermum comorense*" and Baillon labeled *Boivin s.n.* and *Boivin 3180* as "*Tarenna comorensis*". Homolle (1938) used the name "*Enterospermum comorense*" to indicate this species. All these names are nomina nuda.

5. *Paracephaelis comorensis* sp. nov. strongly resembles *P. cinerea* in flower and fruit morphology. This is also the case for *P. trichantha*, even though in this species the flowers are markedly smaller than in the two other species. In an early stage of the revision process, the author regarded the three species as too morphologically similar to distinguish them at species level. After thorough revision of all *Paracephaelis* material to evaluate the morphological differences between and within species and taking into account that 1) the three taxa form separate geographic entities that are unlikely to have the opportunity to interbreed, with *P. comorensis* sp. nov. restricted to the Comoro Islands, *P. trichantha* to the Seychelles and the East African coast and *P. cinerea* to Madagascar, 2) the morphological differences between the taxa, and 3) the fact that two taxa already had existing species names, it was decided to recognize them at specific level. The above described process resulted in the annotation of specimens of *P. comorensis* sp. nov. as "*Paracephaelis cinerea* subsp. *comorensis*", a name which was never published. Unfortunately, this nomen nudum was picked up in *La Flore Illustrée de Mayotte* (Barthelat 2019: 527).

Paracephaelis gautieri De Block sp. nov.
urn:lsid:ipni.org:names:77260708-1
Figs 2E, 10

Diagnosis

Differing from *Paracephaelis aristata* sp. nov. by having rounded to retuse leaf tips (vs shortly aristate), glabrous lower leaf surfaces (vs densely covered with long erect or spreading hairs), shorter bracteoles (0.7–1.2 mm vs 3–5 mm long), shorter calyx lobes (1.2–1.5 mm vs 2.5–3 mm long in flowering stage, 4–5 mm long in fruiting stage), and the inner surface of the calyx tube densely covered with long appressed hairs (vs glabrous).

Etymology

The species is named in honour of Dr Laurent Gautier from the Conservatoire et Jardin botaniques de la Ville de Genève (G), who collected the type specimen.

Type material

MADAGASCAR – **Antsiranana Province, Sava Region, Vohemar District** • commune Daraina, Daraina, forêt de Bobankora, partie nord, 1 km NNE du point coté 607, ruisseau à côté du campement;

330 m a.s.l.; 2 Mar. 2003; fl; *Gautier, Wohlhauser & Nusbaumer 4188*; holotype: G scan; isotype: BR[BR00000929990].

Other material studied

MADAGASCAR – **Antsiranana Province, Sava Region, Vohemar District** • commune Daraina, Daraina, forêt de Bobankora, partie nord, à 460 m du point coté 454 au 196°; 313 m a.s.l.; 17 Jan. 2005; fl; *Nusbaumer & Ranirison 1423*; BR, G n.v.

Description

Shrub, 5–6 m tall; pubescence whitish. Young shoots blackish brown, glabrous; older branches greyish, glabrous; internodes short, 0.3–2.5 cm long. Petioles 2–6 mm long, glabrous. Leaf blades narrowly obovate or narrowly elliptic, 4–7 × 0.4–1.7 cm, coriaceous, drying dark brown or greenish and not discolorous, upper surface glossy, both surfaces glabrous; base attenuate; tip rounded to retuse; ciliate pit domatia sometimes present; 5–8 secondary veins on each side of midrib; secondary and higher order venation inconspicuous on both surfaces. Stipules caducous, triangular with short needle-like awn, outer surface of youngest stipule pairs sparsely to moderately covered with short appressed hairs at the base and tip, inner surface glabrous with row of colleters at the base; sheath 1.5–2.5 mm long; awn 1–1.5 mm long. Inflorescences sessile, 1.5–2.5 × 1.5–3.5 cm, with 12–35 flowers; inflorescence parts sparsely or moderately (base of inflorescence) to densely (higher up) covered with short appressed hairs; first order axes 0.5–1.5 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted or linear leaf-like, 1.5–6 mm long, tips acute; bracteoles on pedicel somewhat below ovary, subopposite, stipular parts absent, foliar parts narrowly triangular or linear, 0.7–1.2 mm long, tips acute. Flowers shortly pedicellate, pedicels 2–6 mm long. Calyx densely covered with appressed hairs outside; tube ca 1 mm long, inner surface with ring of long appressed hairs; lobes oblong, 1.2–1.5 mm long, somewhat keeled, inner surface moderately covered with short appressed hairs in lower half, ± glabrous in upper half, margins ciliate, tips obtuse or rounded. Corolla tube 8–9 mm long, inner surface moderately covered with spreading hairs except at base; lobes 4–4.5 mm long, margins ciliate. Anthers 4.5–5 mm long, completely exserted from corolla tube at anthesis; filaments ca 1 mm long. Ovary 1–1.2 mm long, longitudinally ribbed (when dried), densely covered with appressed hairs; per locule 3–4 ovules arranged at periphery (mostly at base and top) of placenta attached to middle of septum. Style and stigma 15–16 mm long, exserted for 6–8 mm; style densely covered with long spreading hairs from ca 3 mm from base to somewhat below papillate zone; stigmatic lobes 6–7 mm long. Fruits, pyrenes and seeds unknown.

Distribution

Only known from Daraina in Vohemar District, Sava Region (Antsiranana Province) (Fig. 23A).

Habitat and phenology

Low-elevation semi-deciduous forest; elev. ca 300 m. Flowers: January–March; Fruits: unknown.

Provisional IUCN assessment

Critically Endangered: CR B2ab(iii). Since *P. gautieri* sp. nov. is only known from two collections (collected in 2003 and 2005), the extent of occurrence (EOO) cannot be calculated. The area of occupancy (AOO) is 8 km^2, which complies with the Critically Endangered category under criterion B2. The species is known from a single location, which also complies with the Critically Endangered category under subcriterion 'a' of criterion B2. The type specimen is from Bobankora Forest within the Loky-Manambato Protected Landscape, created in 2005 and managed by a Malagasy non-governmental organization, Association Fanamby (Wahlert *et al.* 2019). Before 2005, no protective measures had been taken for this region, which forms the junction between humid and dry forests and lowland and montane forests and

is therefore very variable in vegetation types (Nusbaumer *et al.* 2010). Loky-Manambato is known as a region with high species diversity and endemicity (Rakotondravony 2006). Recent large-scale collecting resulted in the discovery of ca 50 new plant species (Nusbaumer *et al.* 2010), among which *P. gautieri*

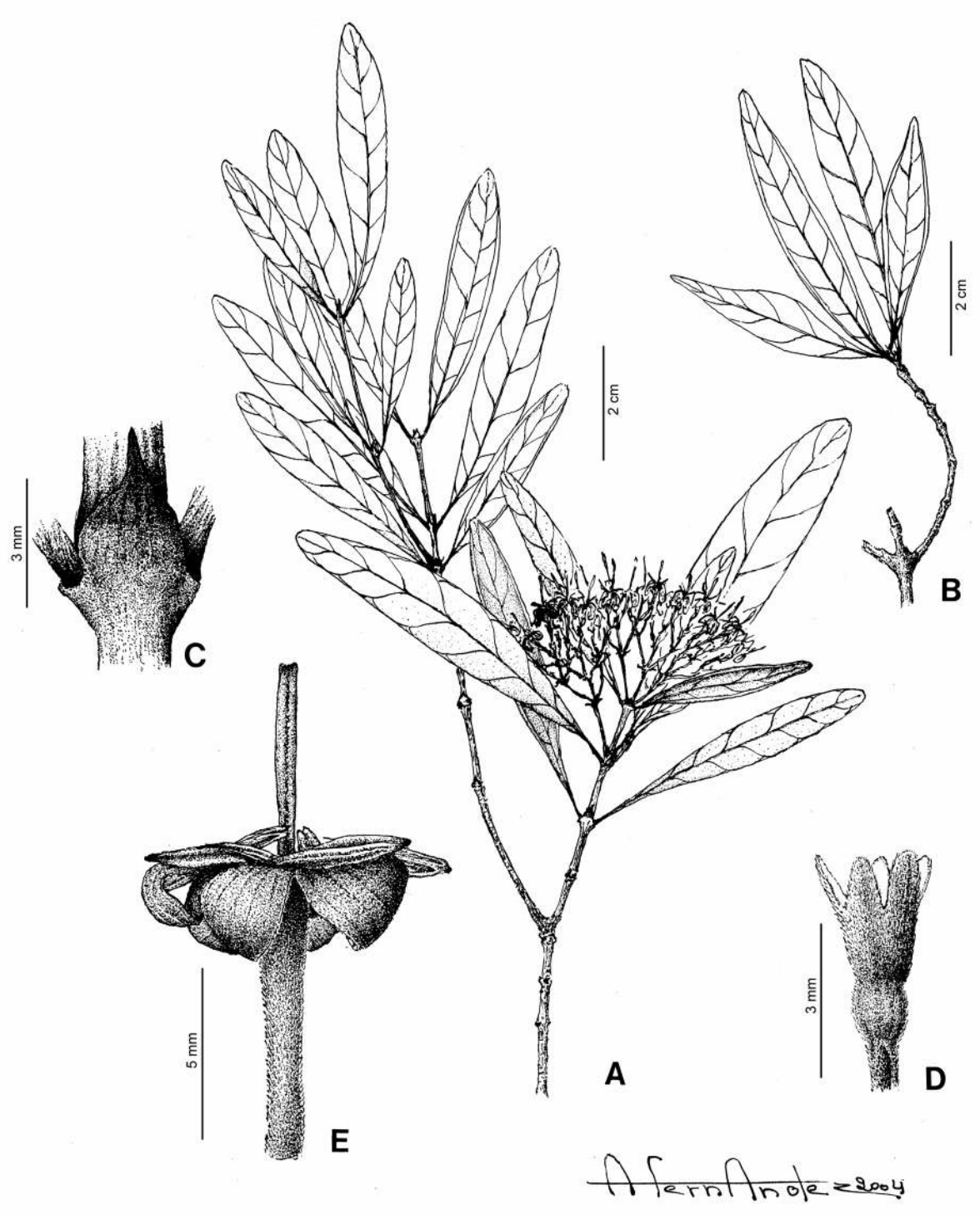

Fig. 10. *Paracephaelis gautieri* De Block sp. nov. **A**. Flowering branch. **B**. Vegetative branch showing short internodes. **C**. Stipule. **D**. Bracteole, ovary and calyx. **E**. Corolla, stamens, style and stigma. Drawn by Mr A. Fernandez. From *Gautier, Wohlhauser & Nusbaumer 4188*.

sp. nov. (and *P. ranirisonii* sp. nov.). *Paracephaelis gautieri* sp. nov. occurs in lowland semi-deciduous forest. The main threat to the species is loss of habitat as a result of subsistence farming, illegal logging for timber and charcoal, burning for pasture, and artisanal gold mining (Rakotondravony 2009; Nusbaumer *et al.* 2010), activities that also take place within the protected area. Therefore, a reduction in the extent and quality of the habitat of *P. gautieri* sp. nov. is inferred. This fact, in combination with the low AOO and the single location, qualifies the species for Critically Endangered status.

Notes

1. *Paracephaelis gautieri* sp. nov. is similar to *P. aristata* sp. nov. by the relatively small and narrow leaves, the small inflorescences with relatively few flowers, the short internodes and the greyish branches. *Paracephaelis gautieri* sp. nov. differs from *P. aristata* sp. nov. by the glabrous petioles and young shoots (vs densely covered with ± short appressed hairs in *P. aristata* sp. nov.), the glabrous lower leaf surfaces (vs densely covered with tawny, erect or spreading hairs), the shape of the leaf tips (rounded or retuse vs shortly aristate), the shorter stipular awns (1–1.5 mm vs 2–4 mm long), the longer pedicels (2–6 mm vs 0–3 mm long), the shorter bracteoles (0.7–1.2 mm vs 3–5 mm long), the shorter calyx lobes (1.2–1.5 mm vs 2.5–3 mm long in flowering stage), the fewer ovules per locule (3–4 vs 6–10), and the shape of the ovary in dried condition (longitudinally ribbed vs smooth). Furthermore, *P. gautieri* sp. nov. occurs in northern Madagascar whereas *P. aristata* sp. nov. is restricted to south-eastern Madagascar.

2. Ciliate pit domatia are present in *Gautier et al. 4188* but absent in *Nusbaumer & Ranirison 1423*.

Paracephaelis grandifructa De Block sp. nov.
urn:lsid:ipni.org:names:77260709-1
Figs 3, 11

Diagnosis

Differing from *Paracephaelis capitulifera* sp. nov. by having larger fruits (15–20 × 10–15 mm vs 10–13 × 8–10 mm), hair tuft domatia (vs domatia absent), stipules with acute tips or more rarely acuminate with awn up to 2.5 mm long (vs acuminate with needle-like awn 1.5–4 mm long), longer calyx tubes (6.5–12 mm vs 3–8 mm long), shorter bracteoles (1.5–2.5 mm long, with acute tips vs 3–3.5 mm long, with acuminate tips), and calyx lobes with rounded to obtuse tips (vs acuminate, reflexed tips).

Etymology

The species epithet is based on the robust fruits.

Type material

MADAGASCAR – **Toamasina Province, Analanjirofo Region, Mananara District** • commune Vanono, fkt. Anjian'ny Madiorano, suivant la piste vers Ambodimanga Sahavalanana, à environ 1 km de vol d'oiseau SE d'Anjian'ny Madiorano; 834 m a.s.l.; 21 Jul. 2007; fr; *Ravelonarivo et al. 2570*; holotype: MO; isotypes: BR[BR0000022757630], P[P05402966], TAN.

Other material studied

MADAGASCAR – **Toamasina Province, Alaotra-Mangoro Region, Moramanga District** • Phelps Dodge project site, ca 15 air-km NE of Moramanga, ca 11 km E of Antanambao, Ambatovy-Sud; 975 m a.s.l.; 15 Feb. 1997; fl; *Andriatsiferana et al. 2148*; MO, P. – **Analanjirofo Region, Soanierana-Ivongo District** • Andapafito, Iampirano, Ambatovaky RS, 4 km S of village; 520 m a.s.l.; 14 Dec. 2003; fl; *Rakotonasolo, Beentje, Ralimanana & Rakotoarinivo 700*; BR, K, P online, TAN. – **Vavatenina District** • Ambohibe, Ambatoharanana, Moango, le long de la piste vers Antevibe, Zahamena PN; 697 m a.s.l.; 15 Jul.

2004; fr; *Andriamihajarivo, Ratovoson, Andrianjafisoa & Rapaoly 309*; K, MO, P online • Beranomaso, fir. Sahatavy; 16 Jan. 1958; fl; *Ramarokoto 9466-RN*; P online, TEF. – **Antananarivo Province, Vakinankaratra Region, Ambatolampy District** • 16.2 km SE de Tsinjoarivo, forêt d'Ankilahila, le long de la rivière d'Andrindrimbola; 1450 m a.s.l.; 21 Jan. 1999; fl; *Messmer & Andriatsiferana 748*; G, K, P online. – **Fianarantsoa Province, Vatovavy-Fitovinany Region, Ifanadiana District** • Ranomafana PN, Vohipara, 38.3 km NE of Fianarantsoa; 1100 m a.s.l.; 2 Nov. 1997; fl, fr; *Davis, Andriantiana, Gower & Malcomber 1041*; BR, K, P online, TAN • Ranomafana PN, parcelle 3, S of RN 25 at 7 km W of Ranomafana; 950–1150 m a.s.l.; 7 Oct. 1993; fr; *Solo & Randrianasolo 25*; BR, K, MO, P, TAN.

Description

Tree, 4–15 m tall, dbh to 20 cm, more rarely large shrub; pubescence tawny. Young shoots reddish brown, densely covered with short erect hairs; older branches reddish brown, often flaking, glabrescent. Petioles 1.2–2.2 cm long, densely covered with short erect hairs. Leaf blades occasionally anisophyllous (*Solo & Randrianasolo 25*; *Rakotonasolo et al. 700*), elliptic, somewhat obovate or somewhat ovate, 5–20 × 2.5–9 cm, coriaceous, drying brown and hardly discolorous, upper surface somewhat glossy, moderately covered with short erect hairs (with pubescence on midrib and secondary veins somewhat denser), lower surface densely covered with somewhat longer erect hairs; base cuneate to obtuse; tip acuminate with acumen 0.5–2 cm long; hair tuft domatia present; 10–15 secondary veins on each side of midrib, raised below; higher order venation hardly visible above, somewhat raised below. Stipules triangular, keeled, gradually tapering into an acute tip or, more rarely, with short needle-like awn, outer surface densely covered with short erect hairs, inner surface glabrous with 2–3 rows of colleters at the base; sheath 8–12 mm long; awn, if present, up to 2.5 mm long. Inflorescences sessile, capitate, 1.5–2(–4 in fruit) × 3–4(–8 in fruit) cm, with 15–40 flowers; inflorescence parts densely covered with short erect hairs; first order axes 0.2–0.8 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted, faintly keeled, 3–5 mm long, tips acute; bracteoles at base of ovary, opposite, stipular parts absent, foliar parts triangular, 1.5–2.5 mm long, tips acute. Flowers sessile. Calyx densely covered with short erect hairs outside, inner surface densely covered with minute appressed hairs all over but most dense at the base; tube 6.5–12 mm long, longitudinally ribbed (when dried); lobes ovate, 1–2 mm long, faintly keeled, margins ciliate, tips obtuse to rounded. Corolla tube 12–20 mm long, inner surface unknown; lobes 5–12 mm long. Ovary ca 3 mm long, strongly ribbed longitudinally (when dried), densely covered with short erect hairs; per locule 7–14 ovules arranged at periphery of placenta attached to middle of septum. Style and stigma unknown. Fruits ovoid, 15–20 × 10–15 mm, strongly ribbed longitudinally (when dried), densely covered with short erect hairs; fruit wall well-developed, with multi-layered anastomosing network of sclerified vascular bundles; pyrenes sub-hemispherical, ca 9 × 8 mm, thin, crustaceous, with rounded base, rounded tip, small adaxial opening somewhat below the middle and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 4–8 per fruit, 4.5–5.5 × 3–4 mm.

Distribution

Restricted to eastern Madagascar. Present in: Moramanga District, Alaotra-Mangoro Region, and Soanierana-Ivongo and Vavatenina Districts, Analanjirofo Region (Toamasina Province); Ambatolampy District, Vakinankaratra Region (Antananarivo Province); Ifanadiana District, Vatovavy-Fitovinany Region (Fianarantsoa Province) (Fig. 23A).

Habitat and phenology

Mid-elevation humid forest; elev. 500–1450 m. Flowers: November–February; Fruits: July–November.

Vernacular names

Lelanangaka, molotrangaka (*Andriatsiferana et al. 2148*); voatalanina (*Ramarokoto 9466-RN*).

Provisional IUCN assessment

Vulnerable: VU B1ab(iii) B2ab(iii). This assessment is based on 8 herbarium specimens collected between 1958 and 2007. The EOO of *P. grandifructa* sp. nov. is estimated to be 8777 km^2, which complies with the Vulnerable category under criterion B1. The AOO is 32 km^2, which complies with the Endangered

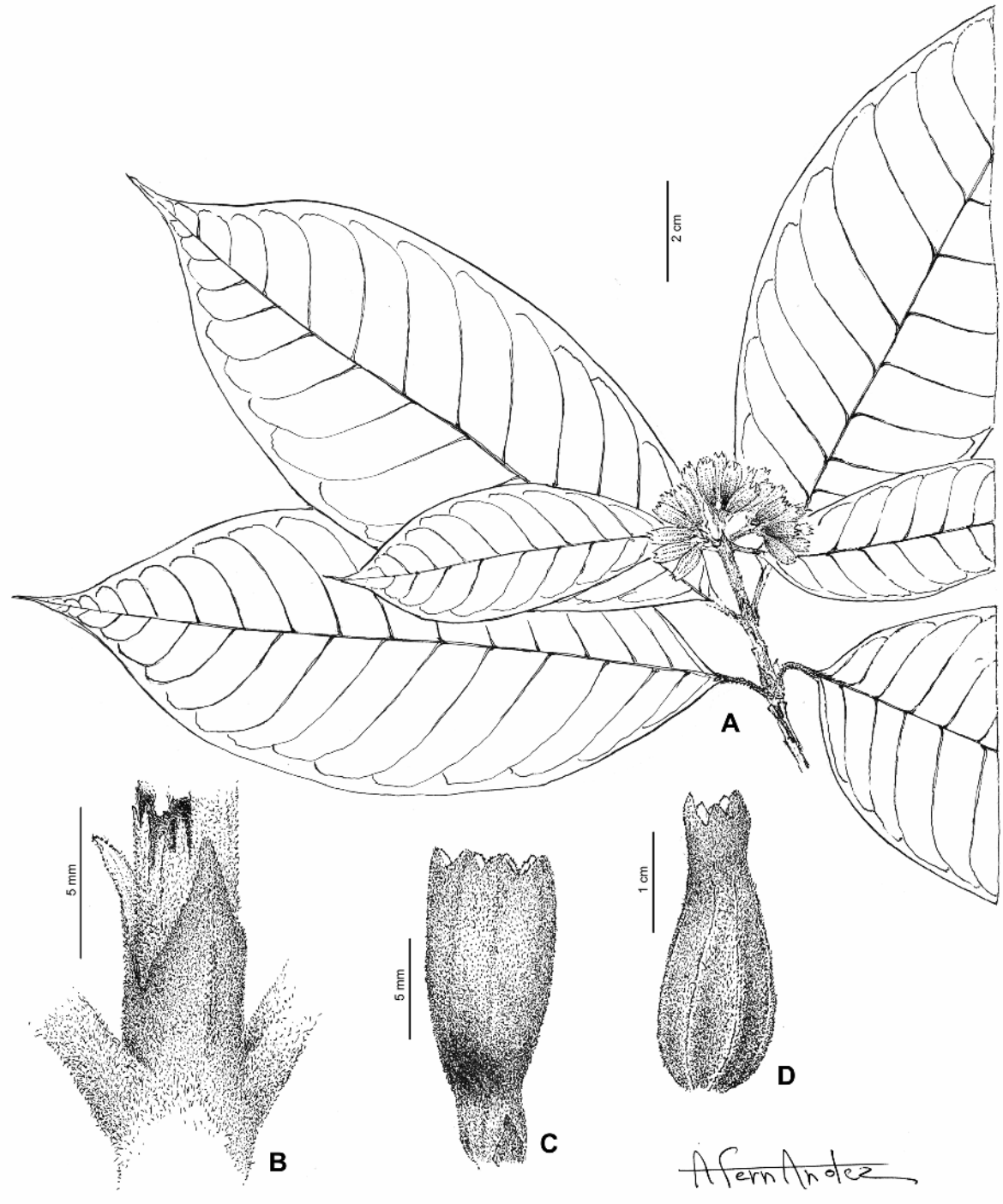

Fig. 11. *Paracephaelis grandifructa* De Block sp. nov. **A**. Flowering branch. **B**. Stipules. **C**. Bracteole, ovary and calyx. **D**. Fruit. Drawn by Mr A. Fernandez. From *Rakotonasolo et al. 700* (A–C) and *Solo & Randrianasolo 25* (D).

category under criterion B2. The species occurs in 6 locations, which complies with the Vulnerable category under subcriterion 'a' of criterion B2. *Paracephaelis grandifructa* sp. nov. occurs in the Ranomafana and Zahamena National Parks and the Ambatovaky Special Reserve. These protected areas suffer from clearing of forest for subsistence agriculture, grazing of cattle, human settlement (Zahamena), and artisanal gold mining (Ranomafana). Furthermore, illegal logging, production of charcoal, collection of non-timber forest products, and hunting take place (Nicoll & Langrand 1989; Thompson & Evans 1992; Wright 1997; Hannah & Boltz 2003; Jones 2018; BirdLife International 2020a). Outside the protected areas, these threats are even more prominent. Because of the above-mentioned facts, a reduction in the extent and quality of the habitat of *P. grandifructa* sp. nov. is inferred. This fact, in combination with the low EOO and AOO and the low number of locations, qualifies *P. grandifructa* sp. nov. as Vulnerable.

Note

1. *Paracephaelis grandifructa* sp. nov. resembles *P. capitulifera* sp. nov. by the similar pubescence on vegetative and reproductive parts, the stipular sheaths of the same size, the capitate inflorescences, the sessile flowers, the well-developed calyx tubes and the large ovoid fruits. The two species differ by the shape of the tips of the stipular sheaths (usually acute, more rarely with short awn up to 2.5 mm long in *P. grandifructa* sp. nov. vs with needle-like awn 1.5–4 mm long in *P. capitulifera* sp. nov.), the absence/presence of hair tuft domatia (present in *P. grandifructa* sp. nov. vs absent in *P. capitulifera* sp. nov.), the shape and size of the bracteoles (1.5–2.5 mm long and tips acute vs 3–3.5 mm long and tips acuminate), the length of the calyx tube (6.5–12 mm vs 3–8 mm long), the shape of the tip of the calyx lobes (round to obtuse and not reflexed vs acuminate and reflexed) and the size of the fruits (15–20 × 10–15 mm vs 10–13 × 8–10 mm). *Paracephaelis grandifructa* sp. nov. occurs in mid-elevation humid forest, elev. 500–1150 m, whereas *P. capitulifera* sp. nov. occurs in high plateau and gallery forest, elev. 1200–1700 m.

2. Two specimens with (near-)mature flowers were seen online (P). In *Ramarokoto 9466-RN*, the corolla tube is ca 20 mm long and the corolla lobes 6–7 mm long. In this specimen, the corolla tubes are split longitudinally over their entire length. In *Messmer & Andriatsiferana 748*, the flowers are mature buds, with the corolla tube ca 12 mm and the corolla lobes ca 5 mm long. The flowers of these two specimens could not be studied.

Paracephaelis longipedicellata De Block sp. nov.
urn:lsid:ipni.org:names:77260710-1
Figs 2C, 4A–B, E, G, M–N, 12

Diagnosis

Differing from *Paracephaelis sericea* by having narrower leaves (1.5–3.5 cm vs 4.5–12 cm wide), shorter petioles (2–5 mm vs 1–3 cm long), longer pedicels (8–20 mm vs 0–2 mm long or rarely up to 5 mm long in case of reduction), shorter calyx tubes (0.75–1 mm vs 2–5 mm long), and smaller, spherical fruits (4–7 mm in diameter vs ovoid or more rarely subspherical, 10–12 × 8–11 mm) with thin fruit walls (vs thick fruit wall with network of anastomosing sclerified vascular bundles).

Etymology

The species epithet is based on the long pedicels.

Type material

MADAGASCAR – **Antsiranana Province, Diana Region, Nossi-Be District** • Sambirano, forêt de Lokobe, Nossi-Be; 13–15 Mar. 1964; fl; *Capuron 23451-SF*; holotype: P[P04525149]; isotypes: BR[BR0000022757647], P[P04525148], TEF.

Other material studied

MADAGASCAR – **Antsiranana Province, Diana Region, Ambanja District** • Ampasindava, forêt de Betsitsika, à 582 m du point côté 69, au 294°; 65 m a.s.l.; 22 Jan. 2009; fl; *Ammann, Madiomanana & Tahinarivony 324*; BR, G n.v. • Ampasindava, forêt de Betsitsika, à 375 m du point côté 264, au 274°; 230 m a.s.l.; 17 Nov. 2009; fr; *Ammann, Madiomanana & Tahinarivony 358*; BR, G n.v. • Antseva, Tsaratanana massif; 450 m a.s.l.; 9 Apr. 2000; fl; *Antilahimena, Ratovoson, Ravelonarivo & Rabenantoandro 458*; BR, MO • Bemanevika, Bandrakorony, forêt primaire subhumide de basse altitude de Bandrakorony, près du ruisseau de Betsitsiky sur la presqu'île d'Ampasindava; 272 m a.s.l.; 20 Jan. 2009; fl; *Bernard et al. 1298*; BR, MO • Sambirano, presqu'île d'Ambato; 16 Mar. 1964; fl, fr; *Capuron 23425-SF*; BR, P, TEF • Sambirano, Antsalabe, entre Djangoa (Ambanja) et Ankaramybe; 12 Oct. 1966; fr; *Capuron 24838-SF*; BR, P, TEF • Bekaka; 150 m a.s.l.; 20 Mar. 1950; fl; *coll. ignot. 3163-SF*; P, TAN, TEF • Manongarivo RS, Besinkara, 1 km NW d'Ambalafary, relevé R 70; 300 m a.s.l.; 22 Jun. 1994; fr; *Gautier, Chatelin & Derleth 2404*; BR, G n.v., K, TAN • Manongarivo RS, Ambahatra, cours supérieur, crête entre les deux bras de l'Ambahatra, 500 m WNW du point côté 1037, relevé TL1; 850 m a.s.l.; 28 Feb. 1999; fl; *Gautier, Messmer & Andriatsiferana 3431*; BR, G n.v., P online • Ampasindava, forêt de Betsitsika, à 906 m du point côté 69, au 145°; 150 m a.s.l.; 1 Nov. 2009; fr; *Gautier, Ammann, Madiomanana & Tahinarivony 5268*; BR, G n.v. • massif de Manongarivo; 800 m a.s.l.; Apr. 1909; fr; *Perrier de la Bâthie 3854*; P • chaîne de Bekaka; 150 m a.s.l.; s.dat.; fl; *Saboureau 59*; P • forêt d'Andranomatavy; 196 m a.s.l.; 26 Sep. 2013; fr; *Tahinarivony 736*; G n.v., P online, MO n.v., TAN n.v. – **Nossi-Be District** • Nossi-Be, RNI 6, Lokobe; 0–30 m a.s.l.; 19 May 1994; fr; *Antilahimena 121*; BR, K, MO, P • Nossi-Be, Junea, protection zone around RNI 6, Lokobe; 105 m a.s.l.; 13 Jan. 2007; fl; *Groeninckx, Rakotonasolo & De Block 82*; BR, MO, TAN • Nossi-Be, forêt de Lokobe; Mar. 1962; fl; *Keraudren 1581*; BR, P • Nossi-Be, Andokobe, Lokobe; 12 Mar. 1956; fl; *Lebosaka 9397-RN*; BR, P, TEF • Andokobe, Hell-Ville; 12 Mar. 1957; fl; *Lebosaka 9447-RN*; P • Nossi-Be; 1840; fr; *Richard 362*; P • Nossi-Be;1840; fr; *Richard 643*; P • Nossi-Be; 1848; fr; *Richard 2058*; P • Marovalia, RNI 6, Lokobe, Nossi-Be; 2 Mar. 1951; fl; *Rakoto 2724-RN*; BR, P, TAN. – **Sava Region; Vohemar District** • forêt d'Analalava, S de la basse Fanambana; 18 Mar. 1967; fl; *Capuron 27547-SF*; BR, P, TEF • Vohemar-Sambava road, ca 8 km S of Fanambana river and village, 32 km S of Vohemar; 50 m a.s.l.; 28 Jul. 1985; fr; *Puff, Igersheim & Rajemisoa 850728-1/3*; K, WU • fir. Fanambana, forêt d'Analalava-Antsoha; 61 m a.s.l.; Apr. 2001; fl; *Rabenantoandro, Ranaivojaona & Rakoto 489*; BR, K, MO, P online • fir. Tsarabaria, fkt. Manakana, forêt d'Ambondrobe; 53 m a.s.l.; 15 Jul. 2003; fr; *Rabevehitra, Razakamalala & Rakotomamonjy 312*; BR, K, MO • fir. Tsarabaria, fkt. Manakana, Ambondrobe; 26 Oct. 2002; fr; *Rabevohitra, McPherson, Rabenantoandro & Ranarivelo 4212*; BR, MO, P online • fir. Tsarabaria, fkt. Manakana, forêt sublittorale E d'Ambondrobe; 2 Mar. 2003; fl; *Rabevohitra, Rabenantoandro & Razakamalala 4574*; BR, MO, P online • ibid.; 13 Mar. 2004; fl; *Razakamalala, Rabevohitra & Faralahy 1009*; BR, K, MO • ibid.; 20 May 2004; fr; *Razakamalala & Rabehevitra 1322*; BR, K, MO, P.

Description

Shrub or tree, 1–10 m tall; pubescence whitish. Young shoots brown or reddish brown, densely covered with appressed to spreading or, more rarely, erect hairs; older branches reddish brown, flaking, glabrescent. Petioles 2–5 mm long, densely covered with appressed or spreading hairs. Leaf blades narrowly elliptic, narrowly ovate, narrowly obovate, elliptic, ovate or obovate, 2.4–11 × 1.5–3.5 cm, papyraceous to subcoriaceous, drying brown, dark brown or, more rarely, greenish above and somewhat paler below, upper surface (somewhat) glossy, sparsely to moderately covered with short ± appressed hairs or glabrous, lower surface densely covered with long, erect hairs (lanate); margin ciliate; base cuneate; tip conspicuously acuminate, acumen narrow, (0.4–)0.8–1.8 cm long; domatia absent; midrib glabrous or sparsely covered with appressed hairs above, densely covered with appressed hairs below; 5–9 secondary veins on each side of midrib, glabrous or sparsely covered with appressed hairs above, raised and densely covered with appressed hairs below; higher order venation inconspicuous on both surfaces. Stipules triangular

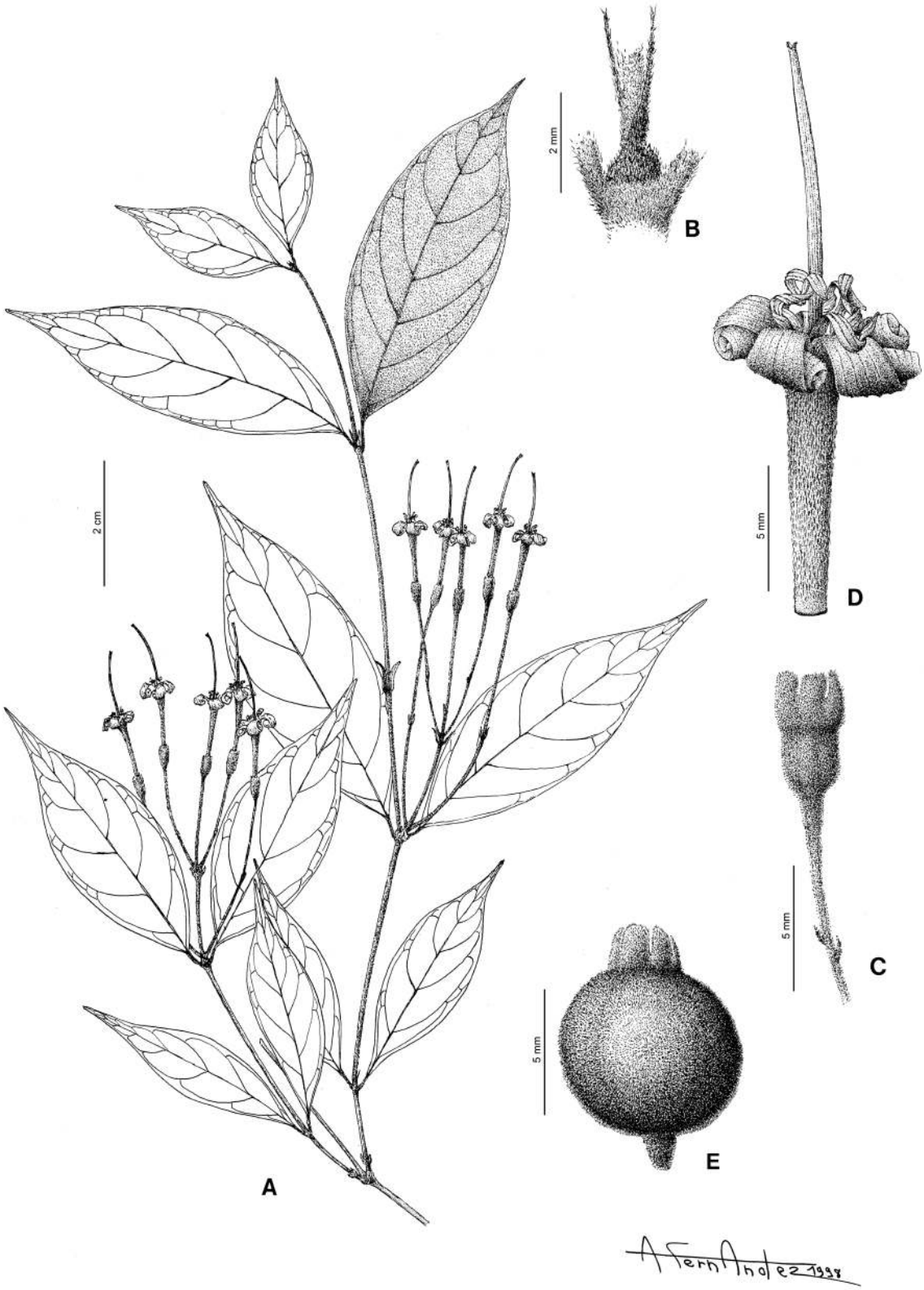

Fig. 12. *Paracephaelis longipedicellata* De Block sp. nov. **A**. Flowering branch. **B**. Stipules. **C**. Bracteoles, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *coll. ignot. 3163-SF* (A, C–D), *Capuron 23451-SF* (B) and *Puff et al. 850728-1/3* (E).

with needle-like awn, outer surface densely covered with appressed hairs, inner surface glabrous in basal half but sparsely to moderately covered with appressed hairs higher up and with row of colleters interspaced with long hairs at the base; sheath 1–3 mm long; awn 2–4 mm long. Inflorescences sessile or pedunculate, lax, 2–6 cm × 3–10 cm, with (1–)3–15(–30) flowers; inflorescence parts densely covered with short appressed or spreading hairs; if present, then peduncle up to 3 cm long; first order branching point usually 1–5 mm displaced above subtending bract pair; first order axes 0.4–4.5 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted or linear, 2–5 mm long, or rarely leaf-like, up to 10 mm long; bracteoles on pedicel 1–10 mm below ovary, not opposite, stipular parts absent, foliar parts triangular, ≤1 mm long, tips acute. Flowers pedicellate, pedicels 8–20 mm long. Calyx densely covered with short erect or spreading hairs outside, inner surface densely covered with short appressed hairs; tube 0.75–1 mm long; lobes quadrangular or shortly oblong, 0.7–1.2 mm long, often somewhat keeled, margins ciliate, tips rounded. Corolla tube 8–10 mm long, inner surface moderately to densely covered with short erect hairs except for 2–3 mm at base; lobes 6–8 mm long, margins ciliate. Stamens inserted ca 1 mm below level of throat; anthers ca 8 mm long, basal part (2–2.5 mm long) included in corolla tube at anthesis, exserted part spirally contorted; filaments up to 1 mm long. Ovary 1.5–2 mm long, longitudinally ribbed (when dried), densely covered with short erect hairs; per locule (2–)4–6 ovules arranged at periphery of placenta attached somewhat above middle of septum. Style and stigma 15–24 mm long, exserted for 7–12 mm; style densely covered with upwardly directed hairs for 5–7 mm below papillate zone; stigmatic lobes 9–11 mm long. Fruits spherical, 0.4–0.7 cm in diam., densely covered with short erect hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical, ca 6 × 5 mm, membranous adaxially, crustaceous abaxially, with rounded base, shortly acuminate tip, small adaxial opening in the upper half and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a faint depression below it. Seeds 5–8 per fruit, 3–4 × 2–3 mm.

Distribution

Coastal species, mostly collected from Lokobe on Nossi-Be, but also present in the surroundings of Ambanja and Manongarivo on the west coast and south of Vohemar on the east coast. Present in: Ambanja and Nossi-Be Districts, Diana Region, and Vohemar District, Sava Region (Antsiranana Province) (Fig. 23C).

Habitat and phenology

Littoral, sublittoral or low-elevation humid forest; on sandy soil or rocky substrate; elev. 0–450(–850) m. Flowers: (January–)March–April; Fruits: March–November. Flower buds were collected in January (3 specs), February (1 spec.) and March (1 spec.). Anthetic flowers were collected in March (flowering peak) and April (2 specs).

Vernacular names

Balaniry (*coll. ignot. 3163-SF*); fatora (*Gautier et al. 2404*); malemisisika (*Tahinarivony 736*); tembariky (*Gautier et al. 2404*); tsifolaky (*Rakoto 2724-RN*).

Provisional IUCN assessment

Vulnerable: VU B1ab(iii) B2ab(iii). This assessment is based on 32 herbarium collections with detailed locality data, collected between 1840 and 2013. The EOO of *P. longipedicellata* sp. nov. is estimated to be 2200 km^2 (ca 2100 km^2 on the west coast, ca 100 km^2 on the east coast), which complies with the Endangered category under criterion B1. The AOO is 72 km^2, which also complies with the Endangered category under criterion B2. The species occurs in 8 locations, which complies with the Vulnerable category under subcriterion 'a' of criterion B2. The species is present in Lokobe National Park and Manongarivo Special Reserve. Manongarivo Special Reserve is threatened by deforestation for slash-and-

burn agriculture. Illegal logging for construction wood and firewood takes place, as well as hunting, cattle grazing, and the collection of non-timber forest products, e.g., medicinal plants (Nicoll & Langrand 1989; BirdLife International 2020b). The same threats occur in Lokobe National Park albeit to a lesser extent (Nicoll & Langrand 1989). Outside the protected areas, anthropogenic pressure is even more important. Therefore, a reduction in the extent and quality of the habitat of *P. longipedicellata* sp. nov. is inferred. This fact, in combination with the low AOO and EOO and the low number of locations, qualifies the species for Vulnerable status.

Notes

1. *Paracephaelis longipedicellata* sp. nov. is easily recognized by the lax inflorescences, the long pedicels with the subopposite bracteoles positioned well below the ovary, the quadrangular or shortly oblong calyx lobes, ± equal in length to the calyx tube, and the small spherical fruits.

2. The species was recognised as new for science by Homolle, who published the name "*Tarenna nossibensis*" (Homolle 1938), but gave no description or type specimen. This nomen nudum was also used by Capuron (1973).

3. Prior to the synonymization of *Homollliella* with *Paracephaelis* (De Block *et al.* 2015), herbarium specimens were annotated by the author as "*Homolliella longipedicellata*", a name which was never published.

Paracephaelis orientalis De Block sp. nov.
urn:lsid:ipni.org:names:77260711-1
Fig. 13

Diagnosis

Differing from *Paracephaelis sericea* by having shorter stipules (2.5–5 mm vs 8–30 mm long), smaller leaves (4.5–10.5 × 1–4 cm vs 7–21 × 4.5–12 cm), glabrous upper leaf surfaces (vs moderately to densely covered with short erect hairs or, rarely, blade glabrous but midrib and sometimes secondary veins pubescent), usually glabrous lower leaf surfaces (vs densely covered with short erect hairs), shorter calyx tubes (1.5–2 mm long in flowering stage and ca 3 mm long in fruiting stage vs 2–5 mm long), shorter corolla tubes (ca 7 mm long vs 6–17 mm long), longer filaments (2–2.5 mm vs 1–1.5 mm long), and sparsely pubescent connectives (vs connectives glabrous).

Etymology

The species epithet is based on the distribution of the species along the east coast of Madagascar.

Type material

MADAGASCAR – **Fianarantsoa Province, Atsimo-Atsinanana Region, Midongy-Atsimo District** • Manombo; 30 m a.s.l.; 4 Feb. 2006; fl; *Tosh, De Block & Rakotonasolo 341B*; holotype: BR[BR0000022757555]; isotypes: BR[BR0000022757562], BR[BR0000022757692], E, G, K, MO, NY, P, UPS, TAN, TEF, WAG.

Other material studied

MADAGASCAR – **Toamasina Province, Analanjirofo Region, Fenoarivo Atsinanana District** • fir. Ampasimaningoro, fkt. Tampolo, forêt littorale de Tampolo (forêt classée); 0 m a.s.l.; 4 Jul. 2001; fl; *Rabenantoandro, Razakamalala, Razafindrainibe & Ludovic 559*; BR, K, MO. – **Maroantsetra District** • commune Rantabe, Beanana; 175 m a.s.l.; 27 Feb. 2002; fr; *Antilahimena, David & Rajao 943*; BR, MO. – **Soanierana Ivongo District** • Manompana, fkt. Tanambao Ambodimanga, forêt de Menagisy;

26 May 2010; fr; *Lehavana & Zackarie 700*; MO n.v., P online, TAN n.v. • commune Manompana, village le plus proche Tanambao-Maritaina, forêt de Menagisy-Pointalare [Pointe à Larrée], 3 km vol d'oiseau S de Tanambao-Ambodimanga; 52 m a.s.l.; 12 Apr. 2011; fr; *Randrianaivo, Rakotonandrasana, Razafindrabeaza, Olivier, Tsivakia & Odon Sanga 1836*; BR, CNARP n.v., MO, P, TAN. – **Atsinanana Region, Vatomandry District** • commune Ambalabe, fkt. Ambinanindrano II, forêt de Vohibe à Antenanala, 4 heures de marche d'Ambalabe; 671 m a.s.l.; 16 May 2011; fl, fr; *Randrianaivo, Razanatsima, Rakotondrajaona, Randrianasolo, Mamy, Dedesy, Kôtsy & Dimby 1861*; BR, CNARP n.v., MO, P, TAN • Ambalabe, Ambinanindrano II, E de Toby Foara; 590 m a.s.l.; 12 May 2006; fr; *Razanatsima 110*; MO n.v., P online, TAN n.v. • Ambalabe, Ambinanindrano II, forêt de Vohibe, direction NW du Toby Foara; 637 m a.s.l.; 21 Aug. 2015; fr; *Razanatsima 1394*; MO n.v., P online, TAN n.v. – **Toliara Province**. **Anosy Region**. **Taolagnaro District** • ca 117 km N of Fort Dauphin, ca 7 km N of Manantenina forest remnant called Analalava; 50 m a.s.l.; 8 Nov. 1989; fr; *McPherson 14410*; K, MO, P, TAN, TEF • Iabakoho, Antsotso; 25 May 2006; fl; *Rajoharison, Antilahimena, Ramisy & Maharavo 207*; BR, MO, P, TAN.

Description

Tree, up to 20 m tall, dbh up to 30 cm; pubescence tawny or whitish. Young shoots brown or reddish brown, glabrous to densely covered with short appressed hairs; older branches brown or reddish brown, flaking, glabrous. Petioles 2–12 mm long, glabrous to densely covered with short appressed hairs. Leaf blades obovate or narrowly obovate, 4.5–10.5 × (1–)1.5–4 cm, coriaceous, drying brown or dark brown and hardly discolorous, upper surface glossy and glabrous, lower surface densely covered with minute erect hairs all over (*Tosh et al. 341B*) or glabrous and then sometimes with midrib sparsely to moderately covered with short appressed hairs; base attenuate; tip acuminate with acumen 0.4–1.2 cm long; hair tuft domatia often present; 5–10 secondary veins on each side of midrib, raised below; higher order venation inconspicuous on both surfaces. Stipules caducous, triangular, 2.5–5 mm long, gradually tapering into an acute tip or with short awn ≤1 mm long, outer surface of youngest stipule pairs moderately to densely covered with short appressed hairs, inner surface glabrous with 1–3 rows of colleters at the base. Inflorescences sessile, 1.5–4 × 2–5 cm, with 12–60 flowers, partial inflorescences compact; inflorescence parts densely covered with short appressed hairs; first order axes 0.5–3 cm long; higher order bracts with stipular parts reduced or absent and foliar parts triangular, 2–4 mm long, tips acute; bracteoles at base of ovary, opposite, stipular parts absent, foliar parts triangular, 1.5–2 mm long, tips acute or obtuse. Flowers sessile. Calyx densely covered with short appressed hairs outside; tube 1.5–2 mm long in flowering stage, ca 3 mm long in fruiting stage, inner surface densely covered with long appressed hairs in basal half, upper half densely covered with appressed hairs in the region of the sinuses, glabrous or sparsely covered with appressed hairs below the lobes; lobes quadrangular, somewhat keeled, 1.–1.5 mm long, inner surface glabrous or sparsely covered with short appressed hairs, margins ciliate, tips rounded. Corolla tube ca 7 mm long, inner surface moderately to densely covered with spreading hairs in upper half; lobes 5.5–6.5 mm long, margins ciliate. Anthers 4–5 mm long, completely exserted from corolla tube at anthesis; filaments 2–2.5 mm long; connective sparsely covered with appressed hairs (filament not pubescent). Ovary 1.5–2 mm long, longitudinally ribbed (when dried), densely covered with short appressed or spreading hairs; per locule 4–7 ovules arranged at periphery of placenta attached to upper half of septum. Style and stigma 12–19 mm long, exserted for 5–12 mm; style densely covered with long spreading hairs for 3–5 mm below papillate zone; stigmatic lobes 8–9 mm long. Fruits spherical, 0.8–1 cm in diam., faintly ribbed longitudinally (when dried), moderately covered with short appressed or spreading hairs; fruit wall thin, with sclerified vascular bundles; mature pyrenes and seeds unknown.

Distribution

Occurring along the east coast from south of the Masoala Peninsula to Taolagnaro. Present in: Amparafaravola District, Alaotra-Mangoro Region, Soanierana Ivongo and Fenoarivo Atsinanana Districts, Analanjirofo Region, and, Vatomandry District, Atsinanana Region (Toamasina Province); Midongy-Atsimo District, Atsimo-Atsinanana Region (Fianarantsoa Province); Taolagnaro District, Anosy Region (Toliara Province) (Fig. 23C).

Habitat and phenology

Littoral or low-elevation humid forest; on sandy soil; elev. 0–700 m. Flowers: November (Taolagnaro: *McPherson 14410*, buds), February (Atsimo-Atsinanana: *Tosh et al. 341B*), May (Taolagnaro: *Rajoharison et al. 207*); Fruits: February–August.

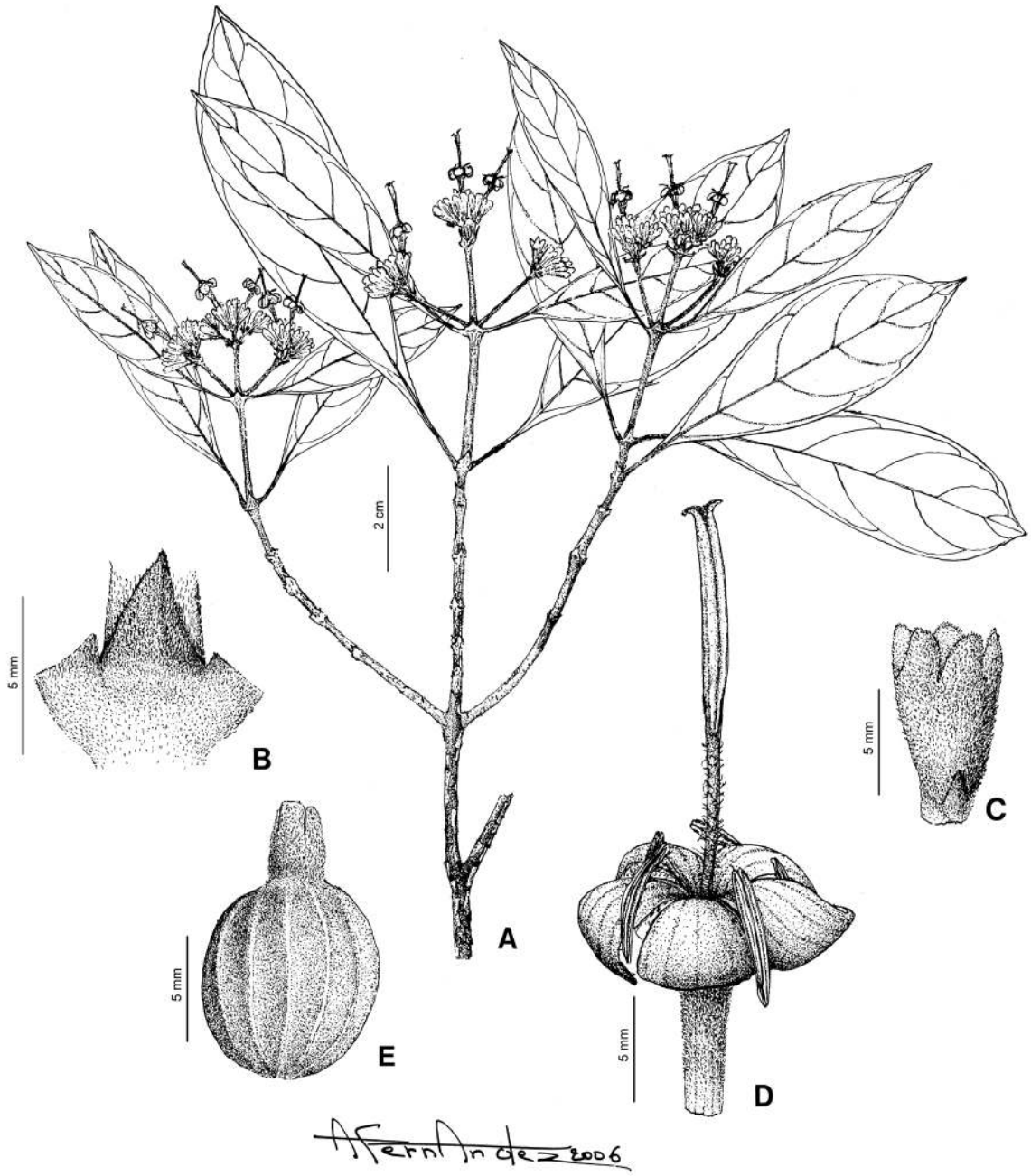

Fig. 13. *Paracephaelis orientalis* De Block sp. nov. **A**. Flowering branch. **B**. Stipule. **C**. Bracteole, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *Tosh et al. 341B* (A–D) and *Randrianaivo et al. 1836* (E).

Vernacular names

Maraintsiatoraka (*Rajoharison et al. 207*); mentalady (*Antilahimena et al. 943*); oditrovy (*Razanatsima 1394*).

Provisional IUCN assessment

Vulnerable: VU B2ab(iii). This assessment is based on 10 herbarium collections, all collected after 1989. GeoCAT calculates the EOO of *P. orientalis* sp. nov. as 30 125 km^2, exceeding the upper limit for the Vulnerable category under criterion B1. However, this must be considered an overestimation since most littoral and low-elevation humid forest along the east coast has already been destroyed (Green & Sussman 1990; Consiglio *et al.* 2006; Moat & Smith 2007). The AOO is 32 km^2, which complies with the Endangered category under criterion B2. The species occurs in 7 locations, which complies with the Vulnerable category under subcriterion 'a' of criterion B2. *Paracephaelis orientalis* sp. nov. occurs in Manombo Special Reserve and Tampolo Protected Area. All along the east coast, littoral and low-elevation humid forest is under high anthropogenic pressure (Green & Sussman 1990; Consiglio *et al.* 2006; Moat & Smith 2007). To a lesser extent, this is also the case for forests within protected areas. Manombo suffers from slash-and-burn agriculture, bushfires, logging, hunting, and unsustainable use of non-timber forest products (Nicoll & Langrand 1989; Ralainasolo *et al.* 2008). Tampolo is mostly affected by logging for timber, firewood and the production of charcoal, the collection of non-timber forest products such as *Pandanus* leaves for making mats, hunting, and fishing (Ratsirarson & Ranaivonasy 2002). Because of the above-mentioned facts, a reduction in the extent and quality of the habitat of *P. orientalis* sp. nov. is inferred. This threat, in combination with the low AOO and the low number of locations, qualifies *P. orientalis* sp. nov. as Vulnerable.

Note

This is the only species in the genus currently known to have a sparsely ciliate connective. It should be noted, though, that mature flowers were unavailable for study in several species.

Paracephaelis pauciflora De Block sp. nov.
urn:lsid:ipni.org:names:77260712-1
Figs 1B, 14

Diagnosis

Differing from *Paracephaelis sericea* by having smaller stipules (4–9 mm vs 8–30 mm long), smaller leaves (2–15 × 1–5.5 cm vs 7–21 × 4.5–12 cm), smaller inflorescences (1–2 × 1.5–3.5 cm with first order axes 0.3–0.7 cm long and 3–12 flowers vs 1.5–7 × 3–9 cm with first order axes 0.3–4 cm long and 15 to numerous flowers), longer corolla tubes (1.1–3.3 cm vs 0.6–1.7 cm long), less exserted styles and stigmas (exserted for 2–6 mm vs 6–17 mm), and longer calyx tubes (4–10 mm vs 2–5 mm long).

Etymology

The species epithet is based on the few-flowered inflorescences.

Type material

MADAGASCAR – **Toamasina Province, Alaotra-Mangoro Region, Moramanga District** • 1–2 km S of Hotel de la Gare at Andasibe (Perinet); 1000 m a.s.l.; 5 Mar. 1988; fl; *Schatz, Dransfield & Henderson 1941*; holotype: MO; isotypes: BR[00000822147], K[K000176002], P[P04023495], TAN.

Other material studied

MADAGASCAR – **Toamasina Province, Alaotra-Mangoro Region, Ambatondrazaka District** • Nonokambo, forêt aux confins du pays Sihanaka; 18 Aug. 1937; fr; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *2791*; P • commune Antanandava, fkt. Antanandava, 3 km SW d'Ankosy; 1157 m a.s.l.; 27 Jan. 2001; fl; *Randrianasolo, Rakotozafy, Ratovoson, Andrambolantsoa & Rajoelison 186*; K, MO, P • Manaka-Est; 23 Mar. 1960; fl; *coll. ignot. 11251-RN*; P • partie NW de la RNI 3, Zahamena, 1 km SW du village d'Antenina, commune Imerimandroso; 910 m a.s.l.; 15 Aug. 1994; fr; *Randrianjanaka & Zafy 203*; BR, K, MO, P, TAN. – **Amparafaravola District** • forêt d'Andranovakoana, W de Manohilahy, Andrazaka; 1100–1300 m a.s.l.; 30 Aug. 1958; fr; *Capuron 18761-SF*; BR, P, TEF • sables d'Andilana; 1100 m a.s.l.; 7 Jan. 1945; fl; *Cours 2208*; P, TAN • ibid.; 1000 m a.s.l.; 7 Jan. 1945; fl; *Homolle 2208*; P. – **Moramanga District** • Ambohibary, Ampitambe, Ambatovy, environ 22 km NE de Moramanga, Analamahy; 1042 m a.s.l.; 16 Mar. 2005; fl; *Andriatiana & Razafindasy 162*; BR, MO, P, TAN • Andasibe, Menalamba, forêt d'Ambatovy; 15 Feb. 1997; fr; *Andriatsiferana, Rakotomamonjy, Rafamantanantsoa, Leporaka & Rolland 2516*; BR, MO, P • Andasibe, Berano, Ambatovy forest, Analamay; 1117 m a.s.l.; 2 Mar. 2005; fl; *Antilahimena & Razafindasy 3534*; BR, MO, P, TAN • commune Ambohibary, fkt. Ampitambe, Sahaviana forest; 1147 m a.s.l.; 13 Feb. 2007; fl; *Antilahimena 5314*; MO n.v., P online, TAN n.v. • Morarano, Marovoay, Ankosy forest; 1111 m a.s.l.; 24 Apr. 2009; fr; *Antilahimena, Bernard, Edmond, Ravelonarivo, Ratodimanana & Radona 7076*; BR, MO, P, TAN • Ambohibary, Ampitambe, Ambatovy, Betsingilo forest; 1041 m a.s.l.; 7 Aug. 2012; fr; *Antilahimena, Ratolojanahary & Felix 8428*; BR, MO, P, TAN • Ambohibary, Ampitambe, Andranovery, Ambatovy; 1019 m a.s.l.; 10 Jun. 2009; fr; *Bernard, Antilahimena, Edmond & Radona 1443*; BR, MO • Ambohibary, Ampitambe, Ambatovy, zone de défrichement 22; 1069 m a.s.l.; 28 Apr. 2010; fr; *Bernard, Ratodimanana, Randrianasolo & Ramahenina 1563*; BR, MO, P, TAN • Perinet-Analamazaotra; 8–9 Aug. 1961; fr; *Capuron 20320-SF*; P, TEF • Perinet; 27 Mar. 1951; fr; *coll. ignot. 3322-SF*; P, TAN, TEF • Analamazaotra-Perinet; 27 Mar. 1957; fr; *coll. ignot. 3732-SF*; P, TAN, TEF • S du parc des orchidées, Analamazaotra; 13 Feb. 1980; fl; *coll. ignot. 29692-SF*; TEF • limite droite de Mananara PN, Mantadia, fkt. Faliarana, fir. Andasibe; 850–1250 m a.s.l.; 14 Oct. 1993; fr; *coll. ignot. 34483-SF*; TEF • station forestière d'Analamazaotra, environs de la parc des orchidées; 880 m a.s.l.; 23 Feb. 1999; fl; *De Block & Rakotonasolo 848*; BR, G, K, MO, P, TAN, WAG • ibid.; 880 m a.s.l.; 23 Feb. 1999; fl; *De Block & Rakotonasolo 855*; BR, G, K, MO, P, TAN, WAG • parc Mitsinjo (Analamazaotra); 880 m a.s.l.; 22 Jan. 2006; fl; *De Block, Tosh & Rakotonasolo 1908*; BR, MO, TAN, UPS • Andasibe, station forestière d'Analamazaotra; 900 m a.s.l.; 2 Apr. 1999; fl; *Labat, Haevermans & Rabenantoandro 3079*; BR, K, P, TAN, WAG • Ambatovy, NE of Moramanga, azonal forest S of Dynatec offices, on slope below flat area; 1110 m a.s.l.; 12 Apr. 2006; fr; *Lowry, Antilahimena & Andriamahefarivo 6798*; MO n.v., P online • Ambatovy, 10 km NE de Moramanga; May 1969; fr; *Morat 3224*; P • Moramanga, RN 2, PK 6 after Moramanga; 900 m a.s.l.; 21 Aug. 1999; fr; *Rakotonasolo 97*; BR, G, MO, TAN • 4.5 km NNW of Moramanga; 1030 m a.s.l.; 6 Oct. 2002; fr; *Rakotonasolo 428*; BR, K • commune Ambohibary, fkt. Ampitambe, Ambatovy, environ 22 km NE de Moramanga; 1123 m a.s.l.; 1 Mar. 2005; fl; *Rakotovao, Razafindasy & Edmond 1415*; BR, MO, P, TAN • ibid.; 1123 m a.s.l.; 1 Mar. 2005; fl; *Rakotovao, Razafindasy & Edmond 1445*; BR, MO, P, TAN • ibid.; 1141 m a.s.l.; 2 Mar. 2005; fl; *Rakotovao, Razafindasy & Edmond 1459*; MO, TAN • ibid.; 1060 m a.s.l.; 4 Mar. 2005; fl; *Rakotovao, Razafindasy & Edmond 1510*; BR, MO, P, TAN • Ambohibary, Ampitambe, Ambatovy, Saviraha, by pass; 1042 m a.s.l.; 23 Feb. 2010; fl; *Ramahenina, Edmond, Rasolofoniaina & Rakotonandrasana 16*; MO n.v., P online, TAN n.v. • Andasibe, Analamazaotra-Perinet PN, Amboasary; 1022 m a.s.l.; 14 Feb. 2013; fr; *Rasoazanany, Antilahimena, Bernard, Razafindraibe, Edmond & Ratolojanahary 358*; BR, MO, P, TAN • Ambohibary, Antsily, Andakana, forêt de Bekomy; 902 m a.s.l.; 7 Sep. 2012; fr; *Razakamalala & Randrianaivo 6984*; MO n.v., P online, TAN n.v. – **Atsinanana Region, Vatomandry District** • commune Ambalabe, fkt. Ambinanindrano II, forêt de Vohibe à Antenanala, 4 heures de marche d'Ambalabe; 986 m a.s.l.; 2 Jun. 2007; fr; *Ravelonarivo 2484*; BR, MO, P, TAN. – **Vohibinany District** • commune Maroseranana, fkt. Ambodilendemy, Ankerana; 921 m a.s.l.; 25 Mar. 2011; fr; *Antilahimena 7823*; BR,

MO • Anjahamamy, Anivoranokely, Ankerana forest; 1092 m a.s.l.; 20 Jan. 2012; fr; *Antilahimena 8005*; BR, MO, P, TAN • entre Sahalampona et Sahamalaza; 1200 m a.s.l.; 21 Jan. 1945; fl, fr; *Cours 2635*; BR, P, TAN • Maroseranana, Ambodilendemy, vers le sommet d'Ankerana; 804 m a.s.l.; 20 Mar. 2011; fr; *Ravelonarivo, Felix, Edmond & Lejoma 3742*; BR, MO • Vohimanana, commune Maroseranana, fkt. Ambatolampy, point 2 d'atterrissage d'hélicoptère d'équipe qui avait fait le sondage (Héliport); 805 m a.s.l.; 23 Jan. 2012; fl; *Ravelonarivo, Edmond & Laindrirana 4169*; BR, MO • Maroseranana, fkt. Ambatolampy, Ankerana; 735 m a.s.l.; 2 Feb. 2012; fl; *Ravelonarivo & Edmond 4292*; BR, MO, P, TAN • forêt de Tampina; Dec. 1936; fr; *Ursch s.n.*; L. – **Mahajanga Province, Sofia Region, Mandritsara District** • Ambilobe, Bandabe, suivant la piste vers Antsiradava, 5 km E de Bandabe à vol d'oiseau, W de la forêt de Makira, à la limite de la province de Tamatave et de Majunga, Ambolotsangana, une ligne de crête; 3910 ft a.s.l.; 25 Apr. 2007; fr; *Ravelonarivo, Lehavana, Tsiady & Manankaja 2338*; BR, MO, P, TAN. – **Antananarivo Province, Analamanga Region, Anjozorobe District** • Anjozorobe; 28 Jan. 1987; fl; *Rakotozafy & Raharilala 1822*; TAN • Vanjamanitrabe; 30 Jan. 1989; fl; *Rakotozafy & Raharilala 2440*; TAN. – **Without locality** • s.dat.; fr; *Baron 3114*; K • s.dat.; fl; *Homolle s.n.*; BR, P • s.dat.; fr; *Homolle J5*; BR, P.

Description

Shrub or tree, 2–8(–15) m tall; pubescence tawny. Young shoots brown to reddish brown, densely covered with short erect hairs; older branches pale or greyish brown, flaking, glabrescent. Petioles 0.4–2 cm long, densely covered with short erect hairs. Leaf blades obovate, elliptic, narrowly obovate or narrowly elliptic, 2–15 × 1–5.5 cm, coriaceous, drying brown or dark brown and hardly discolorous, upper surface somewhat glossy, sparsely to moderately covered with short erect hairs or glabrous with pubescence restricted to midrib and secondary veins, lower surface densely covered with longer erect hairs or glabrous with pubescence restricted to midrib and secondary veins; margin ciliate; base cuneate, obtuse, unequal or somewhat attenuate; tip acuminate with acumen 0.3–1.5 cm long or rarely acute; hair tuft domatia usually present; midrib sparsely to densely covered with short erect to appressed hairs on both surfaces; 8–13 secondary veins on each side of midrib, somewhat impressed above, raised below, glabrous or sparsely to moderately covered with short erect or appressed hairs on both surfaces; higher order venation inconspicuous on both surfaces (in mature leaves). Stipules triangular, often somewhat keeled, 4–9 mm long, gradually tapering into an acute or, more rarely, obtuse tip, outer surface densely covered with short erect hairs, inner surface glabrous with 2–3 rows of colleters at the base. Inflorescences sessile, compact, 1–2 × 1.5–3.5 cm, with 3–12 flowers; inflorescence parts densely covered with short erect hairs; first order axes 0.3–0.5(–0.7) cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted, 3–4 mm long; bracteoles at base of ovary, opposite, stipular parts absent, foliar parts triangular, 1–2 mm long, tips acute. Flowers sessile or shortly pedicellate, pedicels 0–1.5 mm long. Calyx densely covered with short erect hairs outside, inner surface densely covered with minute appressed hairs all over but most dense at the base; tube 4–10 mm long; lobes triangular or quadrangular, (0.5–)1–2 mm long, often somewhat keeled, tips rounded, obtuse or acute. Corolla tube 1.1–3.3 cm long, inner surface moderately covered with long erect hairs in upper ⅔; lobes 5–9 mm long. Anthers 5–7 mm long, completely exserted or basal part (ca 1 mm long) included in corolla tube at anthesis; filaments ca 1 mm long. Ovary 2–3 mm long, longitudinally ribbed (when dried), densely covered with short erect hairs; per locule 6–9 ovules arranged at periphery of placenta attached just above middle of septum. Style and stigma 1.5–3.7 cm long, exserted for 2–6 mm; style densely covered with long upwardly directed hairs for 3–8 mm below papillate zone; stigmatic lobes 7–15 mm long. Fruits ovoid, longitudinally ribbed and glossy (when dried), 9–12 × 7–10 mm, densely covered with short erect hairs; fruit wall well-developed, with multi-layered anastomosing network of sclerified vascular bundles; pyrenes hemi-ovoid, 8–10 × 5–6.5 mm, crustaceous, with rounded base and tip, small adaxial opening in the upper half and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 6–10 per fruit, ca 4.5 × 3 mm.

Distribution

Restricted to central eastern Madagascar (Alaotro-Mangoro, Atsinanana and Analamanga Regions), also known from Makira Forest on the border between Toamasina and Mahajanga Province. Present in: Ambatondrazaka, Amparafaravola and Moramanga Districts, Alaotra-Mangoro Region, and Vatomandry and Vohibinany Districts, Atsinanana Region (Toamasina Province); Mandritsara District, Sofia Region (Mahajanga Province); Anjozorobe District, Analamanga Region (Antananarivo Province) (Fig. 23C).

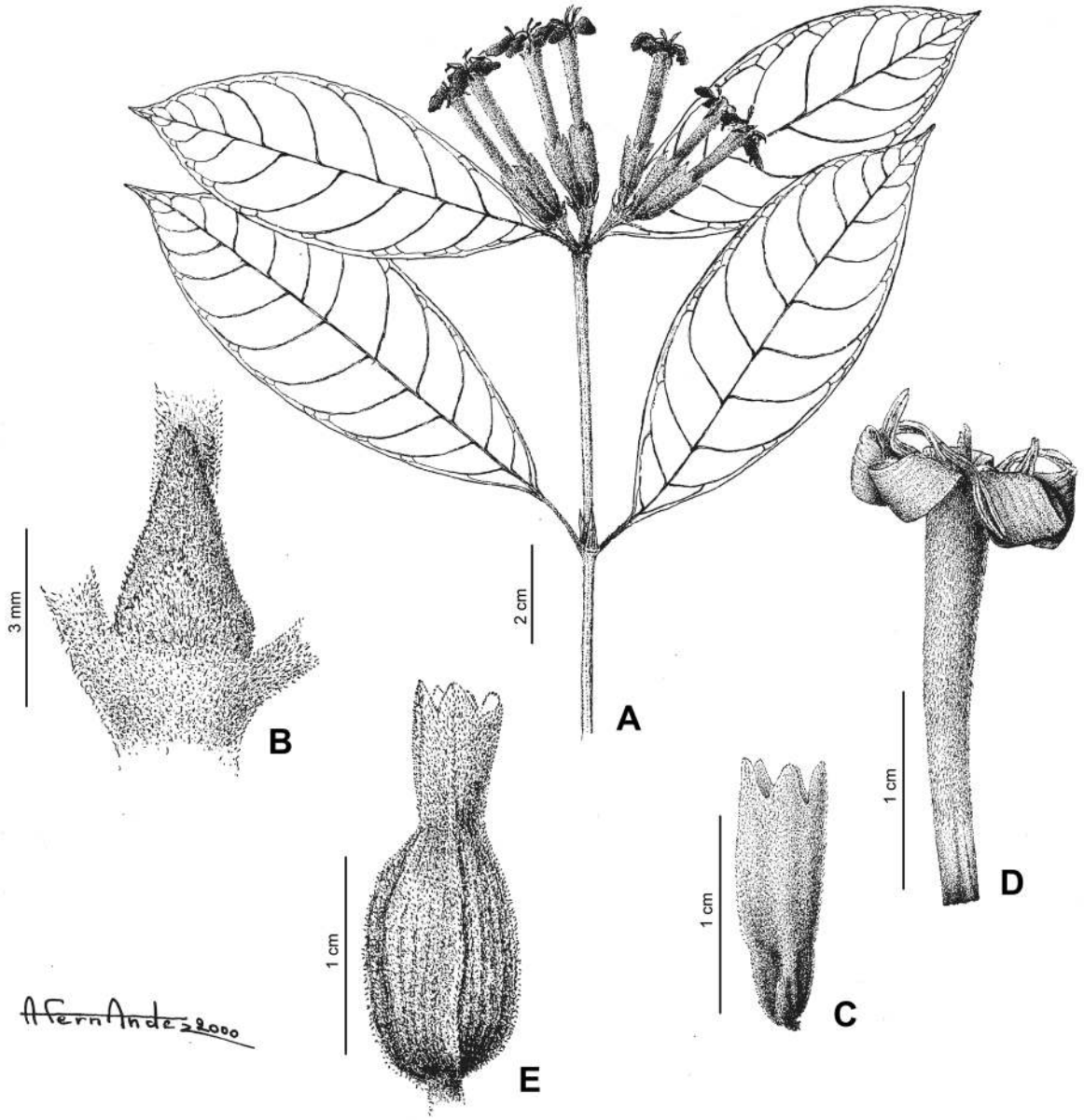

Fig. 14. *Paracephaelis pauciflora* De Block sp. nov. **A**. Flowering branch. **B**. Stipule. **C**. Bracteole, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *Schatz et al.* 1941 (A–D) and Ravelonarivo 2484 (E).

Habitat and phenology

Mid-elevation humid forest; elev. 700–1400 m. Flowers: January–March, one collection reported flowering in April (*Labat et al. 3079*); Fruits: March–December.

Vernacular names

Ankahatra (*Cours 2635*); hazo mafany (*Ursch s.n.*); kafeala *(coll. ignot. 3322-SF* and *3732-SF*); sofintsoy (*Antilahimena 8005*); taolananafotsy (*coll. ignot. 29692-RN*); tsotsorovarika (*coll. ignot. 11251-RN*).

Provisional IUCN assessment

Near Threatened. This assessment is based on 46 herbarium collections with detailed locality data, collected between 1937 and 2013. The EOO of *P. pauciflora* sp. nov. is estimated to be 22 340 km^2, which somewhat exceeds the upper limit of the Vulnerable category under criterion B1. The AOO is 116 km^2, which complies with the Endangered category under criterion B2. The species occurs in 15 locations, which exceeds the upper limit for Vulnerable category under subcriterion 'a' of criterion B2. However, circa 30% of the specimens of *P. pauciflora* sp. nov. were collected at Ambatovy, which is the site of the world's largest lateritic nickel mine, where open pit nickel and cobalt mining is ongoing (http://www.ambatovy.com). The mining location will be completely cleared within the next thirty years, which will reduce the number of locations to 14 and have a negative effect on the AOO, but not on the EOO. *Paracephaelis pauciflora* sp. nov. occurs in the Andasibe-Mantadia and Zahamena National Parks and in Makira Natural Park (1 specimen currently known). Outside the protected areas, clearing of forest (Harper *et al.* 2007), mainly for subsistence agriculture, continues at a rapid pace. Inside the protected areas, land clearing for subsistence farming, cattle grazing, and human settlement also occurs, as well as logging, production of charcoal, collection of non-timber forest products, and hunting (Nicoll & Langrand 1989; Hannah & Boltz 2003; Rasolofoson *et al.* 2007; Dolch 2008). The Andasibe-Mantadia National Park, close to the capital Antananarivo, is one of the main destinations for tourists interested in Madagascar's nature. But the remote location of Zahamena and Makira and the limited resources for the management of these protected areas (both monetary and in terms of staff) are negative factors not aiding the conservation of these protected areas. Because of the above-mentioned facts, a reduction in the extent and quality of the habitat of *P. pauciflora* sp. nov. is inferred and a future reduction in the AOO, the number of locations, the habitat and the number of mature individuals is projected. Because of the size of the EOO and the number of locations, *P. pauciflora* sp. nov. does not qualify for Vulnerable status. However, because the EOO is only just over 20 000 km^2 and the number of locations is 14 (taking into account the future destruction of the Ambatovy location), the species is assessed as Near Threatened.

Notes

1. *Paracephaelis pauciflora* sp. nov. is easily recognized by the pauciflorous inflorescences and the flowers with well-developed calyx tubes.

2. Prior to the synonymization of *Homolliella* with *Paracephaelis* (De Block *et al.* 2015), herbarium specimens were annotated by the author as "*Homolliella pauciflora*", a name which was never published.

Paracephaelis ranirisonii De Block sp. nov.
urn:lsid:ipni.org:names:77260713-1
Figs 1F, 15

Diagnosis

Differing from *P. gautieri* sp. nov. by having densely pubescent young shoots, petioles, and leaves (vs glabrous), longer stipules (7–12 mm vs 3.5–4 mm long), longer bracteoles (ca 3 mm vs 0.7–1.2 mm long),

sessile flowers (vs pedicels 2–6 mm long), longer calyx tubes (2–2.5 mm long in flowering stage, up to 4 mm long in fruiting stage vs ca 1 mm long), and a different pubescence on calyx and ovary (densely covered with long, tawny hairs, appressed to spreading on the calyx and erect on the ovary in *P. ranirisonii* sp. nov. vs densely covered with shorter, whitish, appressed hairs in *P. gautieri* sp. nov.).

Etymology

The species is named in honour of Dr Patrick Ranirison, who collected the type specimen in northern Madagascar.

Type material

MADAGASCAR – **Antsiranana Province, Sava Region, Vohemar District** • commune Daraina, Daraina, forêt d'Antsahabe, à 1060 m du point côté 938, au 287°; 840 m a.s.l.; 2 May 2004; fr; *Ranirison 781*; holotype: G n.v.; isotype: BR [BR0000022757579].

Description

Shrub, ca 1.5 m tall; pubescence tawny. Young shoots brown or greyish brown, densely covered with short erect hairs; older branches corky, brown to greyish brown, glabrescent; internodes short, 1–2 cm long. Petioles 3–6 mm long, densely covered with short erect hairs. Leaf blades obovate, 4–6.5 × 1.5–3 cm, coriaceous, drying brown above, tawny (because of abundant pubescence) below, upper surface glossy, moderately to densely covered with short erect hairs, lower surface sericeous; base cuneate; tip obtuse to retuse; domatia absent; 7–8 secondary veins on each side of midrib, somewhat impressed above, somewhat raised below; higher order venation inconspicuous on both surfaces. Stipules caducous, triangular, keeled, 0.7–1.2 cm long, gradually tapering into an acute tip or with short awn < 2 mm long, outer surface of youngest stipule pairs moderately to densely covered with short erect to spreading hairs, inner surface glabrous with 1–3 rows of colleters at the base, margin ciliate. Inflorescences sessile, 2–3 × 3–5 cm, with 15–30 flowers; inflorescence parts densely covered with short erect to spreading hairs; first order axes 0.5–1.5 cm long; higher order bracts trilobed, lobes triangular or narrowly triangular, central lobe 3–5 mm long, lateral lobes up to 2 mm long; bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts triangular, ca 3 mm long, tips acute. Flowers sessile. Calyx densely covered with long spreading to erect hairs outside, inner surface densely covered with short appressed hairs all over but most dense at the base; tube 2–2.5 mm long in flowering stage, reaching 4 mm in fruiting stage; lobes triangular or ovate, 1.2–2 mm long, tips acute or shortly acuminate. Mature corolla, stamens, style and stigma unknown. Ovary ca 2.5 mm long, densely covered with long spreading to erect hairs; per locule 5–6 ovules arranged at periphery of placenta attached just below middle of septum. Fruits ovoid, 0.8–1 × 0.6–0.9 cm, strongly ribbed longitudinally and glossy (when dried), densely covered with long spreading to erect hairs; fruit wall ± thick, with sclerified vascular bundles; pyrenes hemi-ovoid, ca 7 × 5 mm, crustaceous, with rounded base, acute tip, small adaxial opening somewhat below the middle and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 4–8 per fruit, 3–4 × 2.5–3 mm.

Distribution

Only known from Antsahabe Forest near Daraina in Vohemar District, Sava Region (Antsiranana Province) (Fig. 23C).

Habitat and phenology

Dry forest; elev. ca 840 m. Flowers: unknown; Fruits: May.

Provisional IUCN assessment

Critically Endangered: CR B2ab(iii). *Paracephaelis ranirisonii* sp. nov. is only known from a single collection, which means that the extent of occurrence (EOO) cannot be calculated. The area of occupancy (AOO) is 4 km^2, which complies with the Critically Endangered status under criterion B2. The species is known from a single location, which also complies with the Critically Endangered status under sub criterion 'a' of criterion B2. The type specimen was collected recently (2004) in the Loky-Manambato

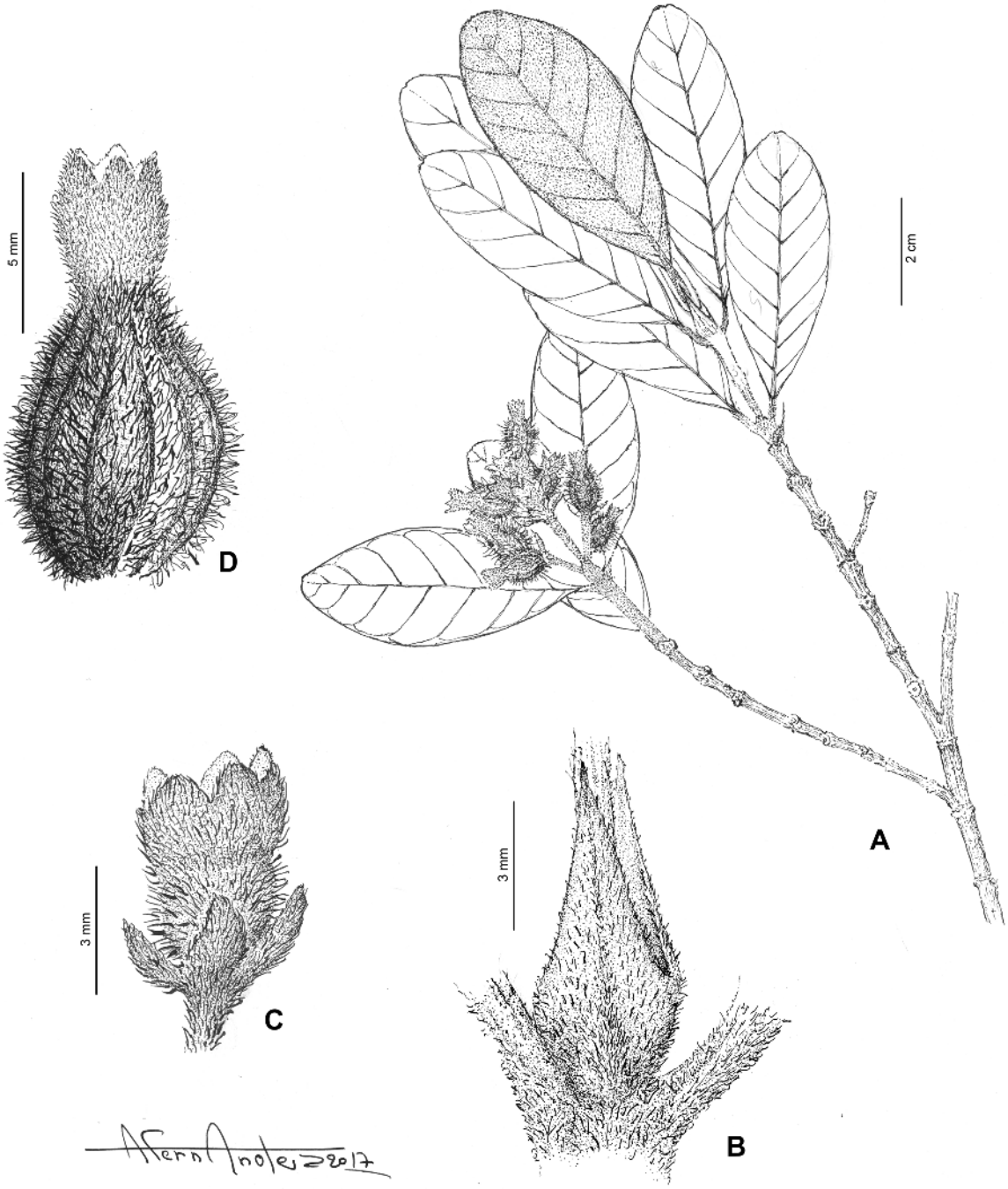

Fig. 15. *Paracephaelis ranirisonii* De Block sp. nov. **A**. Fruiting branch. **B**. Stipules. **C**. Bracts, bracteole, ovary and calyx. **D**. Fruit. Drawn by Mr A. Fernandez. From *Ranirison 781*.

Protected Landscape (Daraina). The region of Loky-Manambato is very diverse in altitude and rainfall, hence a mosaic of different forest types occurs, from dry to humid evergreen, and from lowland to montane forest (Nusbaumer *et al.* 2010). Loky-Manambato is known for its high species diversity and endemicity (Rakotondravony 2006; Nusbaumer *et al.* 2010). As a region of transition it is of high conservation value (Nicoll & Langrand 1989; Ganzhorn *et al.* 1997). While nominally protected within the Loky-Manambato Protected Landscape, *P. ranirisonii* sp. nov. is threatened by habitat loss as a result of clearing for subsistence farming, burning for pasture, logging for timber and charcoal, and artisanal mining for gold (Rakotondravony 2009; Nusbaumer *et al.* 2010). Therefore, a reduction in the extent and quality of the habitat of *P. ranirisonii* sp. nov. is inferred. This fact, in combination with the low AOO and the single location, qualifies the species as Critically Endangered. For further details on the Loky-Manambato Protected Landscape, see *P. gautieri* sp. nov.

Note

The description is based on a single specimen without flowers. Ovary and calyx details are taken from undeveloped fruits. Label information on *Ranirison 781* indicates the habitat as "forêt de transition sèche de haute altitude sur substrat pauvre".

Paracephaelis russata De Block sp. nov.
urn:lsid:ipni.org:names:77260714-1
Figs 1L, 2G–H, 16

Diagnosis

Differing from *Paracephaelis tiliacea* by having shorter petioles (0.5–1.2 cm vs 1–3 cm long), a higher number of secondary veins (8–16 vs 5–8), longer stipular sheaths (0.8–2 cm vs 0.4–0.7 cm long), more lax inflorescences (first order axes 2–7 cm vs 0.5–1.5 cm long and pedicels 0–12 mm vs 0–2 mm long), longer calyx tubes (1–1.5 mm vs 0.5–0.7 mm long), a lower number of ovules (1–4 per placenta vs 4–10), and by not having a *Terminalia* branching pattern (vs present).

Etymology

The species epithet is based on the reddish colour of the pubescence on most of the specimens.

Type material

MADAGASCAR – **Antsiranana Province, Diana Region, Ambilobe District** • Ankarana, close to Mahamasina; 82 m a.s.l.; 27 May 1999; fr; *De Block, Rapanarivo & Randriamboavonjy 1048*; holotype: BR [BR000000933669]; isotypes: BR[BR000000855054], K, MO, P, TAN.

Other material studied

MADAGASCAR – **Antsiranana Province, Diana Region, Ambilobe District** • plateau calcaire de l'Ankarana, W de Mahamasina, Antanatsimanaja; 23 Apr. 1963; fr; *Capuron 22674-SF*; BR, P, TEF • Ankarana, tsingy, ca 3 km NE of Mahamasina, not part of Ankarana PN, on right side of road (going towards Antsiranana) at the second bridge from Mahamasina; 16 Jan. 2002; fl; *De Block, Rakotonasolo & Randriamboavonjy 1252*; BR, G, K, MO, P, TAN • Tanambao-Marivorahona, 5 km E du hameau Betsimiranjana, au lieu dit Andohanantsohihy, partie sud; 65 m a.s.l.; 4 Jul. 2005; fr; *Leopold, Razafitsalama, Guittou & Ndaza dit Tsimihetibe 112*; CNARP n.v., MO n.v., P online, TAN n.v. • Marivorahona, Betsimiranja, Andohan'Antsoha; 40 m a.s.l.; 16 Jul. 2005; fr; *Rakotondrafara, Rakotonandrasana, Randrianaivo, Leopold, Bezara & Benjara 310*; BR, MO, P • Ankarana RS; 11–14 Jan. 2002; fl, fr; *Razafimandimbison & Andrianatoanina 466*; UPS. – **Sava Region, Vohemar District** • commune Daraina, Daraina, forêt de Solaniampilana-Maroadabo; 120 m a.s.l.; 9 Mar. 2004;

fl; *Gautier, Wohlhauser, Nusbaumer & Ranirison 4526*; BR, G • commune Daraina, Daraina, forêt d'Ambohitsitondroina; 140 m a.s.l.; 16 Mar. 2004; fr; *Gautier, Wohlhauser, Nusbaumer & Ranirison 4597*; BR, G.

Description

Shrub or small tree, 1.5–6 m tall; pubescence tawny to reddish brown. Young shoots brown to reddish brown, densely covered with long erect hairs; older branches brown to reddish brown, flaking, glabrous. Petioles 0.5–1.2 cm long, densely covered with long erect hairs. Leaf blades ovate, broadly ovate or elliptic, 11.5–21 × 5–11 cm, papyraceous to subcoriaceous, drying blackish brown above and dark brown below, upper surface glossy and sparsely to moderately covered with long erect hairs (more densely pubescent on midrib and secondary veins), lower surface densely covered with long erect hairs; base obtuse, rounded, unequal or somewhat cordate; tip shortly acuminate with acumen 0.3–1 cm long; domatia absent; 8–16 secondary veins on each side of midrib, somewhat raised above, raised below; higher order venation inconspicuous on both surfaces. Stipules ovate or broadly ovate with needle-like awn, keeled, outer surface densely covered with long erect hairs at the base and along the midrib, elsewhere sparsely pubescent or glabrous, inner surface sparsely covered with short appressed hairs and with row of colleters at the base, margin ciliate; sheath 0.8–2 cm long, awn 2–6 mm long. Inflorescences sessile, 4–10 × 5–13 cm, with numerous flowers; inflorescence parts densely covered with long erect hairs; first order axes 2–7 cm long; branchings often subopposite with bracts displaced 1–4 mm above branching point; higher order bracts with stipular parts reduced or absent and foliar parts narrowly triangular, up to 10(–15) mm long or rarely leaf-like, up to 1 × 0.5 cm long; bracteoles on pedicel somewhat below ovary, subopposite, stipular parts absent, foliar parts linear, 3–5 mm long, tips acute. Flowers pedicellate, pedicels 0–5 mm long in flowering stage (central flower in triad often sessile), 0–12 mm long in fruiting stage. Calyx densely covered with long erect hairs outside; tube 1–1.5 mm long, inner surface densely covered with long appressed hairs; lobes oblong to triangular, 2–4 mm long, inner surface moderately to sparsely covered with appressed hairs, tips acute. Corolla tube 9–11 mm long, inner surface densely covered with long spreading hairs in upper half; lobes 4–6 mm long. Anthers ca 4 mm long, completely exserted or basal part (ca 1 mm long) included in corolla tube at anthesis; filaments 0.2–0.3 mm long. Ovary 1.5–2 mm long, very densely covered with long erect hairs; per locule (1–)2–4 ovules arranged at periphery of placenta attached to middle of septum. Style and stigma 15–19 mm long, exserted for 7–8 mm; style densely covered with long erect hairs for 2–3 mm below papillate zone; stigmatic lobes 7–9 mm long. Fruits ovoid, faintly ribbed longitudinally and glossy (when dried), ca 10 × 8–9 mm, moderately covered with long erect hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemi-ovoid, ca 9 × 6.5 mm, crustaceous, with rounded or truncate base, acuminate tip, small adaxial opening somewhat below the middle and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 2–6(–8) per fruit, 3.5–4.5 × 2.5–3.5 mm.

Distribution

Endemic to northern Madagascar. Only known from Ambilobe District, Diana Region, and Vohemar District, Sava Region (Antsiranana Province) (Fig. 23D).

Habitat and phenology

Low-elevation dry deciduous or semi-deciduous forest; on limestone or limestone covered with sand; elev. 40–150 m. Flowers: January–March; Fruits: January–July.

Provisional IUCN assessment

Endangered: EN B1ab(iii) B2ab(iii). This assessment is based on seven herbarium specimens, collected between 1963 and 2005. The EOO is estimated to be 627 km^2, which complies with the Endangered

category under criterion B1. The AOO is estimated to be 24 km^2, which also complies with the Endangered category under criterion B2. *Paracephaelis russata* sp. nov. is known from five locations, which is the upper limit for the Endangered category under subcriterion 'a' of criterion B2. Three of the seven specimens are found in the Ankarana Special Reserve (1 location), two are found in different forests of the Loky-Manambato New Protected Area (2 locations) and three specimens were collected outside protected areas (2 locations). The main threat to the species is loss of habitat as a result of anthropogenic

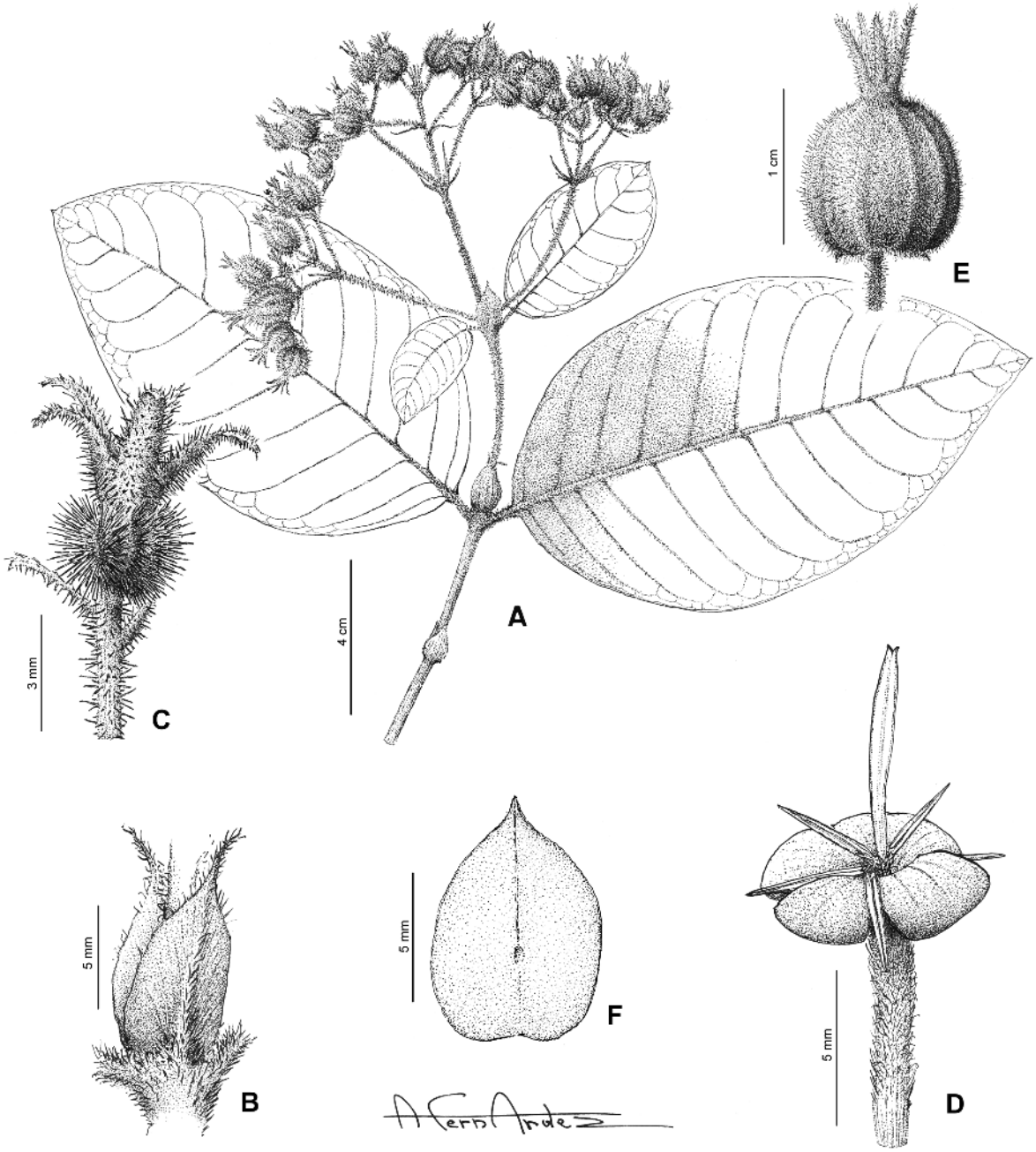

Fig. 16. *Paracephaelis russata* De Block sp. nov. **A**. Fruiting branch. **B**. Stipules. **C**. Bracteoles, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. **F**. Pyrene, adaxial view. Drawn by Mr A. Fernandez. From *De Block et al. 1048* (A–C, E–F) and *Gautier et al. 4526* (D).

factors. This loss of habitat even takes place inside the protected areas. In the Loky-Manambato New Protected Area, an archipelago of forests of different size and different ecology (dry, humid, lowland, montane; Nusbaumer *et al.* 2010), natural vegetation is lost by conversion into fields for subsistence farming, bushfires, and traditional gold mining. Furthermore, there is logging for timber and charcoal, extraction of natural resources, and hunting (Rakotondravony 2009; Nusbaumer *et al.* 2010). All these factors also play an important role in habitat destruction in the Ankarana Special Reserve, although mining there is for sapphires (Nicoll & Langrand 1989; Cardiff & Befourouack 2008). Because of the above-mentioned facts, we infer a reduction in the extent and quality of the habitat of *P. russata* sp. nov. This fact, in combination with the low EOO, low AOO and the low number of locations, qualifies the species for Endangered status.

Paracephaelis sambavensis De Block sp. nov.
urn:lsid:ipni.org:names:77260715-1
Fig. 17

Diagnosis

Differing from *Paracephaelis orientalis* sp. nov. by having larger leaves (13–18 × 5.5–8.5 cm vs 4.5–10.5 × 1–4 cm), larger inflorescences (4–8 × 4–8 cm vs 1.5–4 × 2–5 cm), longer pedicels (1–2 mm long in flowering stage, up to 5(–8) mm long in fruiting stage vs flowers sessile), shorter bracteoles (ca 1 mm vs 1.5–2 mm long), shorter calyx tubes (1–1.5 mm long vs 1.5–2 mm long in flowering stage, ca 3 mm long in fruiting stage), fewer ovules per locule (3–4 vs 4–7), and ovoid fruits (vs spherical).

Etymology

The species epithet is based on the type locality of the species.

Type material

MADAGASCAR – **Antsiranana Province, Sava Region, Sambava District** • S de Sambava; 1–10 Apr. 1967; fr; *Capuron 27702-SF*; holotype: P; isotypes: BR[BR0000022757685], TEF.

Other material studied

MADAGASCAR – **Antsiranana Province, Sava Region, Sambava District** • S de Sambava; 30 Nov.–1 Dec. 1966; fl; *Capuron 27121-SF*; BR, P, TEF.

Description

Tree to 15 m tall; pubescence tawny. Young shoots pale brown, densely covered with short appressed to spreading hairs; older branches pale brown, somewhat flaking, glabrescent. Petioles 1.2–2 cm long, densely covered with short appressed to spreading hairs. Leaf blades elliptic or obovate, 13–18 × 5.5–8.5 cm, thinly coriaceous, drying brown or dark brown and hardly discolorous, upper surface glossy, both surfaces glabrous (except for pubescence on midrib and secondary veins); base cuneate; tip acuminate with acumen 0.8–1.8 cm long; hair tuft domatia present; midrib moderately to densely covered with short appressed hairs in the lower half, sparsely covered with short appressed hairs or glabrous in the upper half on both surfaces; 8–12 secondary veins on each side of midrib, raised and sparsely covered with short appressed hairs or glabrous on both surfaces; higher order venation visible on both surfaces (when dried). Stipules triangular, 5–8 mm long, gradually tapering into an acute tip or with short awn < 1 mm long, outer surface densely covered with short appressed to spreading hairs, inner surface glabrous with 2–3 rows of colleters at the base. Inflorescences sessile, 4–8 × 4–8 cm, with numerous flowers; inflorescence parts densely covered with short appressed to spreading hairs; first order axes 1–3 cm long; higher order bracts with stipular parts reduced or absent, foliar parts triangular and vaulted, 2–10 mm long; bracteoles on

pedicel just below ovary, opposite, stipular parts absent, foliar parts triangular, ca 1 mm long, tips acute. Flowers shortly pedicellate; pedicels 1–2 mm long in flowering stage (immature buds), up to 5(–8) mm long in fruiting stage. Calyx densely covered with short appressed to spreading hairs outside; tube 1–1.5 mm long, inner surface with ring of long appressed hairs at the base and glabrous higher up; lobes quadrangular, ca 1 × 1 mm, somewhat keeled, inner surface glabrous, margins ciliate, tips rounded. Mature corolla, stamens, style and stigma unknown. Ovary 1–1.5 mm long, longitudinally ribbed (when dried), densely covered with short appressed or spreading hairs; per locule 3–4 ovules arranged at periphery of placenta (mostly at base and top) attached just above middle of septum. Fruits ovoid, 8–10 × 5–8 mm, moderately covered with short appressed to spreading hairs; fruit wall well-developed with multi-layered anastomosing network of sclerified vascular bundles; pyrenes hemi-ovoid, 7–9 × 4–5.5 mm, crustaceous

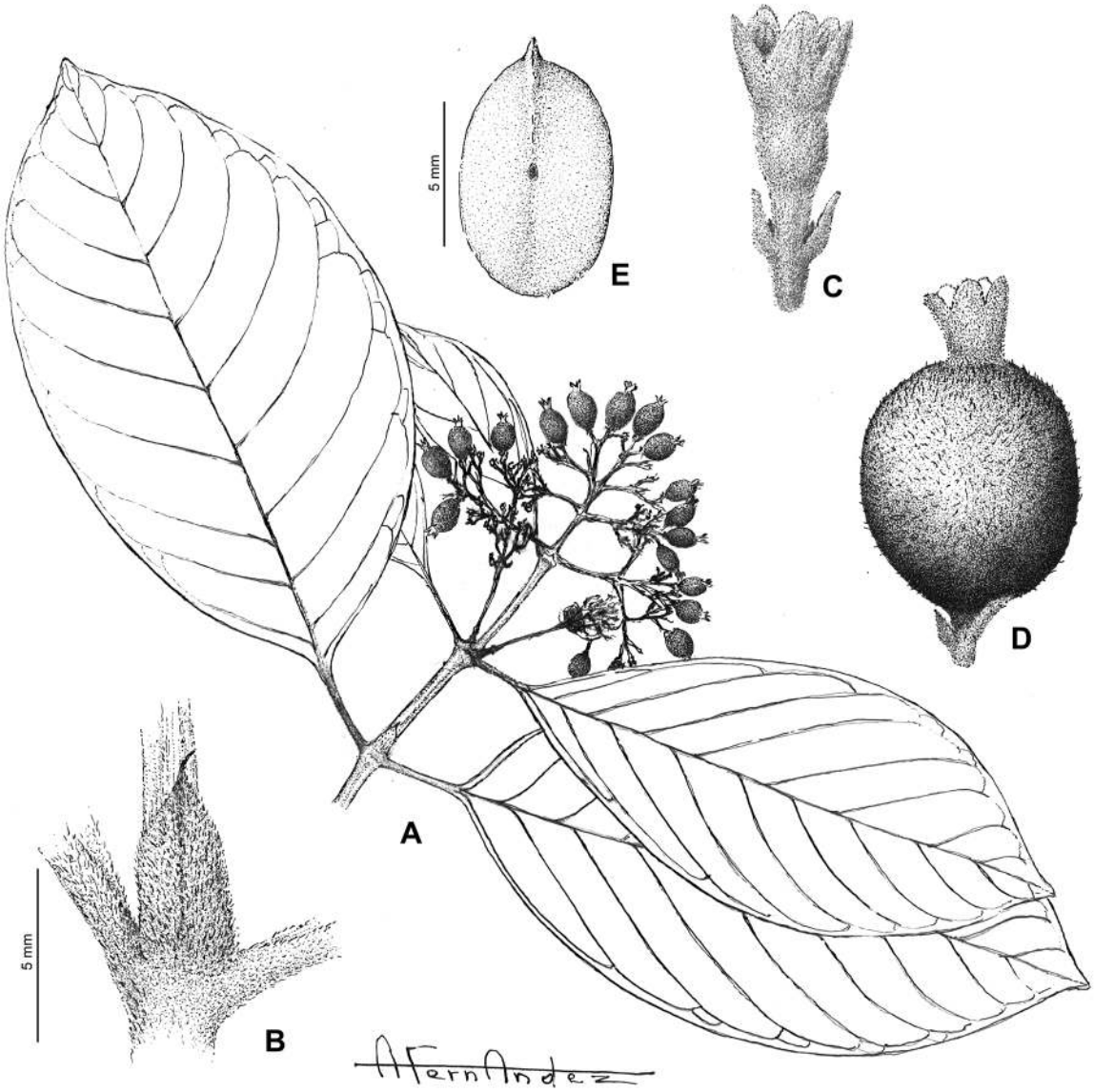

Fig. 17. *Paracephaelis sambavensis* De Block sp. nov. **A**. Fruiting branch. **B**. Stipule. **C**. Bracteoles, ovary and calyx. **D**. Fruit. **E**. Pyrene, adaxial view. Drawn by Mr A. Fernandez. From *Capuron 27702-SF* (A, C–E) and *Capuron 27121-SF* (B).

adaxially, ± stony abaxially, with rounded base, shortly acuminate tip, small adaxial opening somewhat above the middle and longitudinal central ridge running from the apex to the top of the adaxial opening. Seeds (1–)2–4(–8) per fruit, 4–4.5 × 3.5–4 mm.

Distribution

Coastal species, only known from Sambava in Sambava District, Sava Region (Antsiranana Province) (Fig. 23D).

Habitat and phenology

Littoral forest; on sand. Flowers: November (flowers buds); Fruits: April.

Provisional IUCN assessment

Critically Endangered: CR B2ab(iii). *Paracephaelis sambavensis* sp. nov. is only known from 2 specimens, seemingly collected from the same tree with a time lapse of ca 5 months. As a result, the EOO cannot be calculated and the AOO is 4 km^2, which complies with the Critically Endangered category under criterion B2. The species is known from a single location, which also complies with the Critically Endangered category under subcriterion 'a' of criterion B2. Both collections date from the sixties and no recent specimens are known. *Paracephaelis sambavensis* sp. nov. is a large tree from littoral forests on sand in north-eastern Madagascar. These eastern littoral forests on sand were identified as one of the most biodiverse habitats for plants (Dumetz 1999). They are home to ca 13% of Madagascar's native plant species, even though they only occupy less than 1% of Madagascar's surface (Consiglio *et al.* 2006). While littoral forests formed a continuous band along the east coast of Madagascar in the past, less than 10% now remain as isolated and fragmented patches (Consiglio *et al.* 2006). All remaining littoral forests are under severe pressure from local communities through logging for construction and firewood (Consiglio *et al.* 2006), and this would certainly be the case around a large city as Sambava. As a large tree (15 m tall), *P. sambavensis* sp. nov. would certainly be a sought-after resource. Furthermore, littoral forests in the region of Sambava have been cleared for slash-and-burn agriculture as well as for large-scale oil palm plantations (Google Earth, September 2020). Only a few remnant patches of littoral forest remain. Based on the above-mentioned facts, a reduction in the extent and quality of the habitat of *P. sambavensis* sp. nov. is inferred. This threat, combined with the low AOO and the single location, qualifies *P. sambavensis* sp. nov. for Critically Endangered status. The fact that the species has not been collected or observed for more than fifty years, would suggest it is possibly extinct. A targeted survey in the littoral forests of northern and north-eastern Madagascar is needed to confirm or deny the suspicion that the species is extinct in the wild. If living plants of this species were to be found, they should be protected and an ex situ conservation program set up.

Note

Since the collection labels give identical data for both *Capuron 27702-SF* and *27121-SF*, it would seem that the two specimens were collected from a single tree, the collector returning to the locality to collect flowers after having found a specimen in fruit. This species was never collected again.

Paracephaelis saxatilis (Scott Elliot) De Block
Figs 1C, G, 2D, 4C–D, F, I, K, 18

Systematics and Geography of Plants 73: 100 (De Block 2003).

Basionym

Webera saxatilis Scott Elliot, *Journal of the Linnean Society* 29: 25 (Scott Elliot 1891). **Type**: MADAGASCAR – **Toliara Province, Anosy Region, Taolagnaro District** • Fort Dauphin; May [1888–1890]; fr; *Scott Elliot 2885*; lectotype: K, **here designated**. **Syntype**: MADAGASCAR • s.loc.; *Scott Elliot 2683* (n.v.). See Note.

Homotypic synonym

Tarenna saxatilis (Scott Elliot) Homolle, *Bulletin de la Société botanique de France*: 607 (Homolle 1938); *Révision des Rubiacées de Madagascar et des Comores*: 175 (Capuron 1973).

Heterotypic synonyms

Myonima velutina Cordem., *Flore de l'île de la Réunion*: 508 (De Cordemoy 1895). – *Tarenna velutina* (Cordem.) Verdc., *Kew Bulletin* 37: 561 (Verdcourt 1983). **Type**: ?RÉUNION • s.loc.; s.dat.; fl (corollas fallen); *Bernier s.n.* (voyage de M. Boivin, ex Herb. Bernier); holotype: P; isotype: Herb. Cordemoy MARS.

Other material studied

MADAGASCAR – **Toliara Province, Androy Region, Ambovombe-Androy District** • versant méridional du massif de l'Angavo, E d'Antanimora; 23 Jan. 1963; fr; *Capuron 22477-SF*; BR, P • along road between Ambondro and Ambovombe; 100–150 m a.s.l.; 18 Feb. 1975; fr; *Croat 31689*; MO • Antanimora, N d'Ambovombe; 29 Apr. 1931; fr; *Decary 8867*; P • route d'Antanimora; 12 Jan. 1956; fl; *Descoings 1447*; P • Vohipary forest; 539 m a.s.l.; 20 Apr. 2001; fr; *Miles & Randriantarika 142*; K • Antamimora, bifurcation de Bekibio; 16 Feb. 1961; fr; *Peltier J. & M. 2871*; P • Antanimora, on road to Beraketa; 341 m a.s.l.; 18 Dec. 2004; fl; *Rakotonasolo, Hoffmann, Rakotoarisoa & Ralimanana 922*; BR, K. – **Beloha District** • falaise côtière NW du cap Sainte-Marie, vers Lavanono; 1–150 m a.s.l.; 8 Mar. 1955; fl; *Humbert 29322*; P • falaise côtière vers l'embouchure de la Menarandra, Bevoalava-Ankazondranto; 1–150 m a.s.l.; 12 Mar. 1955; fl; *Humbert 29378*; BR, P. – **Bekily District** • vallée supérieure de la Manambolo (bassin du Mandrare), aux environs de Beaka (Pisopiso); 800 m a.s.l.; Jan. 1934; fl; *Humbert 13684*; BR, P • bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, aux dessus de Pisopiso (Beaka); 1100 m a.s.l.; Dec. 1933–Jan. 1934; fl; *Humbert 13684bis*; BR, P. – **Anosy Region, Amboasary-Atsimo District** • vallée du Mandrare; Oct. 1905; fl, fr; *d'Alleizette 3175*; L • near Amboasary, due E of Ambovombe; 150 m a.s.l.; 19 Feb. 2001; fl; *Davis & Rakotonasolo 2731*; BR, K, MO, P, TAN, TEF • Mandrare moyen, environs de Beza Esiva; 27 Feb. 1957; fr; *Descoings 2737*; TAN • bassin supérieure de l'Onilahy (Mangoky), vallée de l'Andranomiforitra; 1000–1200 m a.s.l.; 19 Dec. 1928; fl; *Humbert 7072bis*; P • vallée moyenne du Mandrare, près d'Anadabolava; 200–250 m a.s.l.; Dec. 1933; fl; *Humbert 12399*; P • ibid.; 200–250 m a.s.l.; Dec. 1933; fl; *Humbert 12556*; P • ibid., mont Vohitrosy; 800 m a.s.l.; Dec. 1933; fl; *Humbert 12696*; P • vallée de la Manambolo (bassin du Mandrare), NW de Maromby (Betsioky); 300–400 m a.s.l.; Dec. 1933; fl; *Humbert 12768*; BR, P • vallée de la Manambolo (bassin du Mandrare), rive gauche, aux environs d'Isomony (confluent de la Sakamalio), monts Kotriha et Isomonobe; 400–600 m a.s.l.; Dec. 1933–Jan. 1934; fl; *Humbert 12823*; BR, P • vallée de la Manambolo (bassin du Mandrare), rive droite, aux environs d'Isomony (confluent de la Sakamalio); 400–900 m a.s.l.; Dec. 1933; fl; *Humbert 12954*; BR, P • Marotsiraka, forêt de Betsimalaho, colline Beanivo; 222 m a.s.l.; 20 Apr. 2012; fr; *Raharimampionona, Ravelonarivo & Josso 399*; MO n.v., P online, TAN n.v. • Ranobe, Betsingilo, forêt de Beanivo, complexe Anadabolava Betsimalaho; 282 m a.s.l.; 12 Feb. 2013; fr; *Randrianarivony, Randriatsivery, Botovao & Remanofy 509*; BR, MO n.v., P n.v., TAN n.v. – **Taolagnaro District** • forêt de Vinanibe, près de Fort-Dauphin; 9 Jan. 1963; fl; *Capuron 22314-SF*; BR, P • dune d'Eolala, entre le Vinanibe et Fort-Dauphin; 4 Feb. 1963; fl; *Capuron 22317-SF*; BR, P • Vinanimbe (Ambimanibe), coastal forest 8 km WSW (BRG 237º) of Taolanaro; 10 m a.s.l.; 4 Dec. 1997; fr; *Davis, Andriantiana &*

Gower 1192; K, P, TAN • Fort Dauphin; s.dat.; fl; *Cloisel 196*; BM, P • woods around the airport, W side of Fort Dauphin; 10 m a.s.l.; 10 May 1983; fl, fr; *D'Arcy & Rakotozafy 15413*; MO • ibid.; 10 m a.s.l.; 10 May 1983; fl, fr; *D'Arcy & Rakotozafy 15414*; MO, P • ibid.; 10 m a.s.l.; 10 May 1983; fr; *D'Arcy & Rakotozafy 15418*; MO • Petriky forest; 20 m a.s.l.; 18 Feb. 2001; fl; *Davis & Rakotonasolo 2727B*; BR, K, TAN, TEF • Petriky, Eharake; 47 m a.s.l.; 31 Mar. 2010; fl; *De Block, Groeninckx & Rakotonasolo 2396*; BR, G, K, MO, P, TAN • Petriky, near guard's cabine; 47 m a.s.l.; 31 Mar. 2010; fl; *De Block, Groeninckx & Rakotonasolo 2401*; BR, G, K, MO, P, TAN • Fort-Dauphin; 28 Jun. 1926; fl; *Decary 4207*; P, LISC • Fort-Dauphin; 28 Jun. 1926; fr; *Decary 4208*; P, WAG • Italy, côte W de Fort Dauphin; Mar. 1955; fl, fr; *Descoings 426*; TAN • Mandena; 0–10 m a.s.l.; 10 Mar. 1989; fr; *Dumetz, Gereau & Rabevohitra 557*; K, MO, P, TAN • Mandena; 0–10 m a.s.l.; 23 Jan. 1990; fl; *Dumetz 1230*; K, MO, P, WAG • fir. Mananbaro, Petriky forest, S of large dune near NE corner of lake Andranany, ca 10 km WSW of Tolanaro; 0–10 m a.s.l.; 10 Apr. 1989; fr; *Gereau, Rabevohitra & Dumetz 3343*; BR, K, MO, P, TAN, WAG • dunes de Fort Dauphin; 27 Mar. 2010; fr; *Groeninckx, De Block & Rakotonasolo 289*; BR, K, MO, P, TAN • baie des Galions (Ranofotsy), SW de Fort-Dauphin; 1–100 m a.s.l.; Feb. 1955; fl; *Humbert 28991*; P • Petriky; 14 m a.s.l.; 7 Sep. 2006; fr; *Landry 131*; K • hauts bassins de la Mananara et abords, N d'Imonty, RNI 11, Andohahela; 400–1900 m a.s.l.; 3 Dec. 1960; fl; *Leandri & Saboureau 4224*; P • Petriky, WSW of Fort-Dauphin, at junction of main QMM road and side road; 5 m a.s.l.; 13 Mar. 1998; fl, fr; *Lowry, Smith, Vincelette & Randrihasipara 5025*; BR, K, MO, P • Petriky, along roads near and beyond dune near end of QIT road; 25 m a.s.l.; 8 Dec. 1989; fl; *McPherson & Dumetz 14670*; K, MO, P, TAN • Petriky, along QIT road; 15 m a.s.l.; 12 Jan. 1990; fl; *McPherson, Dumetz & Rabevohitra 14764*; K, MO, P, TAN, TEF • Petriky, along coastline near S end of the most SW lake; 10 m a.s.l.; 22 Jan. 1990; fl; *McPherson, Dumetz & Rabevohitra 14850*; MO • Mandena forest; 2–15 m a.s.l.; 23 Jan. 1990; fl; *McPherson, Dumetz & Rabevohitra 14875A*; MO, P, TAN • 5 km S of Manambaro, 23 km W of Fort Dauphin; 150 m a.s.l.; 30 Mar. 1991; fl; *Miller & Randrianasolo 6231*; K, MO, P, TAN • Fort Dauphin; 1955; fr; *Pernet 38*; TAN • fir. Manambaro, village Ambovo, forêt littorale de Petriky; 6 m a.s.l.; 24 Jun. 2004; fr; *Rabenantoandro, Ramisy, Rajoharison & Randriatafika 1609*; BR, K, MO • Andrakaraka, forêt littorale de dune haute à côté du site de construction du seuil déversoir de QMM; 8 m a.s.l.; 27 Feb. 2007; fr; *Rabenantoandro, Randriatafika, Ramison, Rajoharison & Théodore 1790*; BR, MO n.v., P online, TAN n.v. • Petriky; 5 Dec. 2002; fl; *Rakotonasolo, Randrinaivo, Rabevohitra, Rzafindrabeaza & Ratodimanana 573*; BR, K, P • forêt littorale de Sainte Luce; 8 Jan. 2008; fl; *Ramison & Rabehevitra 514*; MO n.v., P online, TAN n.v. • Ambatoabo, Ankoba, forêt sèche à *Alluaudia* d'Ankoba; 180 m a.s.l.; 24 Feb. 2009; fl, fr; *Randrianaivo, Ratovoson, Razanatsoa, Razafindrahaja, Rasolondrainy Tsimitamby & Fiadana 1749*; BR, MO, P • fir. Manambaro, fkt. Petriky; 18 Feb. 2004; fl; *Randriatafika & Ramisy 400*; BR, MO • Manambaro, forêt littorale de Petriky, située entre le village d'Ambovo et de Loharano; 6 m a.s.l.; 2 Mar. 2004; fl; *Randriatafika, Razafimandimby & Ramisy 475*; MO n.v., P online • Manambaro, Petriky, forêt littorale de Petriky; 15 Mar. 2006; fl; *Randriatafika & Rabenantoandro 710*; MO n.v., P online • ibid.; 22 Mar. 2006; fl; *Randriatafika & Rabenantoandro 717*; MO n.v., P online • Fort Dauphin; s.dat.; fl; *Scott Elliot 2389*; P • Fort Dauphin; Sep. 1890; fl, fr; *Scott Elliot 2389bis*; K • Fort Dauphin; s.dat.; fr; *Scott Elliot 2885*; K. – **Without locality** • Feb. 1955; fl, fr; *Descoings 316*; TAN.

Description

Shrub or small tree, to 4 m tall; pubescence white or tawny; youngest internodes pale or orange brown, rapidly becoming corky, densely covered with appressed or spreading hairs; older branches corky, greyish or fawnish, glabrous. Leaves grouped at the end of lateral short-shoots with short internodes and the older leaves fallen. Petioles 2–5 mm long, densely covered with appressed, spreading or erect hairs. Leaf blades elliptic, ovate, rarely obovate or orbiculate, 1–4 × 0.7–2.8 cm, coriaceous, drying brown, dark brown or greenish above and somewhat paler below, upper surface glossy, moderately to densely covered with short erect hairs or, more rarely, glabrescent, lower surface densely covered with long, erect hairs (hairs often more appressed on midrib and secondary veins); base cuneate, acute, truncate, rounded or somewhat cordate; tip obtuse, rounded or acute, mucronate; domatia absent; midrib sparsely to

moderately covered with ± long appressed or spreading hairs above; 3–6(–7) secondary veins on each side of midrib, impressed above, raised below; higher order venation usually inconspicuous on both surfaces, rarely impressed above. Stipules caducous, triangular with short needle-like awn, keeled; outer surface of youngest stipule pairs densely covered with long appressed or spreading hairs, inner surface glabrous with row of colleters interspaced with long hairs at the base; sheath 1–2.5 mm long; awn 0.5–1.5 mm long. Inflorescences terminal on short lateral shoots with short or longer internodes and leaves fallen but stipules or stipular remnants remaining, sessile but leaves of first order bracts often fallen (giving the impression of short peduncle), compact, 0.6–1.5 × 1–2 cm, with 5–45 flowers; inflorescence parts densely covered with appressed or spreading hairs; first order axes 0.2–1 cm long; higher order bracts with stipular parts reduced or absent, foliar parts triangular and vaulted, 1.5–4 mm long; bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts triangular, 1.5–2.5 mm long, tips acute. Flowers sessile or shortly pedicellate, pedicels 0–2(–3) mm long. Calyx densely covered with appressed to spreading hairs outside; tube (0.2–)0.4–0.7 mm long, inner surface densely covered with appressed hairs; lobes triangular, 0.8–1.5 mm long, inner surface densely covered with appressed hairs all over or pubescence restricted to the base of the lobes, tips acute. Corolla tube 4–7 mm long, inner surface densely covered with long erect hairs in upper ⅔; lobes 3–4.5 mm long. Anthers 3.5–4 mm long, completely exserted or basal part (ca 1 mm long) included in corolla tube at anthesis; filaments 0.5–1 mm long. Ovary ca 1.5 mm long, longitudinally ribbed (when dried), densely covered with appressed to spreading hairs; per locule 3–8 ovules arranged at periphery of placenta attached to top of septum. Style and stigma (8–)10–12.5 mm long, exserted for 4–5 mm; style densely covered with long upwardly directed hairs from ca 2 mm above base to just below papillate zone; stigmatic lobes 5–6 mm long, upper part fusiform; papillae absent along fusiform part, present lower down in longitudinal grooves. Fruits subspherical, 5–7 × 5.5–8 mm, densely covered with short erect hairs, somewhat glossy; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical, ca 5.5 × 5 mm, membranous adaxially, crustaceous abaxially, with rounded tip and base, small adaxial opening somewhat above the middle and slight longitudinal central ridge running from the apex to the top of the adaxial opening. Seeds (2–)4–8 per fruit, 3–4 × 2.5–3 mm.

Distribution

Restricted to south-eastern and southern Madagascar. Present in: Ambovombe-Androy, Beloha and Bekily Districts, Androy Region, and Amboasary-Atsimo and Taolagnaro Districts, Anosy Region (Toliara Province) (Fig. 23D).

Habitat and phenology

Deciduous dry forest and scrub, littoral forest and dune vegetation; on white sand, more rarely on rocky substrate; elev. 0–1200 m. Flowers: September–October, December–March, May; Fruits: throughout the year, but none recorded in February–March.

Vernacular names

Tinoro (*Gereau et al. 3343*); taitsanda (*Randriatafika & Rabenantoandro 710*).

Provisional IUCN assessment

Least Concern: LC. This assessment is based on 61 collections with detailed locality data, collected between 1890 and 2012. The EOO of *P. saxatilis* is estimated to be 23 637 km^2, somewhat exceeding the upper limit of the Vulnerable category under criterion B1. The AOO is 140 km^2, which complies with the Endangered category under criterion B2. The species occurs in more than 15 locations, which exceeds the upper limit for Vulnerable category under subcriterion 'a' of criterion B2. However, at least three locations are severely threatened by mining. QIT Madagascar Minerals (QMM) is a sands mining operation, producing ilmenite, a major source of titanium dioxide, and zircon (https://www.riotinto.com/operations/madagascar/qit-madagascar-minerals). Approximately 1665 ha of

littoral forest habitat is expected to be lost between 2008 and 2050 at Mandena (3 specs), Petriky (14 specs), and Sainte Luce (1 spec.). The mining operation clears the vegetation and removes the soil, thereby destroying the seed bank. While part of the forests will be conserved and the company pledges restoration, the mining activities will have a negative effect on the AOO and the number of mature individuals, but not on the EOO, and the number of locations. The main threat to *P. saxatilis* is the destruction of its habitat, as a result of mining, subsistence farming, charcoal production, and collection of plants for medicinal or

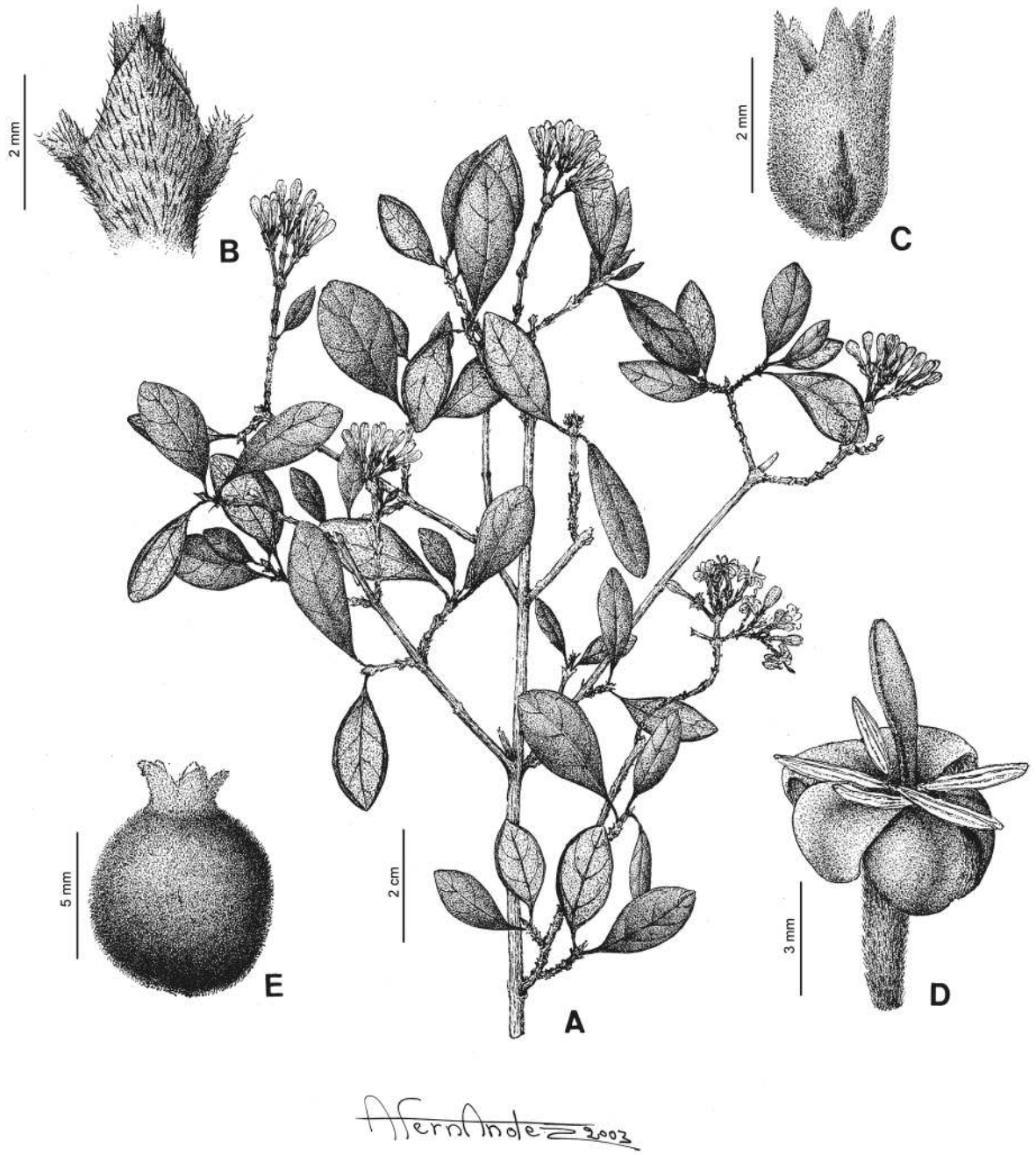

Fig. 18. *Paracephaelis saxatilis* (Scott Elliot) De Block. **A**. Flowering branch. **B**. Stipule. **C**. Bracteole, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *McPherson et al. 14764* (A–D) and *Gereau et al. 3343* (E).

subsistence use (Ingram & Dawson 2006). While a reduction in the extent and quality of the habitat of *P. saxatilis* can be inferred, the number of locations (> 15) and the relatively large EOO does not qualify this species for a threat category. Therefore, *P. saxatilis* is assessed as Least Concern.

Note

Webera saxatilis was described based on two syntypes: *Scott Elliott 2885* and *Scott Elliott 2683* (Scott Elliott 1891). It has proven impossible to locate the second specimen. *Scott Elliott 2885* is only a fragment present in K. There is, however, another specimen of *P. saxatilis* collected by Scott Elliott, notably *2389* (P) and *2389bis* (K). In K, one double of *Scott Elliot 2389bis* is mounted on the same sheet as *Scott Elliott 2885*, with the second double on a separate sheet. The labels of *Scott Elliot 2389* and *2389bis* in both K and P bear the name '*Webera saxatilis*', but the name is absent from the label of *Scott Elliott 2885*. Possibly, Scott Elliott (1891) erroneously cited the number *2683* instead of *2389bis* for the second syntype of *Webera saxatilis*.

Paracephaelis sericea (Arènes) De Block
Figs 1D, 19

Taxon 64: 92 (De Block 2015).

Basionym

Homolliella sericea Arènes, *Notulae Systematicae* 16: 17, Pl. 4, 19–25 (Arènes 1960). **Type:** MADAGASCAR – **Toamasina Province, Alaotra-Mangoro Region, Moramanga District** • forêt d'Analamazaotra; Feb. 1919; fl; *Thouvenot 122*; holotype: P[P00551271]; isotypes: BR[BR00000904508], P[P00551270]. See Note 1.

Other material studied

MADAGASCAR – **Antsiranana Province, Sava Region, Andapa District** • Anjialavabe, Ankiakabe, near Tsaralanto village; 1030 m a.s.l.; Feb. 2006; fl; *Antilahimena, Randriamandimby & Falison 4610*; BR, MO, P, TAN • Anjialavabe, Ankiakabe, forêt d'Antsahaberaoka, 11 km NW d'Anjialavabe; 1002 m a.s.l.; 21 Feb. 2007; fl; *Rakotovao, Razakamalala, Ravelonarivo & Jacky 3703*; BR, G n.v., P online, TAN • Anjanaharibe-Sud RS; 1116–1424 m a.s.l.; 21 Mar.–7 Apr. 1994; fr; *Ravelonarivo, Rasoavimbahoaka, Rafaliarimanana, Rasitefanonirina & Raymond 29*; K, MO, P, TAN • Anjanaharibe-Sud RS, commune Bealampona, quartier de Befingotra, village d'Andranotsarabe, suivant la route d'Andapa vers Bealanana, piste de l'est 1 km à côté droite du ruisseau Andranotsarabe; 890–1041 m a.s.l.; 14 Sep. 1994; fr; *Ravelonarivo, Rabesonina & Ramainty 358*; BR, K, MO, P, TAN • Doany, Tsaralanto, Andongozabe, Ankiakabe; 1293 m a.s.l.; 1 Mar. 2006; fl; *Ravelonarivo, Patriode, Mobel & Germain 1680*; BR, MO, P online, TAN. – **Toamasina Province, Alaotra-Mangoro Region, Ambatondrazaka District** • Didy, forêt de Tsarahonena environ 7 km de Didy; 1108 m a.s.l.; 14 Jan. 2010; fl; *Andrianaivoravelona, Ralimanana, Rakotoarinivo, Rajaonarison, Rakotoroalahy & Ramaherimana 227*; K n.v., P online, TAN n.v. • Mitanonoka, fir. Manakambahiny-Est; 18 Jan. 1963; fl; *Laibosaka 12599-RN*; P, TEF •Manakambahiny-Est; 3 Mar. 1950; fl; *Ramanantoavina 1963-RN*; BR, P, TAN • fir. Manakambahiny-Est, entre Laindrotra et Onibe, 5 km E de Manakambahiny-Est; 900 m a.s.l.; 19 Sep. 2002; fr; *Ratovoson, Rakotondrajaona, Randrianasolo, Rasolohery, Razakanirina & Mananjara 679*; BR, K, MO. – **Toamasina Province, Alaotra-Mangoro Region, Amparafaravola District** • Anony, N du pays Sihanaka; 3 Sep. 1937; fr; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *2939*; P. – **Toamasina Province, Alaotra-Mangoro Region, Moramanga District** • Sandrangato, PK 27 route d'Anosibe; 26 Oct. 1964; fl, fr; *Abraham 187*; TEF • Ambohibary, Ampitambe, Ambatovy, forêt d'Analamay, campement Mahatakatra; 1110 m a.s.l.; 15 Dec. 2004; fr; *Andriamahefarivo, Antilahimena, Ranaivojaona & Edmond 41*; BR, MO, P, TAN • Ambatovy Dynatec; 1115 m a.s.l.; 16 Jan. 2005; fl; *Andriantiana 349*; BR, MO, P • commune Andasibe,

fkt. Menalamba, Ambatovy forest; 996 m a.s.l.; 16 Jan. 2005; fl; *Antilahimena 3173*; BR, MO, P, TAN • commune Ambohibary, fkt. Ampitambe, Vavanaomby forest; 1025 m a.s.l.; 11 Feb. 2007; fl; *Antilahimena, Edmond & Tojoniaina 5277*; MO n.v., P online, TAN n.v. • commune Ambohibary, fkt. Ampitambe, Sahaviana forest; 987 m a.s.l.; 22 Feb. 2007; fl; *Antilahimena & Edmond 5389*; MO n.v., P, online TAN n.v. • commune Andasibe, fkt. Menalamba, Ambatovy, lac Amparihihambana; 1116 m a.s.l.; s.dat.; fl; *Antilahimena, Edmond & Razadindasy 5474*; MO n.v., P online, TAN n.v. • commune Ambohibary, fkt. Ampitambe, Andranovery forest, Ambatovy; 995 m a.s.l.; 21 Oct. 2007; fr; *Antilahimena & Marcelin 5857*; MO n.v., P online, TAN n.v. • Andasibe, Menalamba, forêt d'Analamay; 1142 m a.s.l.; 6 Jun. 2007; fr; *Bernard, Antilahimena & Marcelin 524*; BR, MO, P, TAN • Ambatovy; 996 m a.s.l.; 24 Oct. 2007; fr; *Bernard 692*; BR, MO, P, TAN, TEF • Ambohibary, Ampitambe, Ambatovy, zone de défrichement 22; 1093 m a.s.l.; 26 Apr. 2010; fr; *Bernard, Ratodimanana, Ramahenina, Edmond & Randrianasolo 1556*; MO n.v., P online, TAN n.v. • Befoza, Perinet; 14 Jun. 1950; fr; *coll. ignot. 2610-SF*; P, TAN, TEF • Sahamaloto-Perinet; 10 Jul. 1951; fr; *coll. ignot. 3836-SF*; P, TEF • Sahamaloto-Perinet; 2 Sep. 1952; fr; *coll. ignot. 5748-SF*; P, TEF • Menalamba, Perinet; 27 Feb. 1959; fl; *coll. ignot. 14958-SF*; BR, K, P, TEF • Sahamaloto, Perinet; 18 Jun. 1955; fr; *coll. ignot. 15012-SF*; P, TEF • Analamazaotra, village le plus proche Perinet; 800 m a.s.l.; 6 Apr. 1958; fr; *coll. ignot. 17946-SF*; P, TEF • fir. Marovoa, au bord du ruisseau Andrevodrevoka, village le plus proche Sakalava-Ambany, forêt d'Ankeramadinika; 1100 m a.s.l.; 19 Sep. 1964; fr; *coll. ignot. 21855-SF*; K, P, TEF • réserve Sandrangato, PK 27 route d'Anosibe; 900 m a.s.l.; 26 Oct. 1964; fr; *coll. ignot. 21948-SF*; BR, G, K, P • station forestière d'Analamazaotra, environs de la parc des orchidées; 880 m a.s.l.; 23 Feb. 1999; fl; *De Block & Rakotonasolo 849*; BR, G, K, MO, P, TAN, WAG • ibid.; 880 m a.s.l.; 23 Feb. 1999; fl; *De Block & Rakotonasolo 850*; BR, K, MO, P, TAN • Analamazaotra; 19 Apr. 2010; fr; *De Block, Groeninckx & Razanatsoa 2532*; BR, K, MO, TAN, WAG • forêt d'Analamazaotra; Oct. 1923; fl; *Louvel 182*; P • Andasibe, Menalamba, forêt d'Antsampanandrano; 1114 m a.s.l.; 4 Jun. 2007; fr; *Miandrimanana, Ravelonarivo & René d'Ampitambe 224*; MO n.v., P online, TAN n.v. • forêt d'Analamazaotra; 800 m a.s.l.; Feb. 1912; fl; *Perrier de la Bâthie 8621*; P • Phelps Dodge project site, ca 15 air-km NE of Moramanga, ca 11 km E of Antanambao, between Ambatovy-Sud and Analamy-Est, Torotorofotsy River, Berano; 1000 m a.s.l.; 20 Feb. 1997; fl; *Rakotomalaza, Razafimanantsoa & Andriatsiferana 1152*; MO, P • Ambohibary, Ampitambe, Andranovery, Ambatovy, clearing zone 5; 1000 m a.s.l.; 13 Feb. 2008; fl; *Rakotondrafara, Rakotondrajaona, Rabearivanona, Ratovomanana & Rajerison 586*; MO n.v., P online, TAN n.v. • ibid.; 985 m a.s.l.; 15 Feb. 2008; fl; *Rakotondrafara, Rakotondrajaona, Rabearivanona, Ratovomanana & Rajerison 628*; MO n.v., P online, TAN n.v. • ibid.; 1024 m a.s.l.; 4 Mar. 2008; fl; *Rakotondrafara, Rakotomazava, Ratovomanana, Raymond & Kotosoa 685*; MO n.v., P online, TAN n.v. • RN 2, PK 6 after Moramanga; 900 m a.s.l.; 21 Aug. 1999; fr; *Rakotonasolo 94*; BR, K • Ambatovy, SW d'Ampitambe; 950–1000 m a.s.l.; 5 Oct. 2002; fr; *Rakotonasolo 425*; BR, TAN • Ambohibary, Ampitambe, Ambatovy, Befandrotrarana, by pass; 995 m a.s.l.; 21 Feb. 2010; fl; *Ramahenina, Ravelonarivo & Razafimelison 12*; MO n.v., P online, TAN n.v. • commune Amboasary, fkt. Antsily, village Mangabe, forêt d'Ampahatra; 987 m a.s.l.; 13 Nov. 2012; fl; *Ramahenina, Randrianaivo, Rasoazanany, Razanakoto & Randriamialisoa 149*; MO n.v., P online, TAN n.v. • Perinet, Sahamaloto; 18 Feb. 1948; fl; *Ratovoarison 1337-RN*; P, TAN • Befoza, Perinet; 27 May 1994; fr; *Ravilonombiara s.n.*; P • Ambohibary, Antsily, Andakana, forêt d'Ampahatra; 923–942 m a.s.l.; 11 Sep. 2012; fl; *Razakamalala & Randrianaivo 7045*; MO n.v., P online, TAN n.v. • Ambatovy forest; 1100 m a.s.l.; 1 Feb. 2006; fl; *Rogers & Antilahimena 1004*; BR, MO • ca 19 km S of Moramanga along road to Anosibe An'ala, ca 2 km N of road; 16 Feb. 1991; fl; *Schatz, Spargur, Hines & Thomas 3162*; K, MO, P, TAN • Mantadia, PK 15, site of graphite mine; 1058 m a.s.l.; 21 Jan. 2006; fl; *Tosh, De Block & Rakotonasolo 248*; BR, G, K, MO, P, TAN, WAG. – **Toamasina Province, Analanjirofo Region, Mananara Avaratra District** • forêt d'Ibanda; 500 m a.s.l.; 20 Jul. 1990; fr; *Raharimalala 1077*; P. – **Maroantsetra District** • environs de la baie d'Antongil, Antandrokolaka, entre les bassins de la Rantabe et de la Fananehana; Feb. 1954; fl; *Capuron 9040-SF*; K, MO, P, TEF. – **Vavatenina District** • Sahatavy; 25 Apr. 1960; fr; *Laibosaka 10950-RN*; MO, P, TEF. – **Atsinanana Region, Toamasina II District** • RN 3, Mangabe; 13 Feb. 1952; fl; *Botoalma 3724-RN*; BR, K, MO, P,

TAN • RNI 1, Betampona, 1 km de la poste de Rendrirendry, piste principale, fkt. Andrantabe, fir. Ambodiriana; 20 Mar. 1999; fl; *Iambana, Bernard & Birkinshaw 138*; MO n.v., P online, TEF n.v. – **Vatomandry District** • Ambalabe, forêt de Vohibe, piste sortant du plot vers Ambinanin'i Sahamahirana; 644 m a.s.l.; 19 Sep. 2010; fr; *Raharimampionona, Rasoaviety & Lezafy 365*; MO n.v., P online, TAN n.v. • Ambalabe, Ambinanindrano II, Vohibe forest, WSW of Foara Toby, along trail towards Tsitondroina waterfall; 667 m a.s.l.; 20 Nov. 2013; fl; *Randrianasolo, Razanatsima, Foara, Zafindrafeno & Mamy 1453*; MO n.v., P online, TAN n.v. • Ambalabe, Ambinaninandro II, E de Toby Foara; 589 m a.s.l.; 11 May 2006; fr; *Razanatsima 106*; MO n.v., P online, TAN n.v. • Ambalabe, Ambinanindrano II, forêt de Vohibe, rivière Vakoanina; 697 m a.s.l.; 21 Aug. 2015; fr; *Razanatsima 1419*; MO n.v., P online, TAN n.v. • Ambalabe, Ambinanindrano II, Vohibe, Vohibe forest; 609–648 m a.s.l.; 19 Apr. 2010; fr; *Rothrock, Kuhlman, Rakotoarivelo, Rasoarivety, Zafindrafeno, Yhomad & Florentin 339*; BR, MO. – **Mahajanga Province, Sofia Region, Mandritsara District** • Tsaravilona Amparihy, Makira, suivant une ligne de crête vers le NE; 1302 m a.s.l.; 26 Feb. 2008; fr; *Ravelonarivo, Gerard & Rasoanaivo 3032*; BR, MO, P, TAN. – **Fianarantsoa Province, Atsimo-Atsinanana Region, Vondrozo District** • Vondrozo forest, along main road; 578 m a.s.l.; 5 Feb. 2006; fl; *De Block, Tosh & Rakotonasolo 1994*; BR, MO, P, TAN, UPS. – **Ihorombe Region, Ivohibe District** • Ivohibe forest, 7 km from Ivohibe village; 801 m a.s.l.; 31 Jan. 2006; fl; *Tosh, De Block & Rakotonasolo 301*; BR, MO, P, TAN. – **Vatovavy-Fitovinany Region, Mananjary District** • Ambodiramiavona; 20 Jul. 1956; fr; *coll. ignot. 14733-SF*; P, TEF. – **Toliara Province, Anosy Region, Taolagnaro District** • RNI 11, Andohahela, forêt humide prés du village Taviala-Andohavondro S d'une rivière Antsororoka, commune Ankaramena; 175–200 m a.s.l.; 29 Jun. 1995; fl; *Eboroke 1043*; BR, MO, P online.

Description

Tree, 5–16 m tall, dbh to 35 cm; pubescence tawny. Young shoots dark brown but rapidly becoming corky and reddish brown, densely covered with short erect hairs; older branches brown, pale or reddish brown, flaking, glabrescent. Petioles 1–3 cm long, densely covered with short erect hairs. Leaf blades obovate or, more rarely elliptic, ovate or broadly obovate, 7–21 × 4.5–12 cm, coriaceous, drying brown to dark brown above and somewhat paler below, upper surface glossy, moderately to densely covered with minute erect hairs (with pubescence on midrib and secondary veins denser), or, rarely, glabrous (with pubescence restricted to midrib and sometimes secondary veins), lower surface densely covered with short erect hairs (with pubescence on midrib and secondary veins identical to that on blade or appressed rather than erect); base cuneate, more rarely obtuse to rounded; tip acuminate (often abruptly), acumen narrow, 0.5–1.5 cm long; hair tuft domatia often present; 8–10 secondary veins on each side of midrib, raised on both surfaces; higher order venation inconspicuous above, visible below. Stipules triangular or ovate, 8–30 mm long, gradually tapering into an acute tip or, more rarely, with short awn 1–2 mm long, outer surface densely covered with short erect hairs, inner surface glabrous with row of colleters at the base; yellow or brownish mucus often present on youngest stipule pair (when dried). Inflorescences sessile, 1.5–7 × 3–9 cm, with 15 to numerous flowers; inflorescence parts densely covered with short erect hairs; first order axes 0.3–4 cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted, 2–6 mm long (up to 10 mm long in second order bracts); bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts triangular, 1–2 mm long, tips acute. Flowers sessile to shortly pedicellate, pedicels 0–2 mm long (rarely up to 5 mm long in case of reduction). Calyx densely covered with short erect hairs outside, inner surface densely covered with minute appressed hairs all over but most dense at the base; tube 2–5 mm long; lobes broadly ovate, 0.5–1.5 mm long, often keeled, margins ciliate, tips rounded, obtuse, acute to minutely acuminate. Corolla tube 0.6–1.7 cm long, inner surface moderately to densely covered with long erect hairs in upper half; lobes 5–8 mm long, margins ciliate. Anthers 5–6.5 mm long, completely exserted from corolla tube at anthesis; filaments 1–1.5 mm long. Ovary 1.5–2.5 mm long, longitudinally ribbed (when dried), densely covered with short erect hairs; per locule 4–7 ovules arranged at periphery of placenta attached to middle of septum. Style and stigma 12–34 mm long, exserted for 6–17 mm; style moderately covered with long erect hairs for

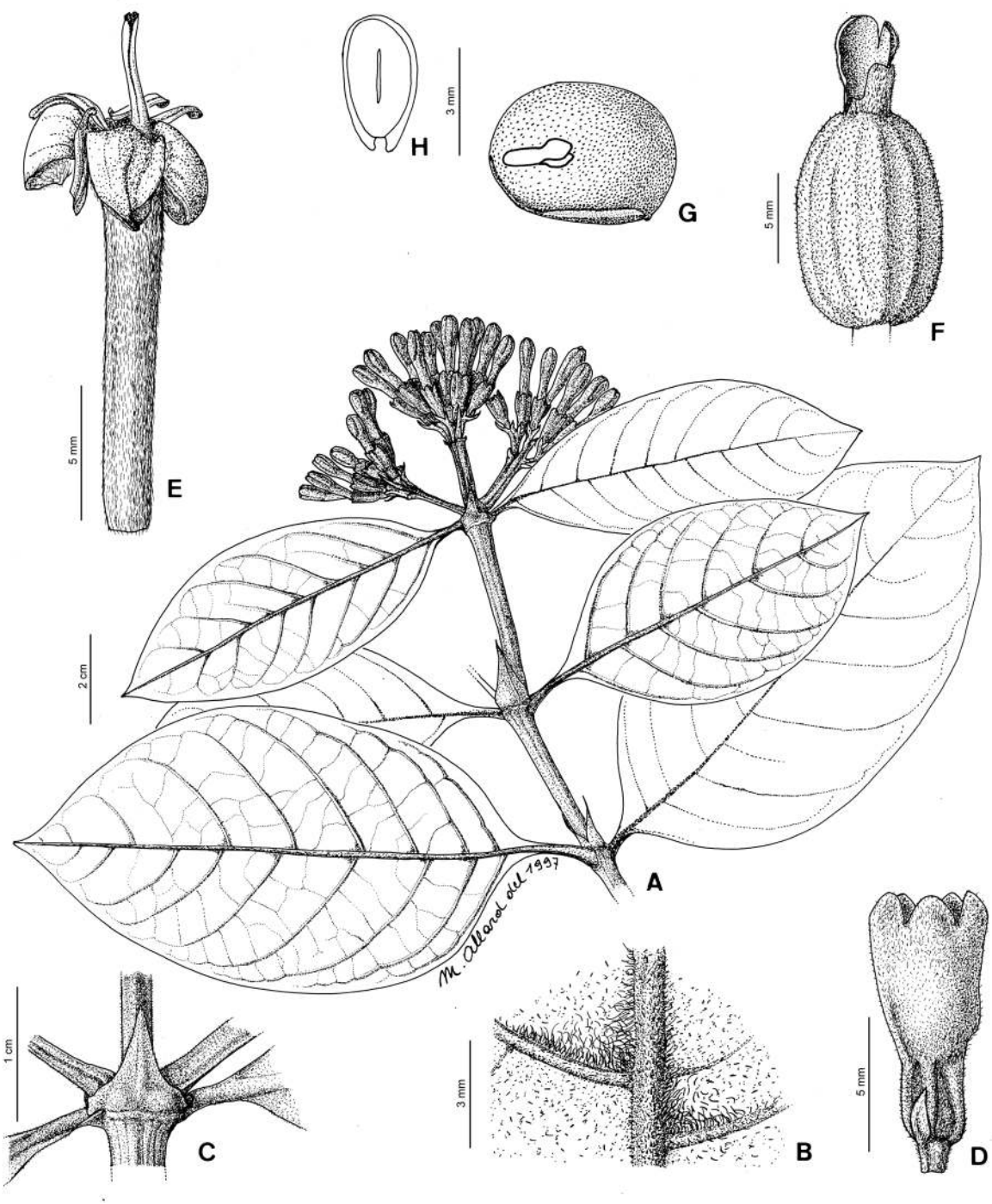

Fig. 19. *Paracephaelis sericea* (Arènes) De Block. **A**. Flowering branch. **B**. Lower leaf surface, showing hair tuft domatia. **C**. First order bracts. **D**. Bracteole, ovary and calyx. **E**. Corolla, stamens, style and stigma. **F**. Fruit. **G**. Seed, position of embryo indicated. **H**. Transverse section through seed, embryonal cavity indicated. Drawn by Ms M. Allard. From *Schatz et al. 3162* (A–D, F–H) and *coll. ignot. 14958-SF* (E).

6–7 mm below papillate zone; stigmatic lobes 7–16 mm long. Fruits ovoid to subspherical, longitudinally ribbed (when dried), 10–12 × 8–11 mm, densely covered with short erect hairs; fruit wall well-developed with multi-layered anastomosing network of sclerified vascular bundles; pyrenes hemi-ovoid, ca 7.5 × 5 mm, thickly crustaceous, with rounded base, shortly acuminate tip, small adaxial opening just above the middle and prominent longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 4–8(–10) per fruit, 4.5–5 mm × 3.5–4 mm.

Distribution

Mostly collected from the Moramanga area, but present along the entire east coast. Present in: Andapa District, Sava Region (Antsiranana Province); Ambatondrazaka, Amparafaravola and Moramanga Districts, Alaotra-Mangoro Region, Mananara Avaratra, Maroantsetra and Vavatenina Districts, Analanjirofo Region, and, Toamasina II and Vatomandry Districts, Atsinanana Region (Toamasina Province); Mananjary District, Vatovavy-Fitovinany Region, Ivohibe District, Ihorombe Region, and, Vondrozo District, Atsimo-Atsinanana Region (Fianarantsoa Province); Taolagnaro District, Anosy Region (Toliara Province); Mandritsara District (eastern part), Sofia Region (Mahajanga Province) (Fig. 23D).

Habitat and phenology

Mid-elevation or lower montane humid forest (500–1450 m a.s.l.), rarely low-elevation humid forest (Toliara: Andohahela: 175–200 m a.s.l.); on laterite soil. Flowers: October–March, flowering peak in February; Fruits: April–December. The single specimen collected from Toliara (Andohahela) flowers in June.

Vernacular names and uses

Most commonly this species is indicated with the names molotrangaka (e.g., *Antilahimena et al. 3173*) or molotrangaka be ravina ("molotrangaka with large leaves", e.g., *coll. ignot. 17946-SF*). Other vernacular names are: afatra (*coll. ignot. 21855-RN*); ampitsikahitra à grandes feuilles (*Louvel 182*); fisatendro (*Thouvenot 122*); halampona (*Rothrock et al. 339*); kisaka (*Andrianaivoravelona et al. 227*); ritsikaludambo (*Botoalma 3724-RN*); sadodoka à grandes feuilles (*Laibosaka 12599-RN*); toalanana(na) (*Abraham 187*, *coll. ignot. 21948-RN*); vandrikala (*Capuron 9040-SF*); vanopotsy (*Laibosaka 10950-RN*); voantalanana (*Ramanantoavina 1963-RN*); voantalanana fotsy (*Ratovoson et al. 679*). The species is used for firewood (*coll. ignot. 14958-SF*, *coll. ignot. 21855-SF*), tool handles (*Ratovoson et al. 679*), and wood for construction (*Abraham 187*, *coll. ignot. 15012-SF*, *coll. ignot. 21948-SF*).

Provisional IUCN assessment

Least Concern: LC. This assessment is based on 68 collections with detailed locality data, collected between 1912 and 2015. The EOO of *P. sericea* is estimated to be 98 231 km^2, far exceeding the upper limit of any threat category under criterion B1. The AOO is 184 km^2, which complies with the Endangered category under criterion B2. The species occurs in ca 20 locations, which far exceeds the upper limit of any threat category under subcriterion 'a' of criterion B2. However, over 20% of the specimens of *P. sericea* were collected at Ambatovy, a location which will disappear within the next thirty years as a result of mining (see *P. pauciflora* sp. nov. for details). This will have a negative effect on the number of locations and the AOO, but not on the EOO. *Paracephaelis sericea* is present in several protected areas, notably the Andasibe-Mantadia, Zahamena, and Andohahela National Parks, the Anjanaharibe-Sud Special Reserve, the Betampona Natural Reserve, the Vohibe Forest New Protected Area, and the Vondrozo Forest Reserve. Throughout Madagascar outside protected areas, clearing of forest continues at a rapid pace (Harper *et al.* 2007). The main causes are subsistence farming, bushfires, and grazing by cattle. Mining also impacts the natural vegetation (Cardiff & Andriamanalina 2007), e.g., graphite mining in Mantadia (https://tirupatigraphite.co.uk/madagascar-projects/), nickel and cobalt mining in Ambatovy (http://www.ambatovy.com). Unfortunately, the protected areas in which *P. sericea* occurs are not spared

from degradation resulting from anthropogenic factors. They suffer from land clearing for subsistence farming, cattle grazing, human settlement (e.g., Zahamena: Hannah & Boltz 2003) or artisanal mining (e.g., Anjanaharibe-Sud: Garreau & Manantsara 2003). Furthermore, logging, production of charcoal, collection of non-timber forest products, and hunting take place (Nicoll & Langrand 1989; Britt *et al.* 2003; Fenn 2003; Garreau & Manantsara 2003; Hannah & Boltz 2003; Rasolofoson *et al.* 2007; Dolch 2008; Rakotoarivelo *et al.* 2015). The remote location of some protected areas, such as Zahamena, Makira, and Anjanaharibe-Sud, and the limited resources for their management are also negative factors. The main threat to *P. sericea* is the destruction of its habitat, notably for subsistence farming and the above-mentioned factors. We therefore infer a reduction in the extent and quality of its habitat. In the future, there will also be a reduction in number of locations (Ambatovy). However, the species has a large EOO and occurs in a high number of locations, some of which have more intact vegetation. Therefore, *P. sericea* is assessed as Least Concern.

Notes

1. Arènes (1960) cited the holotype as "*Perrier 122*". The holotype is in fact a collection made by Thouvenot but donated to the Paris herbarium by Perrier (*Thouvenot in Perrier de la Bâthie 122*). One isotype was donated by Fauchère (*Thouvenot in Fauchère 122*). This last specimen bears a label from the Service de Colonisation listing Ramamantoavolana as collector and a printed label saying "Thouvenot 1919". Another specimen bears only the indication "*Service de Colonisation 122*" (BR). According to Dorr (1997), Thouvenot undertook collecting expeditions for the Service de Colonisation together with Fauchère and Ramamantoavolana.

2. Homolle recognized this species as new and wanted to name it "*Maireana sericea*", but she never finalized the description. Since the name *Maireana* already existed for a genus of the Chenopodiaceae Vent., Arènes (1960) named the new genus for Homolle (*Homolliella*).

3. In his unpublished *Révision des Rubiacées de Madagascar et des Comores*, Capuron (1973: 175) considered *Paracephaelis* to be a section of the genus *Tarenna*. In this section he also placed the type species of *Homolliella* and introduced the combination "*Tarenna sericea*", a combination which was never formally published.

4. The vernacular names molotrangaka or molotrangaka be ravina are also used for *Robbrechtia grandifolia* De Block, another species of Pavetteae characterized by large leaves, stipules and calyces, and which overlaps in distribution and habitat with *P. sericea* (De Block 2003).

5. In some specimens the corolla tubes are slit longitudinally over the whole length at anthesis (e.g., *Antilahimena et al. 4610*).

Paracephaelis seyrigii De Block sp. nov.
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Figs 4H, J, L, O, 20

Diagnosis

Differing from *Paracephaelis saxatilis* by having larger leaves (2–8.5 × 1.5–5 cm vs 1–4 × 0.7–2.8 cm), longer petioles (0.4–1.5 cm vs 0.2–0.5 cm long), larger stipules (sheath 3–7 mm and awn 0–3 mm vs sheath 1–2.5 mm and awn 0.5–1.5 mm long), larger inflorescences (1–3(–6) × 1.5–3(–6) cm vs 0.6–1.5 × 1–2 cm), and longer calyx lobes (1.5–2 mm long in flowering stage, 3–3.5 mm long in fruiting stage vs 0.8–1.5 mm long).

Etymology

The species epithet honours the French collector, André Seyrig, who was a miner and entomologist (Dorr 1997) and collected the type specimen.

Type material

MADAGASCAR – **Toliara Province, Androy Region, Bekily District** • Ampandrandava, entre Bekily et Tsivory; 1000 m a.s.l.; Dec. 1943; fl; *Seyrig 425*; holotype: P; isotype: P, as *coll. ignot.* (*Herbier du Jardin botanique de Tananarive*) *5765*.

Other material studied

MADAGASCAR – **Fianarantsoa Province, Ihorombe Region, Ihosy District** • Plateau de l'Horombe, SW du radin sur l'Ilanana; 17 Dec. 1969; fl; *Capuron 29029-SF*; BR, P • plateaux et vallées de l'Isalo, W de Ranohira; 800–1250 m a.s.l.; 1955; fr; *Humbert 28670*; P • Ranohira, Isalo PN, Analalava; 18 May 2004; fr; *Rakotonasolo & Zachary 783*; K, MO, TAN. – **Toliara Province, Androy Region, Bekily District** • Ampandrandrava, 5 km N of Beraketa; 638 m a.s.l.; 2 Feb. 2006; fr; *Andriamahay & Rakotoarisoa 1298*; K • Ampandrandava; s.dat.; fr; *coll. ignot.* (*Herbier Jardin botanique de Tananarive*) *6439*; P • Ampandrandava, entre Bekily & Tsivory; 1000 m a.s.l.; Apr. 1943; fl; *Seyrig 425B*; P. – **Anosy Region, Betroka District** • PK 65–66, route Ihosy-Betroka; Feb. 1963; fr; *Bosser 17294*; BR, P, TAN • rocailles entre Beraketa et Antanimora; 6 Dec. 1961; fl; *Capuron 20419-SF*; BR, P • road from Beraketa to Betroka, 12 km from Beraketa; 554 m a.s.l.; 9 Feb. 2007; fr; *Groeninckx, De Block & Rakotonasolo 237*; BR, G, K, MO, P, TAN, TEF, UPS • Betroka, 7 km S of Ianabinda; 790 m a.s.l.; 19 Dec. 2004; fl; *Rakotonasolo, Hoffmann, Rakotoarisoa & Ralimanana 933*; BR, K, MO, P, TAN. – **Atsimo-Andrefana Region, Sakaraha District** • Zombitse-Isoky PN, Zombitse; 612 m a.s.l.; 1 Feb. 2007; fl; *Groeninckx, Rakotonasolo & De Block 175*; BR, G, MO, P, TAN • Zombitse-Vohibasia PN, Isako, W part of Isoky; 4 Dec. 2003; fl; *Razafimandimbison & Bremer 498*; UPS. – **Toliary II District** • N d'Andranohinaly, PK 43 de la route Tulear-Sakaraha; 12 Dec. 1962; fl; *Capuron 22276-SF*; BR, P. – **Without locality** • s.dat.; fr; *Homolle 1610*; P.

Description

Shrub or small tree, to 4 m tall; pubescence tawny or, more rarely, whitish. Young shoots pale brown, densely covered with long, appressed or spreading hairs; older branches greyish or brown, glabrous. Leaves grouped at the end of lateral branchlets. Petioles 0.4–1.5 cm long, densely covered with long, erect or spreading hairs. Leaf blades ovate or elliptic, rarely broadly ovate, broadly elliptic or orbiculate, (2–)2.5–8.5 × 1.5–5 cm, thickly coriaceous, drying brown or greenish brown above and somewhat paler below, upper surface densely covered with short to ± long, erect hairs (hairs often somewhat longer and spreading on midrib and secondary veins), lower surface densely covered with long, erect hairs (hairs often more appressed on midrib and secondary veins); base acute, truncate, rounded or somewhat cordate; tip obtuse, acute or broadly acuminate, often mucronate; domatia absent; 5–9 secondary veins on each side of midrib, impressed above, raised below; higher order venation somewhat impressed above, somewhat raised below. Stipules caducous, triangular, keeled, gradually tapering into an obtuse or acute tip or, more rarely, with short needle-like awn; outer surface of youngest stipule pairs densely covered with long appressed or spreading hairs; inner surface glabrous with row of colleters interspaced with long hairs at the base; sheath 3–7 mm long; awn, if present, up to 3 mm long. Inflorescences terminal on short lateral shoots with short internodes and leaves fallen but stipules or stipular remnants remaining, sessile, compact or partial inflorescences compact, 1–3(–6) × 1.5–3(–6) cm, with 15 to numerous flowers; inflorescence parts densely covered with long, spreading or erect hairs; first order axes 0.3–2(–4) cm long; higher order bracts with stipular parts reduced or absent, foliar parts narrowly triangular and vaulted or trilobed, 0.5–1 cm long; bracteoles at base of ovary, opposite, stipular parts absent, foliar parts narrowly triangular, 1.5–2.5 mm long, tips acute. Flowers sessile. Calyx densely covered with ± long, erect or

spreading hairs outside, inner surface densely covered with long appressed hairs; tube 0.5–1 mm long; lobes triangular, 1.5–2 mm long in flowering stage, 3–3.5 mm long in fruiting stage, tips acuminate, acute or obtuse. Corolla tube 5–7 mm long, inner surface densely covered with long erect hairs in upper ⅔; lobes 4–5.5 mm long. Anthers 4–5 mm long, completely exserted or basal part (ca 1 mm long) included in corolla tube at anthesis; filaments 0.5–1 mm long. Ovary 1.5–2 mm long, densely covered with long, erect or spreading hairs; per locule (1–)4–8 ovules arranged at periphery of placenta attached to upper half of septum. Style and stigma 10–15 mm long, exserted for 5–7 mm; style densely covered with long upwardly directed hairs from ca 3 mm above base to just below papillate zone; stigmatic lobes 6–7 mm long, upper part fusiform; papillae absent along fusiform part, present lower down in longitudinal grooves. Fruits spherical, 5–7 mm in diameter, faintly ridged longitudinally and glossy when dried, densely covered with ± long erect hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemi-ovoid, ca 6 × 4 mm, membranous adaxially, crustaceous abaxially, with rounded tip and base, small adaxial opening somewhat above the middle and faint longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds (2–)4–8 per fruit, 2–4 × 1.5–3 mm.

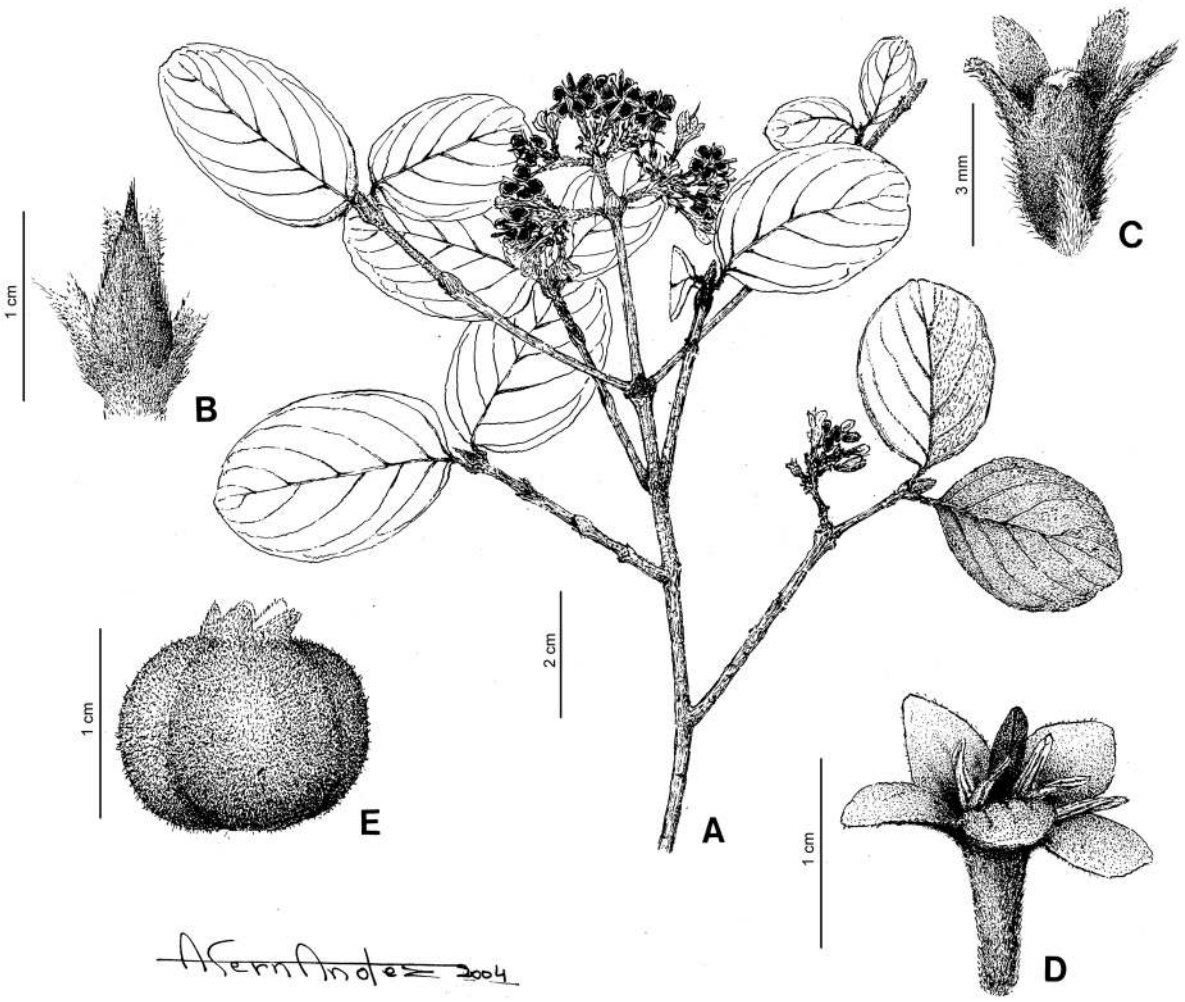

Fig. 20. P*aracephaelis seyrigii* De Block sp. nov. **A**. Flowering branch. **B**. Stipule. **C**. Bracteole, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *Seyrig 425* (A, C–D), *coll. ignot. 5765* (B) and *Bosser 17294* (E).

Distribution

Restricted to southern Madagascar from Ihosy in the north and east to Toliara in the west and Beraketa in the south. Present in: Ihosy District, Ihorombe Region (Fianarantsoa Province); Bekily District, Androy Region, Betroka District, Anosy Region, and, Sakaraha and Toliary II Districts, Atsimo-Andrefana Region (Toliara Province) (Fig. 23C).

Habitat and phenology

Deciduous and semi-deciduous dry forest; on sandy soil or rocky substrate; elev. 550–1250 m. Flowers: December–January, one collection reported flowering in April (*Seyrig 425B*); Fruits: February–May.

Vernacular uses

Edible fruits (*Homolle 1610*); vermifuge (*Homolle 1610*).

Provisional IUCN assessment

Vulnerable: VU B2ab(iii). This assessment is based on 15 collections with detailed locality data, collected between 1943 and 2007. The EOO of *P. seyrigii* sp. nov. is estimated to be 24 441 km^2, exceeding the upper limit of the Vulnerable category under criterion B1. The AOO is 44 km^2, which complies with the Endangered category under criterion B2. The species occurs in 8 locations, which complies with the Vulnerable category under subcriterion 'a' of criterion B2. *Paracephaelis seyrigii* sp. nov. is present in the Isalo and Zombitse-Vohibasia National Parks. Both parks are threatened by yearly bushfires, penetrating forested or woody areas, resulting in an impoverishment of the natural vegetation and limited regeneration. Local populations enter the parks to extract construction and firewood. Charcoal is illegally produced in Zombitse. Areas are deforested for subsistence agriculture. Hunting and gathering of non-timber forest products, e.g., honey, is common (BirdLife International 2020d, 2020e; Nicoll & Langrand 1989). Sapphire mining is becoming a problem in Isalo (BirdLife International 2020e). These threats are even more important outside the protected areas. Therefore, a reduction in the extent and quality of the habitat of *P. seyrigii* sp. nov. is inferred. This fact, in combination with the low AOO and the low number of locations, qualifies the species for Vulnerable status.

Notes

1. *Paracephaelis seyrigii* sp. nov. is similar to *P. saxatilis* but more robust in most of its characters: e.g., larger leaves, longer petioles, larger inflorescences, longer calyx lobes. The distribution of the two species does not overlap. The distribution area of *P. seyrigii* sp. nov. lies to the west and north of that of *P. saxatilis*.

2. Leroy distinguished *P. seyrigii* sp. nov. as a distinct species of *Paracephaelis* under the name "*Paracephaelis recurva*". He annotated several specimens in the P herbarium, e.g., *Seyrig 425* and *425B*, *Homolle 1610*, *Humbert 28670*, *coll. ignot. 6439* and *5765*, but never formally published the name.

Paracephaelis tiliacea Baill.
Figs 1H, 2A, A', B, 21

Adansonia 12: 316 (Baillon 1879); *Histoire des Plantes* 7: 496 (Baillon 1880); *Notulae Systematicae* 16: 9, pl. 1, 1–7 (Arènes 1960). **Type:** MADAGASCAR – **Mahajanga Province, Boeny Region, Soalala District** • Ambongo; 14 Feb. 1841; fr; *Pervillé 633*; holotype: P[P00274300]; isotypes: K, P[P00115282], P[P00274301].

Other material studied

MADAGASCAR – **Mahajanga Province, Boeny Region, Soalala District** • Ambongo; Jan. 1906; fr; *d'Alleizette 1472*; P. – **Mahajanga I District** • Majunga, dunes; Jan. 1921; *Perrier de la Bâthie 13452*; K, L, P. – **Melaky Region, Antsalova District** • forêt de Tsimembo, E d'Ambereny (Antsalova); 29–31 Mar. 1966; fr; *Capuron 24573-SF*; BR, P, TEF. – **Toliara Province, Menabe Region, Morondava District** • forêt de Marosalaza, 50 km N de Morondava; 0 m a.s.l.; 28 May 1974; fr; *Abraham 88*, part A; BR, P • Kirindi forest, along RN 8 to Belo-Tsiribihina; 64 m a.s.l.; 21 Feb. 2018; fl; *Atalahy, Razafindrahaja, Swenson & Razafimandimbison 111*; BR n.v., MO n.v., P online, S n.v., TAN n.v. • forêt de Kirindi (forêt d'Andalandahalo), Pandanus walk, by the river Kirindry, 45 km NE of Morondava; 20 m a.s.l.; 21 Feb. 2000; fr; *Davis, Rakotonasolo & Wilkin 2580*; BR, K, P, TAN • between Marofadilia and Tsimafana, on road to Belo, ca 68.5 km (GPS) NE of Morondava; 5 m a.s.l.; 22 Feb. 2000; fl; *Davis, Rakotonasolo & Wilkin 2585*; BR, K, P, TAN • Kirindi forest, N part, piste vers le point de vue km 7; 89 m a.s.l.; 19 Jan. 2007; fl; *De Block, Rakotonasolo, Groeninckx & Dessein 2172*; BR, K, MO, P, TAN • Lamboukily, 14 km of basement camp in Kirindi; 30 m a.s.l.; 20 Jan. 2007; fl; *Groeninckx, Rakotonasolo, Dessein & De Block 113*; BR, G, MO, P, TAN • commune Bemanonga, Andranomena Reserve; 18 Mar. 2011; fr; *Kainulainen, Razafimandimbison, Razafindraibe & Wikström 167*; BR, S.

Description

Shrub, 2–5 m tall, or small tree, 5–6 m tall, dbh 2–10 cm; *Terminalia*-branching pattern; pubescence reddish brown, tawny or whitish. Young shoots brown or reddish brown (because of pubescence), densely covered with long erect hairs; older branches greyish or greyish brown, glabrous. Leaves clustered at the end of long and short shoots, probably deciduous. Petioles 1–3 cm long, densely covered with long erect hairs. Leaf blades broadly elliptic or broadly ovate, often orbiculate, 7–20 × 5–15 cm, papyraceous to subcoriaceous, drying brown or greenish brown above and somewhat paler below, upper surface moderately to densely covered with short erect hairs (hairs denser and somewhat longer on midrib and secondary veins), lower surface densely covered with long erect hairs; base strongly cordate, cordate or unequally truncate; tip shortly acuminate, acumen 2–10 mm long; domatia absent; 5–8 secondary veins on each side of midrib, impressed above, prominently raised below; higher order venation visible or inconspicuous above, visible below. Stipules caducous, triangular with short needle-like awn, keeled; outer surface of youngest stipule pairs densely covered with long erect hairs, inner surface glabrous with row of colleters interspaced with long hairs at the base; sheath 4–7 mm long; awn 0.5–2 mm long. Inflorescences terminal on short lateral shoots with leaves fallen, later becoming pseudo-axillary, sessile, compact, 1–7 × 2–7 cm, with numerous flowers; inflorescence parts densely covered with long erect hairs; first order axes 0.5–1.5 cm long; second order bracts with stipular parts broadly triangular, up to 4 mm high, and foliar parts trilobed, consisting of a basal sheath 1–1.5 mm long, topped by triangular lobes, central lobe 4–8 mm long, lateral lobes 1–2 mm long; higher order bracts with stipular parts reduced or absent, foliar parts triangular and vaulted, 3–4 mm long, or trilobed with central lobe up to 4 mm long; bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts narrowly triangular, 2–3 mm long, tips acute. Flowers sessile or shortly pedicellate, pedicels 0–2 mm long. Calyx densely covered with ± long erect hairs outside, inner surface densely covered with long appressed hairs; tube 0.5–0.7 mm long; lobes triangular, (1.5–)2–3.5 mm long, tips acute. Corolla tube 7–9 mm long, inner surface sparsely covered with appressed hairs over entire length; lobes 4.5–5 mm long. Anthers ca 5 mm long, basal part (ca 1 mm long) often included in corolla tube at anthesis; filaments ca 0.5 mm long. Ovary 2–3 mm long, densely covered with ± long erect hairs; per locule 4–10 ovules arranged at periphery of placenta attached to upper half of septum, rarely with some ovules on abaxial surface of placenta. Style and stigma 14–18 mm long, exserted for 5–8 mm; style moderately covered with long upwardly directed hairs from ca 3.5 mm from base to just below papillate zone; stigmatic lobes 7–9 mm long. Fruits ovoid, faintly ribbed longitudinally (when dried), ca 7 × 5 mm, densely covered with ± long erect hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemi-ovoid, ca 5 × 3 mm, crustaceous, with rounded

base, acute tip, small adaxial opening somewhat above the middle and longitudinal central ridge running from the apex to the top of the adaxial opening and continuing into a longitudinal depression below it. Seeds 1–2(–6) per fruit, 3–3.5 × 2.7–3 mm.

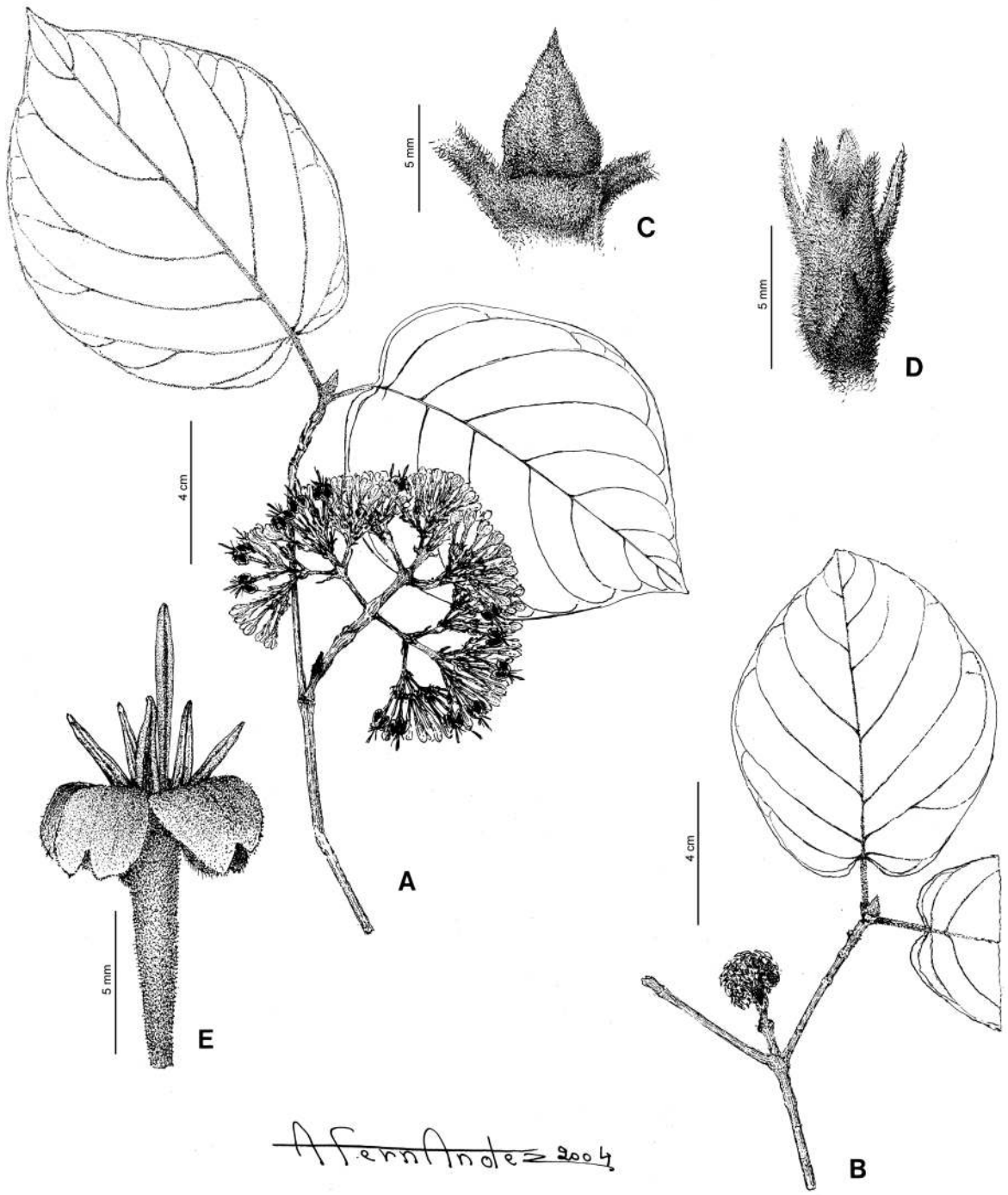

Fig. 21. *Paracephaelis tiliacea* Baill. **A**. Flowering branch. **B**. Branch bearing young infructescence. **C**. Stipule. **D**. Bracteole, ovary and calyx. **E**. Corolla, stamens, style and stigma. Drawn by Mr A. Fernandez. From *Davis et al. 2585* (A, C–E) and *Pervillé 633* (B).

Distribution

Restricted to western Madagascar. Recent material is only known from the region of Kirindy Forest in Morondava. Present in: Soalala and Mahajanga I Districts, Boeny Region, and Antsalova District, Melaky Region (Mahajanga Province); Morondava District, Menabe Region (Toliara Province) (Fig. 23D).

Habitat and phenology

Low-elevation dry deciduous forest; on white sand or laterite; elev. 0–650 m. Flowers: January–February; Fruits: February–May.

Vernacular name

Papolany (*Abraham 88*).

Provisional IUCN assessment

Endangered: EN B2ab(iii). This assessment is based on 11 collections with detailed locality data, collected between 1841 and 2018. Using GeoCAT, the EOO of *P. tilia* is estimated to be 39 353 km^2, far exceeding the upper limit of any threat category under criterion B1. However, this seems to be an overestimation since it includes a large inland region, whereas *P. tiliacea* typically occurs less than 50 km from the coast. The AOO is 36 km^2, which complies with the Endangered category under criterion B2. The species occurs in 4 locations, which complies with the Endangered category under subcriterion 'a' of criterion B2. Most specimens are collected from the Menabe-Antimena Protected Area, and more specifically from Kirindi Forest (1 location). A second location is in the protected area of Tsimembo Manambolomaty. From the other two locations (Majunga and Ambongo), no specimens were collected after 1921. The dry deciduous forests in western Madagascar are being destroyed at a more rapid pace than any other Malagasy forest type (Moat & Smith 2007). Clearing for subsistence farming, bushfires, and logging for wood and for the production of charcoal are the main threats (Moat & Smith 2007). These threats also affect the two protected areas, Menabe-Antimena and Tsimembo Manambolomaty (Filou 2019; BirdLife International 2020c). Another important factor in the Menabe-Antimena Protected Area is the clearance of forest for the production of the cash crop corn. Rates of deforestation in the region are unprecedented with predictions that more than 80% of the forest in the Menabe-Antimena region could be cleared by 2025 (Vieilledent 2016; Filou 2019; Hudson *et al.* 2020). The main threat to *P. tiliacea* is the destruction of its habitat for the above-mentioned factors and a reduction in the extent and quality of its habitat is inferred. This, in combination with the low AOO and the low number of locations, qualifies the species for Endangered status.

Note

Fruit and seed characters are based on a single fruiting specimen, *Abraham 88*, from which two immature fruits were studied. In one fruit, each of the two pyrenes enclosed a single developing seed and several aborted ones, resulting in two potentially viable seeds. In the other fruit, the two pyrenes developed, but one of these only contained aborted seeds, resulting in a single viable seed. It is presumed here that more seeds can develop within a single fruit. The fruit size given is the size of the boiled immature fruits.

Paracephaelis trichantha (Baker) De Block
Fig. 22

*Systematics and Geography of Plant*s 73: 100 (De Block 2003); *Flora Zambesiaca, Rubiaceae, Part 3*: 619, tab. 122 (Bridson 2003); *Trees & Shrubs Mozambique*: 1015 (Burrows *et al.* 2018).

Basionym

Pavetta trichantha Baker, *Bulletin of Miscellaneous Information, Kew* 1894 (89): 148 (Baker 1894); *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 21: 91 (Schinz 1897); *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 26: 552 (Voeltzkow 1902); *Bulletin of Miscellaneous Information, Kew* 1919 (3): 123 (Hemsley 1919). **Type**: SEYCHELLES – **Aldabra islands** • s.loc.; Oct.–Dec. 1892; fl, fr; *Abbott s.n.*; lectotype: K, **here designated**; isolectotypes: P[P00885879], US[US00138555].

Homotypic synonym

Tarenna trichantha (Baker) Bremek., *Repertorium Novarum Specierum Regni Vegetabilis* 37: 207 (Bremekamp 1934); *Philosophical Transactions of the Royal Society, Biological Sciences* 260: 218, 225 (Fosberg 1971); *Philosophical Transactions of the Royal Society, Biological Sciences* 260: 231 (Renvoize 1971); *Phytologia* 41: 355 (Fosberg 1979); *Kew Bulletin* 34: 401, figs. 2F, 3V–W (Bridson 1979); *The Flora of Aldabra and Neighbouring Islands*: 161 (Fosberg & Renvoize 1980); *Bulletin du Jardin botanique national de Belgique* 55: 102, figs 7–9 (Bridson & Robbrecht 1985); *Flora of Tropical East Africa, Rubiaceae, Part 2*: 602 (Bridson 1988); *Kenya Trees, Shrubs and Lianas*: 547 (Beentje 1994); *Flora des Seychelles: Dicotyledones*: 604, pl. 194 (Friedmann 1994).

Other material studied

SEYCHELLES – **Aldabra Atoll** • s.loc.; pubescent form; 1892; fl, fr; *Abbott s.n.*; K, P • s.loc.; pubescent form; 28 Dec. 1906; fl; *Dupont 87*; K • s.loc. (from living material at Conservatoire et Jardins botaniques de Nancy); 23 Oct. 1996; st; *Friedmann 833385*; UPS • s.loc.; pubescent form; 1909; fl; *Fryer 86*; K • s.loc.; glabrous form; 1973; fl; *Hnatiuk 732022*; US online • Anse Grande; pubescent form; 2 Mar. 1973; fr; *Hnatiuk 732026*; US online. – **Grande Terre (South Island)** • Cinq Cases; glabrous form; 18 Jan. 1968; fl; *Fosberg & Grubb 48885*; US online • SE of Cinq Cages camp, 300–500 m from coast; glabrous form; 18 Jan. 1968; fl; *Fosberg 48911*; MO, US online • just SE of Cinq Cases camp, 200–500 m back of coast; glabrous form; 19 Jan. 1968; fl; *Fosberg 48921*; MO, US online • ibid.; glabrous form; 19 Jan. 1968; fl; *Fosberg 48924*; MO, US online • just ENE of Cinq Cases camp; glabrous form; 23 Jan. 1968; fl; *Fosberg 49023*; US online • point Hodoul; glabrous form; 25 Jan. 1968; st; *Fosberg 49048*; US online • 5 km W of point Hodoul; glabrous form; 4 Feb. 1968; fl; *Fosberg 49209*; MO, US online • 3.5 km W of point Hodoul; glabrous form; 4 Feb. 1968; st; *Fosberg 49210*; US online • SE coast, 0.6 km E du bord de la mer Takamaka; glabrous form; 7 Feb. 1968; fl; *Fosberg 49246*; MO, US online • Takamaka area; glabrous form; 7 Feb. 1968; fl, fr; *Fosberg 49249*; US online • Takamaka well; glabrous form; 8 Feb. 1968; fr; *Fosberg 49259*; MO, US online • Takamaka well; glabrous form; 12 Feb. 1968; fl; *Fosberg 49346*; MO, US online • S of Takamaka grove; glabrous form; 16 Feb. 1968; fl; *Fosberg 49383*; MO, US online • dune Jean-Louis, landwards of dunes; glabrous form; 18 Feb. 1968; fl, fr; *Fosberg 49387*; MO, US online • ibid.; glabrous form; 18 Feb. 1968; fl; *Fosberg 49388*; MO, US online • N de Anse Mais; glabrous form; May 1983; fl; *Friedmann 4550*; P • environs de la dune Jean-Louis; glabrous form; May 1983; fl; *Friedmann 4733*; P • vicinity of dune Jean-Louis; glabrous form; 3 Mar. 1974; fl; *Hnatiuk 731506*; US online • Takamaka grove; glabrous form; 8 Aug. 1974; fr; *Hnatiuk 731706*; US online • near Willson's well; glabrous form; 19 Sep. 1974; fr; *Hnatiuk 731899*; US online • near Takamaka grove; glabrous form; 25 Mar. 1974; fl; *Hnatiuk 732054*; US online • Takamaka grove; glabrous form; 20 Aug. 1973; fr; *Merton 7047*; K • along trail from hut at dune de Messe to lagoon; glabrous form; 12 Aug. 1992; fr; *Potter & Harrington 920812-08-01*; P online • SE coast, 0.6 km E du bord de la mer, Takamaka area; glabrous form; 30 Jan. 1968; fl; *Renvoize 873*; K, US online • Cinq Cases dune; glabrous form; 3 Feb. 1968; fr; *Renvoize 914*; BR, K, L, LISC, P, US online • Cinq Cases dune, 50 yards NE of dune; glabrous form; 3 Feb. 1968; fl; *Renvoize 915*; K, P, US online • near coast, 0.4 km N of point Hodoul; glabrous form; 10 Feb. 1968; fl; *Renvoize 1006*; BR, K, L, LISC, P, US online • S of Takamaka; glabrous form; 24 Feb. 1968; fl; *Renvoize 1117*; BR, K, L, LISC, P, UPS, WAG • near dune Jean-Louis; glabrous form;

14 Mar. 1968; fr; *Renvoize 1308*; BR, K, L, LISC, P, US online • dune de Messe; glabrous form; 22 Mar. 1968; fr; *Renvoize 1394*; K • Trou Nenez; glabrous form; 20 Aug. 1967; fr; *Stoddart 976*; K, P, US online. – **Euphrates (Esprit Island)** • near W end of island; pubescent form; 13 Jan. 1968; fl; *Fosberg 48770*; MO, US online • s.loc.; glabrous form; Jun. 1983; fl; *Friedmann 4823*; P. – **Michael (Michel Island)** • s.loc; pubescent form; 15 Feb. 1968; fl; *Fosberg 49352*; MO, US online • s.loc.; pubescent form; 15 Feb. 1968; fr; *Fosberg 49355*; MO, US online • around coconut / *Casuarina* grove; pubescent form; 15 Feb. 1968; fl; *Renvoize 1045*; BR, K, L, LISC, P, US online. – **Picard (West Island)** • près bassin Lubines; pubescent form; May 1983; fr; *Friedmann 4548*; P • along back path; pubescent form; Jan. 1974; fl; *Hnatiuk 731508*; US online • path to bassin Cabri; pubescent form; 8 Aug. 1973; fr; *Merton 7018*; K • along back path; pubescent form; 11 Feb. 1992; fl; *Potter & Harrington 920211-08*; P online • behind settlement; pubescent form; 12 Jan. 1968; fl; *Renvoize 739*; BR, K, L, LISC, P, US online • bassin Cabri; pubescent form; 15 Mar. 1972; fl; *Wood 1664*; US online. – **Malabar (Middle Island)** • E end of island; pubescent form; 27 Jan. 1968; fl; *Fosberg 49073*; MO, US online • près camp Gionnet; pubescent form; 1983; st; *Friedmann 4705*; P • N of dune Blanc; glabrous form; s.dat.; fl; *Hnatiuk 731504*; US online • s.loc.; glabrous form; 27 Jul. 1973; fl; *Hnatiuk 732028*; US online • s.loc.; pubescent form; 10 Jun. 1992; fr; *Potter & Harrington 920610-01*; P online • SW corner, W of passe Houareau, along lagoon trail coccid transect; pubescent form; 13 Sep. 1992; fr; *Potter & Harrington 920913-05*; P online • 250 m W of middle camp; pubescent form; 19 Jan. 1972; fl; *Wood 1636*; K, US online. – **Polymnie Island** • s.loc.; pubescent form; 21 Mar. 1974; fl; *Hnatiuk 731314*; US online • NW corner of island on ridge ca 200 m E of grande passe and 30 m S from edge of sea cliff along northern edge of island; pubescent form; 7 Jul. 1992; fr; *Potter & Harrington 920707-07*; P online. – **Cosmoledo Atoll** • s.loc.; glabrous form; s.dat.; *Dupont 279*; K. – **Astove Island** • Grand Anse; pubescent form; 5 Mar. 1968; fr; *Fosberg 49720*; MO, US online • behind coconut grove N of settlement; pubescent form; 5 Mar. 1968; fr; *Renvoize 1204*; BR, K, L, LISC, P, US online • s.loc.; pubescent form; 5 Nov. 1968; fl; *Ridgway 92*; US online. – **Assumption Island** • s.loc.; glabrous form; Jul. 1910; fr; *Dupont 116*; K • centre of W coast, along tractor path; glabrous form; 9 May 1973; fl; *Frazier 608*; US online • 200 m inland of south settlement; pubescent form; 29 Nov. 1973; fl; *Frazier 716*; US online • centre of island; pubescent form; 30 Nov. 1973; fl; *Frazier 747*; US online.

African mainland

KENYA – **K7** • Lamu district, Kitwa Pembe hill; 0–50 m a.s.l.; glabrous form; 15–16 Jul. 1974; fr; *Faden R.B. & A.J. 74/1104*; K, WAG • Tana river, Shekiko; 5 m a.s.l.; pubescent form; 21 Aug. 1988; fr; *Luke & Robertson 1376*; EA, K • Lamu district, Ras Tenewi; 20 m a.s.l.; glabrous form; 22 Nov. 1988; fr; *Luke & Robertson 1436*; EA, K • Lamu district, Kiwayu, KWS/WWF Camp; 20 m a.s.l.; glabrous form; 18 Nov. 1998; fl; *Luke 5483*; K • Lamu district, Pate Island; pubescent form; Jul.–Aug. 1980; fl; *Marquis s.n.*; K • N coast, Kijini conservancy (02° S, 40° E); glabrous form; 10 Nov. 2006; fr; *Dowsett-Lemaire 2034*; BR.

MOZAMBIQUE • Tecomaze Island; glabrous form; 29 Mar. 1961; fl; *Gomes e Sousa 4673*; COI, K, PRE n.v. • Nampula, Mossuril district, Matibane, entre a floresta de Crucsee (Cruce) e a Praia; pubescent form; 20 Feb. 1984; fl; *Groenendijk, De Koning & Dungo 1188*; K, MO, WAG.

TANZANIA – **T6** • Uzaramo district, Wazo hill, ca 25 km NNW of Dar es Salaam; 75 m a.s.l.; pubescent form; 3 Aug. 1969; fr; *Harris & Tadros 3038*; BR, K • Pwani, Bagamoyo district, Kiono Forest Reserve; glabrous form; 25 Aug. 1989; st; *Rulangarana, Mbago & Suleiman 267*; WAG.

Description

Shrub or small tree, to 4 m tall; pubescence white. Young shoots brown or dark brown, moderately to densely covered with short appressed or spreading hairs or glabrous except in the region of the nodes (there moderately or sparsely covered with short appressed hairs); older branches corky, glabrous, pale brown, greyish brown, brown or fawn, flaking. Petioles 7–22 mm long, moderately to sparsely covered with ± long appressed hairs. Leaf blades obovate, elliptic, somewhat ovate or rarely suborbicular, (2.5–)3.5–

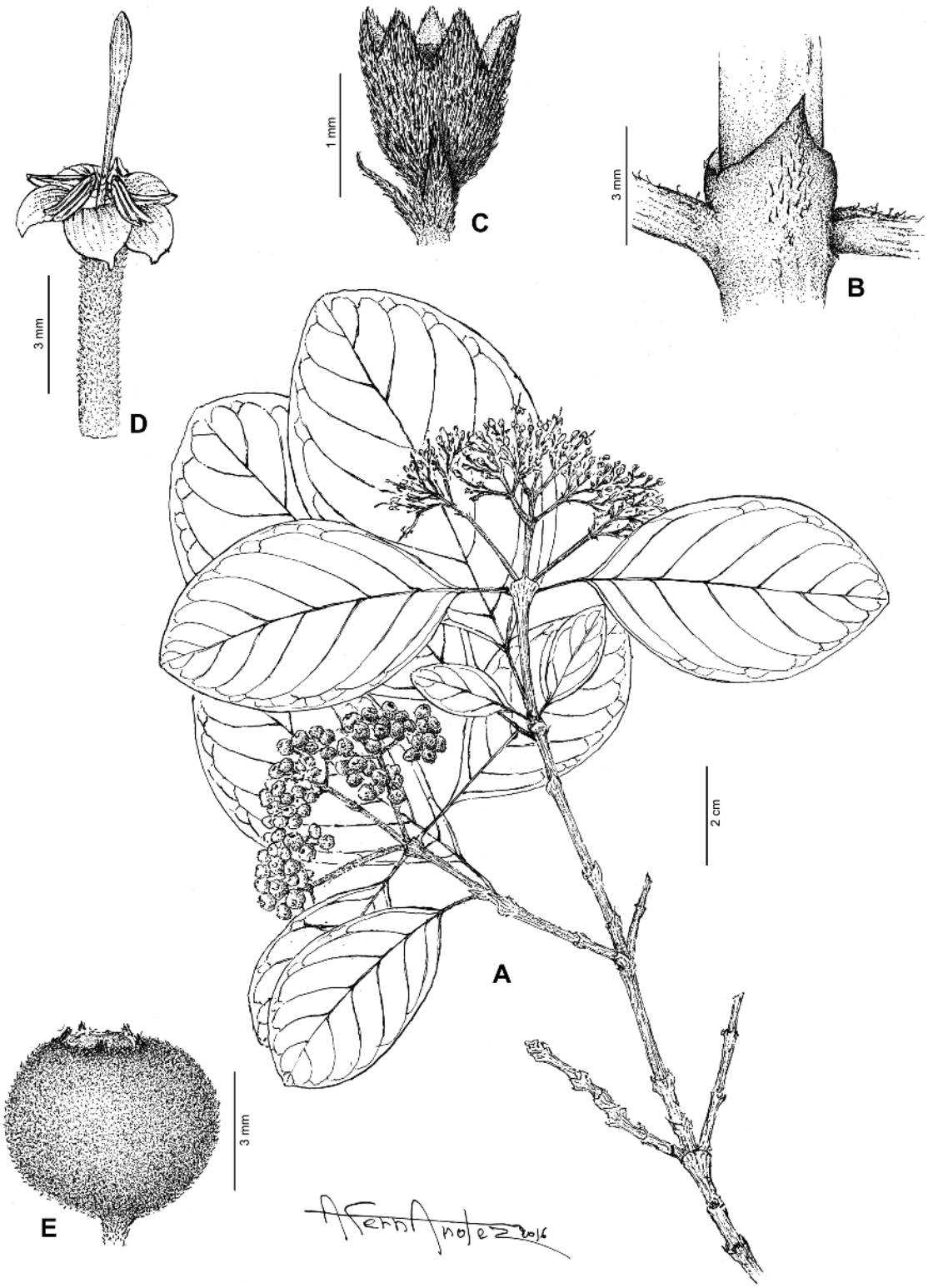

Fig. 22. *Paracephaelis trichantha* (Baker) De Block. **A**. Flowering branch. **B**. Stipule. **C**. Bract, bracteole, ovary and calyx. **D**. Corolla, stamens, style and stigma. **E**. Fruit. Drawn by Mr A. Fernandez. From *Fosberg 49387* (A), *Fosberg 49259* (B), *Renvoize 1006* (C–D) and *Renvoize 1308* (E).

13 × 2.5–8 cm, coriaceous, drying brown and not discolorous, upper surface glossy, moderately to densely covered with short erect hairs (appressed hairs in young leaves), glabrous or with pubescence restricted to midrib, secondary veins and margin, lower surface densely to moderately covered with long erect hairs or glabrous except for midrib and secondary veins; margin sparsely ciliate; base cuneate, obtuse or rarely rounded; tip rounded or obtuse and mucronate, or, retuse; hair tuft or ciliate pit domatia often present; midrib moderately to sparsely covered with long appressed hairs or glabrous above, sparsely to densely covered with long appressed hairs below; 6–10 secondary veins on each side of midrib, usually glabrous but rarely with sparse appressed hairs above, somewhat raised and moderately to sparsely covered with ± long appressed hairs below; in case of glabrous leaves, higher order venation conspicuous below because of paler colour, glabrous above, glabrous or very sparsely covered with ± long appressed hairs below. Stipules triangular with needle-like awn, outer surface moderately to sparsely covered with short appressed hairs, or, more often, pubescence restricted to the base and the region of the midrib, inner surface glabrous with row of colleters interspaced with long hairs at the base; sheath 1.5–3 mm long; awn 0.5–2 mm long. Inflorescences sessile, 1.5–7 × 1.5–11 cm, with numerous flowers; inflorescence parts densely covered with ± long appressed or somewhat spreading hairs; first order axes 0.3–3.5 cm long; higher order bracts with stipular parts absent and foliar parts linear, 0.75–2 mm long (up to 4 mm long in second order bracts); bracteoles on pedicel just below ovary, opposite, stipular parts absent, foliar parts linear, 0.5–0.75 mm long, tips acute. Flowers sessile or shortly pedicellate, pedicels 0–2 mm long. Calyx densely covered with short appressed hairs outside; tube ca 0.2 mm long, inner surface with ring of long appressed hairs; lobes triangular, 0.25–0.5 mm long, inner surface sparsely covered with appressed hairs, tips obtuse. Corolla tube 3.5–5.5(–6) mm long, inner surface moderately covered with long erect hairs in upper half; lobes 1.2–2 mm long. Anthers 1.5–2 mm long, completely exserted from corolla tube at anthesis (spreading on top of corolla lobes); filaments 0.1–0.2 mm long; connective often drying reddish brown. Ovary 0.75–1 mm long, densely covered with short appressed hairs; per locule 1–3 ovules pendulous from small placenta attached to upper half of septum. Style and stigma 6.5–11 mm long, exserted for 3–5 mm; style densely covered with long erect hairs from ca 2 mm above base to ca 2 mm below papillate zone; stigmatic lobes 2.5–3 mm long, upper 1.5–2 mm fusiform; papillate grooves running along fusiform part and further down for ca 1 mm. Fruits 0.3–0.4 × 0.4–0.5 cm, wrinkled when dried, moderately to densely covered with short appressed hairs; fruit wall thin, with sclerified vascular bundles; pyrenes hemispherical, ca 3 mm in diam., parenchymatous adaxially, thinly crustaceous abaxially, with rounded base, truncate tip, and small adaxial opening somewhat above the middle. Seeds (1–)2–4 per fruit, 2–3.5 × 1.5–2.5 mm.

Distribution

Occurring on the African mainland along the coast in Kenya, Tanzania, and Mozambique as well as on the islands of the Aldabra group (Outer Islands of the Seychelles), notably on Assumption Island, Cosmoledo Atoll, Astove Island, and Aldabra Atoll (islands Grande Terre, Malabar, Picard, Euphrates, Michael, Polymnie) (Fig. 25).

Habitat and phenology

Thicket, mixed open and closed scrub; on limestone (outcrops and coral champignons), more rarely on sand; elev. 0–650 m. Flowers: November–February(–July); Fruits: February–December. Most specimens flower in January and February. Anthetic flowers were also collected in November (4 specs), March (5 specs), May (3 specs); June (1 spec.), and July (2 specs).

Provisional IUCN assessment

Vulnerable: VU B2ab(iii). This assessment is based on 74 collections with detailed locality data, out of 81 collected between 1892 and 2006. The EOO of *P. trichantha* cannot be estimated using GeoCAT since the species is coastal and most of the EOO calculated automatically is part of the Mozambique

Channel. The EOO is estimated to be 3680 km^2 and comprises the combined surface area of the Aldabra Atoll, Assumption Island, Astove Island, and the Lamu Archipelago (ca 180 km^2) as well as a 2 km wide strip along the east coast of Africa from 2° to 15° S (3500 km^2). This EOO complies with the Endangered category under criterion B1. The AOO is 136 km^2, which also complies with the Endangered category under criterion B2. The species occurs in 10 locations (the different islands of the Aldabra and Astove Atolls are counted as single locations), which is the upper limit for the Vulnerable category under subcriterion 'a' of criterion B2. Most specimens of *P. trichantha* are collected from the Aldabra Atoll, a world heritage site, which is well-protected as a result of its remoteness. Invasive alien species, climate change, and oil spills are possible threats to *P. trichantha* on this atoll (World Heritage List 2020). The natural vegetation on the Assumption and Astove Islands, which are vulnerable for the same threats, is much less preserved (Ministry of Environment, Energy and Climate Change 2020) and this is also the case for the locations along the east African coast. Coastal forest in east Africa is under high anthropogenic pressure and the once continuous forest cover has been reduced to small remnant patches (Burgess *et al.* 1998; Habel *et al.* 2017). Forest clearance occurs for subsistence farming, agro-forestry plantations, the development of tourist infrastructure, mining (e.g., Wazo Hill in Tanzania; Richard & Nyundo 2018). Less destructive threats are logging for construction wood, firewood or the production of charcoal, the gathering of edible and medicinal plants, hunting, and the collection of honey (Burgess *et al.* 2000; Habel *et al.* 2017). The main threat to *P. trichantha* is the destruction of its habitat for subsistence farming and the above-mentioned factors, especially on the east coast of continental Africa. A reduction in the extent and quality of the habitat is therefore inferred. This fact, together with the low AOO and the low number of locations, qualifies this species as Vulnerable.

Notes

1. In *Paracephaelis trichantha*, a glabrous and a pubescent form occurs. In the Aldabra Atoll, specimens of the glabrous form are restricted to South Island, whereas specimens of the pubescent form occur on all islands of the Aldabra Atoll except for South Island. The two forms mainly differ in the presence or absence of pubescence on the young shoots and on the lower and upper leaf surfaces. Furthermore, specimens of the pubescent form tend to have somewhat smaller leaves, inflorescences, and flowers than those of the glabrous form and their stems are brown, greyish or pale brown vs pale brown to fawnish. Both forms of *P. trichantha* occur on the African mainland, in Tanzania, Kenya, and Mozambique.

2. Like in *Paracephaelis cinerea*, the anther connective in *P. trichantha* often dries reddish brown.

3. As mentioned in Note 5 of *Paracephaelis comorensis* sp. nov., the author initially considered *P. cinerea*, *P. comorensis* sp. nov. and *P. trichantha* as belonging to the same species. This resulted in the annotation of specimens of *P. trichantha* as "*Paracephaelis cinerea* subsp. *trichantha*", a name which was never published.

Discussion

In the present revision, thirteen new species are described in *Paracephaelis*. The species number is raised from five to eighteen, twelve of which are endemic to Madagascar. Most species occur in dry vegetation types; they are characterized by a short calyx tube and calyx lobes that are equal in length or longer than the tube ('*Paracephaelis*'type). Some species, however, are found in more humid vegetation types: they often are more robust and usually have a calyx tube that is longer than the calyx lobes ('*Homolliella*' type). In this broadened delimitation (with the inclusion of the '*Homolliella*' type), *Paracephaelis* is present throughout Madagascar in both dry and humid vegetations. While Madagascar is clearly the centre of diversity for the genus, *P. trichantha* occurs in the Seychelles and on the east coast of mainland Africa and *P. comorensis* sp. nov. is endemic to the Comoro Islands.

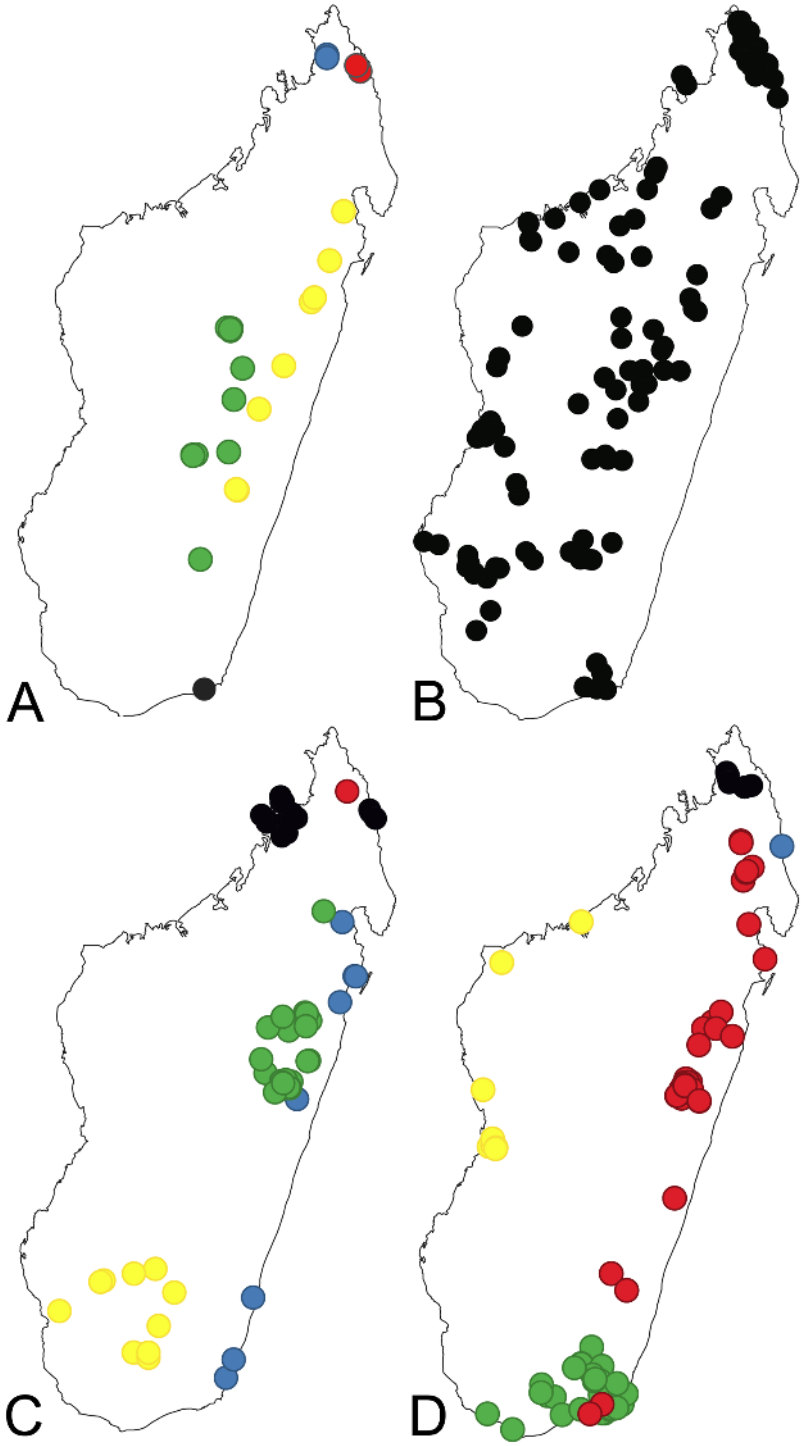

Fig. 23. Distribution maps of Malagasy species of *Paracephaelis*. **A**. *P. aristata* De Block sp. nov. (black dot), *P. bardotiae* De Block sp. nov. (blue dot), *P. capitulifera* De Block sp. nov. (green dot), *P. gautieri* De Block sp. nov. (red dot), and *P. grandifructa* De Block sp. nov. (yellow dot). **B**. *P. cinerea* (A.Rich. ex DC.) De Block (black dot). **C**. *P. longipedicellata* De Block sp. nov. (black dot), *P. orientalis* De Block sp. nov. (blue dot), *P. pauciflora* De Block sp. nov. (green dot), *P. ranirisonii* De Block sp. nov. (red dot), and *P. seyrigii* De Block sp. nov. (yellow dot). **D**. *P. russata* De Block sp. nov. (black dot), *P. sambavensis* De Block sp. nov. (blue dot), *P. saxatilis* (Scott Elliot) De Block (green dot), *P. sericea* (Arènes) De Block (red dot), and *P. tiliacea* Baill. (yellow dot).

Fig. 24. Distribution map of *Paracephaelis comorensis* De Block sp. nov.

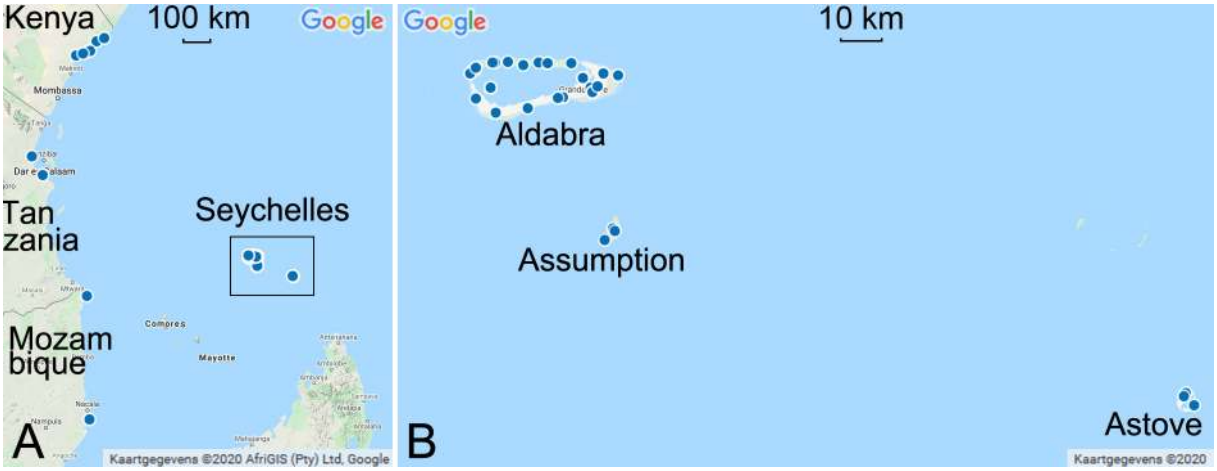

Fig. 25. Distribution map of *Paracephaelis trichantha* (Baker) De Block. **A**. Overview. **B**. Detail: islands of the Aldabra group.

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