

Novitates Gabonenses 93: a fresh look at Podostemaceae in Gabon following recent inventories, with a new combination for *Ledermanniella nicolasii*

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Academic editor: Brecht Verstraete ♦ Received 15 October 2022 ♦ Accepted 1 February 2023 ♦ Published 1 March 2023

Abstract

Background and aims – Podostemaceae is a family of strictly aquatic plants found in rapids and waterfalls. Despite a recent treatment in the Flore du Gabon, the family remained poorly known, with no major studies including Gabonese collections, and almost no targeted inventories since 1966. We present the first large-scale inventory of this family in Gabon, targeting Podostemaceae throughout the country, providing new additions to the flora of Gabon and many new records of poorly known species.

Material and methods – Fieldwork was conducted in Gabon between 2017 and 2021. The collected specimens were primarily preserved in ethanol with associated silica gel-preserved material and photographs. Material available at BR, BRLU, LBV, MO, P, WAG, and Z/ZT was examined. For each species, information on distribution and ecology is presented, as well as a distribution map in Gabon.

Key results – The 500 newly collected specimens represent 91.4% of all known collections of Podostemaceae from Gabon. Three taxa are newly recorded for the country, including one genus (*Inversodicraea tenax*, *Ledermanniella schlechteri*, and *Saxicolella nana*). New distribution records are also presented for 13 little-known species. Four taxa are excluded from the Gabonese flora (the genus *Dicraeanthus*, *Inversodicraea ledermannii*, *Ledermanniella sanagaensis*, and *Macropodiella garrettii*). To date, 20 species belonging to five different genera are known to occur in Gabon. A new combination is proposed for *Ledermanniella nicolasii*, and *Inversodicraea tanzaniensis* is now considered as a synonym of *Inversodicraea tenax*.

Keywords

aquatic plants, Central Africa, Gabon, hydropower, Lower Guinea, Podostemaceae, taxonomy

INTRODUCTION

The flora of the Republic of Gabon is one of the richest in tropical Africa: a national checklist was published by Sosef et al. (2006) and recorded 4710 species of vascular plants for the country, but a recent account (Texier et al. 2022) recorded 5039 species, of which 396 are considered as endemic. Nevertheless, the knowledge about the flora is still far from perfect, because large areas are not well-explored (Texier et al. 2021), and many taxonomic groups have not been revised recently. The Flore du Gabon series started in 1960 and currently covers 164 families and ca 76% of the flora, while new volumes are regularly published (e.g. Aubriot 2020; van der Burg and Bidault 2020; Beentje 2021; Harris et al. 2022; Schaefer 2022).

Podostemaceae is a family of strictly aquatic species, known from 313 species in 53 genera (Katayama et al. 2022) and is mostly pantropical, with one species (*Podostemum ceratophyllum* Michx.) in the temperate regions of North America. In Africa and Madagascar, 106 species in 17 genera are known (Ameka et al. 2010; Cheek and Lebbie 2018). Podostemaceae is among the most under-sampled and under-studied groups in Gabon, largely due to their peculiar ecology, and the fact that they are immersed during a large part of the year.

Until 2018, the date of the publication of the Flore du Gabon treatment of Podostemaceae (Ghogue 2018), the available studies on Podostemaceae of Gabon were limited to the founding work of Colette Cusset, a specialist of the family based at Paris' Muséum national d'Histoire naturelle (Cusset 1973, 1974, 1978, 1980, 1983, 1984; Cusset and Cusset 1988a, 1988b, 1988c). These studies were based on the limited material available at that time. Indeed, no botanist had performed systematic inventories targeting Podostemaceae in Gabon before. Consequently, only few specific sites were visited, often large and remarkable rapids (e.g. the rapids of Booué, on the Ogooué river) or waterfalls (e.g. Kinguélé falls in the Monts de Cristal). Moreover, most of the sampling sites of Podostemaceae were close to roads and easily accessible. Sampling was thus strongly biased.

At the time of Cusset's works, the known diversity of Podostemaceae of Cameroon and Gabon was rather similar, and reflected the importance of Atlantic Central Africa as the centre of diversity for the family in Africa. This was highlighted in her revision of *Ledermanniella* Engl. (Cusset 1983, 1984), including subgenus *Phyllosoma*, whose species were later transferred to the resurrected genus *Inversodicraea* Engl. ex R.E.Fr. (Thiv et al. 2009; Cheek and Haba 2016). *Inversodicraea* and *Ledermanniella* s.s. are now the most diverse genera of Podostemaceae in Africa (Cheek et al. 2017). In 1984, according to Cusset, 14 species of *Ledermanniella* s.l. (including *Inversodicraea*) were known to occur in Gabon, a number that remained constant until 2018. Between 1978 and 2017, only 12 collections of Podostemaceae were made in Gabon, which brought the country's total number of known collections for the whole family to 48. In the meantime, sampling of

Podostemaceae in Cameroon increased, which resulted in the description of five species of *Ledermanniella* s.s. and four species of *Inversodicraea* between 1984 and 2018 (Cheek 2003; Schenk and Thomas 2004; Cheek and Ameka 2008; Kita et al. 2008; Schenk et al. 2015; Cheek et al. 2017). In addition, several recent discoveries were made in other Podostemaceae genera in Cameroon, including *Stonesia* G.Taylor (Pfeifer et al. 2009) and *Djinga* C.Cusset (Ghogue et al. 2013). The most recent account of Podostemaceae for Cameroon (Kuetegue et al. 2019) lists 43 species of Podostemaceae, including 10 species of *Inversodicraea* and 17 species of *Ledermanniella*. In comparison, the recently published Flore du Gabon (Ghogue 2018) lists 19 species of Podostemaceae in the country, including seven species of *Inversodicraea* and nine species of *Ledermanniella*.

However, due to the opportunistic (rather than systemic) nature of the inventories carried out in Central Africa, many Podostemaceae species are still known from very few collections and sites. Large-scale inventories, specifically designed to target Podostemaceae, have yet to be conducted in several countries, including Cameroon (Kuetegue et al. 2019). At the same time, both Cameroon and Gabon are facing an unprecedented phase of planning and construction of multiple hydroelectric dam projects of varied size and power. Due to their particular ecology and restricted habitat, Podostemaceae are inherently threatened by such projects (Cheek et al. 2017).

In 2017, the Missouri Botanical Garden and the Herbarium National du Gabon initiated a series of inventories specifically targeting Podostemaceae, which first took place in the Monts de Cristal area (Estuaire province, north-western part of the country), and then, starting from 2018, expanded to other areas of Gabon. Targeted inventories were designed to visit as many potentially suitable areas for Podostemaceae as possible, and multiple collections of the same taxa were gathered, in order to cover the morphological variability and the distribution of the encountered species. This approach, to our knowledge implemented in the field in Central Africa for the first time, allowed for the accumulation of 500 collections of Podostemaceae between 2017 and 2021.

Based on those recent collections, this paper contains the first large-scale inventory of Podostemaceae in Gabon, providing new additions to the flora of Gabon, and many new records of poorly known species.

MATERIAL AND METHODS

Sampling of Podostemaceae in Gabon targeted all kinds of rivers, from the largest rivers under sunny conditions (the Ogooué, Ivindo, and Ngounié rivers) to the smallest forested rivers with rapids and waterfalls under shadier conditions. Suitable habitats for Podostemaceae in Gabon were sampled between 30 and 590 m in elevation.

A site of occurrence was defined as a linear portion of a single river showing homogenous geomorphological

characteristics. This approach is proposed to accommodate for collections with different coordinates but collected on a single, large site, such as the Ogooué rapids at Booué, the Kongou falls on the Ivindo, or the Poubara falls on the Ogooué. Collecting areas situated close to each other, but considered as having different geomorphological characteristics or belonging to different rivers, were not considered as similar sites.

Collections were primarily preserved in 50% ethanol and collected in two duplicates or more. Silica gel-preserved material was gathered for most of the collections. Herbarium specimens were made only when living material was abundant. Additional data results from the study of other herbarium and spirit collections in BR, BRLU, LBV, MO, P, WAG, and Z/ZT (herbarium acronyms follow Thiers 2023). Collections made in the framework of this study were first pre-identified at the genus level in Libreville, then identifications were made at P, BRLU, and Z/ZT, using historical collections available at those institutions and the available literature whose references are cited throughout this paper. Material was ultimately stored at BRLU in 50% ethanol, in plastic bottles for long-term conservation. The new combinations and synonymizations follow the current International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018).

For each species, information on general distribution and ecology is presented. A distribution map in Gabon is provided, using the QGIS software, version 3.14 (QGIS Development Team 2023) and the coordinate system as WGS84/Pseudo-Mercator. A list of all collections of the 20 species that are present in Gabon and that are discussed in this paper can be found in Supplementary material 1. For each collection, the identifier of the record in MBG's database Tropicos is provided. When available, institutional barcodes are provided. In the case of recent collections without barcode, or when the barcode could not be retrieved, the acronyms of the institutions where the collections were studied are provided. Updated determinations made by Ehoarn Bidault, Rolf Rutishauser, and Attila Mesterházy are provided, as well as the basic necessary information linked with each collection: collectors, collection number, Gabonese province and locality of collection, collection date, elevation, and geographical coordinates.

RESULTS

Podostemaceae sampling

The 500 collections of Podostemaceae were collected between 2017 and 2021 in 70 different sites spanning most of the country, but with the exception of the north-eastern and southern parts (Fig. 1). Some sites that were explored in the past were sampled again, such as the Kingué falls on the Mbé river, the Ogooué rapids at Booué, and the Chutes de l'Impératrice on the Ngounié river near

Fougamou. All other sites include rivers and tributaries for which Podostemaceae had never been sampled before, among which the largest are the Offooué, Louéti, and Komo rivers.

To date, there are 20 Podostemaceae species, belonging to five different genera, occurring in Gabon. Overall, the collections made since 2017 and the beginning of the systematic collection of Podostemaceae and targeted field effort represent 91.4% of all known Podostemaceae collections made in the country. For 15 of the 20 species, the collections gathered since 2017 represent between two-third and the entirety of the total number of known collections made within the country. These inventories managed to collect 14 of the 19 species of Podostemaceae mentioned in Ghogue (2018), often representing a drastic increase in their number of collections and known sites of occurrence. Similar to Cameroon, the most diverse genera in Gabon are *Ledermanniella* (nine species) and *Inversodicraea* (seven species). *Macropodiella* Engl. is represented by two species, while *Tristicha* Thouars and *Saxicolella* Engl. are represented by only one each.

Knowledge gaps

Despite our efforts, no collections have been made since 2017 for four species known to occur in Gabon: *Inversodicraea cristata* Engl., *Inversodicraea gabonensis* (C.Cusset) Cheek, *Ledermanniella boloensis* C.Cusset, and *Ledermanniella letestui* (Pellegr.) C.Cusset. Even if recent inventories allowed for a significant increase in the knowledge on Podostemaceae in Gabon, six species (ca a third of all Gabonese species) are still known from only five or less collections: *Inversodicraea boumiensis* (C.Cusset) Cheek, *Inversodicraea nicolasii* (C.Cusset) E.Bidault, Rutish. & Mesterházy, and the four species mentioned above. Among these, three are still only known in the country from one collection (made between 1926 and 1968): *Inversodicraea cristata*, *I. gabonensis*, and *Ledermanniella boloensis*.

Site richness and species abundance

Since all taxa were systematically collected each time a population was encountered at a given site, the number of collections known for each taxon provides useful information on their abundance on specific sites and country-wide. However, the number of known sites of occurrence better allows to appreciate their distribution within the country (Fig. 2). Before 2017, all species of Podostemaceae occurring in Gabon were known from only three sites or less. The recent inventories revealed that *Ledermanniella pusilla* (Warm.) C.Cusset (30 different sites), *Tristicha trifaria* (Bory ex Willd.) Spreng. (27 different sites) and *Ledermanniella aloides* (Engl.) C.Cusset s.l. (15 sites) are the most common Podostemaceae species in Gabon. In addition, *Saxicolella nana* Engl. was found at eight different sites, and is now considered as one of the most commonly found species in

Gabon, despite the fact that it was considered as a point endemic in Cameroon before 2017 (Cheek et al. 2022). On the other hand, a majority of them (13 of the 20 species known to occur in Gabon) are still known from five or less different sites, confirming the overall rareness of these species in Gabon.

The richest location for Podostemaceae in Gabon is the Ogooué rapids at Booué, where at least eight different species are currently known. The main rapids are located west of the city, which form an area of ca 750 m long and up to 570 m wide. This site was historically known as the richest in Gabon since 29 Jul. 1966, when Nicolas Hallé and Annick Le Thomas collected six different species, identified by Colette Cusset as *Inversodicraea thollonii* (Baill.) Cheek, *Inversodicraea annithomae* (C.Cusset) Rutish. & Thiv, *Macropodiella hallaei* C.Cusset, *Macropodiella heteromorpha* (Baill.) C.Cusset, *Ledermanniella pusilla*, and *Inversodicraea nicolasii* (initially as *Ledermanniella*,

transferred to the genus *Inversodicraea* in this study). Cusset described three species from these collections (*I. annithomae*, *M. hallaei*, and *I. nicolasii*), including two that were considered as endemic to the site until 2017 (*I. annithomae* and *I. nicolasii*). Recent inventories since 2019 allowed us to rediscover five of the six species initially mentioned in 1966. In addition, two species were recently discovered at this site, *Tristicha trifaria* and *Saxicolella nana*, that were not collected by Nicolas Hallé and Annick Le Thomas in 1966. The two site-endemics, *Inversodicraea annithomae* and *Inversodicraea nicolasii*, were also recently collected at other sites in Gabon (in the Ogooué and Ivindo rivers), and as a consequence, no species are known to be endemic to Booué anymore. The rapids of the Ogooué, west of Booué, now represent the second richest location in Africa for Podostemaceae, after the Lobé falls, where ten species are currently known to occur (Cheek et al. 2017).

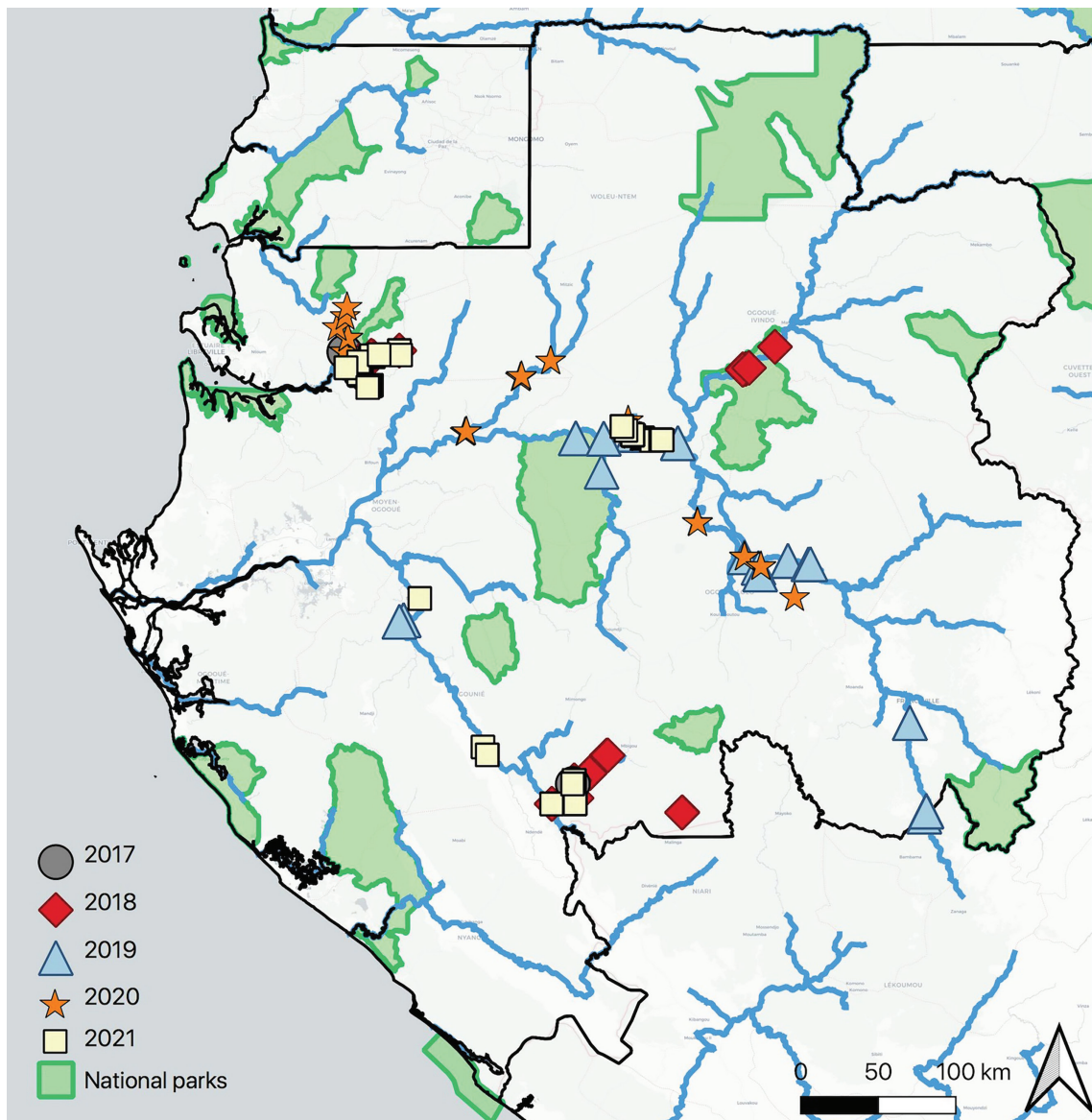


Figure 1. Location of the 70 collection sites sampled by the MBG-HNG team between 2017 and 2021 for the inventory of Podostemaceae (500 collections).

Three other sites of importance in Gabon are located on the Louétsi river, which were never explored before 2017: Issala, Ndoubi, and Dibwangui. These sites represent, after Booué-West, the richest sites in Gabon, where authors and colleagues observed six different species of Podostemaceae, including taxa new to science, in each of those three sites. Three other sites are known to harbour five different species of Podostemaceae in Gabon: Poubara and Booué-East, both on the Ogooué river, and Boukondzo on the Louétsi river. More than half (43 over 70) of the total number of sites where Podostemaceae have been collected in Gabon harbour only one or two species (with a national average of 2.5 species per site).

The taxa presented in the species list below concern 20 species in five genera. Among them are three additions

to the flora of Gabon: *Inversodicraea tenax* Engl. ex R.E.Fr., *Ledermanniella schlechteri* (Engl.) C.Cusset, and *Saxicolella nana*. The list also includes one genus new to the country: *Saxicolella*. New records are also presented for 13 little-known species. Three species, as well as one genus, are presented in a list of taxa excluded from the Gabonese flora: *Inversodicraea ledermannii* Engl., *Ledermanniella sanagaensis* C.Cusset, *Macropodiella garrettii* (C.H.Wright) C.Cusset, and *Dicraeanthus* Engl. *Inversodicraea ledermannii* and *Ledermanniella sanagaensis* were reported in the country by Ghogue (2018) based on misidentifications. The list of studied material for this work is provided in Supplementary material 1. The list presents 405 Gabonese collections that were seen by the authors, corresponding to the 20 species

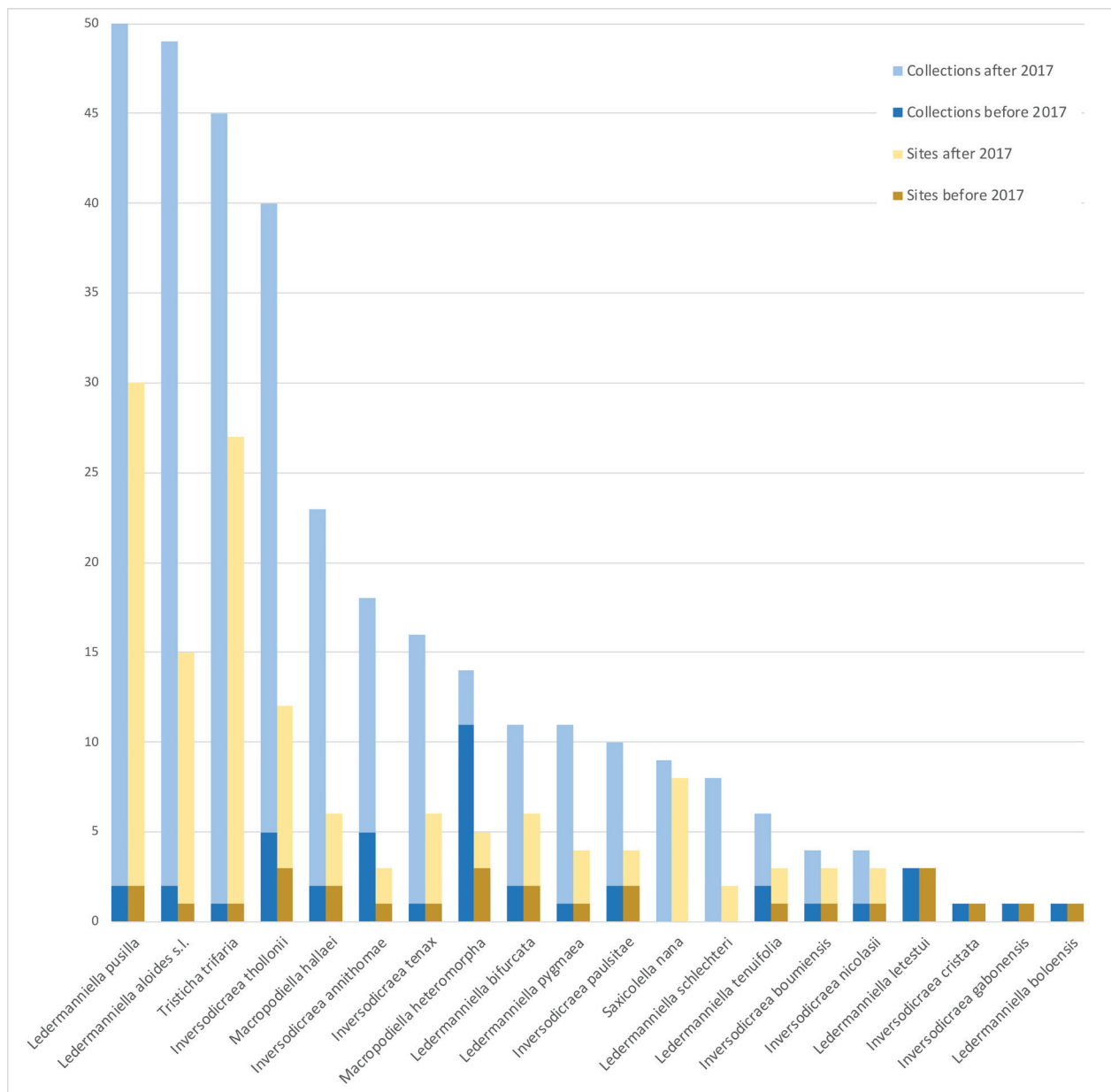


Figure 2. Number of collections and known sites of occurrence, before and after 2017, for each of the 20 currently known Gabonese species of Podostemaceae. The y-axis is limited to 50 for better visualization, but the number of collections of *Ledermanniella pusilla* in Gabon is 119.

known to occur in the country. The 405 collections cited include 361 that were made between 2017 and 2021 in the frame of this study, and 44 historical collections gathered between 1884 and 2007.

SPECIES IN GABON

Inversodicraea annithomae (C.Cusset) Rutish. & Thiv (Thiv et al. 2009: 72)

Figs 3A, B, 4A

Ledermanniella annithomae C.Cusset (Cusset 1983: 377, plate 6)

Type. GABON • Booué; 29 Jul. 1966; [0°05'24"S, 11°55'59"E]; 165 m; fl., fr.; *N. Hallé & A. Le Thomas* 206; holotype: P [P00179254].

Distribution. Gabon, Republic of the Congo. Before 2017, this species was only known from two collections: the type collected in 1966 at Booué in the Ogooué river in Gabon, and a collection made by Sita at the Mandoro rapids in the Republic of the Congo, in a tributary of the Kouilou river. Between 2018 and 2020, six collections were made, and its presence was confirmed at Booué. It was also discovered at another site in the Ogooué, the Poubara falls, and it is therefore probably present elsewhere on the Ogooué river, though it has not yet been collected at several other visited sites along the river. One collection is also known from the Okano river, a tributary of the Ogooué. The collection by Sita was determined by Colette Cusset in 1998, but since the P (P00179255) specimen shows stems branched multiple times, it was mentioned as doubtful in the synoptic revision of the genus (Cheek et al. 2017), though not providing a different determination since they did not observe the specimen. Cheek et al. (2017) also described *Inversodicraea tchoutoi* Cheek, to which they associate the collection *Letouzey 10299*, initially determined as *I. annithomae* by Cusset. Cheek et al. (2017) hence consider *I. annithomae* as a species endemic to the Booué rapids. Since recently collected material revealed morphological variability in *I. annithomae* (see Notes), we chose to stick with Cusset's determination of the Sita collection, and to consider this species as present in the Republic of the Congo. Moreover, since this species was found at Poubara (only ca 150 km away from Sita's collection site), it is also probably present in the Ogooué river upstream of Poubara, where rapids are present only ca 100 km away from the Sita collection site.

Habitat and ecology. Rapids and falls in rivers from ca 90 to 410 m wide, 160–400 m in elevation. It appears to be quite rare at the sites where it has been encountered. Flowers and fruits were collected in July and August, and fruits in September. It is mostly found in micro-habitats submitted to strong currents, but can also be found in slower-running water.

Notes. Recent collections revealed a strong morphological variability: the collection *Boupoia et al. 2698* shows cable-like horizontal stems more than 5 mm thick and up to

30 cm long, sparsely covered by scale-leaves, and bearing axillary, short flowering shoots abundantly covered by scale-leaves, while the collection *Boupoia et al. 2684* shows upright flowering shoots of up to 2 cm long, with stems up to 1.5 mm in diameter, abundantly covered by scale-leaves, and attached to a ribbon-like root. Intermediate forms were also collected (*Boupoia et al. 2672* and *2682*), showing typical features of *I. annithomae*, but with upright to horizontal shoots up to 5 cm long and 3 mm thick, still covered by scale-leaves on ca 50–60% of their surface. The three forms (small and upright, medium and upright to horizontal, large and horizontal) may be developmental stages as well as environmental modifications, but more precise field observations and habitat characterization is needed to explain this morphological variability. The morphological variability of *I. annithomae* was previously indirectly postulated by Cusset, who determined the sterile specimen *Letouzey 10299* as *I. annithomae*, probably considering that the absence of long, flexible flowering stems (as for the typical form of the species) was the result of a juvenile stage (Cheek et al. 2017).

Inversodicraea boumiensis (C.Cusset) Cheek (Cheek and Haba 2016: 55)

Figs 3C, 4A

Ledermanniella boumiensis C.Cusset (Cusset 1983: 370, plate 3)

Type. GABON • Boumi waterfalls at Mbigou [“Chutes de la Boumi à Mbigou”]; 5 Jul. 1927; [1°54'16"S, 11°54'31"E]; 665 m; fl., fr.; *Le Testu* 6536; holotype: P [P00179270]; isotypes: BM [BM000910485], BR [BR0000006267230], P [P00179271].

Distribution. Endemic to the Louétsi river, south-eastern Gabon. Before 2017, this species was only known from a single collection made at Boumi falls, near Mbigou. In 2018, it was discovered at two additional sites on the same river, at Issala and Dibwangui.

Habitat and ecology. Rapids and falls in rivers from ca 30 to 50 m wide, 380–665 m in elevation. It appears to be very rare at the sites where it has been encountered. Flowers and fruits were collected in July and August. At Dibwangui, it grows intermingled with *I. aff. annithomae*, in strong currents.

Notes. *Inversodicraea boumiensis* can be distinguished from *I. annithomae* mainly by its much smaller stature (stem < 1 mm thick and up to 2–3 cm long vs stem up to 3 mm thick and 20 cm long), stem scales (thin and spreading in *I. boumiensis* vs thick and appressed in *I. annithomae*), and pollen as dyads (vs monads in *I. annithomae*). The collection *Letouzey 15339* from the Ntem river (Cameroon) was attached to *I. boumiensis* by Cusset, but later determined as *I. tchoutoi* (Cheek et al. 2017). After examination of this collection, we choose to follow Cheek et al. (2017).

Inversodicraea cristata Engl. (Engler 1915: 276)

Ledermanniella cristata (Engl.) C.Cusset (Cusset 1974: 273)

Type. CAMEROON • Makaka Station [“Makaka, gr. Steine & Felsen in reissendem Bach im gebirgigen Walde”]; 21 Nov. 1908; [4°55'00"N, 9°57'00"E]; 500 m; fl.; *Ledermann 1173*; holotype: B; isotypes: BM [BM000910414], U [U0005650].

Distribution. Central African Republic, Cameroon, Equatorial Guinea, Gabon, Angola. This species is known

from Gabon by only one collection, *N. Hallé 4451*, collected in 1968 at the Kinguélé waterfall on the Mbé (Mbei) river in Monts de Cristal. The species is known from at least 15 other collections elsewhere, mainly in Cameroon (12 collections).

Habitat and ecology. Rapids and falls in rivers from ca 25 to 180 m wide, 5–1500 m in elevation. No information could be found regarding its abundance on sites where it has been found. Flowers and fruits were collected in January, February, and March (in Cameroon and Gabon), in August (in Angola), and in November (Cameroon).



Figure 3. Photographs illustrating a selection of species treated in this paper. **A, B.** *Inversodicraea annithomae* (A: Boupoya et al. 2444; B: Boupoya et al. 2689). **C.** *Inversodicraea boumiensis* (Boupoya et al. 1748). **D, E.** *Inversodicraea nicolasii* (D: Texier et al. 2247; E: Texier et al. 2334). **F, G.** *Inversodicraea paulsitae* (Boupoya et al. 1750). **H, I.** *Inversodicraea tenax* (H: Boupoya et al. 2432; I: Boupoya et al. 2430). Photographs: Igor Nguimbit (A), Archange Boupoya (B, C, F–I), Nicolas Texier (D, E).

Its sole collection from Gabon also contained a few individuals of *I. tenax*, indicating that both species probably grow intermingled at this site (Kinguélé waterfalls). *Ledermanniella bifurcata* (Engl.) C.Cusset and *L. letestui* were also collected at this site, but no information is provided on the habitat partitioning.

Notes. According to Cheek et al. (2017), Cusset had a morphologically broad concept of the species. Recent examination by Cheek et al. (2017) of material associated to this species by Cusset revealed that some collections belong to other species, such as *Inversodicraea digitata* H.E.Hess or *I. tchoutoi*. Cheek et al. (2017) consider

that this species may even be restricted to Cameroon, with records from Equatorial Guinea, Angola, C.A.R., and Gabon representing other species, but they did not examine all collections and did not provide new identifications for the non-Cameroonian collections. Examination of the Gabonese material in Paris did not reveal significant differences from the original description. Hence, we choose to consider the collection N. Hallé 4451 as belonging to *I. cristata*. Recent inventories were carried out at the Kingulé waterfall by the authors and colleagues and revealed that the site is now completely devoid of Podostemaceae. The construction of two hydroelectric

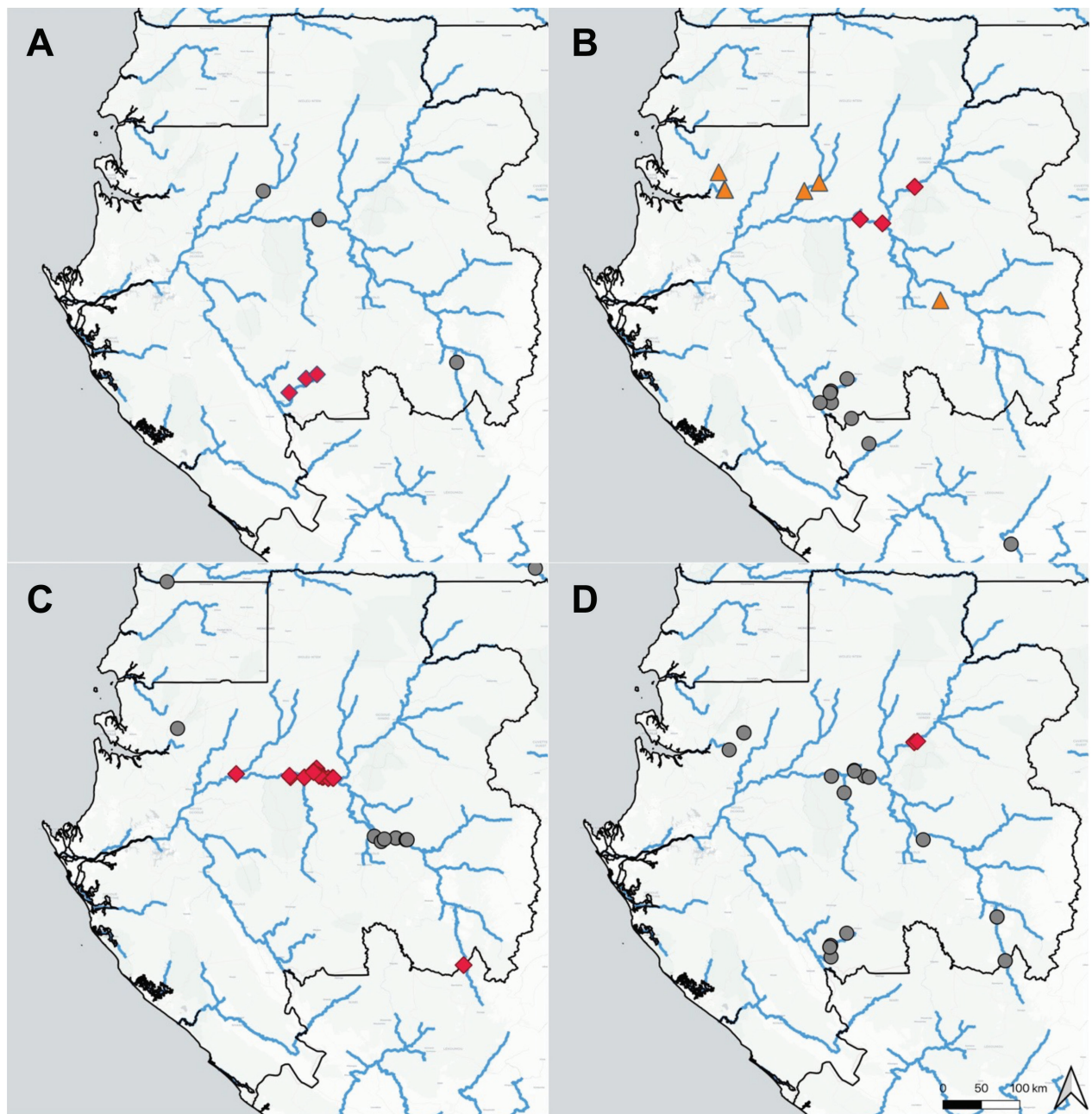


Figure 4. Distribution maps of Podostemaceae in Gabon. A. *Inversodicraea annithomae* (grey circles), *I. boumiensis* (red diamonds). B. *Inversodicraea nicolasii* (red diamonds), *I. paulsitae* (grey circles), *I. tenax* (orange triangles). C. *Inversodicraea thollonii* (red diamonds), *Ledermanniella bifurcata* (grey circles). D. *Ledermanniella aloides* (grey circles), *L. schlechteri* (red diamonds).

dams between 1969 and 1978 deeply modified the water availability at the site. *Inversodicraea cristata* was not collected elsewhere in Gabon.

Inversodicraea gabonensis (C.Cusset) Cheek (Cheek and Haba 2016: 2)

Ledermanniella gabonensis C.Cusset (Cusset 1983: 368, plate 2)

Type. GABON • Ogoulou rapids at Mitingo [“Haute Ngounyé, rapides de l’Ogoulou à Mitingo”]; 19 Jul. 1926; [1°55’00”S, 11°18’00”E]; 200 m; fl., fr.; *Le Testu 6017*; holotype: P [P00179287]; isotype: BM [BM000910486].

Distribution. Gabon, Republic of the Congo. This species is solely known from five collections. Three are known from the Foulakari waterfalls (a tributary of the Congo river) and one from waterfalls on the Nyanga river in Mouvougou, all in the Republic of the Congo. The only Gabonese collection, *Le Testu 6017*, was made on the Ogoulou river, a tributary of the Ngounié river, in 1926.

Habitat and ecology. Rapids and falls in rivers from ca 60 to 190 m wide, 130–200 m in elevation. No information could be found regarding its abundance on sites where it has been found. Flowers were collected in May and July, fruits in July, August, September, and October. Another species is found at the Foulakari waterfalls (*Ledermanniella bifurcata*), though the precise habitat partitioning at this site is unknown.

Notes. The type locality (in Gabon) has not been visited since 1926, nor other sites on the Ogoulou river. Sampling on the Ngounié river by authors and colleagues resumed only in 2019 with the exploration of the Impératrice waterfalls in Fougamou, far downstream, and did not lead to the collection of this species.

Inversodicraea nicolasii (C.Cusset) E.Bidault, Rutish. & Mesterházy, **comb. nov.**

urn:lsid:ipni.org:names:77315006-1

Figs 3D, E, 4B, 5

Ledermanniella nicolasii C.Cusset, Bulletin du Muséum National d’Histoire Naturelle, Section B, Adansonia. sér. 4, Botanique Phytochimie 6(3): 274. (Cusset 1984: 274)

Type. GABON • Ogooué river at Booué [“Lit de l’Ogooué à Booué”]; 29 Jul. 1966; [0°05’24”S 11°55’59”E]; 165 m; fl., fr.; *N. Hallé & A. Le Thomas 205*; holotype: P [P00179341]; isotypes: P [P00179342, P00179343].

Distribution. Endemic to the Ogooué and Ivindo rivers, in Gabon. Before 2017, this species was only known from a single collection made at Booué rapids on the Ogooué. In 2018, it was discovered on the Kongou falls, on the Ivindo river. In 2019, it was discovered on the Touné falls on the Ivindo river, less than 4 km upstream from the confluence with the Ogooué river, 30 km east of the type locality at Booué, and ca 60 km south-west of the Kongou falls. Recent efforts of Podostemaceae inventory at Booué rapids (west of the city) allowed for the rediscovery of this

species at its type locality. Nevertheless, it seems very rare at this site, since only one of the 70 collections made at this site between 2019 and 2021 represents this species. Given the considerable size of the rapids area, which is not yet fully explored, it is possibly more abundant than suggested by our data. The type material collected in 1966 includes a lot of individuals, suggesting that the species was, at least then, abundant on site. A natural, partial replacement of this population by another species cannot be excluded.

Habitat and ecology. Rapids and falls in large rivers from ca 100 to 500 m wide, 165–425 m in elevation. It appears to be quite abundant at Kongou falls, but rare at Booué and Touné falls. Flowers and fruits were collected in February, July, and August. The species grows intermingled with *Ledermanniella schlechteri* and *Macropodiella hallaei* at the Kongou falls. It appears to grow with *M. hallaei*, *M. heteromorpha*, and *L. pusilla* at the Touné falls. It was collected in micro-habitats submitted to strong currents. It is apparently consumed as a vegetable by local people around the Kongou falls in Gabon (boiled in water). Recent footage taken from the Kongou falls also showed an elephant potentially feeding on Podostemaceae, even though it is unclear if this species in particular is targeted. **Notes.** The recent material collected at Kongou falls on the Ivindo river revealed the presence of few, small but conspicuous triangular to wart-like, patent stem scales, most of them with a distal black dot, mostly grouped below the inflorescences, and very scarce along the stem. Closer examination of the type collection revealed similar stem-scales that were overlooked by Cusset, who initially placed this species in subgenus *Ledermanniella* rather than subgenus *Phyllosoma*. Because of the presence of clear stem-scales, we consider that this taxon belongs to the genus *Inversodicraea*. The recent collections from the Ivindo river show minor differences with the type collection, such as shorter and wider leaves and longer flowers and capsule stalks (up to 3 cm long vs up to 2 cm long), ca 60% of them bearing 3 stamens (vs 2 stamens), but they are otherwise very similar. We do not consider those differences as sufficient to distinguish another taxon. *Inversodicraea nicolasii* is solely known from four collections, which suggests a morphological variability that was unsuspected until now, and that remains largely undocumented.

Inversodicraea paulsitae (C.Cusset) Cheek (Cheek and Haba 2016: 55)

Figs 3F, G, 4B

Ledermanniella paulsitae C.Cusset (Cusset 1983: 378, plate 7)

Type. GABON • Litsila rapids on the Ngounié river, at Moupoundi [“Moupoundi, rapide Litsila de la Ngounyé”]; 20 Jun. 1927; [2°25’00”S, 11°50’00”E]; 250 m; fl., fr.; *Le Testu 6510*; holotype: P [P00179346]; isotype: BR [BR0000006265069].



Figure 5. Drawing of *Inversodicraea nicolasii*. **A.** Sterile shoot tip with young leaves and stem scales (scale bar: 0.5 mm). **B.** Fertile shoot before anthesis (scale bar: 5 mm). **C.** Capsule, one valve removed (scale bar: 1 mm). **D.** Flower at anthesis (scale bar: 2 mm), ovary with two stigmas dropped. **E.** Cross-section of the ovary (scale bar: 0.5 mm). **F.** Detail of the ovary (scale bar: 1 mm). **G.** Fertile lateral shoot and portion of the main stem (scale bar: 1 cm). A, E, F: *Texier et al.* 2247; B: *Nguimbit et al.* 8; C, D: *Boupoaya et al.* 2445; G: *Nguimbit et al.* 7. Drawings by Anne-Hélène Paradis, based on preliminary drawings by Rolf Rutishauser.

Distribution. Gabon, Republic of the Congo. This species is only known from southern Gabon in the Ngounié and Louétsi rivers, and the Bibaka and Bouenza rivers in the Republic of the Congo.

Habitat and ecology. Rapids and falls in large rivers from ca 50 to 80 m wide, 150–580 m in elevation. It appears to be quite abundant at the few sites where it has been encountered. Flowers and fruits were collected in January, June, and August. Grows intermingled with *Inversodicraea annithomae* and *I. boumiensis* in the Louetsi river. This species was solely found in micro-habitats submitted to strong currents.

Notes. Before 2017, this species was only known from two collections in Gabon (in 1927 and 1933), and two in the Republic of the Congo (in 1965 and 1975). One of the Gabonese collections was made at the Byoko falls on the “Louétoie” river, that presumably corresponds to the Bongolo falls on the Louetsi river, near Lébamba, a site that was recently explored by authors and colleagues, but without any success. A small hydroelectric facility was built downstream of these rapids, which might have caused the disappearance of this species’ subpopulation. Another species was nevertheless collected at this site, suggesting that *I. paulsitae* may be less resilient to disturbances and may have been replaced. This hypothesis remains speculative until a complete inventory of these rapids is undertaken. Recent inventories made in the Ngounié river did not collect this species, but the exploration of this major Gabonese river remains largely fragmentary.

Inversodicraea tenax (C.H.Wright) Engl. ex R.E.Fr.
(Fries and Rosen 1914: 56)

Figs 3H, I, 4B

Dicraea tenax C.H.Wright (Baker and Wright 1909: 125)
– Type: same as for *Inversodicraea tenax*.

Ledermanniella tenax (C.H.Wright) C.Cusset (Cusset 1974: 275) – Type: same as for *Inversodicraea tenax*.

Inversodicraea tanzaniensis Cheek, **syn. nov.** (Cheek et al. 2020: 31) – Type: TANZANIA • Distr. Iringa c. 1700 m Ruhudji river [“Stromgebiet des oberen Ruhudje, Landschaft Lupembe, nördlich des Flusses”]; 22 Aug. 1931; [9°18’31”S, 35°11’20”E]; 1700 m; fl., fr.; *Schlieben 1131A*; holotype: K; isotypes: B†, BM, BR [BR0000017827522], EA, G, LISC, P [P00179369], PRE, Z, ZT.

Type. ZAMBIA • Victoria Falls, Livingstone Island; [17°55’26”S, 25°51’14”E]; 885 m; fl., fr.; 17 Sep. 1906; *Kolbe 3149*; holotype: K [K000435188]; isotypes: BM [BM000797689], BOL [BOL135706].

Distribution. Gabon, Democratic Republic of the Congo, Angola, Namibia, Tanzania, Botswana, Zambia, Zimbabwe. Though recent collections revealed the presence of this species in Gabon, it has in fact been collected in the country as early as in 1926 (*Le Testu 5983*), but it was misidentified as *I. ledermannii* by Cusset (see Notes under that species). In addition, examination

of the collection *N. Hallé 4451* collected on the Kinguéle waterfall on the Mbé river (Monts de Cristal) in 1968, and identified as *I. cristata* by Cusset, revealed the presence of one fertile individual identified by us as *I. tenax*, now as the collection number *N. Hallé 4451B*, separated from *N. Hallé 4451A*, which represents *I. cristata*. Material associated with *I. ledermannii* from the Democratic Republic of the Congo and Angola was not examined for this study, but should be checked for their pollen. If monads are observed (i.e. not dyads as typical for *I. ledermannii*), this material would be best associated to *I. tenax*, which could link this species’ original distribution with the newly discovered Gabonese subpopulations.

Habitat and ecology. In Gabon, rapids and falls in rivers from ca 10 to 40 m wide, 50–510 m in elevation (up to 1,700 m in Tanzania). It appears to be quite rare at the few sites where it has been encountered. In Gabon, flowers and fruits were collected in January, June, July, and August. It grows intermingled with *I. cristata* (*N. Hallé 4451A* and *4451B*) and close to *L. pusilla* in the Monts de Cristal area. Collections made from small rivers in Monts de Cristal (north-western part of Gabon), as well as larger rivers (Komo, Abanga, Offooué) revealed important ecological tolerance, previously unsuspected for this species.

Notes. The discovery of *I. tenax* in Gabon is surprising, but the pollen as monads shown by the Gabonese material and the close examination of material from southern Africa leaves no doubt about the identity of the Gabonese collections. The recently collected Gabonese material revealed important morphological variability: stem-scales appear to have a variable number of dorsal projections (from 0 to 2, often on the same individuals) and of lobes (3 to 5), whereas Cusset’s description of the species (Cusset 1983) mentioned 3-dentate stem-scales (or with 3 lobes), and most often with 2 dorsal appendages. The Gabonese material also shows a great variety in the proportion of dorsally appendaged stem-scales versus dorsally smooth stem-scales, with some individuals nearly or completely devoid of dorsal appendages. Nevertheless, the pollen as monads consistently observed on this material allows to rule out *I. ledermannii* (that has pollen as dyads). The examination of the Paris isotype of the recently described *I. tanzaniensis* (*Schlieben 1131A*) showed a similar pattern of stem-scales variation, bearing 3 to 5 lobes and from 0 to 2 dorsal appendages, despite the original description (Cheek et al. 2020) mentioning the clear absence of dorsal appendages as a strong difference with *I. tenax*. Stem-scale variation appears more important at the tip of shoots, on stem-scales subtending spathellae, in both the Gabonese collections as well as *I. tenax* material and the isotype of *I. tanzaniensis*. Stem-scale morphological variability within the genus *Inversodicraea* (including in *I. tenax*) was already described by Cusset (1983), who mentioned differences in shape and size of stem-scales depending on their position in the stem. Considering the clear continuum between the presence and absence of dorsal appendages, we consider that their absence cannot be used to discriminate material from an otherwise similar

species. In addition, all dried capsules observed on the isotype of *I. tanzaniensis* as well as the Gabonese material showed 8-ribbed capsules, including two commissural ribs clearly visible, whereas Cheek et al. (2020) mentioned *I. tanzaniensis* as having 6 ribs instead of 8 being a strong difference with *I. tenax*. Among other differences between *I. tenax* and *I. tanzaniensis* are the lengths of the tepals and gynophore. The Gabonese collections showed tepals of ca 0.8 mm of length, similar to what was described for *I. tanzaniensis*, but slightly longer than mentioned on the original description of *I. tenax* (0.5 mm), and a gynophore of ca 0.5 mm, similar to what was described for *I. tenax*, but slightly longer than mentioned for *I. tanzaniensis*. We believe those differences are not relevant, especially since some variability has also been observed by the authors on other species. Finally, another important character mentioned by Cheek et al. (2020) to discriminate *I. tanzaniensis* from *I. tenax* is the length of stem, of up to 20 cm for *I. tenax* whereas *I. tanzaniensis* has 5–8 cm long stems. The recently collected Gabonese material showed both stemless individuals (Boupoya et al. 2418, 2420, 2422, 2423), or with stems of up to 3 cm long (Boupoya 1709, 2429, 2430, 2432). We suggest a cautious approach when considering the length of stem as a character to discriminate species. If some Podostemaceae species clearly never show elongated stems, especially in *Ledermanniella* (*L. thalloidea* (Engl.) C. Cusset and *L. aloides*, for instance), the prolific material collected by authors and colleagues suggests a strong intraspecific variability in that matter, that was only sporadically mentioned by Cusset (1983) in *Ledermanniella* (*L. pusilla* and *L. bifurcata*), and that was largely unsuspected for *Inversodicraea* until now. Recent material collected in Gabon shows that *I. annithomae*, *I. thollonii*, and *I. tenax* (among others) can show stemless shoots as well as developed stems, sometimes on single individuals. In addition, such variability is not surprising considering species that are widespread and known from a variety of micro-habitats, such as *I. tenax*. When developed stems are observed for a given species, stem length might therefore better reflect ecological preferences. Our observations also suggest that developed stems are often associated with strong currents. For all the above-mentioned reasons, we believe it is best to consider *I. tenax* as a widespread, morphologically variable (with continuums) and ecologically ubiquitous species, which comprises *I. tanzaniensis*.

Inversodicraea thollonii (Baill.) Cheek (Cheek and Haba 2016: 55)

Figs 4C, 6A, B

Podostemum thollonii Baill. (Baillon 1890: 877)

Ledermanniella thollonii (Baill.) C. Cusset (Cusset 1983: 388)

Type. GABON • Lopé rapids in the Ogooué [“Ogooué, rapides de Lopé”]; Jul. 1887; [0°05′38″S, 11°35′24″E]; 115 m; fl., fr.; *Thollon* 825; holotype: P [P00179381]; isotype: BM [BM000910405].

Distribution. Endemic to the Ogooué river and its tributaries, in Gabon. Before 2007, this species was only known from two collections, one from the Booué rapids on the Ogooué (*N. Hallé* 202b, collected in 1966) and one from the rapids of the Ogooué at Lopé (*Thollon* 825, collected in 1887). In 2007, three sterile collections were made in the Lenké (or Langke) river near Booué (*Kato et al.* GB11, GB12, and GB13, as mentioned in Koi et al. 2012) that were not identified as *I. thollonii* until this study. Since 2019, it has been collected 35 times in the Ogooué, and in various tributaries: the Lopé, Létili, Okano, Bissoubilam, Offooué, and Lenké rivers. All of these collections were made less than 2 km upstream from the confluence with the Ogooué river, except for the collection from the Bissoubilam river (ca 6 km away). Most (38 of the 40) of the collections were made in or along a ca 130 km long portion of the Ogooué between Alembé and Makokou in central Gabon, with the exception of two collections made in the Létili river at the border between Gabon and the Republic of the Congo. Those collections are separated from the easternmost others by ca 300 km, and it is expected that *I. thollonii* is also present in between.

Habitat and ecology. Rapids in rivers from ca 20 to 600 m wide, 45–500 m in elevation. It appears to be abundant where encountered. Flowers and fruits were collected in July, August, and September. It was collected with or near to *Ledermanniella aloides*, *L. pusilla*, *Macropodiella hallaei*, and *Tristicha trifaria*. Collections made from small Ogooué tributaries (Lopé, Bissoubilam, and Lenké rivers), larger tributaries (Okano, Létili, and Offooué rivers) as well as the Ogooué river itself revealed important ecological tolerance, previously unsuspected for this species. It has been noticed in strong as well as slow currents. It has surprisingly not been found on the Ivindo river, even at the Touné falls, close to its confluence with the Ogooué. However, only one day was dedicated to the exploration of this site, and this species may have been overlooked.

Notes. As for other species in this study, the newly collected material revealed great morphological variability. *Inversodicraea thollonii* is among the Podostemaceae species showing both stemmed and stemless shoots, whereas it was originally described as having short stems 1–2 cm long (Cheek et al. 2017). If both forms were usually collected separately, a few recent collections showed stemmed and stemless shoots on single individuals (*Boupoya* 1948 and 1968, for instance). Stem-scales also show variability, most of them being narrowly triangular with rounded apex as described by Cusset (1983), but in some cases almost linear (*Boupoya* 2452). Stem-scales are usually spreading and quite delicate (thin). On stemmed individuals, stem-scales are scarce, as described by Cusset (1983), and never covering more than 50% of the stem as the key to all species provided in Cheek et al. (2017) mentions. On stemless individuals, stem-scales are forming a dense crown below the spatheae. With 40 collections to date, *I. thollonii* is now considered as one of the most common Podostemaceae species in Gabon, even

though it is yet to be found in other watersheds than that of the Ogooué river.

Ledermanniella aloides (Engl.) C.Cusset (Cusset 1974: 273)

Figs 4D, 6C

Inversodicraea aloides Engl. (Engler 1915: 271, 273, plate 175)

Type. CAMEROON • Adamaoua, Pass Tchape; 27 Feb. 1909; [7°23'00"N, 11°55'00"E]; 1500 m; fl.; *Ledermann* 2785; holotype: B; isotype: BM [BM000910397].

Distribution. Sierra Leone, Nigeria, Cameroon, Central African Republic, Gabon, Angola. This species was first collected in Gabon in 1993 by Lee White at Lopé, probably not in the Ogooué river, but in a small tributary. We have not been able to retrieve this collection and confirm the



Figure 6. Photographs illustrating a selection of species treated in this paper. A, B. *Inversodicraea thollonii* (A: Boupoya et al. 1948; B: Boupoya et al. 1943). C. *Ledermanniella aloides* (Boupoya et al. 1749). D, E. *Ledermanniella bifurcata* (D: Boupoya et al. 1954; E: Boupoya et al. 1958). F, G. *Ledermanniella pusilla* (F: Boupoya et al. 1733; G: Boupoya et al. 1735). H. *Ledermanniella pygmaea* (H: Boupoya et al. 1764). Photographs: Archange Boupoya.

identification made by Sosef in 2017. In 2007, another collection, *Kato et al. GB-10*, was made in the Lenké river near Booué (erroneously labelled as *Ledermanniella bifurcata* by Koi et al. 2012, see Notes). Since 2017, it has been collected 47 times by the authors and colleagues, including 13 collections from the Louétsi river, 11 from the Komo river, and 23 from the Ogooué or its tributaries. *Ledermanniella aloides* is the second most commonly found Podostemaceae species in Gabon.

Habitat and ecology. In Gabon, rapids in rivers from ca 10 to 450 m wide, 85–550 m in elevation (up to 1,500 m in Cameroon). It appears to be very abundant where encountered, forming dense, monospecific mats. In Gabon, flowers and fruits were collected in March, July, August, and September, elsewhere also in May, November, and December. In Gabon, it appears to share the same micro-habitat as *I. thollonii*, *L. pusilla*, *Tristicha trifaria*, and was once found near *Saxicolella nana*. *Ledermanniella aloides* is often found in relatively slow-running currents.

Notes. *Ledermanniella aloides*, unlike *I. thollonii* or *L. pusilla*, never shows developed stems. Nevertheless, some characters used by Cusset (1984) to distinguish it from morphologically close species seem to be more variable than suspected. We observed that the distichous arrangement of leaves and the absence of ramification of the blade are constant throughout the recently collected material, but the presence and shape of stipules, the presence and size of the sheath, and the length and overall shape of the blade can vary. We have noticed three morphogroups occurring in Gabon: one characterized by having all leaves of reproductive rosettes without stipules, with sheaths enlarged but folded and imbricate, and with ensiform (laterally flattened) leaf blade; another group characterized by most leaves with 1–2 stipules at base, with sheaths enlarged but less folded, and leaf blades less obviously ensiform; and a third group with enlarged sheaths bearing obscure (rounded) stipules, and with leaf blade widening on their apical portion, most of them showing a conspicuous midrib. Nevertheless, we are reluctant to name and describe these morphogroups as separate entities, as all characters mentioned here show continua, including in collections from West Africa. Morphological continua between these character states can sometimes even be observed on single shoots, with strong polymorphism of leaves depending on their position relatively to the spathellae. Most of the Gabonese collections studied could be assigned to either one of the three morphogroups based on the observation of the numerous individual shoots they each comprise (usually several dozens or even hundreds of shoots), but all of them also comprise a significant portion of shoots displaying intermediate character states. We believe it is best for now to consider *L. aloides* as a morphologically variable species, occurring from Sierra Leone to Central African Republic and to Angola. *Ledermanniella aloides* remains recognizable from any other *Ledermanniella* species mainly by the combination of always stemless shoots, leaves arranged distichously, blade always entire,

the presence of two stamens, and pollen as monads, among other minor differences. In light of the new information on the morphological variability of sheath, stipules, and leaf blade, the validity of *L. sanagaensis* may be questioned. The description provided by Cusset (1984), as well as the only collection of this species we could study (*Kato et al. CMR134* from the type locality at Nachtigal on the Sanaga river, Cameroon), are both included within the morphological range of variation observed on the Gabonese material. Nevertheless, we consider it premature to stop considering *L. sanagaensis* as a valid and different species until more material from Cameroon is made available and allows for better comparison. In addition, we believe a phylogenetic analysis should be conducted on this group of species, to help untangle this complex and to confirm the hypothesis of *L. aloides* as a widespread, variable species.

Ledermanniella bifurcata (Engl.) C.Cusset (Cusset 1974: 273)

Figs 4C, 6D, E

Inversodicraea bifurcata Engl. (Engler 1915: 273, plate 178) – Type: same as for *Ledermanniella bifurcata*.

Inversodicraea minima Engl. (Engler 1915: 273, plate 176) – Type: CAMEROON • Rapids of the Kienké river, ca 50 km east of Grand Batanga [“in den Schnellen des Kienke oder Kribi-Baches, c. 50 km östlich Groß-Batanga”]; Jun. 1911; [2°48’00”N, 10°21’00”E]; 90 m; fl., fr.; *Mildbraed* 5952; lectotype (**designated here**): U [U 0005647]; isolectotypes: B, BM [BM000910384].

Inversodicraea zenkeri Engl. (Engler 1915: 273, plate 179) – Type: CAMEROON • Bipindi; Nov. 1908; fl., fr.; *Zenker* 3811; lectotype (**designated here**): BM [BM000910385]; isolectotypes: B, WU [WU 0037875].

Type. CAMEROON • Rapids of the Kienké river, ca 50 km east of Grand Batanga [“in den Schnellen des Kienke oder Kribi-Baches, c. 50 km östlich Groß-Batanga”]; Jun. 1911; [2°48’00”N, 10°21’00”E]; 90 m; fl., fr.; *Mildbraed* 5951; holotype: B, isotype: BM [BM000910386].

Distribution. Cameroon, Gabon, Republic of the Congo. Kuetegue et al. (2019) as well as Ghogue (2010) mention that this species is present in Equatorial Guinea, but they did not cite collections. We have not been able to find any collection clearly from Equatorial Guinea, aside from *Letouzey* 15334 from the Ntem river at the border with Cameroon. The presence of this species in this country is nonetheless most probable since it was collected on the Ntem river, and in Gabon. In Gabon, this species is known from one collection (*Bogner* 761) made at the Kinguélé falls in the Monts de Cristal, but recent inventories at this site revealed it has since disappeared due to the construction of two hydroelectric dams on the Mbé river. We have not been able to retrieve this collection and confirm the identification made by Cusset, although she mentioned it as being deposited in Paris. This species has not yet been found again elsewhere in the Monts de

Cristal area, despite recent efforts since 2017. In Gabon, *L. bifurcata* is also present on the Ogooué river around Lastoursville, as attested by a collection made by Le Testu (7424) in 1929, and nine recent collections made in 2019.

Habitat and ecology. In Gabon, rapids in rivers from ca 50 to 450 m wide, 150–350 m in elevation (up to 600 m in Cameroon). It appears to be quite rare where encountered. Flowers and fruits were collected in January, February, May, June, July, November, and December. Recent Gabonese fertile collections were only made in July. In Gabon, it has been found once near *Saxicolella nana*, in the Ogooué. At the Kingué falls, past collections made by Nicolas Hallé comprised *L. letestui*, *I. cristata*, and *I. tenax*, along with *L. bifurcata*, but no information on habitat partitioning was collected. In Gabon, this species was mostly found in fast-flowing water.

Notes. The recently collected Gabonese material confirmed observations already made by Cusset (1984) concerning the morphological variability of this species, especially the presence of stemless shoots as well as elongated stems. *Boupoya* 1953 to 1957 and *Nguimbit* 16 all show only stemless shoots, while *Nguimbit* 15 shows elongated stems up to 2 cm long. The collection *Boupoya* 1958 displays elongated stems up to 5 cm long, as well as a few stemless, fertile shoots, on the same individuals. The leaves appear to be variable in shape, most dwarf collections showing no or rarely forked leaves. On individuals with clearly developed stems, most leaves are usually 1–2-times forked. Stipules are also variable, from absent to present, more or less rounded at apex, depending on the material studied, and in variable proportions. *Ledermanniella bifurcata* appears to generally have two stamens, but in the collection *Nguimbit* 16, ca 5–10% of its flowers have only one stamen. When it has a dwarf habit, this species is morphologically very close to *L. pusilla*, except this latter species has pollen as dyads, whereas *L. bifurcata* has pollen as monads. It is also very similar to another dwarf species with pollen as monads: *L. aloides*. It can still be differentiated from this species by the combination of at least some leaves being dichotomously divided (vs always entire in *L. aloides*), and most importantly the conspicuously stalked spathellae, that show a tapered portion at base (stalk) variable in size, up to 7.5 mm long on *Boupoya* 1957 (vs spathellae never stalked in *L. aloides*). The numerous collections of *L. aloides* now allow for a better understanding of its morphological variability and its boundaries, therefore permitting a better selection of truly discriminative characters. It is nevertheless not yet the case for *L. bifurcata* that, despite its wide range of distribution in Central Africa, remains a rarely collected and poorly known species. Phylogenetic studies may also help in clarifying its position relative to allied species such as *L. aloides*.

Ledermanniella boloensis C.Cusset (Cusset 1984: 272)

Type. GABON • Waterfall on the Bolo river, a tributary of the Gnyé, itself a tributary of the Ntem [“Cascade de

la Bolo, affluent de la Gnyé, qui du Ntem”]; 27 Aug. 1933; [2°07'42"N, 11°45'21"E]; 580 m; fl., fr.; *Le Testu* 9257; holotype: P [P00179263]; isotypes: BM [BM000910388], BR [BR0000006264734, BR0000009211674], P [P00179264, P00179265], WAG [WAG0194844].

Distribution. Endemic to Gabon. This species is only known from the type collection, *Le Testu* 9257, gathered in 1933 at “Cascade de la Bolo, affluent de la Gnyé, qui du Ntem” (waterfall on the Bolo river, a tributary of the Gnyé river, itself a tributary of the Ntem river). The name “Gnyé” was unfortunately misspelled as “Ngounyé” by Cusset (1984), leading to confusion about the locality where this species was collected. The Ngounyé (or Ngounié) river is one of Gabon’s largest, and flows in the southern part of the country, whereas the Gnyé river is a small tributary of the Ntem river, located at the border of Gabon and Cameroon, in the Woleu-Ntem province.

Habitat and ecology. Rapids and falls in rivers ca 30 wide, 580 m in elevation. No information could be found regarding its abundance on the site where it has been found. Flowers and fruits were collected in August. No other Podostemaceae was collected at the type locality.

Notes. The northernmost part of Gabon (including the portion of the Ntem river located in the country and its tributaries) has never been explored for Podostemaceae except for this single collection made by Georges Le Testu in 1933. Future explorations in this region could lead to the rediscovery of this enigmatic species, which has surprisingly not been collected in the Ntem river despite recent collecting efforts conducted in Cameroon.

Ledermanniella letestui (Pellegr.) C.Cusset (Cusset 1974: 274)

Inversodicraea letestui Pellegr. (Pellegrin 1927b: 525)

Type. GABON • Douvouca river in Kwango territory [“Terre de Kwango dans la Douvouca”]; 17 Jul. 1908; [2°55'00"S, 11°05'00"E]; 300 m; fl., fr.; *Le Testu* 1347; holotype: P [P00179329]; isotypes: BM [BM000910389, BM000910390], BR [BR0000006267568], P [P00179330, P00179331].

Distribution. Equatorial Guinea, Gabon. This species is so far known from four collections only. Two collections were made in southern Gabon by Georges Le Testu in 1908 and 1927 in the Douvouca and Ngounié rivers. In 1968, Nicolas Hallé collected *L. letestui* at the Kingué waterfall on the Mbé river.

Habitat and ecology. Rapids in rivers from ca 10 to 50 m wide, 150–600 m in elevation. No information could be found regarding its abundance on sites where it has been found. Flowers were collected in January and June, fruits in June and July. *Inversodicraea cristata*, *I. tenax*, and *Ledermanniella bifurcata* have been collected at the Kingué waterfall, but the precise habitat partitioning occurring at this site before its modification is unknown.

Notes. No recent inventories took place in the Douvouca river, and samples gathered from the Ngounié river in 2019 did not allow for the rediscovery of this species,

though the type locality has not been visited again. The authors and colleagues visited the Kinguélé waterfall in Monts de Cristal, where Podostemaceae have now disappeared. Despite its relatively large distribution range, *L. letestui* remains rare.

Ledermanniella pusilla (Warm.) C.Cusset (Cusset 1974: 273)

Figs 6F, G, 7A

Sphaerotherylax pusilla Warm. (Warming 1899: 146, pl. 39)

Dicraeanthus pusillus (Warm.) C.H.Wright (Baker and Wright 1909: 127)

Inversodicraea pusilla (Warm.) Engl. (Engler 1926: 461)

Type. CAMEROON • Bipindi, in the Lokundje rapids [“Bipinde, an den Lokundje-Schnellen”]; 10 Aug. 1896; [3°05'00”N, 10°25'00”E]; 70 m; fl., fr.; *Zenker 1050*; holotype: B; isotypes: BM [BM000910383], G [G00014258, G00014259], K [K000959889], L [L0035207, L0035208], M [M0108129], U [U0005651], W [W18980001777], WAG [WAG0002675].

Distribution. Cameroon, Gabon, Democratic Republic of the Congo. Before 2017, this species was known from nine collections throughout its range, including two from Gabon, in the Ogooué river at Booué and the Ogoulou river at Mitingo. The authors and colleagues have collected this species 119 times since 2017, which makes it the most commonly collected Podostemaceae species of Gabon. In Gabon, *L. pusilla* is found in all the rivers explored by authors and colleagues in the Monts de Cristal area, as well as the Ogooué, Ngounié, and Louetsi rivers, and the Offooué and Ivindo rivers, near their confluence with the Ogooué. This species is expected to be present in Equatorial Guinea as well as in the Republic of the Congo.

Habitat and ecology. In Gabon, rapids in rivers from ca 10 to 650 m wide, 35–590 m in elevation. It is usually abundant where encountered, forming dense and large mats. Flowers and fruits were collected in July, August, and September, as well as in January, February, and November outside of Gabon. In the Ogooué river, it seems to share micro-habitats with *Inversodicraea annithomae*, *I. thollonii*, *Ledermanniella aloides*, *Macropodiella hallaei*, and *Tristicha trifaria*. It is also often the only species found in rapid areas of small forested rivers in the Monts de Cristal area. In Gabon, this species is very ecologically tolerant, being found in slow or fast-flowing water.

Notes. The Gabonese material corresponds to the specific concept of Cusset, who already noticed the ability of this species to produce stemless fertile shoots as well as developed stems. The recent collections mostly comprise stemless individuals, but some collections (*Boupoya 1751*, 1935, and 1936) show elongated stems up to 4 cm long. The root morphology appears also quite variable, with most collections displaying ribbon-like roots up to 3 mm wide, but sometimes also crustose root, up to 8 mm in diameter (*Boupoya 1467*, for instance). All leaves are linear, varying in length (up to 2.5 cm long in *Boupoya 1935*), with a

good proportion of them being dichotomously divided at least once, the proportion varying depending on the collection. Exceptionally, all leaves can be entire, which brings the question of the validity of *L. linearifolia*. This species, endemic to southern Cameroon, always shows entire thread-like leaves up to 2 cm and may represent a local form of the more widespread *L. pusilla*. In addition, both *L. linearifolia* and *L. pusilla* belong to the same subclade within the *Ledermanniella*-Dyad group (see molecular data and illustrations in Moline et al. 2007: fig. 6A–G; Thiv et al. 2009; Koi et al. 2012). While in *L. pusilla*, most leaves bear stipules, some are also lacking such features, sometimes on single shoots. Exceptionally, some double-sheathed leaves (between two spathellae on a single stemless fertile shoot) can show up to four stipules (*Boupoya 1731*). Double-sheathed leaves are a peculiarity of many podostemoid members in America and Africa, always positioned at the fork of dichotomously branching stems (see Cook and Rutishauser 2007: 306; Moline et al. 2007: 163). One collection showed a couple of flowers having only one stamen (*Boupoya 1725*), and a couple of flowers amongst the several hundred observed showed three stigmas instead of two. Despite important morphological variability, *L. pusilla* can be recognized by the combination of pollen as dyads, leaves distichously arranged, linear, and almost never strictly entire, flowers with (usually) stalked spathellae, almost always bearing two stamens, among other minor characters.

Ledermanniella pygmaea (Pellegr.) C.Cusset (Cusset 1984: 266)

Figs 6H, 7B

Sphaerotherylax pygmaea Pellegr. (Pellegrin 1927a: 268)

Type. GABON • Samba waterfall in the Ngounié river, near Sindara [“Chutes de Samba, Sindara, dans la Ngounyé”]; 30 Jun. 1917; [1°02'23”S, 10°41'44”E]; 35 m; fl., fr.; *Le Testu 2202*; holotype: P [P00179351]; isotype: BM [BM000910392].

Distribution. Endemic to the Ngounié and Louetsi rivers, in Gabon. Before 2017, this species was solely known from the type collection made at Samba (or Tsamba) falls on the Ngounié river, west of Sindara (*Le Testu 2202*, gathered in 1917). It was found again one century later, in 2018, at three different sites on the Louetsi river, a tributary of the Ngounié, and collected 10 times in 2018 and 2021. Surprisingly, recent inventory at the type locality did not allow to collect this species again, despite the apparent lack of disturbance and immediate threat to this site.

Habitat and ecology. Falls in rivers from ca 35 to 170 m wide, 35–450 m in elevation. It is very localized when encountered, but forming dense, apparently monospecific mats. Flowers and fruits were collected in June and August. In the Louetsi river, it has been found in close vicinity with *L. aloides* and *L. pusilla*. This species seems restricted to falls, in fast flowing water, as it was not collected in smaller rapids areas in the Louetsi river.

Notes. The presence of both stemless shoots and developed stem up to 8 mm long was already mentioned by Cusset (1984), and is confirmed by the recent observations. This species is recognizable by the combination of ribbon-like root, pollen in dyads, a single stamen, leaves arranged all around the stem (not distichous), that are linear, entire to 3–4 times forked. When a developed stem is present, the leaves at base are usually shorter, sometimes damaged, which can give the impression of stem-scales. Nevertheless, there is a continuum in length and shape between basal and apical leaves, which suggests no true stem-scales (as typical for *Inversodicraea*) are present in this species.

Ledermanniella schlechteri (Engl.) C.Cusset (Cusset 1974: 275)

Figs 4D, 8A, B, C

Dicraeia schlechteri Engl. (Engler 1909: 381) – Type: same as for *Ledermanniella schlechteri*.

Inversodicraea schlechteri Engl. (Engler 1915: 273) – Type: same as for *Ledermanniella schlechteri*.

Inversodicraea tenuissima Haum. (Hauman 1944: 180) – Type: D.R. CONGO • Near Kinshasa [“Environs de Léopoldville”]; Aug. 1902; [4°19’00”S, 15°19’00”E]; 270 m; fl., fr.; *Gillet s.n.*; holotype: BR [BR0000008975133].

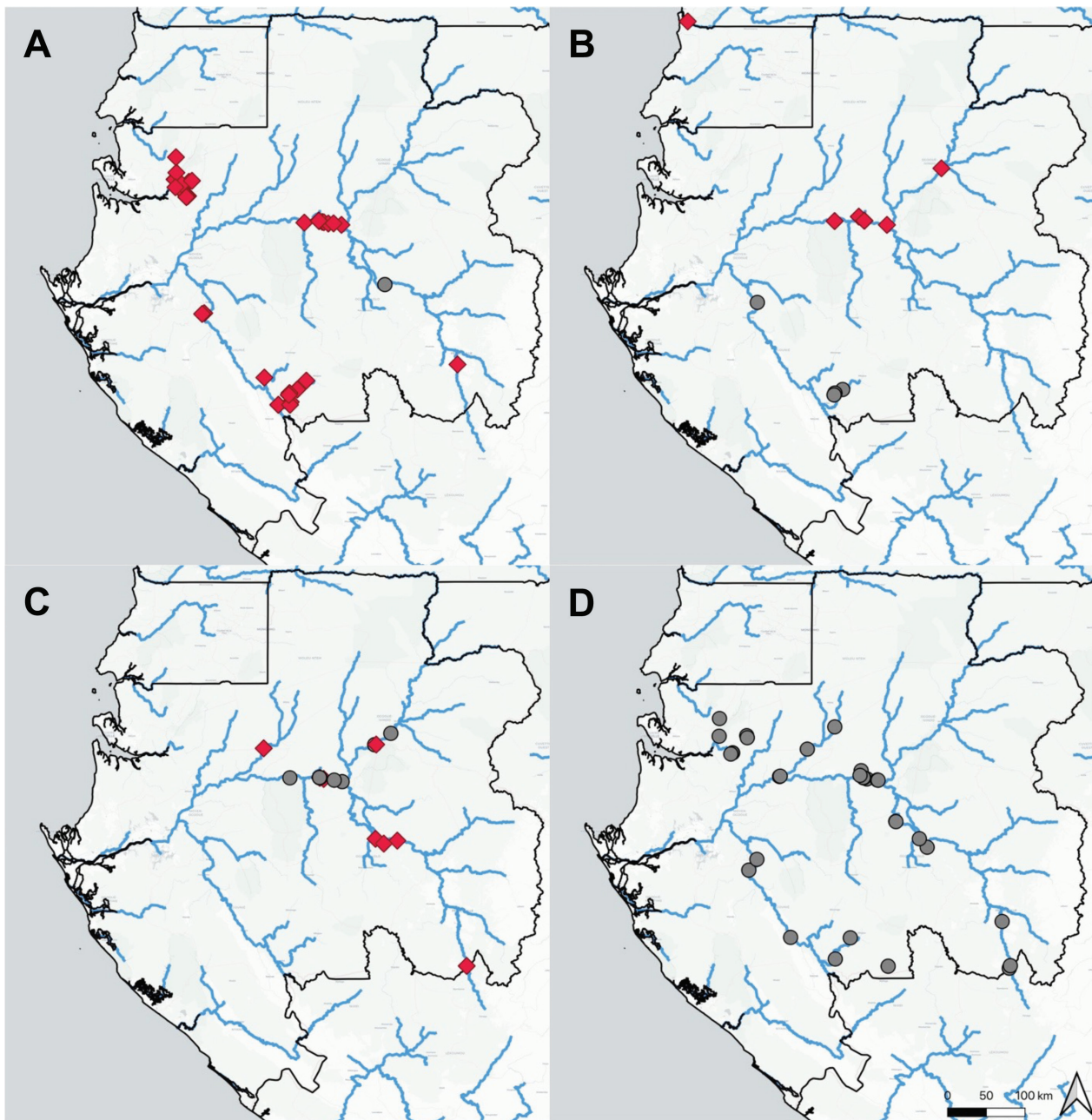


Figure 7. Distribution maps of Podostemaceae in Gabon. A. *Ledermanniella pusilla* (red diamonds), *L. tenuifolia* (grey circle). B. *Ledermanniella pygmaea* (grey circles), *Macropodiella heteromorpha* (red diamonds). C. *Macropodiella hallaei* (grey circles), *Saxicolella nana* (red diamonds). D. *Tristicha trifaria* (grey circles).

Ledermanniella tenuissima (Haum.) C.Cusset (Cusset 1974: 275) – Type: same as for *Inversodicraea tenuissima*.

Type. D.R. CONGO • Stanley Pool; Jun. 1899; [4°12'00"S, 15°33'00"E]; 270 m; fl., fr.; *Schlechter 12574*; holotype: B; isotypes: BM [BM000910391], BR [BR0000008974969].

Distribution. Cameroon, Gabon, Republic of the Congo, Democratic Republic of the Congo. Before 2018, this species was known from 29 collections, including 25 from the area of Brazzaville and Kinshasa, in the Congo and Djoué rivers. Three collections are known from Cameroon, in the Edea and Kribi regions, and in between. In 2018, Nicolas Texier collected this species seven times in Gabon, all of them from the Kongou waterfalls on the Ivindo river. It has not been found elsewhere in Gabon. This species is expected to occur in Equatorial Guinea. One collection is reported from Ivory Coast (*Aké Assi 5259*), but was not identified by Cusset, and likely represents another species.

Habitat and ecology. Falls in rivers from ca 100 to 1800 m wide, 10–460 m in elevation. According to the Gabonese collections, it is very localized when encountered, but forming dense, apparently monospecific mats. At the Kongou falls, it was found in fast-flowing current, but also at the base of falls, on rocks constantly receiving droplets from the falls, located ca 2 m above the water level, and mixed with an undetermined Poaceae species. Flowers and fruits were collected in February in Gabon, and from April to December elsewhere. In the Ivindo river, it has been found in close vicinity with *Inversodicraea nicolasii*, and *Macropodiella hallaei*, though apparently not sharing micro-habitats. This species seems restricted to falls, in fast flowing water of the largest rivers (the Congo, Djoué, Ivindo, Kienké, Nyong, and Sanaga rivers), as it was not collected in smaller rapids of those large rivers, nor in smaller rivers. Interestingly, the species was noted as edible on the collection *Descoings 5667*.

Notes. As for other species of *Ledermanniella*, *Inversodicraea*, and *Macropodiella* mentioned in this study, *L. schlechteri* can also produce flowering individuals without developed stems (*Texier 2250, 2251, 2349, and 2445*), presumably when the species is not in the ideal conditions (slower-flowing waters). More typical forms, with developed stems, were also collected at the same place (*Texier 2272, 2274, 2335*). In the absence of stems, *L. schlechteri* can still be recognized by the combination of having pollen as dyads, two stamens (exceptionally 1 or 3), linear leaves that can be divided, the absence of stipules, and, most importantly, the clearly up to 2 mm spathe stalk. When a stem is present, most of the leaves tend to be forked several times and some may bear long, narrowly triangular stipules, the spathe stalk can be up to 11 mm long, and the pedicel up to 7 mm long after anthesis.

Ledermanniella tenuifolia (G.Taylor) C.Cusset (Cusset 1974: 275)

Figs 7A, 8D, E

Inversodicraea tenuifolia G.Taylor (Taylor 1953: 72, plate 11)

Type. NIGERIA • Ogoja Province: on the Boje-Aboabam path crossing the Afi river; 13 Dec. 1950; [6°12'00"N, 8°56'35"E]; 100 m; fl.; *Keay FHI28241*; holotype: K, spirit [21952.000]; isotype: BM [BM000910401].

Distribution. Sierra Leone, Nigeria, Cameroon, Gabon. The type collection (*Keay FHI28241*) is the only known collection from Nigeria (Afi river, Ogoja Province). Cusset later identified the two Gabon collections *Le Testu 7273bis* and *Le Testu 7413* from the Ogooué river near Lastoursville (see Notes), as belonging to this species. Two collections from Cameroon are cited on GBIF (*Thomas 546 and 2655*, this latter under a wrong number) but the identifier is unknown. Since 2017, four collections were made in Gabon that most probably belong to this species. However, they were made in the Okano river, and no recent collections of this species are known from the Ogooué, despite the recent inventories in the surroundings of Lastoursville.

Habitat and ecology. Falls in rivers from ca 35 to 500 m wide, 50–220 m in elevation. It appears to be very rare, and its ecology and micro-habitats are not yet well understood. Flowers and fruits were collected in June and August in Gabon, and from October to December elsewhere. In the Okano river, it has been found in close vicinity of *Inversodicraea tenax*, *Saxicolella nana*, and *Tristicha trifaria*, though it is unclear whether they share similar micro-habitats.

Notes. The taxonomic concept associated with this species remains unclear. Examination of the two older collections *Le Testu 7413* and *Le Testu 7273bis* revealed that they lack the typical phyllotaxy of *L. tenuifolia*, as having leaves distichously arranged, whereas Cusset described them as whorled. Moreover, some leaves of the two *Le Testu* collections were forked, which is inconsistent with Taylor (1953) and Cusset (1974). In that sense they come close to dwarf members of *L. bifurcata*. However, we have not been able to examine the type collection of *L. tenuifolia* for confirmation. For now, and until more material is available, we choose to follow Cusset's conception and determinations of this species, that include the Gabonese collections *Le Testu 7413* and *Le Testu 7273bis*. We believe this name best accommodates for the recent collections made in the Okano river, even though those show longer leaves than described by Cusset (up to 7 mm long in *Boupoya 2424*), and lack the typical widening at base. Leaves are nonetheless arranged in a whorl, which is coherent with the original description of *L. tenuifolia*.

Macropodiella hallaei C.Cusset (Cusset 1978: 300)

Figs 7C, 8F, G

Type. GABON • Ogooué river at Booué ["Lit de l'Ogooué à Booué"]; 29 Jul. 1966; [0°05'24"S, 11°55'59"E]; 165 m; fl., fr.; *N. Hallé & A. Le Thomas 203*; holotype: P [P00179111]; isotypes: BR [BR0000009211575], P [P00179112, P00179113, P00179114], WAG [WAG0194843].

Distribution. Endemic to the Ogooué and Ivindo rivers, in Gabon. Before 2018, this species was solely known from three collections: *Hallé 203* (the type collection) from the Ogooué rapids at Booué, *Thollon 728* from the Ogooué rapids at Lopé, and *Courtet s.n.*, supposedly from the Chari or Congo rapids. However, collections attributed to Henri Courtet are highly suspicious with respect to their geographical origin. According to Cusset (1978, see Notes under *Macropodiella heteromorpha*), Courtet did collect a few specimens during Auguste Chevalier's 1902–1904

expedition in the “Haut-Chari” region. But it is unsure if Courtet's collections from the d'Alleizette Herbarium were collected by him or are Chevalier's collections that were wrongly attributed to Courtet by Charles d'Alleizette. In addition, all collections from Central Africa labelled as Karmann or d'Alleizette are suspected to be nothing more than fragments of other collections made in Central Africa mainly by Georges Le Testu or Théophile Klaine, as it has been proven by examination of the material from other plant families made by Olivier



Figure 8. Photographs illustrating a selection of species treated in this paper. A, B, C. *Ledermanniella schlechteri* (A: *Texier et al.* 2335; B: *Texier et al.* 2274; C: *Texier et al.* 2250). D, E. *Ledermanniella tenuifolia* (D: *Boupoya et al.* 2417; E: *Boupoya et al.* 2426). F, G. *Macropodiella hallaei* (*Texier et al.* 2249). H, I. *Saxicolella nana* (*Boupoya et al.* 1952). Photographs: Nicolas Texier (A–C, F, G), Archange Boupoya (D, E, H, I).

Lachenaud and the authors of this paper. In the case of the Courtet collection of *M. hallaei*, we can thus not be sure it was indeed collected in the Chari river by Courtet (which would represent a significant and quite surprising extension of the distribution range of the species) or if it is a collection initially collected by Chevalier, or even if it is a fragment of *Thollon* 728. Until more research is done on the d'Alleizette Herbarium, we prefer to consider the latter as the most probable explanation. Between 2018 and 2021, 22 collections of this species were gathered by the authors and colleagues, mostly at and around the type locality near Booué, in the Ogooué river. In 2018 and 2019, *M. hallaei* was discovered at two different sites on the Ivindo river: at the Touné falls (located 3.5 km away from the confluence with the Ogooué) and the Kongou falls. Inventories carried out upstream in the Ogooué river, especially around Lastoursville, Poubara, and at the border with the Republic of the Congo, did not yield this species. *Macropodiella hallaei* is the most commonly found *Macropodiella* species in Gabon.

Habitat and ecology. Falls and rapids in rivers from ca 390 to 750 m wide, 110–465 m in elevation. This species appears to be very abundant when encountered. It appears to be found mostly in the middle of rivers rather than on the rocky banks, and in fast-flowing water, where it forms dense monospecific mats. At the Booué rapids, it has also been found mixed with *I. thollonii*, *L. pusilla*, and *Tristicha trifaria*. Flowers and fruits were collected in February, July, and August. Old fruits were observed in early September.

Notes. The recently collected material is very consistent with Cusset's original description of *M. hallaei* (Cusset 1978). Minor morphological variations can nonetheless be reported. Most individuals show elongated stems, but a few stemless fertile shoots were also observed. In addition, a few stigmas are clearly papillose, among most of them being globose (sometimes bilobed) as mentioned by Cusset. Most flowers bear three stamens, but can occasionally have two, or rarely four.

Macropodiella heteromorpha (Baill.) C. Cusset (Cusset 1978: 298)

Fig. 7B

Sphaerotherylax heteromorpha Baill. (Baillon 1890: 876) – Type: same as for *Macropodiella heteromorpha*.

Macropodiella mildbraedii Engl. (Engler 1926: 466, plate 4) – Type: CAMEROON • Nyong river, south of Yaoundé [“Auf Felsblöcken im Nyong, südlich von Jaunde”]; Jan. 1914; [3°30'30"N, 11°29'33"E]; 640 m; fl.; *Mildbraed* 7749; holotype: B [B 10 0294990].

Type. GABON • Rapids in the Ogooué river at Lopé [“Rapides de Lopé”]; Feb. 1887; [0°05'38"S, 11°35'24"E]; 110 m; fl., fr.; *Thollon* 729; holotype: P [P00179126]; isotypes: P [P00179127, P00179128].

Distribution. Ivory Coast, Cameroon, Gabon. This species was originally described based on material collected by Thollon in 1885 and 1887 in the Ogooué river, at the Lopé

rapids. It is also known from the Ivindo river (*Florence* 527) and the Ogooué rapids at Booué (*N. Hallé* 201 and *N. Hallé* 204). In Cameroon, it is known from the Nyong (at Mbalmayo and south of Makak) and Ntem rivers (Mvéle and Campo falls). A single collection is known from Ivory Coast: *Guillaumet* 1569 on the Cavally river. A collection from Courtet, without collection number, is available in Paris, but its locality data are considered as very doubtful (see Notes for *M. hallaei*). Since 2019, it was collected three times by the authors and colleagues, in the Lenké river (a small tributary of the Ogooué near Booué) and in the Ivindo river (at the Touné falls near its confluence with the Ogooué).

Habitat and ecology. Falls and rapids in rivers from ca 40 to 600 m wide, 40–640 m in elevation. Unlike *M. hallaei*, this species is widely distributed, but appears to be rare when encountered. It is apparently restricted to micro-habitats submitted to fast-flowing water. In the Lenké river, it has been found mixed with *I. thollonii* and *L. aloides*. In Gabon, flowers and fruits were collected in January, February, and July, and in Cameroon in January, February, July, and December. In Gabon, old fruits were observed in early September.

Notes. Surprisingly, recent inventories carried out at the Ogooué rapids near Booué in 2019, 2020, and 2021 did not allow to rediscover this species at this site, though having been collected there in 1966 by Nicolas Hallé and Annick Le Thomas, and then noted as being abundantly present. Nevertheless, recent inventories revealed its presence in the Lenké river only 8 km northwest of Booué, and the Touné falls of the Ivindo, 30 km east of Booué. We cannot exclude the possibility of a natural replacement of this species by *M. hallaei* over time, which shares the same micro-habitats and was recently noted as very abundant at Booué. Such mechanisms are only postulated and would need further studies to be confirmed and understood. Even though *M. heteromorpha* was not recently collected at Booué, its absence from this large area of rapids (ca 550 × 900 m), difficult to access in their entirety, is not certain. This site does not seem to have suffered from any particular human-induced impact, but it is yet unknown whether past stochastic events (such as exceptional natural disturbances of the seasonal variations of water levels) may have favoured one species over another. It is also possible that in such a dynamic environment, natural species replacement may occur without any human-induced impact or natural stochastic extreme climatic events. Long-term surveys of selected areas should be designed to explore these questions, and the Booué rapids seem a good candidate, being located near the city and comprising eight different species.

Saxicolella nana Engl. (Engler 1926: 456)

Figs 7C, 8H, I

Type. CAMEROON • Nyong river, south of Yaoundé [“Auf Felsblöcken im Nyong, südlich von Jaunde”]; Jan.

1914; [3°30'30"N, 11°29'33"E]; 640 m; fl., fr.; *Mildbraed 7749a*; holotype: B [B100294988]; isotype: U [U1518023].

Distribution. Cameroon, Gabon. Before 2018, this species was only known from two collections made at Mbalmayo, Cameroon, in the Nyong river. Johannes Mildbraed collected the first specimen in 1914 (*Mildbraed 7749a*), and in 2007, a second specimen (*Kato et al. CMR-129*) was discovered at the type locality. Since 2018, the authors and colleagues collected *S. nana* nine times in Gabon, where it is now known from the Ogooué, Ivindo, and Okano rivers. It is expected to occur in other rivers in Gabon, as well as in Equatorial Guinea (since it occurs in Cameroon as well as Gabon) and the Republic of the Congo, since it has been collected at its border with Gabon.

Habitat and ecology. Falls and rapids in rivers from ca 50 to 900 m wide, 160–650 m in elevation. This species is widely distributed, but appears to be rare when encountered. In Gabon it is apparently restricted to micro-habitats submitted to slow-flowing water. It seems to form small, monospecific patches. In Booué, it was found in the vicinity of *L. pusilla*, and may share the same micro-habitat. In Gabon, flowers and fruits were collected in February, July, and August, in Cameroon, in January and February.

Notes. Cheek et al. (2022), in their taxonomic monograph of *Saxicolella*, mention that the recent material collected by the authors of the present study and colleagues most likely represent a new, yet undescribed species that they mention as an unplaced “sp. A”, being morphologically close to *S. nana* (subg. *Saxicolella*). The preliminary description provided by Cheek et al. (2022) mentions that it would differ from *S. nana* by having roots long and ribbon-like with the shoots lacking visible stems, and arising along the margins of the root in rows (vs disc-like, crustose, the shoots with visible stems, arising from the centre of the root in a cluster); leaves entire, linear, and not trifold from a point ca 1.5 mm from the base; the ovary sessile (the staminal filament inserted at its base), not with a distinct gynophore; fruit 8-ribbed (not 6-ribbed). However, as stated by the authors, they did not have access to the Gabonese material, and these observations were made from the associated pictures of living plants made in the field. After close examination of the Gabonese material against the characters mentioned by Cheek et al. (2022), as well as the collection *Kato et al. CMR-129* from the type locality of *S. nana* and widely accepted as belonging to this species, we noted that both the Gabonese and Cameroonian material showed all roots as not crustose, but ribbon-like, 0.5 to 1.5 mm wide. Branching root-ribbons may produce a carpet-like “crust” by creeping over each other. In addition, the drawing 37C by Pohl in Engler (1930: 48), displays a ribbon-like root, ca 1 mm wide, inconsistent with his own description of the species. Unfortunately, Cusset’s description in *Flore du Cameroun* (Cusset 1987), solely based on the type material, is not very helpful for this particular character either: “partie basale thalloïde foliacée, profondément divisée” is a rather

generic statement that could either correspond to crustose root or ribbon-like root. We believe it is best to consider *S. nana* as having ribbon-like roots that may produce a carpet-like crust by creeping over each other (hence Engler’s probable mistake). Regarding shoots arising along the margins of the root in rows (vs arising from the centre of the root in a cluster), our examination of *Kato et al. CMR-129* showed all roots carrying short-shoots along the flanks or margins, not at the centre. Again, the Gabonese material shows a similar feature. Unlike stated by Cheek et al. (2022), *Saxicolella nana* is described by Cusset (1987) as having stemless or sub-stemmed shoots (“pousses acaules ou subacaules”). The recently collected Gabonese material is also consistent with this description. Leaves of the Gabonese material were mentioned as entire and linear by Cheek et al. (2022) (vs trifid for *S. nana*). Close observation of the material revealed the presence of bifid leaves, and observations on *Kato et al. CMR-129* showed not only trifid leaves, but also bifid and linear ones. We believe this character can be variable, and a clear overlap suggests it may not be possible to differentiate the Gabonese material from the Cameroonian based on this feature. In addition, the ovary was mentioned as sessile on the Gabonese material by the authors of the monograph, but close observation shows that this material has a distinct gynophore, with the filament not inserted at the base of the ovary. Finally, Cheek et al. (2022) mentioned the Gabonese material as having 8-ribbed fruits, versus 6-ribbed for *S. nana*. The Gabonese collections indeed show eight ribs, including two commissural, but it is also the case for the collection *Kato et al. CMR-129* from the type locality. The original description by Engler (1926) mentioned “6-nerviium” in Latin, but Pohl’s drawings (Engler 1930: 48) show an ovary with six ribs in addition to two commissural ribs that are rather drawn as depressions. In addition, “ribs” on ovaries at anthesis do not appear to be prominent, but rather as darker lines, and commissural ones are indistinct from non-commissural at this stage, whereas, as suggested by Pohl’s drawings, the non-commissural ribs become prominent on the fruit, unlike the commissural two. We believe Engler was referring only to the six non-commissural ribs when writing “6-nerviium”. Cusset, in *Flore du Cameroun*, as well as Kato (2013) state that *S. nana* has eight ribs. As a consequence, the recently collected Gabonese material is consistent with Cusset’s updated description of *S. nana*, as having eight ribs (including the commissural ones). For all these reasons, we choose to consider the Gabonese material as a member of this species, and not as a separate, undescribed species.

Tristicha trifaria (Bory ex Willd.) Spreng. (Sprengel 1824: 22)

Fig. 7D

Type. MAURITIUS • fl., fr.; *Bory de Saint Vincent s.n.*; holotype: P [P00632465]; isotype: B [B -W 00085 -01 0].

Distribution. Tropical Africa, South and Central America, Madagascar, and islands of the western Indian Ocean. Before 2018, this species was known from Gabon from a single collection made by Frans Breteler in the Okano river (in 1978). Since 2018, 46 collections have been made in Gabon, in most of the rivers that were explored by authors and colleagues, to the notable exception of the Ivindo river. *Tristicha trifaria* is now considered one of the most common Podostemaceae species in Gabon.

Habitat and ecology. Falls and rapids in rivers from ca 20 to 600 m wide, 15–575 m in elevation (in Gabon). This species is widely distributed, and appears abundant and ecologically ubiquitous. It has been found in the largest rivers (Ogooué) as well as in small, forested rivers (Bibaka, Méba, etc.). Apparently, it can form small, monospecific patches, but was often found in association with other Podostemaceae species. In Gabon, flowers and fruits were collected in July, August, and September.

Notes. *Tristicha trifaria* is here considered as a single, very polymorphic and ubiquitous species, as suggested by Cook and Rutishauser (2007). Nevertheless, several subspecies were described, but their validity remains uncertain, and more phylogenetic studies are needed to untangle this complex (Kita and Kato 2004; Koi et al. 2015). A complete synonymy is provided in Cusset and Cusset (1988a) and is not reproduced here. The discovery of the commonness of *T. trifaria* in Gabon is less surprising than the fact that it was not discovered earlier. This is probably the result of an historic sampling bias towards the larger Podostemaceae species, even during the few inventories targeted on this family. As an example, Nicolas Hallé and Annick Le Thomas collected six species at Booué in 1966, but not *T. trifaria*, which the authors and colleagues have collected five times at this site in 2019 and 2021.

TAXA EXCLUDED FROM GABON

Dicraeanthus Engl. (Engler 1905: 94)

Distribution. Endemic to Cameroon. *Dicraeanthus africanus* Engl. is widely distributed in Cameroon, and *D. zehnderi* H.E.Hess is restricted to the Sanaga and Mbam watershed.

Habitat and ecology. Rapids and falls in rivers ca 50 to 600 m wide, 5–1050 m in elevation.

Notes. *Dicraeanthus* was mentioned as present in Gabon by Sosef et al. (2006), based on one collection (*Reitsma* 2431) gathered in 1986 at the Poubara waterfalls on the Ogooué river. The collection was determined by the collector and was not observed by Cusset. This collection was supposedly deposited at WAG but could not be retrieved there. Duplicates of *Reitsma* collections are also present in NY, but this number could not be retrieved there either. The presence of this genus in Gabon could not be confirmed, despite the fact that the Poubara site was visited again in 2019. This collection by *Reitsma* might have been misidentified as *Dicraeanthus*, especially since

a species name was not assigned by the collector. Since a hydroelectric dam was built at Poubara between 2008 and 2013, it is also possible that the *Dicraeanthus* population sampled by *Reitsma* in 1986 has since disappeared due to disturbance to the local environment, though four other Podostemaceae species were collected there in 2019: *Ledermanniella pusilla*, *L. aloides* s.l., *Inversodicraea annithomae*, and *Tristicha trifaria*. The presence of the genus *Dicraeanthus* in Gabon remains uncertain, and we choose to not accept it as present until the collection *Reitsma* 2431 can be observed by a specialist, or the species is collected in the field.

Inversodicraea ledermannii (Engl.) Engl. (Engler 1915: 274)

Distribution. Sierra Leone, Guinea, Ivory Coast, Cameroon, Democratic Republic of the Congo, Angola. This is, with *I. tenax*, one of the most widespread species in the genus. However, some collections from the southernmost part of its range may have been misidentified and may represent *I. tenax* (see Notes). Cheek et al. (2017) mention that all collections from West Africa may represent other taxa, since some material originally identified as such later proved to be separate species, e.g. *I. pygmaea* and *I. harrisii* (C.Cusset) Cheek. No complete revision of the available material was made for this study, we thus consider its distribution as mentioned by Cheek et al. (2017) with the exception of its presence in Gabon.

Habitat and ecology. Rapids and falls in rivers, 5–750 m in elevation.

Notes. This species was known in Gabon from a single collection, *Le Testu* 5983, collected in 1926 in the Offooué river (mistakenly mentioned as the Ogooué river by Cusset) on the road from Mimongo to Koulamoutou in the Ogooué-Lolo province, and identified as such by Cusset (1983). However, recent examination of pollen of this material revealed monads, while *I. ledermannii* is described as having pollen as dyads. This excludes the possibility that this material represents *I. ledermannii* and we consider this collection to represent *I. tenax* instead. *Inversodicraea ledermannii* is therefore excluded from the flora of Gabon for the moment. Its presence in the country remains plausible, as this species seems abundant in Cameroon.

Ledermanniella sanagaensis C.Cusset (Cusset 1984: 256)

Distribution. Endemic to the Sanaga and Mbam rivers, in Cameroon.

Habitat and ecology. Rapids and falls in large rivers from ca 300 to 800 m wide, ca 400–450 m in elevation. Flowers were collected in March. This species has apparently never been collected on smaller tributaries of the Mbam and Sanaga rivers, but we are unaware of potential recent inventories.

Notes. This species was included in the Flore du Gabon volume dedicated to this family (Ghogue 2018) following preliminary identifications made on material collected by the authors and colleagues in 2017. Nevertheless, additional material collected since revealed the unsuspected morphological variability of *L. aloides*. This discovery has led us to consider the Gabonese material as belonging to this species rather than to *L. sanagaensis*. This species is thus excluded from the flora of Gabon.

Macropodiella garrettii (C.H.Wright) C.Cusset (Cusset 1978: 302)

Distribution. Liberia, Sierra Leone, Guinea, Ivory Coast. This species is endemic to West Africa, where it seems common and present in multiple watersheds.

Habitat and ecology. Falls in rivers from ca 30 to 300 m wide, 20–520 m in elevation. It appears to be quite common, but not abundant when encountered. It was recorded on medium-sized to large rivers with fast-flowing current. Flowers and fruits were collected in January, February, October, and November. In Liberia, it has been found in the vicinity of *Ledermanniella aloides* and *Tristicha trifaria*.

Notes. *Macropodiella garrettii* was not mentioned as being present in Gabon in the available literature (Sosef et al. 2006; Ghogue 2018). Nevertheless, one collection from this country is available at P (*Thollon 846*), made in the Ogooué river at the Lopé rapids. This collection was identified as *M. garrettii* by Cusset in 1976, but this information was surprisingly not reproduced in her study of the genus *Macropodiella* published two years later (Cusset 1978). Recent examination of this material revealed that it does not belong to this taxon, differing from it by having two stigma lobes (vs cristate, occasionally papillose) and a cylindrical capsule (vs laterally flattened). *Thollon 846* very likely belongs to *L. bifurcata*. *Macropodiella garrettii* is thus excluded from the flora of Gabon.

DISCUSSION

Although flora treatments for both Gabon and Cameroon, as well as useful references such as the synoptic revision of *Inversodicraea* (Cheek et al. 2017), are available, the identification of this unprecedented large collection of Podostemaceae material remains a challenge. The general lack of information on the morphological variability of many taxa currently known from a very limited number of collections, and the important gaps in the understanding of the species distribution, often prevented us from associating Gabonese collections to a species name with certainty. In the context of a rapidly and constantly evolving taxonomy of Podostemaceae, future studies, including molecular data, will undoubtedly deliver new information that will require updates to the results presented here. Nevertheless, we believe that our

present results are of crucial importance for the urgent conservation of this peculiar part of Gabon's natural heritage, and we hope their publication will allow their use by various actors, e.g. in Environmental Impact Assessments and in management plans of protected areas.

These results only represent the first step towards a better understanding of the Podostemaceae distribution and variability in Gabon. They will be completed by additional collections made in 2022, and expected to be made in the upcoming years, which are expected to bring new information on the in-country distribution of the Gabonese species. For this reason, preliminary conservation assessments are not proposed within the framework of this study, and issues on the conservation of this family of aquatic plants will be specifically addressed in a future publication. The identification of this important collection also revealed several taxonomic novelties, not mentioned in this paper, which will be described in future publications.

Despite the encouraging results following these unprecedented efforts towards Podostemaceae sampling in Gabon, the vast majority of the country's rivers and streams are yet unexplored. The Nyanga river has never been explored for Podostemaceae, despite its large size and the presence of numerous rapids visible on satellite imagery, at least in the Mayombe area. The Ntem river and tributaries remain largely unexplored, as well as large portions of the Komo, Okano, and Abanga rivers. Many smaller rivers still lack any Podostemaceae collections, such as the Mvounou river and other tributaries of the Ivindo river. In addition to the first exploration of the above-mentioned rivers, some sites would need to be revisited: the type localities of *Inversodicraea boumiensis* (Boumi falls at Mbigou, on the Louétsi river) and *Ledermanniella boloensis* (Bolo falls, tributary of the Gnyé river), even though several new sites of presence of *I. boumiensis* were discovered on the Louétsi river since 2017. Sites of collections made by Georges Le Testu should also be targeted by future fieldwork efforts to complete the sampling that was made there now more than a century ago: the rapids of the Offooué river on the road from Mimongo to Koulamoutou, the rapids of the Ogoulou river at Mitingo, and the two collection sites of *Ledermanniella letestui* that were not yet re-visited (on the Douvouca and Ngounié rivers). Achieving a satisfactory sampling and level of knowledge on the Podostemaceae in Gabon appears to be a task whose immensity has just started to be understood, as revealed by the numerous novelties, both in distribution as well as in taxonomic distinction and variability of the species. The fact that Podostemaceae were also discovered in small forested rivers and streams (such as in the Monts de Cristal) and not only on waterfalls and large, sunny rapids in the largest rivers (such as the Ogooué, Ivindo, and Ngounié rivers) also expand the possibility of the presence of the family throughout Gabon. Consequently, most of the country's hundreds of streams and small rivers probably

harbour Podostemaceae, and their exploration will need important efforts and time.

ACKNOWLEDGEMENTS

This paper draws on the result of numerous field trips conducted in Gabon by the Missouri Botanical Garden (MBG) and the Herbar National du Gabon, undertaken under the Memorandum of Understanding between the MBG and the Centre National de la Recherche Scientifique et Technologique (CENAREST). We thank the director and vice-director of IPHAMETRA (Institut de Pharmacopée et de Médecine Traditionnelle), Sophie Aboughe Angone and Nestor Engone Obiang, for allowing our research. Part of our fieldwork was supported technically by the Agence Nationale des Parcs Nationaux (ANPN), and funded by the Prince Albert II de Monaco Foundation and the Communauté française de Belgique; persons from these institutions are warmly thanked. CENAREST also provided the necessary research permits for our field work (permit AR0045/19/MESRSTT/CENAREST/CG/CST/CSAR). Some field activities were conducted for the Environmental and Social Impact Assessments of the Kinguélé Aval, Ngoulmendjim, and Dibwangui hydroelectric projects, as well as the Boué sand extraction project. Staff from BIOTOPE (especially Rénaud Boulnois) and TERE (especially Amélie Morin) are warmly thanked, as well as the staff of Asokh and Louetsi Energy (Cédric Mezui), Asohna (Landry Ngala), SETRAG (Société d'Exploitation du Transgabonais) (Sounthia Ousmane), and SEEF (Société Equatoriale d'Exploitation Forestière) for granting access to the sites. We are also grateful to Jean-Philippe Biteau (Jardi-Gab) and to the Wildlife Conservation Society (WCS) Gabon for assistance provided during each of our trips to Gabon, to Eric Akouangou, Dimitri Bikissa, Christ Dibouba-Kombil, Jean de Dieu Kaparidi, Hughes Ngoké, Diosdado Nguema, Gildas Nguimbit, and Raoul Niangadouma for their assistance in the field. We are grateful to all the villagers and local authorities who granted access to their rivers, rapids, and falls, and quite often guided us to these sites. Anne-Hélène Paradis (MBG) is warmly thanked for her beautiful line drawings of *Inversodicraea nicolasii*, based on preparatory drawings by Rolf Rutishauser. Finally, we wish to thank the herbarium curators of BR, BRLU, LBV, MO, P, WAG, and Z/ZT for their assistance while working in their institutes and/or for sending specimens on loan. Simon Verlynde (NYBG) is thanked for enquiring about the Reitsma collections at NY. MNHN (P) gave access to the collections in the framework of the RECOLNAT national Research Infrastructure (ANR-11-INBS-0004). Pete Lowry is warmly thanked for his comments that helped improve the manuscript.

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SUPPLEMENTARY MATERIAL

Supplementary material 1

A list of all collections of the 20 species that are present in Gabon and that are discussed in this paper.

Link: <https://doi.org/10.5091/plecevo.96359.suppl1>