Evolutionary relationships, biogeography and morphological characters of *Glinus* (Molluginaceae), with special emphasis on the genus composition in Sub-Saharan Africa

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Abstract

Glinus is a small genus of Molluginaceae with 8–10 species mostly distributed in the tropics of the World. Its composition and evolutionary relationships were poorly studied. A new molecular phylogeny constructed here using nuclear (ITS) and chloroplast (rbcL, trnK-matK) markers confirmed the monophyly of the genus. Based on ITS analysis, the following well-supported lineages are present within Glinus: the G. bainesii lineage is recovered as sister to the remainder of the genus followed by G. oppositifolius. Three other clades are: G. hirtus with G. orygioides; G. radiatus and G. lotoides; the latter is represented by a sample from North America, and G. zambesiacus as sister to G. setiflorus + G. lotoides + G. dictamnoides. On the plastid gene tree, G. bainesii + G. oppositifolius form a sister clade to all other Glinus species. The next clade is formed by G. hirtus and G. orygioides followed by G. radiatus plus an American sample of
G. lotoides. The next branch comprises G. setiflorus as sister to G. zambesiacus + G. lotoides + G. dictamnoides. Glinus seems to have originated from Africa around the Late Eocene or Early Miocene, with further radiations to Australia and the Americas during the Late Miocene or Late Pliocene. Compared with the previous limited character set used for the diagnostics, we have found ten new morphological and carpological traits distinguishing Glinus members. In both trees based on nuclear and plastid datasets, the major phylogenetic clades cannot be characterized by the peculiar morphological characters. Many shared character states leading to their contrasting pattern in the multivariate analysis model are interpreted as a high homoplasy in the phylogenetically distant species. We paid special attention to the composition of the genus in Sub-Saharan Africa, a region with the greatest species diversity. Our results provide new insight into the taxonomy of Glinus in this region. Glinus lotoides var. virens accepted in many previous works is a synonym of G. dictamnoides that is closely related to G. lotoides based on molecular analysis and morphological characters. The status of the American populations of G. lotoides needs further investigation due to different characters of the specimens from the Old and the New World. Many specimens previously identified as G. lotoides var. virens and as the intermediates G. lotoides × G. oppositifolius belong to G. zambesiacus sp. nov. and G. hirtus comb. nov. (≡ Mollugo hirta); the latter species is resurrected from synonymy after 200 years of unacceptance. In some African treatments, G. hirtus was known under the invalidly published name G. dahomensis. Glinus zambesiacus is distributed in the southern and eastern parts of tropical Africa, and G. hirtus previously assumed to be endemic to West Africa is indeed a species with a wide distribution across the tropical part of the continent. Glinus microphyllus previously accepted as endemic to West Tropical Africa together with other new synonyms (G. oppositifolius var. lanatus, G. herniarioides, Wycliffea rotundifolia) is considered here as G. oppositifolius var. keenanii comb. nov. (≡ Mollugo hirta var. keenanii), a variety found across the entire distribution of G. oppositifolius (Australia, Asia, and Africa). The presence of the American G. radiatus in Africa is not confirmed, and all records of this species belong to G. hirtus. The lectotypes of some names (G. dictamnoides, G. herniarioides, Mollugo hirta, M. setiflora, Pharnaceum pentagynum, Wycliffea) as well as a neotype of G. trianthemoides are designated. A new key to the identification of all Glinus species in Sub-Saharan Africa is provided. A checklist is given of all accepted species in this region (G. bainesii, G. hirtus, G. lotoides, G. oppositifolius s.l., G. setiflorus, and G. zambesiacus) with their nomenclature, morphological description and geographical distribution.

**Keywords**
Biogeography, Glinus, Molluginaceae, molecular phylogeny, Sub-Saharan Africa, taxonomic revision

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Introduction

*Glinus* L. comprises six to ten species distributed in the warm regions of the world (Backer 1951; Endress and Bittrich 1993; Thulin et al. 2016). It includes annual and perennial herbs and rarely subshrubs covered with simple or stellate hairs, with exstipulate, lanceolate to obovate leaves arranged in false whorls of 3–5, several to many vetricillate, sessile or pedicellate flowers, pentamerous perianth consisting of free segments that are green dorsally and white, pink or yellow ventrally, petaloid staminodes often present originating from the outer stamen whorl, 3–30 stamens and 3- or 5-valvate, strongly hydrochastic capsules with numerous small arillate seeds. Among Caryophyllales as well as Molluginaceae, *Glinus* is characterized by the remarkable seed aril divided into two parts: a white, usually well-visible hood covering the funiculus and a large ribbon-like appendage (Pitot 1965; Narayana and Lodha 1972; Endress and Bittrich 1993; Sukhorukov et al. 2018). Molecular phylogenetic analyses based on four species (*G. lotoides* L., *G. oppositifolius* (L.) Aug.DC., *G. radiatus* (Ruiz & Pav.) Rohrb. and *G. setiflorus* Forssk.) suggest the genus is monophyletic (Christin et al. 2011; Thulin et al. 2016).

Species delimitation within *Glinus* is usually based on the pubescence details (stellate vs. simple trichomes; presence of tiny prickles on stem and leaves), leaf dimensions and shape, number of flowers in the leaf axils, and number of stamens (e.g., Bogle 1970; Short 2002; Lu and Hartmann 2003; Vincent 2003). These character sets are
sufficient for the delimitation of *G. lotoides* and *G. oppositifolius*, the most widespread species in the Old World (e.g., Hutchinson and Dalziel 1927; Backer 1951; Jeffrey 1961; Gonçalves 1978; Hargreaves 1995; Gilbert 2000; Short 2002; Retief and Meyer 2017). In some cases, seed size and ultrasculpture are useful tools for identification, e.g., in the characterization of *G. setiflorus*, *G. orygiodes* F.Muell. and *G. bainesii* (Oliv.) Pax (Sukhorukov et al. 2018). Additional characters (pubescence density and pedicel length) were used for the intraspecific descriptions of the morphologically heterogeneous *G. lotoides* and *G. oppositifolius* (Gonçalves 1965, 1970, 1978). There was an attempt to divide *Glinus* into two subgeneric groups called *Euglinus* (≡*Glinus*) and *Pseudoglinus* Endl. mainly based on stellate vs. non-stellate pubescence (Endlicher 1840), but this classification was never used.

The members of the genus are unevenly distributed across the tropics and subtropics of the world with most species present in Africa. In total, seven *Glinus* species are currently accepted in all parts of the continent (Klopper et al. 2006; APD 2019). *Glinus lotoides* is present throughout Africa (Jeffrey 1961; Maire 1962; Gonçalves 1978; APD 2019). *Glinus oppositifolius* possesses a similarly wide distribution, but is not reported from North Africa (Maire 1962; Boulos 1999; Hassan et al. 2005). Other species are considered to be restricted to smaller regions. *Glinus setiflorus* is widespread in E and NE Africa (Jeffrey 1961; Gilbert 1993a, 2000). *Glinus dahomensis* A.Chev. and *G. microphyllus* Hauman are considered to be local endemics to different territories of West Africa (Chevalier 1938; Hauman 1949; Lebrun and Stork 2003). Another African species, *G. bainesii* is restricted to Botswana, Mozambique, Zimbabwe and the eastern part of South Africa (Adamson 1961; Gonçalves 1978). A single adventive species *G. radiatus* (Ruiz & Pavon) Rohrb. from the Americas was referenced in some West African countries (Berhaut 1967, 1979; Lisowski 2009; Thiombiano et al. 2012; Schmidt et al. 2017). Additionally, it is postulated that *G. lotoides* and *G. oppositifolius* seem to freely hybridize in Africa with a large number of intermediates (Adamson 1961; Jeffrey 1961; Gonçalves 1970, 1978). Numerous specimens usually labelled as “*G. lotoides* × *G. oppositifolius*” are present in many herbaria. The reason for this identification is because of the less prominent stellate pubescence in these *Glinus* specimens compared to the typical densely pubescent specimens of *G. lotoides*. However, such hybrids were not reported from other parts of the Old World.

In a previous carpological study of all Molluginaceae (Sukhorukov et al. 2018), the disparity of many specimens belonging to the same *Glinus* species in the herbaria visited was noted. In fact, the limited number of diagnostic characters used and absence of detailed taxonomic treatment do not allow for an evaluation of the real diversity of *Glinus* in tropical Africa, the most species-rich region of the genus in the world. For this reason, a critical study of the taxonomy, morphology and distribution of the genus in Sub-Saharan Africa would be desirable. Therefore, the main aims of the present study are: (1) to conduct an expanded molecular phylogenetic analysis of *Glinus* worldwide, with further implications on its divergence and origin; (2) to deeply investigate the morphology and species distribution of *Glinus* in tropical Africa, the most species-rich region, and to provide precise diagnoses through an updated taxonomic treatment.
Material and methods

Phylogenetic analysis

Taxon sampling

In the molecular phylogenetic analysis, 149 accessions representing 31 species and 10 genera including outgroups were sampled. Except for the Indian *G. ononoides* where samples could not be amplified because of no recent collection, all other *Glinus* species were sampled. In total, nine *Glinus* species representing their entire distribution were sampled. A list of all samples used in this study is presented in Table 1.

**Table 1.** Voucher information and GenBank accession numbers for the species of Molluginaceae and outgroups included in the phylogenetic analysis (arranged in alphabetical order). The newly sequenced samples are highlighted in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Voucher</th>
<th>ITS</th>
<th>rbcL</th>
<th>trnK-matK</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Glinus bainesii</em> 8</td>
<td>Botswana, Khwai River floodplain, Moremi Game Reserve, 21 Nov 2007, <em>A. Heath &amp; R. Heath</em> 1417(K);</td>
<td>MW280260</td>
<td>MW275761</td>
<td>MW286109</td>
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<td><em>Glinus bainesii</em> 40</td>
<td>Zimbabwe, Mavingo prov., Chiredzi, 31 May 1971, <em>S. Mari</em> 1273 (LE);</td>
<td>MW280259</td>
<td>MW275762</td>
<td>MW286110</td>
</tr>
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<td><em>Glinus dictamnoides</em> 18</td>
<td>Yemen, Habbán, 2 Mar 1997, <em>M. van Slageren &amp; A. Al Gifri</em> s.n. (LE);</td>
<td>MW280251</td>
<td>MW275753</td>
<td>MW286101</td>
</tr>
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<td><em>Glinus dictamnoides</em> 41</td>
<td>India, [without exact location] 20 Feb 1955, <em>Baldev</em> 7 (MW);</td>
<td>MW280250</td>
<td>MW275752</td>
<td>MW286100</td>
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<tr>
<td><em>Glinus hirtus</em> 3</td>
<td>Tanzania, Kagera region, Njara, 6 Sep 1960, <em>R. Tanner</em> 5126 (BR000017454308);</td>
<td>MW280247</td>
<td>MW275760</td>
<td>MW286108</td>
</tr>
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<td><em>Glinus hirtus</em> 6</td>
<td>Malawi, Central Region, Nkhatako dist., 13 May 1986, <em>I.H. Petel &amp; R.B. Kaufa</em> 3184 (BRU0026262);</td>
<td>MW280249</td>
<td>MW275758</td>
<td>MW286106</td>
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<td><em>Glinus hirtus</em> 32</td>
<td>Mali, nr Bamako, Niger river, Soutuba, 4 Jul 1973, <em>D. N’Golo</em> 1291 (WAG0319754);</td>
<td>MW280248</td>
<td>MW275759</td>
<td>MW286107</td>
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<td><em>Glinus lotoides</em> 20</td>
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<td>MW286096</td>
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<td><em>Glinus oppositifolius</em></td>
<td>USA, California, <em>Erter</em> 8854 &amp; 8859 (NY);</td>
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<td><em>Glinus oppositifolius</em> 34</td>
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<td><em>Glinus oppositifolius var. keenanii</em> 4</td>
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<td>MW275756</td>
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<td>Suessenguthiella selenanthoides</td>
<td>South Africa, Acoks 18950 (K)</td>
<td>KT907390</td>
<td>FN824473</td>
<td>FN825756</td>
</tr>
<tr>
<td>Trigastrotheca bollaginica</td>
<td>Australia, Telford 11746 (CANB)</td>
<td>KT907408</td>
<td>FN824443</td>
<td>FN825725</td>
</tr>
<tr>
<td>Trigastrotheca penaphylla</td>
<td>India, n/a</td>
<td>KT907377</td>
<td>FN824455</td>
<td>FN825737</td>
</tr>
</tbody>
</table>

**DNA extraction, amplification and sequencing**

5–10 mg of dried herbaria leaf samples was used to isolate DNA using the CTAB protocol (Doyle and Doyle 1987). One nuclear (the nuclear ribosomal internal transcribed spacer, nrITS) and two plastid markers (the coding gene rbcL and the region encompassing trnK introns and matK coding genes, trnK-matK) were selected for phylogenetic analysis. The primers ITS4 and ITS5 (White et al. 1990) were used to amplify the ITS region. The rbcL and matK-trnK primer sequences were taken from Christin et al. (2011). Due to the fact that the samples were taken from herbaria and had a rather long storage term, various combinations of the forward primers trnK-matK_For A, C, G, and H and the reverse primers trnK-matK_Rev C, D, F and I were used. For rbcL, two external rbcL_4_For and rbcL_1353 and two internal primers rbcL_629_For and rbcL_760_Rev were used (Christin et al. 2011).

PCR reactions for all primers were performed in a total volume of 25 μl, using 5 μl DNA (10 ng/μl), 1 μl of each primer, 0.5 μl Encyclo polymerase (Evrogen, Russia), 0.5 μl 50× dNTP, 5 μl 10× Encyclo buffers and 14.5 μl mQ.
PCR amplification of nrITS primers was performed under the following conditions: initial denaturation for 3 min at 94 °C; 37 cycles of 1 min denaturation at 94 °C, 30 s annealing at 51 °C, 150 s extension at 72 °C, and final extension of 10 min at 72 °C (Thulin et al. 2016). PCR amplification for \textit{rbcL} was performed under the following conditions: initial denaturation for 10 min at 94 °C; 34 cycles of 30 s denaturation at 94 °C, 30 s annealing at 48 °C, 150 s extension at 72 °C, and final extension of 10 min at 72 °C. The following PCR program was used for \textit{matK}-\textit{trnK} primers: initial denaturation for 10 min at 94 °C; 34 cycles of 30 s denaturation at 94 °C, 30 s annealing at 51 °C, 2 min extension at 72 °C, and final extension of 10 min at 72 °C.

PCR products were cleaned with Cleanup Mini BC023S Kit (Evrogen, Russia). Sanger sequencing was carried at Evrogen JSC (Moscow, Russia) using the same primers as in the PCR.

**Phylogenetic inference and molecular dating**

Sequences were aligned using MUSCLE v.3.5 (Edgar 2004) and the alignment was adjusted manually using PhyDe (version 0.9971; Müller et al. 2010). Three separate analyses were performed for the nuclear and plastid DNA datasets using maximum parsimony (MP), Bayesian inference (BI) and maximum likelihood (ML). Due to a conflict between \textit{G. zambesiacus} and \textit{G. setiflorus}, all subsequent analyses were conducted using the separate datasets. Models of nucleotide substitution were chosen according to the Akaike information criterion using jModelTestv.2.1.7 (Guindon and Gascuel 2003; Darriba et al. 2012) for each gene separately. The best-fit substitution model for both the nuclear and plastid datasets was GTR + G. For the ML analyses, we used RAxML Version 8 (Stamatakis 2014). Bootstrap analyses were conducted with 2500 replicates for ML. Parsimony analyses were conducted in PAUP* 4.0a162 (Swofford 2002) with the following settings: all characters have equal weight, MaxTrees set to 1000 (auto increased by 1000), TBR branch swapping and with 20000 jackknife (JK) replicates to calculate node support. Final trees were edited in TreeGraph ver. 2.14.0 (Stöver and Müller 2010).

Divergence times for \textit{Glinus} were estimated using a Bayesian uncorrelated log-normal relaxed clock under a birth–death speciation process (Gernhard 2008) for the nuclear and plastid datasets separately. We selected a normal distribution for the secondary calibration with a standard deviation of 8.5, equivalent to the 95% HPD estimate of Yao et al. (2019) for the crown of Molluginaceae. Four independent MCMC analyses were run, each of 20 million generations sampling every 2000. The analyses were run using BEAST 2.4.5 (Bouckaert et al. 2014) on the CIPRES Science Gateway 3.3 (https://www.phylo.org; Miller et al. 2010). Output log files were analyzed using TRACER 1.6 (Rambaut et al. 2014) to assess convergence and ESS of all parameters. As “burn-in”, 10% of samples were removed prior to combining the independent runs using LOGCOMBINER 2.4.5 (Bouckaert et al. 2014). The MCC tree was generated using TREEANNOTATOR 2.4.5 (Bouckaert et al. 2014).
Biogeographical analysis

Geographical distributions of all species were compiled from herbarium specimens and field work (see section “Field and herbarium studies” below). Due to the wide distribution of some species (G. hirtus, G. lotoides, G. oppositifolius, G. radiatus), the biogeographical analysis is based on the continents and not the floristic provinces. Four geographical areas were identified: A – Africa including Madagascar; B – Asia; C – Australia, and D – America (including Galapagos Islands). The BI gene trees were pruned to remove all duplicate accessions and G. dictamnoides using the drop.tip function in the package ape (Paradis et al. 2004). The nuclear and plastid gene trees used for the analyses had 32 accessions each corresponding to 31 species. Two accessions of G. lotoides were included representing the Old World and the American populations. The coded geographic data is available in Table 2.

Ancestral range estimation (ARE) was conducted using the R package “BioGeoBEARS” (Matzke 2013, 2014). Out of the six models explored in this study, the DEC+J model was the best fit based on the AIC and likelihood ratio test (LRT) results (see Table 3). The analyses were unconstrained (without possible dispersal routes or ancestral areas assumed a priori). We allowed the inferred ancestor to occupy a maximum of three areas, corresponding to the maximum number of areas occupied by any extant species.

Based on the likelihood and AIC values, the best fit model was the DEC +J model for both nuclear and plastid datasets (Table 3). Both datasets had the same results and only varied at the divergence times.

Multivariate analysis

The same species set of Glinus as in the molecular phylogenetic analysis were included in the character matrix. The varieties of G. oppositifolius (var. glomeratus and var. keenanii) that deviate in some states of the studied characters as well as G. ononoides and G. sessiliflorus were not included. The multivariate analysis aims to test whether the morphological and carpological character subdivision corresponds with the phylogenetic reconstructions. In our previous papers, multivariate analysis provided a good support for the non-stochastic distribution of the characters in major clades of the entire Molluginaceae (Sukhorukov et al. 2018) and the genus Microtea, Microteaceae (Sukhorukov et al. 2019).

Different Glinus species were classified by group average linkage algorithm of cluster analysis constructed on a Gower similarity matrix (Gower 1971) based on seventeen characters including general morphology (life history, pubescence, leaves) and reproductive traits. This approach recognizes the species grouping based on similar characters, but does not provide a true phylogenetic context. The reliability of grouping was assessed at the level p<0.05 using SIMPROF algorithm (Clarke 1993; Clarke and Warwick 2001). Calculations were performed using PRIMER 6.1.6 statistical software (Clarke and Gorley 2006).
Table 2. The coding of the geographical areas of *Glinus* species and outgroup (all – Molluginaceae).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Geographical areas</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. bainesii</em></td>
<td>A</td>
</tr>
<tr>
<td><em>G. hirtus</em> (known as <em>G. dabomensis</em> nom. inval.)</td>
<td>A</td>
</tr>
<tr>
<td><em>G. lotoides</em></td>
<td>A, B, C</td>
</tr>
<tr>
<td><em>G. lotoides</em> (American sample)</td>
<td>D</td>
</tr>
<tr>
<td><em>G. oppositifolius</em></td>
<td>A, B, C</td>
</tr>
<tr>
<td><em>G. orygioides</em></td>
<td>C</td>
</tr>
<tr>
<td><em>G. radiatus</em></td>
<td>D</td>
</tr>
<tr>
<td><em>G. setiflorus</em></td>
<td>A</td>
</tr>
<tr>
<td><em>G. zambesiacus</em></td>
<td>A</td>
</tr>
</tbody>
</table>

**Outgroup**
- *Adenogramma glomerata* A
- *Adenogramma teretifolia* A
- *Hypertelis cerviana* A & B
- *Hypertelis fragile* A
- *Hypertelis spergulaea* A
- *Mollugo flavescens* D
- *Mollugo floriana* D
- *Mollugo nuodgrassii* D
- *Mollugo tenella* A
- *Mollugo verticillata* D
- *Paramollugo angustijolia* A
- *Paramollugo decandra* A
- *Paramollugo mediautus* A & B
- *Polpoda capensis* A
- *Pharnaceum detonsum* A
- *Pharnaceum incanum* A
- *Pharnaceum lanuginosum* A
- *Psammomphora obvoluta* A
- *Psammomphora quadrangularis* A
- *Suesenguthiella scleranthoides* A
- *Trigastrotheca molluginea* C
- *Trigastrotheca pentaphylla* B

Table 3. Results of the biogeographical analysis using BioGeoBEARS.

<table>
<thead>
<tr>
<th></th>
<th>Nuclear and plastid datasets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LnL</td>
</tr>
<tr>
<td>DEC</td>
<td>-51.29</td>
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<tr>
<td>DEC+J</td>
<td>-48.91</td>
</tr>
<tr>
<td>DIVALIKE</td>
<td>-53.03</td>
</tr>
<tr>
<td>DIVALIKE+J</td>
<td>-51.72</td>
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<tr>
<td>BAYAREALIKE</td>
<td>-66.51</td>
</tr>
<tr>
<td>BAYAREALIKE+J</td>
<td>-55.51</td>
</tr>
</tbody>
</table>

Carpological study

The seeds were investigated using scanning electron microscopy (SEM) and anatomically. The hard seed coat does not require any special preparation prior to SEM due to absence of any trichomes on its surface. The seed colliculae if present are the thickenings of the outer walls of the testa cells. After sputter coating the material with gold-palladium, the SEM observations were made with a JSM–6380 microscope (JEOL
L.

The anatomical cross-sections of seeds were prepared using a rotary microtome Micro
crom HM 355S (Thermo Fisher Scientific, USA). Before sectioning, the seeds were soaked in water:alcohol:glycerin (1:1:1) solution, dehydrated in an ethanol dilution series and embedded in Technovit 7100 resin (Heraeus Kulzer, Germany). The cross-
sections were observed using a Nikon Eclipse Ci microscope and photographed with a
Nikon DS-V1 camera (Nikon Corporation, Japan) at the Department of Higher Plants (Moscow State University).

The list of samples used for the SEM is provided in Table 4.

Choosing the territory for taxonomic study

Due to the fact that Glinus has the highest taxonomic diversity in the tropics of Africa but is represented only by a single widespread species (G. lotoides) in North Africa (Maire 1962; Boulos 1999) and a poorly known local endemic in Luxor (G. runkewitzii Täckh. & Boulos), which is closely related to G. lotoides (Täckholm and Boulos 1972), we thus exclude the northern part of the continent (Algeria, Egypt, Libya, Morocco.

Table 4. List of species and vouchers used in the carpological analysis. The specimens used for both anat-
omy and SEM analyses are marked with an asterisk (*) after the herbarium acronym. The samples of the widely distributed species G. lotoides and G. oppositifolius originated from different regions of the World.

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin of the material</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. bainesii</td>
<td>Botswana, Ngamiland, 100 m S of Samudupe newbridge, 19 Feb 2008, B. Farrington et al. 486 (K)*;</td>
</tr>
<tr>
<td>G. dictamnoides</td>
<td>Kenya, South province, Magadi road, 3000 ft, 8 Aug 1943, P.R.O. Belly 2679 (G)*; Sri Lanka, Central province, Sep 1974, D.B. Samithraaanchch 496 (K);</td>
</tr>
<tr>
<td>G. hirtus</td>
<td>South Africa, Northern Cape, Henkries, 30 Nov 1897, B. Schlechter s.n. (G); Malawi, Zomba, 2500–3500 ft, [without date] A. Whyte s.n. (G); Senegal, [without exact location and date] Perrottet 373 (G); Somalia, Ganaane to Marro Mogale Umberto I, Mar 1893, D. Rivat 736 (G); Nigeria, Niger prov., Bida distr., 1 Mar 1968, B.O. Derameola &amp; A. Bitouy 61930 (K)*; Burkina Faso, Kompienga, 40 km E of Tindangou, 2 May 2003, L. Sansu &amp; M. van Slagteren 1552 (K); DR Congo, Inkisi river, 17 Oct 2007, Niemondiene 2060 (BR000000530230).</td>
</tr>
<tr>
<td>G. lotoides</td>
<td>Indonesia, Java, 1908, H. Winkler s.n. (BM); Madagascar [Boeny Region], Madimorako, 4 Oct 1930, M. Decary 8194 (G); Israel, Upper Jordan valley, 19 Jul 1943, T. Kushnir s.n. (HUJ)<em>; Australia, Northern territory, Simpson desert, Jul 1968, A.E. Orchard 759 (K)</em>; Nigeria, Kainji Lake, 21 Jul 1973, R. Limnahoori s.n. (H1209977)*; Niger, 100 km S of Agadez, 23 Nov 1985, C. Pas 3149 (K);</td>
</tr>
<tr>
<td>G. oppositifolius</td>
<td>[India, leg. D. Freyn] (G10080773)*;</td>
</tr>
<tr>
<td>G. erythrostigma</td>
<td>Philippines, [no location and year] Blanco 385 (LE); India [state of Assam], Cachar [distr.], Mar 1873, R.L. Keenan s.n. (G); Malawi, Zomba, 2500–3500 ft, [without date] A. Whyte s.n. (G); Senegal, [without exact location and date] Perrottet 373 (G); Somalia, Ganaane to Marro</td>
</tr>
</tbody>
</table>
and Tunisia) from our investigations. The territory under study corresponds to the geographical concept designed for the framework for the investigation of biodiversity and conservation of Sub-Saharan plants (Gautier et al. 2006; Klopper et al. 2006).

Field and herbarium studies

Field investigations were conducted by the first author (APS) in many regions of Namibia in 2017–2018, Tanzania (Arusha and Kilimanjaro Regions, Unguja Island) in 2019 and 2020, in surroundings of Victoria Falls (Zimbabwe), Livingstone (Zambia) and Kasane (Botswana) in 2020. Alison and Roger Heath, Honorary Research Associates at RBG Kew, UK and Research Affiliates at University of Botswana, carried out a 20-year botanical research project in the Okavango Delta and surrounding areas of the Kalahari Desert and published interim results of the floristic investigations as a book (Heath and Heath 2009). The study of the herbarium material was undertaken by the first author (APS) at B (images), BACH (images), BM, BOL (images), BR, BRLU, COI (images), E, FI (images), FR, FT (images), G, H, HUJ, K, L (incl. U & WAG), LE, LICS (images), M, MHA, MSB, MW, P, PE (images), PRE (images), RO, STU (images), W, WU, Z (images). Only a part of the images seen from BOL, LISC and PRE were exactly identified and cited in the present article; other specimens from these herbaria requiring more detailed analysis were not cited here. No Glinus specimens were seen from Equatorial Guinea, Lesotho and West Sahara.

Distribution maps are based on the specimens cited in the text and were prepared using SimpleMappr online tool (http://www.simplemappr.net).

Nomenclature

Protologues of each plant name involved were examined for valid publication, legitimacy, and other nomenclatural issues in agreement with the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). As far as possible, original material was traced and type specimens were cited or designated here.

Results

Molecular phylogeny and dating

The combined plastid dataset of rbcL and matK-trnK comprises 4009 aligned bp and 48 accessions while the nrITS dataset has 760 aligned bp and 47 accessions. The ML and BI analyses revealed identical topologies, although slightly different from the MP (see Figs 1, 2). In all three analyses, Glinus is resolved as monophyletic. In the nuclear gene trees, Glinus is sister to Trigastrotheca F.Muell. (Fig 1; BSL 89; PP 0.97) while in the plastid gene trees it is recovered as sister to Mollugo (Fig 2; BSL 100; PP 1). In the parsimony analyses, Glinus is sister to Mollugo in both the plastid (BSP 100) and nuclear (BSP 100) gene trees.
Figure 1. Maximum likelihood phylogenetic cladogram of *Glinus* derived from the nrITS. Values above branches refer to bootstrap values resulting from the ML analysis (only values ≥50). Values below branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.95) and bootstrap values resulting from the parsimony analysis (only values ≥50). An asterisk (*) denotes a branch unsupported by either bootstrap values or posterior probability.
Figure 2. Maximum likelihood phylogenetic cladogram of Glinus derived from the combined plastid matrix (rbcL, trnK-matK). Values above branches refer to bootstrap values resulting from the ML analysis (only values ≥50). Values below branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.95) and bootstrap values resulting from the parsimony analysis (only values ≥50). An asterisk (*) denotes a branch unsupported by either bootstrap values or posterior probability.
In the plastid gene trees, *G. bainesii* + *G. oppositifolius* form a clade sister to all other *Glinus* species. In this clade, *G. hirtus* + *G. orygioideis* are in turn sister to the remaining species. *Glinus radiatus* plus the northern American *G. lotoides* sample are sister to a clade composed of *G. setiflorus*, *G. dictamnoides*, *G. zambesiacus* and *G. lotoides* (Fig. 2).

In the nuclear gene tree, *G. bainesii* is recovered as sister to the remaining species. The *G. oppositifolius* lineage is recovered as sister to a well-supported clade of (1) *G. hirtus* + *G. orygioideis*; (2) *G. radiatus* and the North American *G. lotoides* and (3) *G. zambesiacus* as sister to *G. setiflorus* + *G. lotoides* + *G. dictamnoides* (Fig. 1).

The plastid and nuclear gene trees had a conflict regarding the position of *G. zambesiacus* and *G. setiflorus*. In the plastid gene tree, *G. setiflorus* is well-supported (BSL 100; BSP 100; PP 1) as sister to a clade composed of *G. zambesiacus*, *G. dictamnoides* and *G. lotoides* whereas in the nuclear gene tree *G. zambesiacus* is well-supported (BSL 99; BSP 100; PP 0.98) as sister to a clade composed of *G. setiflorus*, *G. dictamnoides* and *G. lotoides* (Figs 1, 2).

Except for the crown node of Molluginaceae, the other nodes show very different ages for both the nuclear and plastid gene trees. The nuclear gene tree had much older node ages compared to the plastid gene tree (Fig. 3). Molluginaceae started to diversify during the Late Paleocene at ~58.97 mya (95% HPD 42.07–76.03 mya) or ~58.81 mya (95% HPD 41.8–76.03 mya) based on the nuclear and plastid trees, respectively. The diversification of *Glinus* started around the Late Eocene ~39.5 mya (stem age, 95% HPD: 13.33–30.85) or around the Middle Miocene ~13.47 mya (stem age, 95% HPD: 7.82–20.06 mya) for the nuclear and plastid trees, respectively (Fig. 3).

![Figure 3](image-url)
Biogeographical analysis

In the biogeographical analysis, the nuclear and plastid gene trees based on the reduced data showed the same topology but only varied with the divergence times. The nuclear and plastid trees based on the reduced data showed the same topology, as such similar biogeographic results only differing by node ages. The ancestral area of *Glinus* is uncertain (see Fig. 4 ACD: p = 0.21; AD: p = 0.18; ABD: p = 0.16; A: p = 0.10). The ancestral area of the crown node of *Glinus* remains uncertain (Fig. 4; ABC: p = 0.23; A: p = 0.19; AC: p = 0.19; AC: p = 0.19; AB: p = 0.14) even though it seems to be connected to Africa. There have been two shifts from Africa, one to Australia for *G. orygioides* and the other to America for *G. radiatus* and the American *G. lotoides* clade.

Diagnostic characters revisited

We coded 17 characters (14 morphological and 3 anatomical characters) used for the multivariate analyses (see Table 5). Out of the 17 characters coded, 10 are used for species delimitation for the first time (characters 4, 7, 8, 10, 11, 13, 14, 15, 16 and 17; see Table 5). The following characters and states were coded.

1. Life form: annual (0); annual to short-lived perennial herb (1); subshrub (2).
2. Pubescence: soft simple hairs (0); stellate hairs (1).
3. Presence of prickles on the stem, leaves and perianth: absent or scattered and unnoticeable (0); present and distinguishable (1).
4. Leaf veins: adaxially not recessed and abaxially not prominent (0); adaxially recessed and abaxially prominent (1).
5. Presence of pedicel: flowers sessile or subsessile (pedicel up to 5.0 mm long) (0); pedicel more than 5.0 mm long (1).
6. Flower clusters: usually up to 7–10 flowers (0); more than 10 flowers (1).
   Note. Within the state (0), *G. setiflorus* usually has 1–2 flowers in the cluster, and other species – from 4 to 10 flowers. However, this quantitative difference is not strictly expressed in *G. bainesii*, *G. oppositifolius* and *G. zambesiacus*.
7. Flower buds and closed anthocarp (Fig. 5): ovoid or roundish (0); cylindrical (1).
8. Length of perianth segments in fruiting: up to 5.5 mm (0); more than 5.5 mm (1).
9. Number of stamens: 2–7 (0); 10 or more (1).
10. Length of anthers: up to 0.6 mm (0); 0.6–1.0 mm (1); (1.0)1.2–1.8 mm (2).
11. Length of stylodia and stigmas (or style + stigmas): up to 0.6 mm (0); (0.5)0.6–1.0 mm (1); more than 1.0 mm (2).
12. Stigmas (or style with stigmas): 3 (0); usually 5 (1).
   Note. A character “Presence of the style” (united part of the stylodia) is not included in the matrix, because it can be variable within a species. The short style is mentioned in *G. lotoides* (Hofmann 1973). In *G. hirtus*, *G. lotoides*, *G. oppositifolius*, *G. setiflorus* and *G. zambesiacus* the style, if present, is equal in the length to the stigmas.
13. Seed colour: yellow-brown (0); red, brown or reddish-brown (1); dark red or almost black (2).
Figure 4. Ancestral range estimation (ARE) based on the reduced MCC tree (“BioGeoBEARS” DEC+J on Glinus unconstrained ancstates: global optim, three areas max. anagenetic dispersal rate, $d = 0.0063$; extinction rate, $e = 0$; cladogenetic dispersal rate, $j = 0.023$; likelihood ratio test, $\ln L = -48.91$). Coding of biogeographical areas as shown in the legend. Coding of species areas is given in coloured squares left of each species. Pie charts represent the ancestral area probability inferred for each node.
**Table 5.** Coded matrix for multivariate analysis of *Glinus* species. The varieties of the species that deviate in characters compared with the type variety were not included in the Table. To be consistent with the molecular phylogeny, the same species set was used for the multivariate analysis (*G. ononoides* and *G. sessiliflorus* were included in the Table, but they are absent in both molecular and multivariate analyses).

<table>
<thead>
<tr>
<th>Taxon/character states</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
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<th>10</th>
<th>11</th>
<th>12</th>
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<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. bainesii</em></td>
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<td>1</td>
<td>0</td>
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<td><em>G. lotoides</em> (Old World)</td>
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<td><em>G. lotoides</em> (New World)</td>
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<td><em>G. ononoides</em></td>
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14. Seed length: 0.35–0.60 mm (0); 0.7–0.9 mm (1).

15. Seed ultrasculpture (Fig. 6–9): seeds smooth or with barely noticeable colliculae (0); seeds without ridges, only with colliculae (1); seeds with concentric ridges and colliculae (2) (Figs 6A, B, 8G, H).

   Note. Two seed types were observed in *G. hirtus*: seeds with smooth surface found in several specimens only (Fig. 6C, D) and more common colliculate ones (Fig. 6E, F). The colliculate ultrasculpture is the most common type in almost all species and their varieties (Figs 6E, F, 7A–D, 8A–F, 9C–H). All *Glinus radiatus* samples have a smooth seed surface (9A, B), as well as those of *G. ononoides* (Fig. 6G, H) and some specimens of *G. hirtus* (Fig. 6C, D).

16. Stalactites in the testa (Fig. 10): not well-visible (0); prominent (1).

17. Thickness of the seed-coat testa: thin (up to 8 μm) (0); thick (10–30 μm, the thickest area is collicula) (1).

   Note. Due to the presence of the colliculae making the seed coat more robust in these areas, the thickness of the seed coat was measured between them.
Evolution and taxonomy of *Glinus*

**Figure 7.** Seeds of *Glinus* species **A, B** *G. lotoides* (Israel, T. Kushnir s.n., HUJ) **C, D** *G. dictamnoides* (Kenya, P.R.O. Bally 2679, G). Magnification: 120× (**A, C**); 500× (**B, D**).

**Multivariate analysis**

The data of the multivariate analysis were evaluated using the matrix of the characters and their states provided in the Table 5. The results of cluster analysis of all characters suggest the existence of four significantly different groups within *Glinus*, these branches are highlighted in black (Fig. 11): (1) *G. bainesii* + *G. orygioides* (2) *G. setiflorus* (3) *G. lotoides* (Old World) + *G. dictamnoides*, (4) *G. radiatus* / *G. lotoides* (New World) + *G. zambesiaceus* + *G. hirtus* / *G. oppositifolius*. The groups are significantly (p<0.05) distinct on different levels of Gower’s index.

The first group, *G. bainesii* and *G. orygioides*, share 13 characters states, and two of them (3:1, 15:2) are unique and not known in other *Glinus* species. *Glinus lotoides* from the Old World, *G. dictamnoides* and *G. setiflorus* (groups 2 and 3) show morphological similarity based on 15 characters (1:0, 2:1, 3:0, 4:1, 5:0, 6:0, 7:0, 8:1, 9:1, 10:1, 12:1; 13:2, 15:1; 16:1; 17:1). The highest number of the same character states (16 out of 17) is detected in the third group *G. lotoides* (specimens from the Old World) – *G. dictamnoides*. The fourth group unites the species with different character states, and only two of them (1:0 and 3:0) are the same for each species. Within this group, 13 character states are shared between *G. radiatus* and the American populations of *G. lotoides*, and between *G. hirtus* and *G. oppositifolius*. *Glinus zambesiaceus* shares 10 character states (1:0, 3:0, 4:0, 7:1, 12:0, 13:1, 14:0, 15:1, 16:1, 17:1) with both *G. hirtus* and *G. oppositifolius*. 
Figure 10. Seed coat cross-sections A G. bainesii B G. hirtus C G. lotoides D G. oppositifolius E G. or-ygioides F G. radiatus G G. sessiliflorus H G. setiflorus I G. zambesiacus. Scale bar: 10 μm. Glinus dictaminoides has the same seed coat structure as G. lotoides and is not illustrated here. Origin of the material is provided in the Table 4 and is designated with an asterisk (*).

Discussion

Morphological interpretation of the phylogenetic results

Monophyly of Glinus is not surprising because all species share the same unique trait (presence of seed aril) not encountered in other genera of Molluginaceae. Mollugo s.str. was suggested to be closely related to Glinus after the first molecular studies (Christin et al. 2011; Thulin et al. 2016), but this is only partially supported by our results. The merging of Glinus into Mollugo s.l. previously undertaken by several authors (e.g., Bentham in Bentham and Mueller 1866; Oliver 1871; Trimen 1894; Clifton 2003) cannot be accepted, even though species of both Mollugo and Glinus share similar morphological and carpological characters, e.g., whorled leaves, leafy inflorescences, multi-seeded capsules, colliculate seeds with a relatively thick seed coat with stalactites. The carpological differences between the related genera were determined by Sukhorukov et al. (2018) based on an extended seed analysis.

The major clades of Glinus do not possess distinct morphological characters. None of the peculiar character states provided in Table 5 are known in G. bainesii and G. oppositifolius, the earlier diverging lineages of Glinus. Nevertheless, both species share 9 out of 17 character states (2:0, 4:0, 5:1, 6:0, 7:1, 12:0, 14:0, 16:1, 17:1). The longitudinally ridged seeds of G. bainesii are absent in G. oppositifolius and almost all
Evolution and taxonomy of *Glinus* species by group average linkage algorithm of cluster analysis based on 17 characters. Black branches connect significantly (P < 0.05) different groups, red branches – insignificantly different groups.

Other species except in the phylogenetically distant *G. orygioides*. Seeds with concentric ridges and colliculae (character state 15:2) are rather common in many *Mollugo* s.str. (Sukhorukov and Kushunina 2017).

The close relationship between the Australian *G. orygioides* and *G. hirtus* is unexpected from a morphological point of view. These species share only five character states (4:0, 10:1, 12:0, 16:1, 17:1). Compared with other *Glinus* species, *G. orygioides* differs by being a subshrub, while *G. hirtus* has no peculiar character states. Surprisingly, *G. hirtus* shares eleven character states (mostly gross morphological) with the unrelated *G. radiatus*. From the six states distinguishing these two taxa, only one (seed
colour) is visible to the naked eye; however, some *G. hirtus* specimens have yellow seeds (13:0), a usual character state in *G. radiatus*. The other five character states are micromorphological (length of anthers and stylodia, seed ultrasculpture, presence of stalactites in the testa and its thickness). This similarity in the gross morphology has caused the misidentification of both species.

The results of the molecular analysis support the polyphyly of *G. lotoides*: a sample from the New World forms a clade together with *G. radiatus*. The specimens of American *G. “lotoides”* seen by us have yellow or bright brown seeds, like *G. radiatus* (not dark red or almost black as in *G. lotoides* s.str.: state 13:2 in the Table 5), and differ from it by colliculate seed sculpture (e.g., Thieret 1966) and larger perianth segments (Christy 1998). We provisionally accept only one native species in the Americas (*G. radiatus* s.l.). The close relationship between the Old World *G. lotoides* specimens and *G. setiflorus* is supported by many identical character states (Table 5; Figs 7A–D, 10C, H), and they both share nine states with *G. zambesiacus*. In the absence of a well-resolved relationship between *G. lotoides* and *G. dictamnoides* in the plastid and nuclear gene trees, we suggest that *G. dictamnoides* be treated as a synonym to *G. lotoides*, as was proposed in the earlier studies (e.g. Backer 1951; Zohary 1966; Hassan et al. 2005).

Due to the discordance between the gene trees and multivariate analysis of morphological characters, we cannot propose any infrageneric groups within *Glinus*. We assume that character states shared between phylogenetically distant taxa should be interpreted as homoplasies. Similarly, the former genus subdivision proposed by Endlicher (1840) and based on the pubescence details is also not supported.

**Biogeography**

Both the plastid and nuclear gene trees suggest that *Glinus* started to diversify during the Neogene. Even though our results do not indicate a clear origin of *Glinus*, it seems to be connected to Africa (Fig. 4). Origin and adaptation to Neogene aridification in Africa has also been reported in many other plant lineages such as *Acridocarpus* Guill. & Perr., Malpighiaceae (Davis et al. 2002), *Coccinia* Wight & Arn., Cucurbitaceae (Holstein and Renner 2011), *Guibourtia*, Fabaceae (Tosso et al. 2017), *Manilkara* Adans., Sapotaceae (Armstrong et al. 2014) and the tribe Melastomatoideae, Melastomataceae (Veranso-Libalah et al. 2018). The Australian *Glinus oryioides* and the American *G. radiatus* group probably originated during the Late Miocene and Pliocene based on the plastid and nuclear gene trees, respectively. Long-distance dispersal might be the most appropriate explanation for migration of the species to Australia and America during the Neogene.

**Extant geographical distribution**

Two species from the basal clade(s) – *G. oppositifolius* and *G. bainesii* – prefer different climates. *Glinus bainesii* is well adapted to the hot semi-arid climate [climate classification used here is according to Köppen (1936), with additions by Geiger (1961)].
**Glinus oppositifolius** is more frequently found in regions with tropical rainforest and savanna climates. In the regions with hot semi-arid or desert climates, it clearly prefers the habitats near water sources (e.g., river banks). Another widely distributed species, *G. lotoides*, as well as East African *G. setiflorus*, are drought-adapted species and avoid territories with tropical rainforest and monsoon climates.

Altogether, we accept 9–10 species in (sub)tropical parts of the World. These can thrive in different habitats (riversides, deserts, stone outcrops, sandy coastal areas) and sometimes are noxious weeds, especially in the tropics with a humid climate. The species number is unevenly distributed around the World (Fig. 12). Four species occur in Australia (*G. lotoides*, *G. oppositifolius*, *G. sessiliflorus* and *G. orygioides*, endemic to N & C Australia: Short 2002, 2011), with the northern regions being the most species-rich. The Americas are reported to have two species: *G. lotoides*, considered to be an alien from the Old World, and *G. radiatus* (Grayum and Koutnik 1982; Boetsch 2002; Vincent 2003; Vigosa Mercado 2015). However, the presence of *G. lotoides* in the New World is doubtful. Further taxonomic studies are needed to decide whether the carpological and chorological data support the acceptance of the second (presumably native) *Glinus* species in North America. The species number in Asia is two or three: poorly known Indian *G. ononoides* with only two old collections seen by us (G! K!), *G. lotoides* and *G. oppositifolius* (e.g., Backer 1951; Hedge and Lamond 1975; Heller and Heyn 1994; Lu and Hartmann 2003; Townsend 2016; Byalt and Korshunov 2020) with synonyms or insufficiently studied taxa described from Asia (see Taxonomic section below). Only one species (*G. lotoides*) is present in S Europe (Paradis 1993; Tutin et al. 1993) as well as in North Africa (Maire 1962; Boulos 1999). On the contrary, the Sub-Saharan area incorporates two to six species, depending on the regions (Fig. 12). The most species-rich region (5 spp.) is East Africa (Kenya and Tanzania). A large region with a tropical savanna climate is the second richest region with four species.

**Possible mode of species dispersal**

All *Glinus* species have hydrochastic capsules which open when triggered by rain drops (ombrohydrochory). This seems to be a somatic response of the plants to the climates characterized by alternating dry and wet periods. It is also known in many members of the Aizoaceae (Parolin 2006; Kurzweil and Burgoyne 2009) from areas with hot desert and semi-arid climates. In light of the presumable African origin of *Glinus*, such disseminative adaptation allows for a rapid seed dispersal during the rainy season.

In all species of the genus, the dispersal unit is a seed. The rains enable rapid dehiscence of the capsules and further dispersal of the seeds with surface water runoff. Additionally, the dry seeds due to their tiny size can easily roll over the substrate (Sulakshana and Raju 2018). However, it is unlikely that the seeds can move long distances in this manner, and, at least in *G. lotoides*, they remain viable only for several months (Bhatia 1987; Teshome and Feyissa 2015). We suggest that epizoochory may play a significant role in the dissemination, whereby moist substrate particles with seeds attached may inadvertently be carried by animals or humans.
Figure 12. The number of *Glinus* species around the world. Areas coloured in mauve – one species, blue – two species, green – three species, yellow – four species, red – five species. Area boundaries are approximated. *G. ononoides* is a poorly known Indian taxon that needs to be studied further.

Taxonomic treatment of *Glinus* in Sub-Saharan Africa

The following treatment provides a new insight into the identification, taxonomic composition and distribution of *Glinus* in Sub-Saharan Africa where the genus is represented by 6 species.


≡ *Rolofa* Adans., Fam. Pl. 2: 256 (1763), nom. illeg.
      Type: *Glinus lotoides* L.
      Type: *Physa madagascariensis* DC., Prodr. 1: 393 (1824) (= *Glinus oppositifolius* (L.) Aug.DC.)
≡ *Plenckia* Raf., Specch. 1: 194 (1814), nom. rej.
      Type: *Plenckia setiflora* (Forssk.) Raf. (≡ *Glinus setiflorus* Forssk.).
Description. Annual, rarely perennial, prostrate herbs or erect subshrubs with a rootstock, covered with stellate or simple (multiseriate, soft and crispate) hairs, in the latter case additionally with multiseriate, stout thick-walled and broad-based hairs (prickles). Stems branched from the base, often forming mats, rarely erect (G. orygioides). Leaves in false whorls, lanceolate to obovate, entire or denticulate (mostly in their upper half), with several lateral nerves that can be adaxially recessed and abaxially prominent. Flowers usually several to many (up to 20) in leaf axils forming loose or rarely dense inflorescences, bracteate, sessile or pedicellate. Perianth of 5 free oblong, ovate or roundish segments, green (brown) abaxially and white, pinkish or yellowish adaxially, with a green or brown midvein, horizontally spreading when fully opened, sometimes white petaloid staminodes present, always shorter than perianth segments. Stamens (2–4)5–30, outer stamen series corresponding to another staminode whorl (if stamen number is more than 5) often with filaments terminating with teeth (and without anthers), 0.3–1.8 mm, oblong or roundish; anthers yellow; pollen tricolpate (studied in G. lotoides: Perveen and Qaiser 2000). Stylodia 3–5, free or united in lower half into a style. Anthocarp (fruit enclosed by perianth) cylindrical or ovate to roundish. Fruit a hydrochastic loculicidal capsule. Ovary three- or five-carpellate, ovules arranged in two rows. Seeds usually more than 50, yellow, red, brown or black, up to 1.0 mm long, ovoid or reniform, smooth or with numerous colliculae; seed aril divided into two parts: a white, very noticeable hood covering the funiculus and a large ribbon-like appendage, sometimes the hood is reduced. Embryo curved; perisperm abundant and easily visible (in larger seeds) or scanty (in small seeds).

The basic chromosome number in G. radiatus is x = 9 (Lane and Keil 1976), which corresponds with that of other Molluginaceae (Bogle 1970, with references therein). However, Mitra and Datta in Löve (1967) indicated the basic number x = 18 for the Indian populations of Glinus lotoides and G. oppositifolius.

Artificial key to the Glinus species in sub-Saharan Africa based on gross morphology

1 Plants glabrous or with simple (sometimes additionally with prickle-like) hairs mostly localized in young plant parts .................................................................2
   1. Plants covered with stellate hairs ........................................................................3

2 Stems, sometimes leaf petioles and perianth segments with tiny (up to 0.5 mm) stout prickle-like hairs; perianth segments in fruiting 7.0–9.0 mm long; stamens more than 10; anthers 1.3–1.5 mm long; seed surface with longitudinal ridges bearing colliculae .................................................................G. bainesii
   2. All plant parts without stout prickle-like hairs, or such hairs almost unnoticeable; perianth segments in fruiting up to 5.0(5.5) mm long; stamens (3)5(7); anthers up to 1.0 mm long; seed surface smooth or with colliculae, but in latter case without longitudinal ridges .........................................................G. oppositifolius

3(1) Plants white to grayish-green due to abundant stellate hairs; leaves obovate, broadly obovate or roundish, their veins adaxially recessed and abaxially prominent;
flower buds or anthocarp (capsules with the closed perianth) ovoid or roundish, 5.0–12.0 × (3.0)3.5–9.0 mm; stigmas usually 5; seeds dark red to black ..........4

– Plants green; leaves narrowly oblong to obovate, veins neither recessed nor prominent; flower buds and anthocarp cylindrical, 3.0–7.0 × 2.0–3.0 mm; stigmas 3; seeds reddish or brown-red .................................................................5

4 Glomerules of (1)2–4 flowers; perianth in fruiting 8.0–12.0 mm long; seeds 0.7–0.9 mm long; funicular hood often reduced .................. **G. setiflorus**

– Glomerules of 4–12 flowers; perianth in fruiting 5.5–8.5 mm long; seeds 0.5–0.6 mm long; funicular hood easily visible ................................. **G. lotoides**

5(3) Flowers sessile or with short pedicels up to 3.0(4.0–5.0) mm; perianth in fruiting (3.5)4.0–5.0(5.5) mm long; stamens (3–4)5(6–8); anthers 0.6–0.9 mm long; seeds (0.35)0.40–0.50 × 0.25–0.30 mm............................................ **G. hirtus**

– Flowers with well-developed pedicels 5–20 mm long, rarely 2–5 mm long; perianth in fruiting 6.5–8.0 mm long; stamens more than 10; anthers (1.0)1.2–1.8 mm long; seeds 0.5–0.6 × 0.35–0.50 mm .................................. **G. zambesiacus**

List of accepted species in Sub-Saharan Africa (arranged alphabetically)

**Glinus bainesii** (Oliv.) Pax, Nat. Pflanzenfam. 3(1b): 40 (1889).


Type: [BOTSWANA, North-West distr.] “Koobie [Chobe] to N.[orton] Shaw valley, Jan–Mar 1863, T. Baines [s.n.]” (K000232022!).

**Note.** (1) The so-called “Norton Shaw valley” lies close to Ngami Lake (Passarge 1904), and “Koobie” should be applied to “Chobe”; (2) The type specimen indicated by Adamson (1961) as kept at GRA is absent in this herbarium (Tony Dold, pers. comm.).

**Description.** (Fig. 13A–G). Annual or perennial, prostrate or ascending, up to 12 cm tall, often forming large mats up to 1.5 m in diameter. Stems covered with simple crispathe hairs; stems, peduncles and sometimes leaf petioles and midveins additionally covered with small, stout hairs (prickles). Leaves rosulate, short-lived, and cauline, green, stout, entire, 10.0–17.0 × 2.0–4.0 mm, oblanceolate or narrowly oblong, sessile or short-petiolate (petioles up to 3.0 mm), mucronulate, veins neither recessed adaxially nor prominent abaxially. Flowers in clusters of 2–7, distant, pedicellate, pedicels 5.0–16.0 mm, in fruiting up to 20.0 mm; buds and closed anthocarp cylindrical. Perianth segments in flowering 6.0–8.0 mm × 2.5–3.0 mm (10–16 mm in diam.), in fruiting 7.0–9.0 mm long, glabrous or sparsely pubescent, dorsally green or with white margins, ventrally white, creamy, pink or pale mauve. Stamens 10–15, outer stamen series (petaloids) sterile, with filaments terminating in teeth; anthers 1.3–1.5 mm long. Stigmas 3, ~1.2 mm long. Seeds 0.6 × 0.5 mm, almost black, with longitudinal ridges carrying colliculate cells; aril hood clearly visible, 0.25 mm long.

**Remarks.** In the herbaria *G. bainesii* (Fig. 14) is often confused with *G. oppositifolius*, but it is differentiated from the latter species by having small prickles, larger perianth and anthers, and seeds with longitudinal ridges (Table 5).
Figure 14. A herbarium specimen of Glinus bainesii (Botswana, Northern distr., 17 km SE of Maun at Samadupe drift over Botletle river, 23 Jan 1972, H. Biegel & G. Russell 3733, K001394831). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

Habitat. Riverbed sands, flat flood plains, margins of muddy seasonal pans, sparsely vegetated areas at elevations 0–1200 m a.s.l. Associated plants found in Botswana: Dicerocaryum eriocarpum, Pterococcus oppositifolius var. oppositifolius, poor soil
Evolution and taxonomy of Glinus


Distribution (Fig. 15). Botswana: Ngamiland, Kwebe Hills, 3300 ft, 4 Feb 1898, E.J. Lugard 152 (K); Northern Bechuanaland, Sigere pan, 30 miles W of mouth of Nata river, 896 m, 25 Apr 1957, Drummond & Seagrief 5216 (K); Ngamiland, Sehitwa, Lake Ngami, 930 m, 25 Mar 1961, H.M. Richards 14849 (K); Northern distr., 17 km SE of Maun at Samadupe drift over Botletle river, 23 Jan 1972, H. Biegel & G. Russell 3733 (BR0000017454490, K001394831, M, P04577251); Northern distr., Moremi reserve, 19°10.4’S, 23°15.7’E, 26 Jan 1974, P.A. Smith 848 (B101143636, K, WAG1103318); Northern distr., Nata river delta, 21 Apr 1974, J.E. Ngoni 529 (K, PRE0825248); Ngami Lake, 13 Dec 1982, P.A. Smith 3981 (BR0000017454506,
E, K); between Motswiri and TFC [Tsetse Fly control] road, 18°45.671'S, 23°15.033'E, 966 m, 19 Mar 2003, A. Heath & R. Heath 428 (K); 17 km S of Tsetse Fly control road, 18°45.565'S, 23°05.208'E, 964 m, 28 Nov 2004, A. Heath & R. Heath 734 (K); Khwai River floodplain, Moremi Game Reserve, 19°10.505'S, 23°44.176'E, 940 m, 21 Nov 2007, A. Heath & R. Heath 1417 (K); Ngamiland, 100 m S of Samudupe bridge, 20°6'59"S, 23°31'38"E, 938 m, 19 Feb 2008, B. Farrington et al. 486 (K);


South Africa: [Limpopo province] Messina [Musina], alt. 2000 ft, Sep 1917, F.A. Rogers 19299a (BM, G); Transvaal [Limpopo prov.], Messina [Musina], 27 May 1927, R.G. Young 18391 (BM); Transvaal prov., Ellisras, 2900 ft, 24 Feb 1954, L.E. Codde 8491 (K, L1698855); Transvaal [Limpopo prov.], Potgietersrust [Mokopane], Doornpoort Farm, 19 Jan 1955, A.D.J. Meeuse 9522 & 9522a (K, M); Transvaal [Limpopo prov.], Waterberg distr., Tamboetie river, Ellisras–Vila Nova road, 7 Jan 1959, A.D.J. Meeuse & R.G. Strey 10446 (BM, BOL217406, BRLU0026260, K, M, Z-000092195); Transvaal [Limpopo prov.], Kruger NP, 31 Jan 1962, H. Schlieben 9321 (W20978); Mpumalanga prov., Kruger NP, 26 Nov 2015, G. Zambatis 1195 (PRE0990262);

Zimbabwe: [Masvingo prov.] Sabi-Lundi Junction District, Chiribira Falls, 6 Jun 1950, Wild 3448 (B101143602, BR0000018267976, K); [Matabeleland South prov.] Gwanda Distr., 700 ft, Nov 1956, R.M. Davies 2185 (K); [Masvingo prov.] Nuanesi, nr Malipate, 2 May 1961, R.B.Drummond & R.O.B. Rutherford-Smith 7680 (K); [Masvingo prov.] Chiredzi, nr Sabi-Ludi junction, 31 May 1971, S. Mari 1273 (K, LE);

General distribution. Endemic to Zambezi floristic province (according to Takhtajan 1986). Reported from Okavango region, NE Namibia (Friedrich 1966), but the cited specimen (“Lightfoot 65”) has not been found by us (SAM?).

**Glinus hirtus** (Thunb.) Sennikov & Sukhor., comb. nov.
urn:lsid:ipni.org:names:77215157-1

Evolution and taxonomy of *Glinus*


Lectotype (designated here): South Africa. “E Cap. bon. spei” [Cape of Good Hope], *C. Thunberg* (UPS-Thunb 2851; isolectotype UPS-Thunb 2850).


Original material: [Benin] Dahomey, Kouandé à Kontobiri entre Quétécou et Firou [from Kouandé to Kontobiri between Quétécou and Firou], 29 Jun 1910, *A. Chevalier* 24288 (P00461735).

= *Glinus congolanus* Hauman in herb. BR.

**Description.** (Figs 16, 17). Annual, highly branched, with prostrate or ascending stems up to 100 cm long, covered with stellate (sometimes very scattered) and branched hairs, prickles absent. Leaves rosulate, short-lived, and cauline, green or grayish-green turning red at senescence, sparsely to moderately pubescent, rarely glabrous, petiolate (petioles up to 10.0 mm), entire or slightly crisp or scarcely denticulate, ovoid, obovate or oblong-spatulate, 10.0–40.0(45.0) × 3.0–15.0(18.0) mm, acuminate, lateral veins neither recessed adaxially nor prominent abaxially. Flowers in clusters of 8–20, distant or approximated in the upper part of the inflorescence, 8–13 mm in diameter, sessile or with short pedicels up to 3.0(4.0–5.0) mm; buds and closed anthocarp cylindrical. Perianth segments in flowering 3.0–4.2 mm long, in fruiting (3.5)4.0–5.0(5.5) mm long, glabrous or sparsely pubescent, dorsally green or with white margins and ventrally white or mauve; tips ± recurved at fruiting. Stamens (3–4)5(6–8), sometimes with sterile teeth; anthers 0.6–0.9 mm long. Stigmas 3, 0.5–1.0 mm long. Seeds reddish or brown-red, (0.35)0.40–0.50 × 0.25–0.30 mm, colliculate or rarely almost smooth, longitudinal ridges absent.

**Note.** *Mollugo hirta* described from South Africa was very rarely accepted in old taxonomic literature, and only cited as a poorly known species (Fenzl 1836). Otherwise, it has been commonly considered a synonym of *G. lotoides* (e.g., Fenzl 1840; Harvey and Sonder 1860; Just 1879; Adamson 1961; Hedge and Lamond 1975; Gonçalves 1978). We state for the first time that (1) *Mollugo hirta* must be resurrected in specific rank based on both molecular and morphological studies as *G. hirtus*, and (2) this species is conspecific with the name *G. dahomensis*. Specimens of this species were misidentified in collections with various names, particularly *G. lotoides*, *G. lotoides* var. *virens*, *G. lotoides × G. oppositifolius*, *G. spergula*, and *Mollugo glinoides* (both latter names belong to the synonymy of *G. oppositifolius*). Almeida (1998) referred the Indian plants to *G. lotoides* subsp. *hirtus* in the belief that they differ from the European populations (*G. lotoides* subsp. *lotoides*), but he did not indicate any differences between them. However, his description of the subspecies rather belongs to *G. lotoides* based on the number of stamens (>10) and stigmas (5), while *G. hirtus* has up to eight stamens and three stigmas.

The name *G. dahomensis* was originally introduced (Chevalier 1938) with a description in French, whereas the nomenclatural code required a description or diagnosis in Latin. To date the name *G. dahomensis* remains invalidly published because of having been commonly placed in the synonymy of *G. lotoides* var. *virens.*
While considering *G. hirtus* distinct from *G. lotoides*, we resurrect the name published by Thunberg because it is the only one available for the species as circumscribed in our study.

*Glinus hirtus* is morphologically very close to *G. ononoides* Burm.f. described from India (Burman 1768), a species completely forgotten in the past (Dizionario… 1842) and present. The differences between both species are minor and limited to the following characters: (1) the type of *G. ononoides* has stellate hairs that are mostly localized on the young stem parts and leaves and additionally very short (up to 0.4 mm)
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Figure 17. A herbarium specimen of *Glinus hirtus* (Central African Republic, 300 m NW of Gounda, 9°18’N, 21°12’E, alt. 450 m, 28 Jul 1982, J.M. Fay 2763, K001394828 as *G. dahomensis*). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

prickle-like simple hairs present on the stem. In contrast, *G. hirtus* has well-expressed stellate pubescence on stem and perianth, and no prickle-like hairs, and (2) the seeds of *G. ononoides* are smooth, whereas those of *G. hirtus* are usually colliculate (however,
the seeds of the specimens from Senegal, [without date] Perrottet; Botswana, 1982, P.A. Smith; and Somalia, 1893, D. Riva, are smooth). The collections of *G. ononoides* are very scarce, and the variability of the characters mentioned and the distribution of the species in Asia require further investigations. The morphologically very similar, but phylogenetically distant *G. radiatus* distributed in South and Central America has shorter anthers (0.35–0.6 mm long) and stylodia (0.2–0.6 mm long) as well as smooth seeds; by contrast, *G. hirtus* has longer anthers (0.7–0.9 mm) and stylodia (0.5–1.0 mm) and its seeds are usually colliculate (rarely smooth). Also, the distribution areas of both species do not overlap.

**Habitat.** River beds, wetlands, damp areas or as a weed, mostly on sandy soils at elevations 0–2400 m a.s.l. Sometimes, *G. hirtus* is found growing together with *G. oppositifolius* (collections of Cook 405 & 408 from Nigeria, K!). Observations in Botswana recorded the following associated plants (A. Heath & R. Heath 457, K): *Cynodon dactylon, Sida cordifolia, Glinus bainesii, Portulaca oleracea, Cyperus polystachyos, C. compressus, C. longus, Pseudognaphalium luteo-album*. Flowers in early and main rains (obs. in Botswana by A. Heath and R. Heath).

**Distribution** (Fig. 18). The species was originally known as *Mollugo hirta* from South Africa (Thunberg 1794) and not reported as a distinct species from any other African territory. *Glinus dahomensis* was described from Benin (Chevalier 1938), and later reported from Belgian Congo (DR Congo) (Hauman 1951). Hauman (1951) also noted the presence of the species in other territories of tropical Africa (“Du Dahomey au Transvaal”). However, he probably was not sure of that and did not reidentify the specimens from any other countries. We confirm that the range of *G. hirtus* is not restricted to Benin and DR Congo, but the species is distributed in all sub-Saharan Africa and seems to be a common weed in many regions according to the collector’s observations. *Glinus hirtus* has not been previously reported for almost any Sub-Saharan countries (e.g., Adamson 1961; Jeffrey 1961; Berhaut 1967; Gonçalves 1970, 1978; Sita and Moutsambote 1988; Barry and Celles 1991; Mapaura and Timberlake 2004; Phiri 2005; Setshogo 2005; Hassan et al. 2005; Sosef et al. 2006; Germishuizen et al. 2006; Darbyshire et al. 2015). In some West African checklists and manuals it was confused with the American *G. radiatus* (Berhaut 1967, 1979; Boudet et al. 1986; Akoegninou et al. 2006; Lisowski 2009; Thiombiano et al. 2012; Brundu and Camarda 2013; Schmidt et al. 2017). Only a few specimens from Burkina Faso, DR Congo, and Nigeria were correctly identified as *G. dahomensis*.

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1970, R.M. Santos & E. Barroso 2874 (LISC032010); Huila prov., Quipungo, 1200 m, [without date] J.M. Teixeira 12580 (LISC032004);

Benin: see type of G. dahomensis; Atakora [dept.], Toukountouna, 12 Apr 1999, A. Akoegninou et al. 2440 (WAG0235864); Atakora [dept.], Kérou, 16 Apr 1999, A. Akoegninou et al. 2568 (WAG0235868); [Donga dept.] Bassila, 460 m, 30 May 2001, A. Akoegninou 4810 (WAG0235872);

Botswana (new records): Northern distr., Nxauna Pan, 1 Jan 1973, P.A. Smith 318 (K); [North-West distr.] nr Tsau–XaiXai road, 19°55′2″S, 21°24′4″E, 21 Apr 1982, P.A. Smith 3847 (BR0000018269659; PRE0671232, PRE0520975); [Ngamiland distr.] Ngami Lake, 13 Dec 1982, P.A. Smith 3980 (BR0000018269666, E, G, PRE0671267); Ngamiland distr., between Caecae and Gwihaba Hills, 1000 m, 15 Mar 1987, D.G. Long & D.A.H. Rae 300 (E, K); Zibalianja lagoon, 18°34.728′S, 23°32.145′E, 957 m, 23 Jan 2004, A. Heath & R. Heath 457 (BACH, K);
Burkina Faso (new records): Kompienga [prov.], 40 km E of Tindangou, 2 May 2003, L. Sanou & M. van Slageren 1352 (K); Houet [prov.], 18 km NW of Bobo Dioulasso, 12 May 2003, L. Sanou & M. van Slageren 1390 (K);

Burundi (new records): [Karuzi prov.] Nyabibuye, 4500 ft, 15 Nov 1960, R. Tanner 5602 (K, WAG1103206); [Ruyigi prov.] Ruyigi, 2°59'S, 30°28'E, alt. 1450 m, 27 Sep 1978, M. Reekmans 7098 (K);

Cameroon (new records): Southwest region, Mamfe distr., 15 Mar 1953, C.F.A. Onochie et al. 30889 (K); [Centre Province region] 62 km SE of Bafia, 27 Mar 1963, J. Raynal & A. Raynal 10537 (P0456668); [North region] nr Garoua, Benoue river, 18 Dec 1964, W.J.F.O. de Wilde et al. 4959 (WAG0180494); [Litoral region] plaine des Mbo, 7 km E of km 25 Melong–Dechang (Dschang) road, 5°11'24"N, 10°1'12"E, alt. 700 m, 14 Apr 1972, A.J.M. Leeuwenberg & C.C. Berg 9607 (BR0000018268510, K, P04576510, WAG0181531); North region, Bénoué NP, 7 May 1974, C. Geerling & J. Néné 4705 (BR0000018268591, WAG0330521); [Centre region] river Sanaga, bridge nr Nkol Ngok, 4°10'N, 11°01'E, alt. -300 m, 15 Feb 1978, J. Lowe 17675 (K);

Central African Republic (new records): Kémo [pref.], 17 Feb 1892, Anonymous 691 (P04577135); Ouaka pref., Bambari, 7 May 1927, R.P. Tisserant 2180 (P04577138);[Haute-Kotto pref.] 300 m NW of Gounda, 9°18'N, 21°12'E, alt. 450 m, 28 Jul 1982, J.M. Fay 2763 (K001394828);

Chad (new record): [Logone Occidental region] Kim [Krim], 18 May 1969, G. Fotius 1458 (P04576514);

DR Congo (selected): [nr Kinshasa] Stanley Pool [Pool Malebo], 1888, F. Hens 29 (BR0000018268034); [Kongo Central prov.] Kisantu, 1900, J. Gillet 1386 (BR0000018268027); Kongo Central prov.] Kisantu, 1903, J. Gillet 3029 (BR0000018268010); [Kasai prov.] Zambi vill., 27 Jun 1915, Bequaert 7885 (BR0000018268003); [Kwilu prov.] Wombali [Bandundu], Oct 1915, H. Vanderyst 2316 (BR0000018268171); Haut-Katanga prov., Kafuba, 18 Nov 1927, Quarre 804 (BR0000018268386); [Mongala prov.] Bumba, 19 Feb 1931, R. Letouzey & J.F. Villeris 10386 (K, P04576657, WAG0185129); Haut-Uele prov.] Garamba NP, 20 Feb 1950, H. de Saeger 147 (BR0000018268232); Orientale prov., Dungu, 2 Apr 1951, H. de Saeger 1084 (K); Orientale prov.] Haut-Uele prov.] Dungu, Garamba NP, 28 Mar 1951, H. de Saeger 1119 (K); [Lualaba prov.] Dikuluwe, 21 Aug 1956, J. Brynaert 520 (BR0000018268324, K); [Haut-Katanga prov.] Mitwaba, 2 Nov 1956, J. Brynaert 541 (BR0000018268317, K, LE, L1698856, M, W13591); [Tshopo prov.] Yangambi, 5 Feb 1958, R. Devred 2925 (WAG0185147); [Kasai-Oriental prov.] Katanda Territory, 17 Sep 1959, L. Liben 3701 (BR0000017455121); [Maniema prov.] Kabambare Territory, 10 Aug 1959, 570 m, A. Leonard 5736 (BR0000018268201, WAG0185149); [Maniema prov.] Kamisuku, 700 m, 20 Aug 1959, A. Leonard 6034 (BR0000018268218, P04576678, WAG0185148); Yangambi prov., Bangi, Ile Yangambi, 7 Sep 1959, P. Bamps 700 (BR0000018268188, K); [Haut-Lomami prov.] Bukama, Lualaba river, 570 m, 2 Oct 1970, M. Lukuesa 758 (BR0000018268355, WAG0185146); Kongo-Central prov., Kasangulu, Sabuka, 6 Apr 1972, C. Evrard 6929 (BR0000018269673); Haut-Katanga prov., Kumanua, 1150 m, 18 Dec 1975,
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**Ethiopia** (new records): [Amhara region] Begemder prov., [years] 1863–1868, Schimper 1340 (K); [Oromia region] Jimma, Apr 1957, Anonymous S2 (K); Godjam prov. [Amhara region], Bahir Dar, 1800 m, Jun 1968, O. Sebald 2166 & 2255 (M, STU);


**Gambia** (new record): [North Bank Division] Albreda, 1839, Haudelot 100 (G);

**Ghana**: [Oti Region], on road to Oti from Kete Krachi, 18 May 1952, J.K. Morton 7294 (K); [Upper West region] Tumu, edge of Dam, 25 May 1952, J.K. Morton 7554 (K, WAG0185143); [North East region] Gambaga, 26 Dec 1954, J.K. Morton A1378 (K);


**Guinea-Bissau** (new record): [Bafatá Region], Bambadinca, 11 Jun 1945, Anonymous 2065 (K, WAG0185158);

**Ivory Coast** (new records): [Vallée du Bandama distr.] Fétékro, 18 Jan 1947, G. Roberty 6915 (G); [Bouna dept.] Bouna, 1 Dec 1986, P. Poilecot 3833 (G40376);

**Kenya** (new records): [Nairobi] Nairobi Dam, 31 Jan 1961, C. Teesdale 26 (K); Nairobi National Park, 1525 m, 7 Oct 1977, J.B. Gillett & W.T. Staam 21582 (BM, K); [Eastern prov.] 36 km from Embu town, 14 Nov 1979, G.W. Gatheri et al. 79/1 (K);


Republic of the Congo (new record): [Bouenza dept.] Jacob [Nkayi], 27 Sep 1969, *Y. Attims 255* (WAG00034942);

Rwanda (new records): Mutara area, 1400 m a.s.l., 3 Oct 1956, *G. Troupin 2810* (BR0000017455824, K); [Eastern prov.] Nyagatare, 1450 m, 27 Jan 1958, *G. Michel 5077* (BR0000017455817);


Sierra Leone (new records): [Northern prov.] Samaia, 10 May 1914, *N.W. Thomas 245* (K); [Northern prov.] Mange, 21 Feb 1949, *F.C. Deighton 4978* (K); [Northern prov.] Yifin, 23 Mar 1964, *Norton & Gladhill 994* (K, WAG0185139); [Northern prov.] Koinadugu distr., SE of Fadugu, 21 May 2014, *X.M. van der Burgt 1854* (K);

Somalia (new record): [Gedo prov.] nr Ganane, Mar 1893, *D. Riva 736* (G, RO);


South Sudan (new record): [Equatoria Region] Zande, 6 Mar 1940, *J.W.G. Wyld 781* (BM);

Tanzania (new records): [Ruvuma region] 7 km W of Songea, 990 m, 18 Jan 1956, *E. Milne-Redhead & P. Taylor 8355* (BR0000018269017, K); [Rukwa region] Sundu Lake, 1500 m, 13 Dec 1958, *H.M. Richards 10316* (K); Kigoma region, Mugombasi, 1 Sep 1959, *R.M. Harley 9495* (K); [Kagera region] Ngara, 4500 ft,

**Uganda** (new record): [Western region] Kiryadongo, 3200 ft, Mar 1943, *Anonymous* 1338 (K);


**General distribution.** Africa (Sub-Saharan Africa; North Africa: Egypt [WU!]; Madagascar: G! K!).
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The herbarium collections of J. Barrelier are no longer extant (cf. Morton 1970) and had seemingly never been consulted by any botanist because all Barrelier’s legacy but drawings was destroyed by fire after his death (Barrelier 1714a). There were two attempts to lectotypify the name *Glinus lotoides*. Jeffrey (1961) designated a specimen collected by Boccone and kept at OXF; although this specimen is associated with the illustration in Boccone (1674), it was not examined by Linnaeus and therefore is not part of the original material. Jeffrey’s lectotypification is in effect neotypification. Adamson (1961) designated the illustration in Boccone (1674) as lectotype. This lectotypification is correct and supersedes the neotype designated by Jeffrey.


≡ *Glinus dictamnoides* Burm.f., *Fl. Ind.*: 113 (1768). **Lectotype** (designated here): [icon] Plate 356, figure 6 in Plukenet (1705). **Note.** The name *G. dictamnoides* was erroneously attributed by Fenzl to Linnaeus (1771); however, the latter clearly refers to Burman’s “Flora Indica” where *G. dictamnoides* was described (Burman 1768). Burman (1768) cited no specimens in the protologue. Both Burman (1768) and Linnaeus (1771) cited Plukenet (1705) who depicted this plant in the Plate 356, figure 6. This image shows a hairy shoot with the rounded leaves in whorls and almost sessile verticillate flowers. The obovate vs. orbicular leaf shape was the main character known to Burman to distinguish *G. lotoides* and *G. dictamnoides in situ* (Burman 1768; see also a drawing of *G. lotoides* in the table 36, figure 1). The orbicular and greyish-green leaves of *G. dictamnoides* were similar to those of *Dictamnus creticus* Garsault (≡ *Origanum dictamnus* L.), and such plants were found in Madras [now Chennai], India: “dictarni retici facie, maderaspatana”. Based on the protologue of *G. dictamnoides*, Merrill (1921) synonymized this species name with *G. lotoides*. In agreement with Merrill’s opinion, we designate the cited illustration as lectotype and retain Burman’s name in the synonymy of *G. lotoides*. The specimens seen from India usually have rounder leaves with ± scattered pubescence and shorter perianth (usually 5.5 mm long in fruiting) compared to the European populations, which have obovate and usually hirsute leaves and longer perianth reaching 6.5–8.5 mm
in length. These characters were presumably the main argument to consider the Indian plants as *G. lotoides* subsp. *hirtus* (Almeida 1998) based on the name *Mollugo hirta* described from South Africa but erroneously applied to Indian plants (Clarke 1879). *Mollugo hirta* represents the plants with different characters (see also notes under *G. hirtus*). The African plants corresponding with *G. dictamnoides* are present in eastern and southern parts of the continent. It should be noted that the density of pubescence is very diverse in African plants, and those growing in a humid climate (e.g., Nigeria, Cameroon) usually have green leaves with scattered hairs. The intermediate forms in leaf shape and pubescence degree were frequently seen in the herbarium collections. In light of our molecular studies showing a mixed position of *G. lotoides* and *G. dictamnoides*, and scarce morphological differences between them, we prefer to synonymize *G. dictamnoides* with *G. lotoides*.

= *Trypha prostrata* Blume, Bijdr. Fl. Ned. Ind. 11: 549 (1826). **Note.** Described from two localities on the Island of Java, Indonesia: Pamanukan and Cheribon [Cirebon]. The authentic specimens are not traced, but the description of the genus and species (Blume 1826) indicates the identity of *T. prostrata* to *G. lotoides*.

= *Pharnaceum pentagynum* Roxb., Fl. Indica 2: 103 (1832). **Lectotype** (designated here): [without location, year and collector] “Hb. Roxb.” (K000641797!). **Note.** Another authentic specimen was found at BR: “Herb. Roxburghii” (BR0000005227204).

= *Glinus lotoides* var. *virens* Fenzl, Ann. Wiener Mus. Naturgesch. 1: 358 (1836). ≡ *Mollugo glinus* var. *virens* (Fenzl) Oliv., Fl. Trop. Afr. 2: 590 (1871). **Lectotype** (Adamson 1961): South Africa. At the junction of Fish and Orange rivers, left side of the Orange River (ca. -28.1, 17.175): “[Garip, bei Verleptpram, am Ufer des Flusses und in der steinigen Niederung, unter 500 Fuss”, 17 Sep 1830,] J.F. Drège (K000232021; isolecotypes HAL0117929, HBG516708, K000232020, S05-5102, S05-5103). **Note.** In the type citation, the locality information is added from Drège (1843: 92) and the collection date is complemented from Gunn and Codd (1981). When establishing *G. lotoides* var. *virens*, Fenzl (1836) cited several validly published plant names as synonyms (*G. dictamnoides*, *Pharnaceum pentagonum*, *Physa madagascariensis*), and also illustrations and specimens. Since this new name was at the rank of variety and the synonyms were at the rank of species, and Fenzl provided his own description and used his own original material, his variety does not need to be treated as based on any of the synonyms included. Indeed, Adamson (1961) designated a separate type for this varietal name, a specimen collected by Drège in South Africa and cited by Fenzl (1836) in the protologue. This lectotypification is technically correct and should therefore stand. Fenzl (1836) established his variety for the plants that are less villose (or glabrescent at maturity) than the type variety of *G. lotoides*, with the perianth 5 mm long, and without petaloids. The distribution area of this new variety was circumscribed as East India, Timor, Arabia, Madagascar, and South Africa (Fenzl 1836). This variety was accepted by the later authors, and its range was widened to include many regions of tropical Africa (Oliver 1871 sub *Mollugo glinus* var. *virens*; Adamson 1961; Gonçalves 1970, 1978; Figueiredo and Smith 2008; Klaassen and Kwembeya 2013).
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However, many sheets of similar looking species (G. hirtus and G. zambesiacus) were previously identified as G. lotoides var. virens, and this name was therefore used erroneously in many treatments.


Description. (Fig. 19). Annual, stellate pubescent. Stems prostrate or ascending, sometimes reaching 2 m in length, but usually shorter (up to 70 cm), prickles absent. Leaves grey or light green, usually moderately pubescent, sometimes bicolored (light green adaxially and grayish-green abaxially), entire, crisp or denticulate, obovate, broadly obovate or almost roundish; petioles 2–10(15) mm, blades (10)15–60 × 4–20(25) mm, mucronulate. Flowers in clusters of 4–12, distant; sessile or with pedicels up to 15 mm (in fruiting the pedicels, if present, may be up to 20 mm long); white or yellowish, sometimes rusty inside and white abaxially, mid-vein green; flower buds and anthocarp ovoid. Perianth segments (tepals) oblong or ovate, entire or sometimes denticulate, in flowering 5.0–6.5 mm long, in fruiting 7.0–8.5 mm long, with a mucro 0.5–1.0 mm long; white petals (1–3) sometimes present (usually much shorter than tepals). Stamens (5)10–16[∞], obdiplostemonous or alternisepalous, outer stamen series (petaloids) sterile, terminating with 1–3 teeth; anthers 0.7–1.0 mm long. Stigmas (3)5, 0.9–1.5 mm long (sometimes a style is present up to 1.0 mm long). Seeds 0.45–0.6 × 0.40–0.55 mm, dark red or almost black, colliculate and without longitudinal striae; aril hood easily visible, 0.20–0.30 mm long.

Note. The five-staminate and three-carpellate individuals of G. lotoides are considered here as abnormal forms that seem to be very rare. We assume that such specimens investigated earlier in relation to the floral formulae by Müller (1908) rather belong to G. hirtus.

The plants with green or glabrescent leaves are more common in the wet climate (e.g., West Africa), and the densely pubescent populations are most frequent in drier conditions (Fig. 20).

Habitat. Sandy sites in river valleys, limestone, clayey and rocky places, seasonally inundated areas; at altitudes of up to 2000 m. This species prefers semiarid regions and only limited number of specimens from West Equatorial Africa are present in the collections.

Figure 19. Glinus lotoides A an overview of the plant B close-up of the leaves and buds C close-up of the flower D closed anthocarp. Photographer – Ridha El Mokni (Sidi Mechrig – Sejnane, Bizerta Governorate, Tunisia, 23 Oct 2015).

11054 (LISC032003, WAG0104171); [Huila prov.] Chianne, 4 Dec 1970, J.A. de Sousa 86 (K, LISC032011);
BENIN: Zou dept. 8 Mar 1970, L. Aké Assi 11109 (G); [Alibori dept.] Malanville, 13 Nov 1998, V. Adjakiddjé 2593 (WAG0235875); [Alibori dept.] Malanville, 11°52'N, 3°23'E, alt. 270 m, 26 Apr 1999, P. Hourgnon et al. 6507 (BR0000018268560, K, WAG0235862); Atakora dept., Tanguiéta, 20 Jul 2000, B. Sinsin 3667 (WAG0235863);
BOTSWANA: Ngamiland distr., Kwebe hills, 28 Dec 1897, E. Lugard 73 (K); [Bakgatla tribal region] Mochudi, 24°10'S, 26°05'E, 1914, C.C. Harbor 6584 (BM); [Bakgatla tribal region] Mochudi, Jan 1914, F.A. Rogers 6584 (PRE0403681); [Ngamiland distr.] Maun, Dec 1967, F.L. Lambrecht 449A (K); nr Maphaneng, 19°56.75’S, 23°26.2’E, 4 Dec 1977, P.A. Smith 2115 (K);
BURKINA-FASO: [Oudalan prov.] Markoye, 15 Aug 1975, Anonymous 45121 (P04576576); [Sanmatenga prov.] NE of Pissila, 18 Jun 1987, J. Lejoly 87071 (BRLU0026261); [Oudalan prov.] Oursi, 10 Oct 1988, S. Guinko s.n. (WAG0042080); Oudalan prov., Tin Akoff, 7 Oct 1998, S. Kahlheber 1001 (FR-0108631); Oudalan prov., Yomboli, 24 Jul 1999, J. Müller 82 (FR-0014419); Sourou prov., 50 km W of Tougan on road to Kassoun, 13°10’N, 3°25’W, alt. 276 m, 16 Apr 2002, L. Sanou 100 (K);
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**Figure 20.** A herbarium specimen of *Glinus lotoides* (Kayes region, Comitradoougou, 100 km from Diéma, 14°25’N, 8°18’W, alt. 317 m, 25 Feb 2006, *R. Dembele et al. ML-283, K001394833*). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

**BURUNDI:** Bujumbura, plaine de la Ruzizi km 25, alt. 850 m, 28 Sep 1966, *J. Lewalle 1046* (K); Bujumbura, 800 m, 28 Sep 1971, *J. Lewalle 6145* (BR0000018269406, G, WAG0104170); Bubanza prov., Gihungwe, 800 m, 23 Nov 1974, *M. Reekmans 3952*
Figure 21. Distribution map of *Glinus lotoides* in Sub-Saharan Africa (colored in yellow).
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Djibouti: [Tadjourah Region] Andabba [Lake], 6 Jan 1957, *E. Chedeville* 1756 (FT00070026, P04576543);

DR Congo: [Katanga prov.] Kampunda, 3200 ft, 16 Oct 1950, *A.A. Bullock* 3430 (B101143607, K); [Haut-Uele prov.] Garamba, 700–800 m, 19 Nov 1952, *G. Troupin* 74 (K); [North Kivu prov.] Albert Lake, 5 Mar 1954, *D. van der Ben* 1185 (BR0000018269314, K); Katanga, Mitwaba, 21 Aug 1956, *J. Brynaert* 520 (K)


GHANA: [Upper East region] nr Bawku, 12 Dec 1950, C.D. Adams & G.K. Akpabla 4290 (K, P04576600, WAG0185140); [Northern region] 53 miles N of Tamale, 20 May 1952, J.K. Morton 7200 (K, WAG0185141); [Savannah Region] Yapei, 30 Mar 1956, C.D. Adams 3917 (K); Yeji, 11 Apr 1964, J.B. Hall 1251 (K);

GUINEA: [Kouroussa pref.] Kouroussa, Dec 1900, M. Pobeguin 605 (K, P04576530); [Nzérékoré Region] Ouamadou, Dec 1917, J. Berhaut 930 (BR0000018268423); Kankan region, Kankan vill., 23 Apr 1967, S. Lisowski 61907 (BR0000018268508);

KENYA: Makueni county, Kibwezi, 975 m, without date, P. Luke 14330 (K); [Turkana county] Lokitaung, 3000 ft, Jan 1932, A.M. Champion 14 (K); [Eastern prov.] Athi plains, 21 Aug 1938, P.R.O. Bally 7442 (K); South province, Magadi Road, 3000 ft, 8 Aug 1943, P.R.O. Bally 2679 (G, K); [Eastern prov.] Athi River Station, 24 Aug 1947, A. Bogdan 1109 (K); [Marsabit county] 16 miles from Laisamis on road to Marsabit, 2500 ft, 3 Oct 1947, P.R.O. Bally 5471 (K); [Kajiado county] 1 mile S of Kajiado, 1650 m, 21 Feb 1953, R.B. Drummond & J.H. Hemsley 1249 (B101143601, BR0000018268799, FT0007096, K); [Lamu county] Witu, [without date] Thomas 127 (BR0000018269000, G); [Taita-Taveta County] Voi, Sala Gate Rd, 1100 ft, 2 Jan 1967, J.G. Greenway 12937a (K); [Turkana county] Ayangyangi swamp, 1900 ft, 4 Sep 1968, O.M. Mwangangi & D. Gwynne 1235 (BR0000018268829, K); Turkana county, between Lothagam and Kerio delta, 1200 ft, 29 Aug 1968, O.M. Mwangangi & D. Gwynne 1218 (K); [Turkana county] Ayangyangi swamp, 1°55’S, 36°5’E, 12 Jun 1970, B. Mathew & M.D. Gwynne 6768 (FT0007099, K); North Eastern prov., 57 km WS of Wajir, 225 m, 6 Mar 1974, Bally & Carter 16590 (K); Mughwango South swamp, 15 Apr 1972, J. Ament & F.C. Magogo 9 (K); K4, Tana River county, Kora National Reserve, 18 miles from Kora Res. Camp to Asako, 28 Aug 1983, J.G. Mutangah 139 (K); Tana River county, Baomo vill., 30 m, 12 Mar 1990, Q. Luke et al. 141 (K); Embu county, Riakanau, 1125 m, 29 Nov 2000, S.A.L. Smith et al. 253 (K); Isiolo county, Ngare Mara, 0°30’N, 37°39’E, 945 m, 12 Aug 2005, C. Obunyali et al. 261 (K); Machakos county, Kitanga, 1°31’S, 37°11’E, 1660 m, 26 Jan 2005, J.M. Muasya 482 (K); Marsabit county, Log-Logo, 1°59’S, 37°54’E, 520 m, 9 Feb 2005,
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J.M. Muasya et al. 505 (K); [Coast prov.] Tana delta, 2°24'S, 40°18'E, 5 m, 4 May 2011, C. Leauthaud et al. 160 (K);


**Senegal:** [without exact location] May 1825, *Roger 66* (K); [without exact location and date] *Perrottet s.n.* (RO); [without exact location and date] herb. Maire s.n. (RO); Galam, [without date and collector] *s.n.* (P04577294); [Saint Louis region] Richard Toll [village], 26 Feb 1965, *G. Roberty 16845* (G); Djibelor, 17 May 1982, *C. Vanden Berghe 4987* (BR0000018268478);


**South Africa:** [Western Cape prov.] Cape of Good Hope, [without date] *Drège s.n.* (P04576613); [Limpopo prov.] Messina [Musina], [without date] *F.A. Rogers 19446* (G, Z-000092197); River Limpopo, nr Messina [Musina], 27 May 1927, *R.G.H. Young 14664* (BM); [Zululand] Ubombo, Mkuzi Game Reserve, 100 m, 9 Dec 1959, *C.J. Wård 3352* (K, M, PRE0403692, W); [KwaZulu-Natal prov.] Ingwavuma Distr., 12 May 1965, *Vahrmeyer & Tölken 977* (K, PRE0403694, STU); [KwaZulu-Natal prov.] Ingwavuma, 11 Jul 1974, *H. Furness 97* (E); [Limpopo prov.] Soutpansberg, Limpopo river, 4 Apr 1983, *C. Straub 173* (PRE0653966); Limpopo prov., nr Kruger NP, 350 m, 24 Nov 2000, *N.H.G. Jacobsen 2431* (BR945920);

**South Sudan:** [Upper Nile State] bank of the Khor Geyni, Pibor river, 4 Jun 1929, *N.D. Simpson 7032* (K); Jonglei State, 8 km S of Maar, alt. 450 m, 18 Feb 1980, *J.M. Lock 80/26* (K);


**Note.** Plants of both specimens of *Glinus lotoides* and *G. oppositifolius* are present on the same herbarium sheet (Tanzania, *Polhill & Paulo 2077*, K).

Uganda: [Nakapiripirit distr.] Kakamongole, at base of Mt Debasien, Jan 1936, *W.J. Eggeling 2607* (BR0000018268768, K); Karamoja [sub-region], Kidiepo river, 3400 ft, Apr 1960, *J. Wilson 986* (BR0000018268775, K);

Zambia: Lunsemfwa river, 24 Apr 1929, *J. Burtt Davy 897* (K); [Southern prov.] Makambola Farm, Mazabuka, 3300 ft, 28 Apr 1931, *C.F. Trapnell 345* (K); [Eastern prov.] Nsefu Game Camp, 750 m, 15 Oct 1958, *N.K.B. Robson 138* (K); [Eastern
region] Luangwa valley, 13°S, 32°E, 2000 ft, 29 Nov 1957, Stewart 70 (K); [Eastern prov.] Luangwa Game Reserve, Chilongozi Pontoon, 600 m, 11 Oct 1960, H.M. Richards 13333 (K); Zambesi river, Feira [Luangwa], 27 Sep 1962, A. Angus 3350 (K); [Southern prov.] Mazabuka, 2 Oct 1963, H.J. van Rensburg 2515 (K);


General distribution. Africa (Cape Verde, North African countries, Seychelles, Madagascar, Mauritius); W, S & SE Asia; Australia. The distribution in North America is not confirmed in our study.


**Description.** Annual, branched from the base, with numerous prostrate stems often forming mats up to 1 m in diameter; young parts of the stems covered with simple crispate hairs usually arranged along one line; prickles absent or unnoticeable with the naked eye. Leaves rosulate, short-lived, and cauline, green, glabrous or puberulent, shortly petiolate (petioles 3–10 mm long), entire or coarsely denticulate, oblong, ovate, obovate or narrowly obovate, (10)15–45(55) mm × 3–15(20) mm, apically shortly acuminate, lateral veins neither recessed adaxially nor prominent abaxially. Flower clusters interrupted, consisting of (1)2–10 flowers, rarely more; flowers usually with unequal pedicels 7.0–20.0 mm long, or sometimes (sub)sessile; buds and closed anthocarp of cylindrical shape. Perianth segments in flowering (2.7)3.0–3.5 mm long, in fruiting (3.5)4.0–5.0(5.5) mm long, glabrous or sparsely pubescent, dorsally green or pink with white margins and ventrally white or pinkish, sometimes turning red at senescence; petaloids usually absent. Stamens usually 5, rarely 4 or 6–7; anthers (03.–0.5)0.6–0.8(1.0) mm long. Stigmas 3, 0.3–0.6 mm long. Seeds reddish or brown-red, rarely yellow-brown, 0.30–0.50 × (0.25)0.3–0.4 mm, colliculate or rarely smooth, longitudinal ridges absent.

**Note.** *Glinus oppositifolius* is sometimes confused with *Gisekia pharnaceoides* L. (Gisekiaceae). The most remarkable characters of *Gisekia* are the leaves and perianth with white striae (formed by cells with raphides), and its capsules are divided into 5–15 mericarps each containing one exarillate seed (Gilbert 1993b). In contrast to *Gisekia*, *Glinus* species do not have easily visible raphides in any part of the plant and their capsules are multi-seeded with arillate seeds.
Key to the varieties

1. Flowers (1–10 in a cluster, rarely more) with pedicels 7.0–20.0 mm long
   - Flowers often sessile or with short pedicels up to 5.0 mm

2. Upper part of stems ± lanate; leaves up to 15.0 mm long; clusters with less than 10(15) flowers
   - Stems glabrous or sparsely hairy; leaves often longer than 15.0 mm; clusters with 10–20 or even more flowers

Glinus oppositifolius var. oppositifolius

G. oppositifolius var. oppositifolius Figs 22, 23


≡ Physa madagascariensis DC., Prodr. 1: 393 (1824). Type: Madagascar. A. du Petit-Thouars (P?, not found). Note. This plant was originally described by du Petit-Thouars (1806) as a monotypic genus without any species assigned. De Candolle (1824) named the species with a reference to the protologue of the generic name, without any new material involved. The type of Physa madagascariensis is therefore a specimen collected in Madagascar by Petit-Thouars and presumably deposited at P.


≡ Glinus mollugo var. natalensis Sond. in Harvey & Sonder, Fl. Capensis 1: 120 (1860). Lectotype (Jeffrey 1961: 15): South Africa. [Kwa-Zulu] [Port of] Natal [Durban], Gueinzius 138 (S, isolectotype G!). Note. The type of Mollugo serrulata was not labelled by Sonder at G or S. In the latter collection it is stored under Mollugo sp. The specimen seen at G is a typical G. oppositifolius with serrulate leaves.
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Described from Wycliffe (Northern Territory) and Stirling Station (surroundings of Perth) (Ewart and Petrie 1926). Type n.v. (MEL?). Note. The protologue of this species as well as the drawings (figure 1) completely correspond with *G. oppositifolius*, although the seed characters of *W. obovata* were not described.


**Habitat.** Sands, river banks or as a weed; altitude up to 1600 m a.s.l. The most common variety in Sub-Saharan Africa. The associated plants found in Botswana (*A. Heath & R. Heath 456, K*): *Cynodon dactylon, Sida cordifolia, Glinus bainesii, G. hirtus, Portulaca oleracea, Cyperus polystachybas, C. compressus, C. longus, Pseudognaphalium luteo-album* (formerly known as *Helichrysum luteo-album*). Flowers mostly during the main rains (in southern Africa).


Figure 23. A herbarium specimen of *Glinus oppositifolius* var. *oppositifolius* (Kenya, [Lamu county], Kitungu, 55 m NE Lamu, 6 Aug 1961, J.B. Gillespie 167, K001394829). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.
balianja lagoon, 18°34.7’S, 23°32.15’E, 957 m, 23 Jan 2004, *A. Heath & R. Heath* 456 (BACH, K);

**Burkina Faso:** Oudalan prov., Oursi, 22 Sep 1995, *S. Kahlheber* 3076 (FR-0000017455862); Ouagadougou, 8 Jan 1987, *J. Lejoly* 87/020 (BRLU0026274);

**Burundi:** Bujumbura, 800 m, 29 Oct 1968, *J. Lewalle* 3076 (BR0000017455904, H1235324, K, WAG0185122);


Figure 24. Distribution map of *Glinus oppositifolius* var. *oppositifolius* in Sub-Saharan Africa (colored in yellow).
1013 (BR0000017455084, K, WAG0405337); [Tshopo prov.] Lokutu, 7 Nov 2004, Q. Luke et al. 106292 (K); Moenge, Itimbiri river, 360 m, 17 May 2010, Boyekoli Ebali Congo Exp. 501 (BR0000000571554);

ETHIOPIA: [Southern Nations, Nationalities and Peoples’ region, Keffa zone] Gogeb river, Bonga road, 1300 m, 25 Feb 1966, W.J.J.O. de Wilde & B.E.E. de Wilde-Duynjes 10194 (BR0000018270037, K, WAG1103268); [Oromia region] Illubabor zone, Alwero river, Abobo, 630 m, 20 Apr 1982, I. Friis & al. 2475 (K);

GABON: [Ogooué-Maritime prov.] Port Gentil, 12 Sep 1968, E J. Breteler & R.A. van Raalte 5526 (WAG0185127); N of Libreville, 13 Aug 1992, J. Dibata 1055 (WAG0070773);

Note. All other specimens identified as Glinus oppositifolius indeed belong to G. birtus, Gisekia pharnaceoides (Gisekiaceae) and Polycarpaea sp. (Caryophyllaceae).


Note. All other specimens identified as Glinus oppositifolius indeed belong to G. birtus, Gisekia pharnaceoides (Gisekiaceae) and Polycarpaea sp. (Caryophyllaceae).

Note. All other specimens identified as Glinus oppositifolius indeed belong to G. birtus, Gisekia pharnaceoides (Gisekiaceae) and Polycarpaea sp. (Caryophyllaceae).


**Mauritania:** [Tarza Region] Rosso, 11 Oct 1969, *F. N. Hepper 3617* (K, M);

WAG0155677); Zambezia prov., Mamala, 20 Dec 1996, A.R. Torre & M.F. Correia 16648 (BR0000017454469);

Namibia: [Kunene region] Ongonga, 14 Jan 1904, A. Kestilä 30 (K); [Omusati region] Ruacana Falls, 29 Apr 1962, T.T. Kotze 46 (K, M, PRE0823929);

Niger: Niamey, Sep 1957, A. Vaillant 891 (K); 100 km N of Niamey, Niger river, 14 May 1968, A. Geerling & J. Bokdam 2681 (WAG0104161); Niamey, 2 Apr 1987, N. Leman 81 (BR0000018269963);


Republic of Congo: Niari dept., 29 Nov 1951, J. Koechlin 1587 (P04576681); Ubangi river, 20 Feb 1963, de Nere 907 (P04577259); Moutou ya N’Gombé, 12 May 1968, P. Sita 2036 (P04577256); [Pool Malebo] Mbamu, 14 Oct 1969, F. Hallé 1641 (P04577257); nr Brazzaville, 26 Aug 1969, Y. Attims 205 (WAG0034944); nr Brazzaville, 15 Apr 1970, Y. Attims 442 (BR0000018270020); Kouilou Dept., 20 km SE of Pointe-Noire, Cayo Lake, 22 Mar 2017, E. Bidaault & al. 3022 (BRLU0018798);


Sierra-Leone: [Northern prov.] nr Madina, 11 Apr 1892, G.F. Scott Elliot 5561 (BM, K); [Northern prov.] Mokele, Sep 1914, Anonymous s.n. (BM); [Southern prov.]
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Juring, 1 Dec 1926, F.C. Deighton 297 (K); [Northern prov.] Makump, 3 May 1929, F.C. Deighton 1707 (BM, K); [Southern prov.] Baoma, 16 Apr 1936, F.C. Deighton 3166 (K); [Northern prov.] nr Kasanko, 13 May 1951, P. Adams 225 (K); [Southern prov.] Ngokuma (Kori), 22 Jun 1952, F.C. Deighton 5845 (K); [Northern prov.] nr Kambia, Magbema, 25 May 1954, H.D. Jordan 958 (K); [Western Area prov.] Fogbo, 3 Mar 1964, Morton & Jarr 917 (WAG0185090); Somalia: [Puntland State] Ganaane to Marro Mogale Umberto I, Mar 1893, D. Riva 731 (FT0007112) [Note. This specimen was collected in the same locality as FT0007113 (var. lanatus)];


South Sudan: [Sudd region] Bahr el Zeraf, 26 Apr 1930, N.D. Simpson 7790 (BM, K); [Upper Nile State] [Upper Nile State] Sobat river, nr Nyanding, 7 Jun 1929, D. Simpson 7085 (BM, K); [Upper Nile State] Shambe, 14 Jul 1929, D. Simpson 7380 (BM, K);

Swaziland: Blue Jay Ranch, Lubombo Mountains, 30 Oct 1977, J. Culverwell 1114 (K, PRE0498323);

Tanzania: Zanzibar, 1847, L.H. Boivin s.n. (P04577175); Zanzibar, Jul 1873, J.M. Hildebrandt 907 (BM, LE); Kilimanjaro region, [Moshi Rural distr.] Kahe, Apr 1895, G. Volkmann 2188 (E, LE); Pemba [island], [without date] J.H. Vaughan 899 (K); [Lindi region] Masoko, 4 Nov 1912, A. Stolz 1649 (K); [Mbeya region] Kyimbila, N of Lake Nyasa, 1915, A. Stolz K13 (BM, BOL217411, BR0000017454384, K); Tanganyika terr., [Pwani region] Rufiji, 3 Jan 1931, Anonymous 168 (K); Tanga region, Amboni, 6 Jul 1932, Geilinger 661 (K); [Lindi region] 40 km W of Lindi, Lutamba Lake, 29 Nov 1934, H.J. Schlieben 5660 (B101143615, BM, BR0000017454377, G); [Katavi region] Lake Katavi, 3500 ft, 25 Jan 1950, A.A. Bullock 2334 (K); [Mwanza region] 3700 ft, 24 Oct 1952, R.E.S. Tanner 1100 (BR0000017454322, FT0007111, E, K, WAG1103308); [Tanga region] Mkomazi river, 2 miles NE of Lake Manka, 440 m, 1 May 1953, R.B. Drummond & J.H. Hemsley 2347 (B101143612, BR0000017454391, FT0007106, K); Tanga region, Pangani, 500 ft, 23 Jul 1955, R. Tanner 1982 (K); Tanga region, Pangani, 27 Nov 1955, R. Tanner 2369 (BR0000017454339, K); [Pwani region] Utete by river Rufiji, 120 m, 2 Dec 1955, E. Milne-Redhead & P. Taylor 7527 (B101143610, BR0000017454360, K); [Morogoro region] Ilonga, Kilosa, 1700 ft, 18 Jan 1958, M. Cole 58 (K); [Kigoma
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General distribution of the type variety. Tropics of the Old World. Additionally, we report here the first record from North Africa [Egypt: [Sinai Peninsula] Wadi Isleh, Jan 1903, R. Muschler s.n. (GI)].

Glinus oppositifolius var. keenanii (C.B.Clarke) Sukhor., comb. nov.
urn:lsid:ipni.org:names:77215159-1

≡ Mollugo hirta var. keenanii C.B.Clarke, Fl. Brit. India 2: 662 (1879). Holotype: India. [State of Assam], Cachar [District], Mar 1873, R.L. Keenan s.n. (K000641798!).


Lectotype (designated here): [Vietnam] Laisses de la rivière Noire à Tu-Phap, 8 Mar 1888, B. Balansa 3397 (P04601311!).


Habitat. Dry river beds and other water bodies, or as a weed.

Note. A variety with ± villose pubescent stems, shorter leaves (up to 10 mm) and shorter (up to 5 mm) pedicels (Fig. 25). Some individuals also have shorter perianths (2.7–3.6 mm) and anthers (0.3–0.6 mm) as well as brighter (yellow-brown) seeds compared to the type variety, but these characters are not always diagnostic.

This interpretation and circumscription of the variety is undertaken for the first time. In Africa, plants known as G. microphyllus Hauman were considered endemic to DR Congo (Hauman 1949; Lebrun and Stork 2003). Phuphathanaphong (2005) reported G. oppositifolius var. keenanii (as G. herniarioides) from Thailand, but described it as stellate-pubescent. However, the type specimens have simple hairs only, and it is not clear which name should be applied to the Asian plant reported as “G. herniarioides”.

Gagnepain (1918) cited two specimens from Vietnam collected by B. Balansa (no. 3397 & 4613). We found only duplicates numbered 4613 (Environs de Hanoi, dans les rizières après la moisson, June 1891, B. Balansa 4613), which were distributed from
Paris to various herbaria (K000641793!, K! [without a barcode], E!, NY00288837, US00103110), whereas another gathering (Balansa 3397) was traced at P and is designated as lectotype here.

Ewart and Petrie (1926) reported that both Wycliffea obovata (=Glinus oppositifolius s.str.) and W. rotundifolia (=G. oppositifolius var. keenanii) were described from the same locality in Australia. The specimens collected by D. Riva in Somalia [Ganaane to Marro Mogale Umberto I, Mar 1893] also belong to different varieties: the specimen FT0007113 is a typical var. keenanii, while FT0007112 represents var. oppositifolius. Such plants with shorter leaves and pedicels are found in various localities across the distribution area of G. oppositifolius: in Australia, India, Vietnam, many African countries (Gilbert 2000; Fig. 26 in the present article). A specimen of G. oppositifolius var. keenanii used in the molecular study falls within G. oppositifolius subclade (Figs 1, 2). We prefer to consider such plants as a variety of G. oppositifolius, perhaps growing under less favorable drier conditions.

**Distribution** (Fig. 26). ANGOLA: Namibe prov., Tombe [Tombua], 15 Jan 1956, E.J. Mendes 1301 (LISC032017);

BENIN: [Alibori dept.] Malanje, 26 Apr 1999, P. Hounignon et al. 6501 (BR0000017456159, WAG0235844);

CAMEROON: North prov., Bénoué, 22 May 1974, C. Geerling & J. Néné 4858 (BR0000017456128, WAG0330419);

DR CONGO: see the type specimens of G. microphyllus and G. oppositifolius var. lanatus;

ETHIOPIA: [Oromia region] Illubabor zone, S of Abobo, 650 m, 14 Apr 1982, I. Friis et al. 2456 (K);

KENYA: Kwale county, 31 Aug 1953, R.B. Drummond & J.H. Hemsley 4068 (BR0000018268805, FT0007108, K);

MALAWI: [Southern Region] Shire Highlands, Jul 1885, J. Buchanan s.n. (E, K); [Southern region] Njobru, Mulanje, 17 Nov 1955, G. Jackson 1765 (BR0000018269130, K);


SUDAN: [State of Sennar] Sennar, May 1867, A. Figari s.n. (FI059439);

TANZANIA (new records): Morogoro Region, Magogoni, Aug 1930, A. Haarer 1839 (K); Rukwa Region, Rukwa, 2800 ft, 5 Dec 1954, H.M. Richards 3530 (K); [Tanga Region] Handeni distr., Horogwe to Handeni, 18 Nov 1955, E. Milne-Redhead & P. Taylor 7337 (BR0000018269048, K); Rufiji distr., 2 Dec 1955, E. Milne-Redhead & P. Taylor 7526 & 7528 (BR0000018269031, BR0000018269055, K); [Manyara region] Mbulu distr., Tarangire NP, 1066 m, 24 Nov 1969, M. Richards 24759 (BR0000017456005; K);
Figure 25. A herbarium specimen of *Glinus oppositifolius* var. *keenanii* labeled as *G. microphyllus* (Tanzania, Rufiji distr., 2 Dec 1955, E. Milne-Redhead & P. Taylor 7528, K001394830). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.
Zambia: [Eastern prov.] Petauke distr., Luangwa river bridge, 5 Sep 1947, P.J. Greenway & J.P.M. Brenan 8045 (K); Chinsali distr., Mbesuma, 11 Oct 1960, E.A. Robinson 3950 (K, M); Katondwe, 14 Nov 1963, D.B. Fanshawe 8129 (K); Luangwa valley, 4 Dec 1965, W.L. Astle 4166 (K); Western Province, Bulozi plain near Mongu, 15°10’S, 23°06’E, 1000 m, Oct 1993, M.G. Bingham 9743 (K, WAG0334359);

Zimbabwe: [Masvingo prov.] Nuanetsi, nr Malipati, 2 May 1961, R.B. Drummond & R.O.B. Rutherford-Smith 7677 (K);

**General distribution of the variety.** Tropical Africa (incl. Madagascar: WAG!), Asia, Australia.


**Type.** Angola. Pungo Andongo distr., [by a nearly dried swamp between Condo and Quisonde] 2400–3800 ft, [end of March 1857] *F. Welwitsch 1111* (LISU, n.v.; isotypes BM!, BR!, K000221394!, K000221395!).

**Note.** The type label has been complemented with the information from Hiern (1898: 416).

Originally (Gonçalves 1965), the name *G. oppositifolius* var. *glomeratus* was invalidly published with a diagnosis in Latin based on two gatherings without explicit type designation. It was validated later (Gonçalves 1970) by indicating a “lectotype” and providing a full and direct reference to the validating diagnosis.

This variety is characterized by the clusters with >10 flowers, and sessile or shortly (up to 4.0 mm) pedicellate flowers (Fig. 27). It may represent a montane variety of *G. oppositifolius* growing at higher altitudes (1000–2000 m), because one of the specimens cited by Gonçalves (1965) from Bié province, Angola, was collected at the elevation of 1360 m a.s.l. However, we did not include the samples of this variety into the molecular analysis, and further studies are needed to prove its varietal rank.

The plants of *G. oppositifolius* var. *glomeratus* look similar to *G. hirtus*. However, at least two characters distinguish it from the latter species: simple curved hairs vs. stellate pubescence, and shorter (0.3–0.6 mm long) stylodia (as in the type variety) vs. 0.5–1.0 mm long stylodia in *G. hirtus*. This variety was reported from Angola (Gonçalves 1970), but here we extend its distribution into DR Congo, Tanzania and Zambia.

**Distribution** (Fig. 26). Angola: [Cuanza Sul prov.] between Condo and Quisonde [Porto Amboim], Mar 1854, *F. Welwitsch 1111* (BM); Cuando-Cubango prov., Longa, Longa river, 1360 m, 17 Mar 1960, *E.J. Mendes 3155* (BM013839321, LISC032016, M);


Tanzania (new records): Shinyanga Region, Shinyanga, 1932, *R.D. Bax 23* (K);

**General distribution of the variety.** Tropical Africa (south of the equator).

**Glinus setiflorus** Forssk., *Fl. Aegypt.-Arab.*: 95 (1775).

≡ *Plenckia setiflora* (Forssk.) Raf., Specch. 1: 194 (1814).

**Note.** Jeffrey (1961: 16) indicated the “type” of *Glinus setiflorus* at C. He had not seen the material, and failed to distinguish between several sheets in Forsskål’s collection. We designate one of these specimens as lectotype, which was seen and annotated by P. Ascherson in 1881.

The locality information and collection date are complemented from Hepper and Friis (1994).

**Description.** (Fig. 28). Annual with prostrate or ascending stems densely covered with persistent stellate hairs; prickles absent. Leaves shortly petiolate (petioles 2–15 mm long), grey or white, farinose, entire or slightly crisp, 10.0–35.0 × 7.0–25.0 mm, obovate to almost roundish, veins adaxially recessed and abaxially prominent. Flowers in clusters of (1) 2–4, sessile or with pedicels up to 5(10–15) mm long. Perianth segments 5, ovate, in flowering 6.0–7.0 mm long, in fruiting 9.0–11.0 × 7.0–8.0 mm, with a mucro 0.5–1.0 mm long; white or creamy inside, abaxially with dense stellate hairs; flower buds and anthocarp ovoid or almost roundish (Fig. 5A); yellowish multifid petaloids often present. Stamens 5; anthers 0.8–1.0 mm long. Stigmas 5, 0.7–1.2 mm (sometimes a style is present up to 0.7 mm long). Seeds 0.7–0.9 × 0.50–0.60 mm, almost black, colliculate and without longitudinal striae; aril hood often reduced, rarely clearly visible, and in the latter case up to 0.30 mm long.

**Habitat.** Sands, seasonally flooded depressions, rocks, limestones or clayey soils; 0–1300 m.

**Distribution** (Fig. 29).


Figure 27. A herbarium specimen of *Glinus oppositifolius* var. *glomeratus* (Angola, Cuando-Cubango prov., Longa, Longa river, 1360 m, 17 Mar 1960, *E.J. Mendes 3155*, BM013839321).
kana county, Lomesekin, locally very common, 29 Aug 1968, O.M. Mwangangi & D. Gwynne 1218 (K); Turkana county, Lodete, 570 m, 24 Jul 1969, O.M. Mwangangi 1378 (FT0007124, K); [Mandera county] 54 km NE of El Wak, 380 m, 12 Dec 1971, Bally & Smith 14572 (K); Samburu county, nr Wamba, 3 Jul 1974, R.B. Faden & A.J. Faden 74-946 (BR0000017456043, K, WAG1103337); Garissa county, Garissa to Hagadera, 230 m, 29 May 1977, J.B. Gillett 21193 (FT0007126, K); [Tana River county] Kora camp junction, 3 Sep 1983, G.M. Mungai 83/35 (K); [Makueni county] Chyulu plains, Kigelia, 26 Jul 1992, Luke 3204 (K); [Kitui county] Ukasi Dam, 3 Aug 2006, L. Festo & Q. Luke 2813 (K, LE); Makueni county, Kibwezi, 990 m, 22 Nov 2010, Q. Luke 14955 (K);

SOMALIA: [Sanaag region] nr Dofar [El Dahir], 19 Oct 1954, P.R.O. Balley 10115 (FT0007117, K); [Lower Juba Region] Lag Badana, 28 Oct 1971, G. Moggi & R. Bavazzano s.n. (FT0007034); [Bay region] Dinsoor, 16 Feb 1981, J.J. Beckett 1491 (K); [Galguduud region] 27 km S of Guri Ceel, 5°05’N, 45°47’E, 6 Jun 1988, P. Kuchar 17836 (K);

SUDAN: Kassala State, S of Tob el Ahmar, 16 Apr 1961, J.K. Jackson 4143 (K);

TANZANIA: [Dodoma region] 29 miles S of Dodoma, 3500 ft, 15 Aug 1928, R.G. Greenway 773 (BM, K); Dodoma region, Ikowa Dam, 60 km E of Dodoma, 900 m, 29 Jul 1970, M. Thulin & B. Mhoro 515 (K001394832); Dodoma county, Ikowa reservoir, 980 m, 19 Jun 1974, B. Mhoro & I. Backéus 1949 (WAG0192068).

General distribution. East Africa; Arabian Peninsula (Yemen). In addition to the records cited, it is apparently present in Djibouti and Eritrea. In Yemen, where *G. setiflorus* was described from, it is only known from the type locality (Miller 1996).

**Glinus zambesiacus** Sukhor., sp. nov.
urn:lsid:ipni.org:names:77215160-1

Fig. 30

– *Glinus lotoides × G. oppositifolius* p.p., *G. lotoides* auct. non L., *G. lotoides* var. *virens* auct. non Fenzl; *G. bainesii* auct. non (Oliv.) Pax

**Type material.** Holotype: Zambia. Barotseland, [Western province] Mongu, mud at edge of river, 6 Jan 1966, Robinson 6780 (K000865904! iso – M!).

**Description.** Annual up to 70 cm, often forming mats, with numerous prostrate or ascending stems, covered at least in young parts with dense stellate hairs, so that the plant appears greyish; prickles absent. Leaves in false whorls of 2–5, oblong-spatulate or obovate, rarely almost roundish, entire, 10.0–40.0(50.0) × 5.0–15.0(20.0) mm, shortly pedunculate (peduncles up to 15.0 mm), green, scarcely pubescent, rarely subvillose, veins not prominent abaxially. Flowers in clusters of 2–12, pedicellate (pedicels 5.0–20.0 mm long, rarely shorter). Perianth cylindrical (Fig. 5B), perianth segments (5) oblong or ovate, 5.5–7.0 mm long at anthesis, 2.5–3.0 mm wide, abaxially with scattered stellate, easily caducous hairs (at least along mid-vein), abaxially green or pink
Figure 28. A herbarium specimen of *Glinus setiflorus* (Tanzania, Dodoma region, Ikowa Dam, 60 km E of Dodoma, 900 m, 29 Jul 1970, *M. Thulin & B. Mhoro 515*, K001394832). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.
at senescence, adaxially white or creamy, in fruiting reaching 6.5–8.0 mm long, with a mucro 0.5–1.0 mm long. Stamens 10–15, outer stamen series often sterile with filaments terminating with teeth; anthers (1.0)1.2–1.8 mm long (1.0–1.2 mm in plants from higher altitudes). Stylodia 3, 1.0–1.5 mm long (sometimes united in the lower half into a style). Seeds reddish or brown-red, 0.5–0.6 × 0.35–0.50 mm, colliculate, without longitudinal ridges, aril hood clearly visible, ca. 0.25 mm long.

In the herbaria, *G. zambesiacus* was identified as *G. lotoides*, *G. lotoides* var. *virens*, *G. lotoides* × *G. oppositifolius*, and sometimes as *G. bainesii*. *Glinus zambesiacus*, *G. oppositifolius*, *G. bainesii* and *G. hirtus* are found in similar habitats. All character sets for each species are indicated in Table 5. The new species can be easily differentiated from both *G. oppositifolius* and *G. bainesii* by indumentum consisting of stellate trichomes, while *G. hirtus* has much shorter perianth and fewer (up to 8) stamens.
Glinus zambesiacus is related to African *G. lotoides* and *G. setiflorus* (Figs 1, 2) and is easily differentiated from both by cylindrical anthocarp, not recessed leaf veins, length of anthers, number of stigmas, and seed colour (see Table 5).

**Habitat.** Sands, savannas or as a weed at altitudes up to 2200 m a.s.l. The plants growing in montane areas (DR Congo: Katanga province; Kenya; Tanzania) have much shorter pedicels (up to 6.0 mm long), and their flowers are subsessile. Such specimens were labelled in some herbaria as *Glinus zambesiacus* var. *brevipedicellatus* Sukhor. but this characteristic seems to be variable in the specimens collected at lower altitudes.

**Etymology.** The new species is named after the territory of Zambezi river basin as its main distribution area.

Figure 30. Holotype of *Glinus zambesiacus* Sukhor., sp. nov. (Zambia, Barotseland, [Western province] Mongu, mud at edge of river, 6 January 1966, *Robinson 6780*, K000865904). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

*Gilges 748* (K); [Copperbelt prov.] Kaluba, 940 m, 24 Dec 1959, J.-J. *Symoens 6822* (BR0000018269598); [Muchinga prov.] Mbesuma, 11 Oct 1960, E.A. *Robinson 3950* (M); [Central prov.] Mwenda, 12 Dec 1960, J.-J. *Symoens 7942* (BR0000018269383);
Evolution and taxonomy of *Glinus*

The species is only known from the countries listed above.

**General distribution.** The species is only known from the countries listed above.

The most predictable records in the countries where no *Glinus* species were previously collected

Based on the distribution patterns of the species growing in Africa (Figs 15, 18, 21, 24, 26, 29, 31), the following species may occur in Equatorial Guinea, Lesotho and West Sahara.

Equatorial Guinea: *Glinus hirtus*, *G. oppositifolius*.
Lesotho: *Glinus hirtus*, *G. lotoides*, *G. oppositifolius*.
West Sahara: *Glinus lotoides*.

**Records excluded from Sub-Saharan Africa**


**Type:** Chile, habitat in inundatis locis Conceptionis Chile ad Mochita et Carcamo terminum, *H. Ruiz & J.A. Pavón s.n.* (MA?).
= *Mollugo glinoides* Cambess. in Saint-Hilaire, Fl. Bras. Merid. 2: 171 (1830). **Type:** n.v. The protologue (Saint-Hilaire et al. 1829–1833) and the figure 109 show the plant with glabrous seeds. For this reason, *Mollugo glinoides* was synonymized with *Glinus radiatus*. Fenzl (1836) introduced *G. cambessedesii* as a substituting name for both *Mollugo radiata* and *M. glinoides*.

= *Mollugo araucana* Phil., Anales Univ. Chile 85: 170 (1893). **Type:** n.v.

**Note.** The American *Glinus radiatus* was reported for Senegal and some other African countries (Central African Republic, Mali, Nigeria, and South Africa) as an alien species originating from tropical America (Berhaut 1979). It was later reported for Mali, Niger, Central African Republic, and repeatedly for Senegal by Boudet et al. (1986), for Benin by Akoegninou et al. (2006), for Guinea, Sierra Leone, Ghana, Ivory Coast by Lisowski (2009) and for Burkina Faso by Thiombiano et al. (2012) and Schmidt et
al. (2017). We did not see any specimens of true G. radiatus from the whole of Africa, and almost all specimens identified as G. radiatus belong to the morphologically similar G. hirtus. The differences between them are mentioned in the notes under G. hirtus. One of the specimens from Burkina Faso (Gnagna prov., Bogande, FR-0019665) identified as G. radiatus is indeed Zaleya pentandra (L.) C.Jeffrey (Aizoaceae).

Species excluded from Glinus

Glinus chrystallinus Forssk., Fl. Aegypt.-Arab.: 95 (1775).

= Aizoon canariense L.

Type material. Holotype: Egypt. Cairo (“Birket el-hadj”), [August 1762,] P. Forsskål Herb. Forsskål 544 (C10002319).

Note. The protologue (Forsskål 1775) was based on the only specimen indicated by Hepper and Friis (1994) as holotype. Hartmann (2001: 31) designated figure 14 in Forsskål (1776) as lectotype but this choice has no standing.

The locality information and the collection date are complemented from Hepper and Friis (1994).


Glinus mucronatus (Klotzsch) in Peters, Naturw. Reise Mossambique 6 (Bot., 2): 570 (1864). Described from Mozambique.

= Corbichonia decumbens (Forssk.) Exell (see Sukhorukov and Kushunina 2015).

Type material. n.v. Probably described from Mozambique.

Note. No specimens were cited in the protologue (Sprengel 1825), and the description of G. mozambicensis is short and cannot be evaluated properly. According to Don (1834) and Endlicher and Fenzl (1839), it is a synonym of Gisekia pharnaceoides L. sensu lato [incl. G. africana Kuntze] (Gisekiaceae).

Glinus trianthemoides Roth, Nov. Pl. Spec.: 231 (1821).

= Corbichonia decumbens (Forssk.) Exell (see Sukhorukov and Kushunina 2015).

Type material. Neotype (designated here): Hb. Wight in Wallich Cat. 1543 (addenda) (K001113401).

Note. Roth (1821) is an account of plants collected by Benjamin Heyne in India. The corresponding herbarium specimens were donated to Roth, whose collection was purchased by the Berlin Botanical Garden (B) and largely destroyed together with the holdings of that Herbarium in 1943 (Hiepko 1987). Heyne made no records on the
exact provenance of his specimens, and “India Orientalis” (the Indian Peninsula) is the only information published and known.

In the absence of any surviving original material, we used for neotypification one of the classical specimens assigned to the species by Fenzl (1836), who was the first to interpret the name.

Heyne (in Roth 1821) described *G. trianthemoides* as a plant with glabrous stems, obovate leaves with rounded tips, and lax, almost dichotomous inflorescences. Such characters are not found in any *Glinus*. Wight (Wight and Walker-Arnott 1834) accepted the placement of Roth’s species in *Glinus* but doubted its taxonomic position in view of major morphological differences from the latter genus. Under the influence of that account, Fenzl (1836) established a separate genus for this taxon, *Axonothechium* Fenzl, still being uncertain about its precise taxonomic identity. Recent treatments (Gonçalves 1978; Sukhorukov and Kushunina 2015) placed *Glinus trianthemoides* into the synonymy of *Corbichonia decumbens*; this placement agrees with the material used by Fenzl and designated as neotype here.

**Conclusions**

*Glinus* is a monophyletic genus, presumably originating in tropical Africa, with predominant species diversity in Sub-Saharan Africa. Altogether, we accept six species for Sub-Saharan Africa, and none of them can be considered as locally endemic. Only *G. bainesii* and *G. zambesiacus* are restricted in their distribution to the southern and eastern parts of tropical Africa. A wide range of morphological characters can be used for the identification of *Glinus* species. In total, *Glinus* comprises 8–9 species (*G. bainesii*, *G. hirtus*, *G. lotoides*, *G. oppositifolius*, *G. orygioides*, *G. radiatus*, *G. setiflorus*, *G. zambeziacus*, and probably *G. ononoides*), and further research is needed to clarify the status of the American plants labelled as *Glinus “lotoides”*. 

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References


Barrelier J (1714b) Icones plantarum per Galliam, Hispaniam et Italian observatar, ad vivum exhibitarum. S.Ganeau, Paris.


Blume CL (1826) Bijdragen tot de flora van Nederlandsch Indië. Ter Lands Drukkerij, Batavia [Jakarta]. https://doi.org/10.5962/bhl.title.6656


Dizionario delle scienze naturali (1842), Vol. 12 [without authors], V. Batelli & Co., Florence.
Endlicher S (1840) Genera plantarum secundum ordines naturales disposita. F. Beck, Vienna.
Forsskål P (1775) Flora Aegyptiaco-Arabica. Möller, Copenhagen.
Forsskål P (1776) Icones Rerum Naturalium. Möller, Copenhagen.


Täckholm V, Boulos L (1972) Supplementary notes to Student’s flora of Egypt. Publication of the Cairo University Herbarium 5: 3–135.


Thunberg CP (1794) Prodromus plantarum Capensium, quas in promontorio Bonae Spei Africes, annis 1772–1775, collegit Carol Peter Thunberg. Edman, Uppsala. https://doi.org/10.5962/bhl.title.84


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