Journal of Bryology

ISSN: 0373-6687 (Print) 1743-2820 (Online) Journal homepage: https://www.tandfonline.com/loi/yjbr20

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To cite this article: Leonard T. Ellis (2017) *Syrrhopodon spuriodisciformis* Dusén (Calymperaceae) as a distinct species, with taxonomic notes on *Syrrhopodon africanus* (Mitt.) Paris and related taxa, Journal of Bryology, 39:3, 255-266, DOI: 10.1080/03736687.2017.1284634

To link to this article: https://doi.org/10.1080/03736687.2017.1284634

Syrrhopodon spuriodisciformis Dusén (Calymperaceae) as a distinct species, with taxonomic notes on *Syrrhopodon africanus* (Mitt.) Paris and related taxa

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Syrrhopodon spuriodisciformis Dusén is removed from synonymy with *Syrrhopodon africanus* (Mitt.) Paris and reinstated as a distinct species. *Syrrhopodon guineensis* Broth. & Paris is recognised as a synonym of *S. spuriodisciformis*. *Syrrhopodon africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese and *S. africanus* ssp. *mandrakensis* (Tixier) W.D.Reese are reconsidered as species, and the status of *Syrrhopodon obuduensis* Egunyomi & Olar. is discussed.

Keywords: Calymperaceae, *Syrrhopodon africanus sensu lato*, *Syrrhopodon spuriodisciformis*, Taxonomy

Introduction

Syrrhopodon subgenus *Pseudocalymperes* Broth. is justly included in the family Calymperaceae, and although reasonably placed within *Syrrhopodon* Schwägr., its species have sometimes been associated with those in the related genus, *Mitthyridium* H.Rob. (≡ *Thyridium* Mitt., *hom. illeg*.) (see Reese, 1993a). An early modern revision of the group was undertaken by Tixier (1967) as the genus *Calymperopsis* (Müll.Hal.) M.Fleisch. Then, in a series of papers, W. D. Reese (1993a, 1994a, 1994b, 1995, 1999) further rationalised the taxonomy of the group. In the earliest of these (Reese, 1993a), he established its correct name — *Syrrhopodon* subg. *Pseudocalymperes*, and stated that its species were characterised by the possession of 'filiforme gemmae …. borne ventrally along the costa at midleaf, commonly on [modified] deltoid leaves in comae at stem tips'. Previously, when Fleischer (1913) published the group at the generic level as *Calymperopsis*, he also listed among its distinguishing features, the possession of a calyptra deeply lobed from the base. However, Reese (1978) dismissed these lobes (narrow segments) as a defining characteristic, as they were not present in all species of the group. He noted that they were largely lacking in taxa occurring in the Americas, such as *Syrrhopodon parasiticus* (Brid.) Besch., which otherwise possessed leaves and gemmae undeniably characteristic of '*Calymperopsis*', i.e. *Syrrhopodon* subg. *Pseudocalymperes*. However, the lobed calyptrae were not altogether a figment of Fleischer's imagination. The calyptra in the lectotype species of the subgenus, *Syrrhopodon semiliberus* (Mitt.) Paris, does possess deep lobes, where splits have developed distally from the base of the calyptra between linear, evenly spaced longitudinal ribs (see Thailand, Kerr *384*, BM000664956). Lobed calyptrae have also been seen in two other of the taxa discussed below, and with further investigation, the feature may prove to have some taxonomic significance within the subgenus.

A synopsis of the subgenus by Reese (1995) incorporated a subgroup of the included taxa that were linked in his key by their possession of leaves with a marginal strand of stereids (marginal stereome) and a chlorophyllose lamina formed by pluripapillose cells. Reese (1995) referred to these taxa as: *Syrrhopodon africanus* ssp. *africanus* (Mitt.) Paris (with probable synonym *S. obuduensis* Egunyomi & Olar.) and *S. africanus* ssp. *mandrakensis* (Tixier) W.D.Reese from Africa; *S. africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese from the Neotropics, and from Asia *S. semiliberus* (Mitt.) Paris (with probable synonym *Calymperopsis vietnamensis* Ninh). These are the taxa that provide the context within which *Syrrhopodon spuriodisciformis* Dusén, hitherto reduced in synonymy with *S. africanus*, appears a distinct species.

In the course of his investigations during 1994, Reese identified some collections of subgenus *Pseudocalymperes* from NW Africa and Central/East

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DOI 10.1080/03736687.2017.1284634

Africa as *Syrrhopodon africanus*. Among these, one from Cameroon (NW Africa) had originally been collected and described by Dusén (1896) as representing a new species, '*Syrrhopodon spuriodisciformis* Dusén'. Reese (1994a) placed the latter in synonymy with *S. africanus*, stating that his lectotype for *S. spuriodisciformis* (Cameroon, Dusén *exsicc. 500*, in S, and its duplicates in BM, PC), and Dusén's protologue and illustrations for the species were 'an excellent match for *S. africanus*'. However, as noted in Wilbraham & Ellis (2010), while the collections from Central/East Africa determined by Reese as *S. africanus* had features agreeing with those of the type material of *S. africanus* (described from Tanzania), the collections from north-western tropical Africa (represented by *S. spuriodisciformis)* differed consistently in several features of their leaves. Subsequent investigation has indicated that the differences are sufficient to justify removing *S. spuriodisciformis* from synonymy with *S. africanus*, and recognising it as a distinct species.

Also closely linked with *S. africanus* by Reese (1995), but treated as its subspecies rather than as synonyms, were *Calymperopsis mandrakensis* Tixier (≡ *S. africanus* ssp. *mandrakensis* (Tixier) W.D.Reese) and *Syrrhopodon graminicola* R.S.Williams (≡ *S. africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese). On detailed investigation, the latter appeared more similar to *S. spuriodisciformis* than to *S. africanus,* and on present evidence deserves specific status, while the ssp. *mandrakensis* superficially more closely resembled the type subspecies of *S. africanus,* but this too would best be regarded as a distinct species.

Note on terminology: 'Normal leaves' = lingulate, ligulate or lanceolate stem and branch leaves, sometimes bearing filamentous gemmae. 'Modified leaves' = triangular-lingulate to deltoid leaves, mostly forming terminal comae and usually bearing filamentous gemmae.

Key to *Syrrhopodon spuriodisciformis* and Associated Taxa

(Taxa in *Syrrhopodon* subg. *Pseudocalymperes* with leaves possessing a marginal stereome and pluripapillose cells forming the chlorophyllose lamina).

1. Ventral epidermis of costa in leaf base differentiated, formed by unistratose layer of large, thin-walled hyaline cells (resembling cells of hyaline lamina), in cross-sections of costa appearing larger than adjacent guide cells 2
1. Ventral epidermis of costa in leaf base not differentiated, or formed by narrow, thick-walled cells, in cross-sections of costa appearing smaller than adjacent guide cells 3
2. Leaves 3–4 mm long; chlorophyllose limb in normal leaves usually lanceolate with an acute (–acuminate) apex; costa shortly excurrent, a ventral cortex of isodiametric pluripapillose cells restricted to region just above leaf base, often broken or absent, on dorsal surface minute teeth very few or absent; marginal stereome reaching leaf apex, with few teeth or papillae, (north-western tropical Africa) . . . . *S. spuriodisciformis*
2. Leaves 2–3 mm long (occasionally longer); chlorophyllose limb in normal leaves usually lingulate (–lanceolate) with broadly acute (–obtuse), apiculate apex; costa percurrent, ventral surface with extensive cortex of isodiametric pluripapillose cells and dorsal surface with numerous, scattered minute teeth; marginal stereome failing short of leaf apex, well endowed with teeth and small, remote papillae (New World Tropics) . . . . . *S. graminicola*
3. Ventral surface of costa rough, largely formed by protuberant, papillose chlorophyllose cells (Asia) . . . . . *S. semiliberus*
3. Ventral surface of costa largely smooth, formed mostly by stereids 4
4. Longest normal leaves lingulate (tongue-shaped); cells of chlorophyllose lamina 7.5–15(–17.5) × 7.5–10(–12.5) μm, dorsal and ventral surfaces of each cell pluripapillose with 3–5 small papillae; seen in cross-section, cells forming ventral surface of costa in leaf base with broader lumina than underlying stereids (Central/E Africa/ Réunion Island). . . . . *S. africanus*
4. Longest normal leaves ligulate (strap-like); cells of chlorophyllose lamina 5–10 (–15) × 5–8(–12.5) μm, each with a dorsal multifid papilla (ventrally pluripapillose); ventral surface of costa in leaf base largely formed by stereids (Madagascar/ ?E Africa) . . . . . *S. mandrakensis*

Taxonomy and Nomenclature

From among the taxa keyed out above, *Syrrhopodon semiliberus* (Mitt.) Paris is an incontestably distinct species. It serves as the lectotype species for *Syrrhopodon* subg. *Pseudocalymperes* Broth. (*fide* Reese, 1995), and has been described and illustrated in detail by Eddy (1990) and Ellis (2016). More controversially, *Syrrhopodon spuriodisciformis* Dusén, *S. graminicola* R.S.Williams and '*Calymperopsis mandrakensis* Tixier' have been variously closely linked with *Syrrhopodon africanus* (Mitt.) Paris (see Reese, 1995). However, there are significant differences between *S. africanus* and these apparently associated taxa, which are discussed below and summarised in Table 1. First, as a species herein reinstated from synonymy, the key features of *S. spuriodisciformis* are described in detail.

1. ***Syrrhopodon spuriodisciformis*** Dusén, Kongl. Svenska Vetensk. Akad. Handl., 28(3): 35, a–g, f. 1–2 (1896).

(Figure 1)

Table 1 Summary of the differences between *Syrrhopodon spuriodisciformis*, *S. graminicola*, *S. africanus*, and *S. mandrakensis*.

	S. spuriodisciformis	*S. graminicola*	*S. africanus*	*S. mandrakensis*
Normal leaves	3–4 mm long; chlorophyllose limb usually lanceolate with an acute (–acuminate) apex extending from a broad clasping base	2->3 mm long; usually lingulate with a broadly acute (–obtuse), apiculate apex	2–4(−5) mm long; usually lingulate with a broadly acute (–obtuse), apiculate apex	2–4 mm long, ligulate (–narrowly lingulate), with a broadly acute (–obtuse), apiculate apex
Costa	Often slightly excurrent	Usually subpercurrent to percurrent	Usually subpercurrent to percurrent	Usually subpercurrent to percurrent
• Ventral surface (epidermis) in leaf base	Composed of small hyaline cells, thin-walled, in cross-section larger than adjacent guide cells.	Composed of small hyaline cells, thin-walled, in cross-section larger than adjacent guide cells.	Composed of narrow, thick-walled cells, in cross-section smaller than adjacent guide cells.	Epidermis not differentiated, surface largely formed by stereids.
• Ventral surface above leaf base	Largely formed by stereids, some small chlorophyllose cells usually form a limited, often broken, layer just above the hyaline leaf base	Often with an extensive cortex of small pluripapillose, chlorophyllose cells (from apex of hyaline leaf base to beyond mid-limb)	Largely formed by stereids, some small chlorophyllose cells usually form a limited, often broken, layer just above the hyaline leaf base	Largely formed by stereids, some small chlorophyllose cells usually form a limited, often broken, layer just above the hyaline leaf base; occasional remote teeth may occur from mid-leaf towards apex
• Dorsal surface	Largely smooth, minute teeth sparse to absent	With numerous scattered minute teeth	Largely smooth, minute teeth sparse to absent	Largely smooth, but often with a few teeth near leaf apex
Cells of chlorophyllose lamina	Pluripapillose on both surfaces; (5–)7–12.5(−15) × (5–)7–8(−10) µm	Pluripapillose on both surfaces; 7.5–12.5(−15) × (5–)7.5–810(−12.5) µm	Pluripapillose on both surfaces; 7.5–15(−17.5) × 7.5–10(−12.5) µm	Ventrally pluripapillose; dorsally with singular multifid papillae; 5–10(–15) × 5–8(−12.5) µm
Marginal stereome	Usually reaching leaf apex, often with sparse singular papillae and remote teeth	Usually failing short of leaf apex, outer cells often adorned with 2 or 3 papillae; many remote (often double) teeth evident.	Usually failing short of leaf apex; often with sparse singular papillae and remote teeth	Usually failing short of leaf apex, with small, remote teeth, but mostly lacking papillae
Sporophyte				
Seta	3.5–4 mm long (occasionally polysetous)	Up to 3 mm long (often polysetous)	Not seen	>3.5 mm long (unisetous)
Theca	Mostly narrowly cylindrical, 2–2.75 mm long	Cylindrical to slightly ellipsoid, 1–1.5 mm long	Not seen	Not seen
Calyptra	Not seen	Reported to be lobed from the base to beyond mid-calyptra	Not seen	Lobed from the base to beyond mid-calyptra

Type citation: 'Habitat in Camerunia in ramis arborum, ubi ad Ekundu Ndene emporium m. Martio a. 1892 legi. [*leg.* P. Dusén].'

Lectotype (*fide* Reese, 1994a): **Cameroon**. 'Ad Ekundu N'dene emporium', 16 March 1892, *leg.* P. Dusén (*Musci Africani in Camerunia a P. Dusén no. 500.* '*Calymperes subdisciforme* C.M.') (S, sheet B, specimen 7, B181717 !); *isolectotypes*: (BM — BM000663246 !; BM000663241 !; BM000677484 !; H-BR —0811020 !; probable isolectotype: NY — 025938 !).

Notes: This combination was originally published as '*Syrrhopodon spurio-disciformis* Dusén' (see Dusén, 1896).

Another part of *Musci Africani in Camerunia a P. Dusén,* no. *500* in BM (BM000677482) is the holotype of *Syrrhopodon perdusenii* W.D.Reese, a distinct species in the subgenus *Pseudocalymperes* (see Reese, 1994a).

= *Syrrhopodon guineensis* Broth. & Paris in Paris, Rev. Bryol. 34: 94 (1907), *syn.nov.*

Type citation: [French Guinea] Konkouré super. [*leg.* H. Pobeguin]

Holotype: Guinea (French Guinea), Konkouré super., 9 November 1906, *leg.* H. Pobeguin *647* (H-BR —0811016 !); *isotype* —(Hb. Möller, S B180422 !).

Description: *Shoots*: <0.5–3.0 cm high, branched or simple, forming tufts or dense mats on twigs and branches, often terminating with a coma of modified, gemmiferous leaves. *Normal leaves*: <3–4 mm long, with a broadly lanceolate (–lingulate) chlorophyllose limb extending from a broad, suberect, clasping hyaline base, limb patent recurved when moist, incurved and twisted when dry, narrowing to an acute (–acuminate), usually dentate apex (Figure 1A). *Costa*: percurrent to slightly excurrent in a sharp point (Figure 1B, C); ventral surface in hyaline base formed by a unistratose layer of small hyaline cells, some with singular pores in transverse walls (Figure 1D, E), distally (to the leaf apex) ventral surface formed by stereids (Figure 1F, G), largely smooth (sometimes with a few remote teeth),

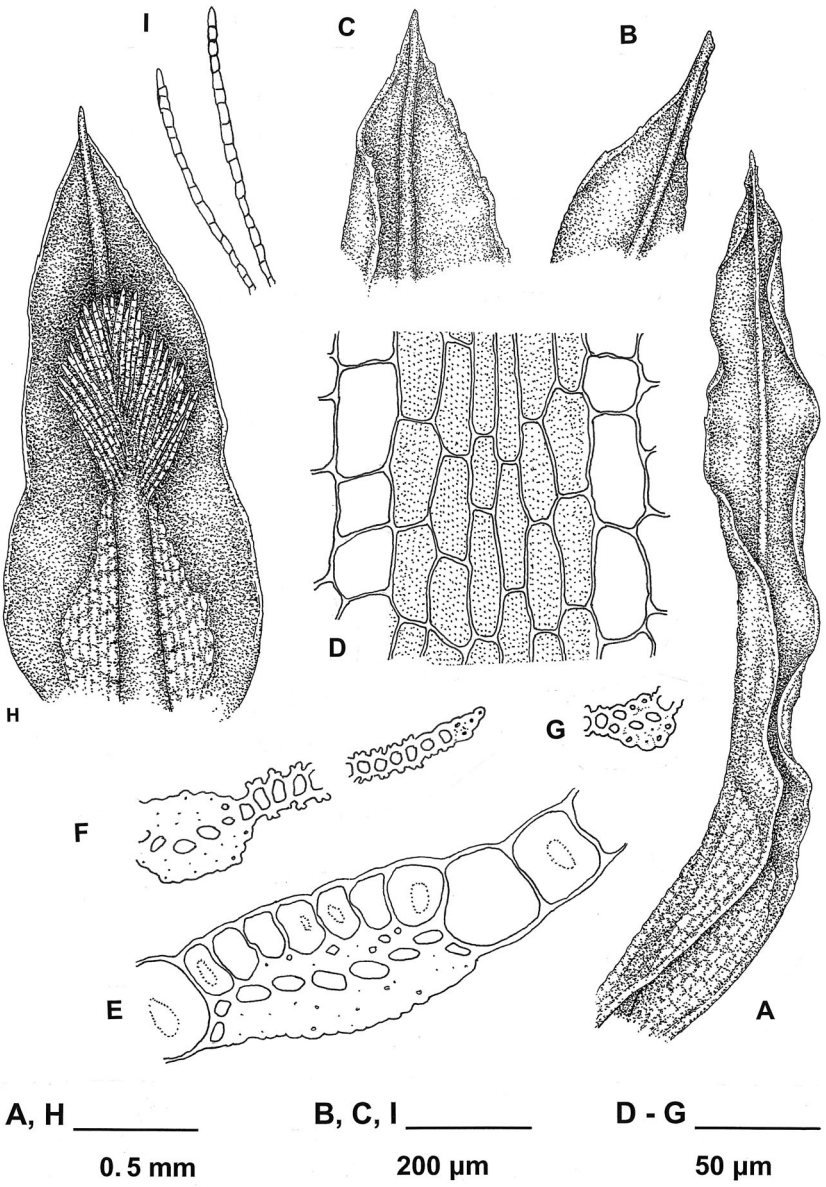

Figure 1 ***Syrrhopodon spuriodisciformis*** **Dusén. (A) Normal leaf in ventral view, with (B, C): detail of apex in (B) dorsal view and (C) ventral view. (D, E) Costa in mid- hyaline leaf base: (D) ventral surface, (E) in cross-section. (F, G) Chlorophyllose limb in cross-section: (F) at mid-limb, (G) at leaf apex. (H) Modified leaf in ventral view with gemmae. (I) Filamentous gemmae. (A, B, D, F) Drawn from Dusén *500* (BM000663246, isolectotype of *S. spuriodisciformis*), (C, E) from Pobeguin *647* (H-BR —0811016, holotype of *Syrrhopodon guineensis* Broth. & Paris); (G – I) from Richards *R7207* (BM000663242).**

but just above the hyaline base small quadrangular, thick-walled and pluripapillose cells (like those of the chlorophyllose lamina) may form a limited, often partial, superficial layer; dorsal surface largely formed by stereids, smooth apart from sparse minute teeth exerted from distal end of some superficial cells. *Chlorophyllose lamina*: often incurved, undulate towards margins, cells thick-walled, polygonal to rounded, isodiametric to slightly longer than broad, (5–)7–12.5(–15) × (5–)7.5–8(–10) µm, ventrally and dorsally pluripapillose (each face mostly with 3–5 papillae) (Figure 1F). *Hyaline lamina*: mostly occupying under a third of leaf length, with a sharply defined acute apex. *Leaf margins*: in leaf base entire, formed by a narrow unistratose band of thick-walled linear cells, distally becoming a strand of stereids (stereome), stereome usually reaching leaf apex, largely entire to distantly toothed (sometimes double toothed, usually toothed near leaf apex), sometimes with remote, simple papilla on outermost cells. *Modified leaves*: similar to normal leaves except: broadly triangular-lanceolate to deltoid, around 2–>3 mm long (Figure 1H), erect-incurved when dry, erect-patent when moist, forming distinct comae (gemmae cups) at apices of some shoots (usually emergent above normal leaves); *costa* incrassate, percurrent to excurrent, with extensive region of small quadrangular, thick-walled and pluripapillose cells forming the ventral surface above the hyaline base (gemmae develop from among these cells); *chlorophyllose*

lamina only slightly undulate, cells similar to those in normal leaves but slightly larger, mostly 10–>17.5 × 7.5–10 µm; *marginal stereome* reaching or almost reaching leaf apex. *Gemmae*: filamentous, uniseriate, produced mostly on modified leaves, arising (often in dense tufts) from lateral cells along the ventral surface of the costa from beyond apex of hyaline lamina to beyond mid-leaf. *Sporophytes*: Perichaetia with 1 (–2) setae; perichaetial leaves similar to normal leaves, but narrowly lanceolate. *Seta* 3.5–4 mm long, smooth, reddish-brown; *theca* narrowly cylindrical, pale brown, 2.0–2.75 mm long, exothecial cells with thick, porose longitudinal walls and thin transverse walls; *peristome* syrrhopodontoid; *operculum* with a long, fine, erect rostrum; spores (only a few seen in old empty capsules) spherical to elliptical, finely papillose, 35–45 µm.

Note: Most perichaetia appear to be unisetous, but polysetous perichaetia were observed in the lectotype (S —B181717) and isolectotypes 0811020 (H-BR) and BM000663241 'A' (BM). For the present study, peristome teeth were not found in sufficiently good condition to describe properly, but were described and illustrated by Dusén (1896; Figure 2), here loosely translated from his Latin text: — teeth 16, extending 240 µm above [rim of] capsule, 40 µm wide, yellow, lanceolate, nodulose, thickened here and there. Similarly, a calyptra was not found in the available material by the present author, but unfortunately, neither was it described in Dusén's protologue.

Taxonomic notes: Reese (1994a) erroneously placed *S. spuriodisciformis* in synonymy with *S. africanus*. The features distinguishing the former species from the latter are detailed below under *S. africanus*, but the most consistent of these relates to the cells forming the ventral surface of the costa in the hyaline leaf base. In *S. spuriodisciformis,* these resemble the cells of the hyaline lamina (albeit smaller). In cross-sections of the costa, they are seen to form a single layer and invariably appear larger than adjacent guide cells; some have singular rounded pores in their transverse walls (Figure 1E). In a study including the NW African collections of *S. spuriodisciformis* cited below, Richards & Edwards (1972) justly employed these supra-costal hyaline cells as a key feature of the species (although erroneously under the name '*Calymperopsis disciformis* (Müll.Hal.) Tixier [*hom. illeg.*]'). This 'ventral hyaline epidermis' is not apparent in costae in *S. africanus* (Figure 2G–I).

Along with *S. spuriodisciformis*, Reese (1995) also placed *Syrrhopodon guineensis* Broth. & Paris in synonymy with *S. africanus*. Described from Guinea in West Africa (Paris, 1907), the type material (Konkouré super., Pobeguin *s.n.*) has features agreeing with those of West African *S. spuriodisciformis*, rather

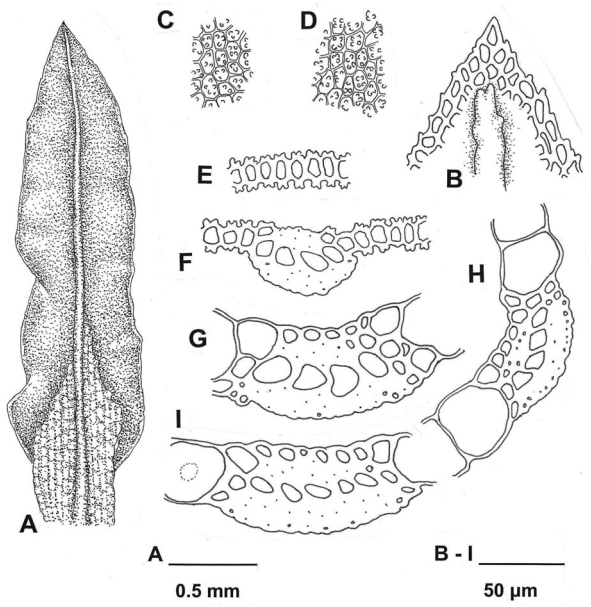

Figure 2 ***Syrrhopodon africanus*** **(Mitt.) Paris. (A) Normal leaf in dorsal view. (B) Margin at leaf apex. (C, D, E) Chlorophyllose lamina: (C) on ventral surface, (D) on dorsal surface, (E) in cross-section. (F – I) Costa in cross-section: (F) through chlorophyllose limb, (G – I) through hyaline leaf base. (A, E, F) Drawn from Uganda, Last *s.n.* (BM000663239 – isotype of *S. africanus*; (B) from Uganda, Last *s.n.* (NY — 00919813 —holotype of *S. africanus*); (C, D, H) from Uganda, Wigginton *U8080d* (BM001226508); (G) from Uganda, Hodgetts *U4557a* (BM001226509); (I) from Congo, Bequeart *s.n.* (BM000677677).**

than those of East African *S. africanus*. As in the other W African specimens, Pobeguin's original collection has leaves with a broadly lanceolate chlorophyllose limb extending from a clasping hyaline base, a percurrent to excurrent costa (Figure 1C), a marginal stereome that usually reaches the leaf apex, and small hyaline cells overlying the costa in the leaf base (Figure 1E). These features indicate that *S. guineensis* is conspecific with the earlier described *S. spuriodisciformis*.

Habitat and distribution: *S. spuriodisciformis* is sparsely but widely distributed within north-western tropical Africa. Apparently often locally frequent, it occurs on twigs and branches of trees in lowland rain forest and savannah. The type was collected from trees in a market place. Fragmentary ecological samples recently collected from south-eastern Madagascar in lowland humid forest (*leg.* S. Stow, 2016, BM) appear to include shoots of *S. spuriodisciformis*.

Specific altitude data were absent from the labels of the collections cited below, but all of the given localities (including hills) seem to be at relatively low altitudes.

Specimens examined: Nigeria: Benin, Okomu Forest Reserve: 24 December 1947, *leg.* E. W. Jones *R3721 pro parte* (BM —BM000677471), 24 January 1948, *leg.* E. W. Jones *3894* BM —BM000663240; 9 December 1947, *leg.* P. W. Richards *3628* (BM —BM000663243);

17 December 1947, *leg.* P. W. Richards *3681* (BM —BM000663244); Benin, Agradi village, near Sapoba, 14 November 1949, *leg.* R. Keay & R. Meikle *U.D.23* (BM —BM000736191). **Sierra Leone:** Kasewe Forest reserve, 27 February 1971, *leg.* P. W. Richards *R7207* (BM— BM000663242). **Cameroon:** Ekumba Liongo: June 1892, *leg.* P. Dusén *s.n.* (S —Hb. Dusén 'sheet B, specimen 1' B234013); June 1892, *leg.* P. Dusén *s.n.* (S —Hb. Möller 'sheet B, specimen 8' B2344014); Ekundu N'dene, *leg.* P. Dusén *s.n.* (Hb. Bescherelle *ex* Hb. Müller, BM —BM000677483).

2. ***Syrrhopodon africanus*** (Mitt.) Paris, Index Bryol. 1244 (1898). (Figure 2)

≡ *Thyridium africanum* Mitt., J. Linn. Soc. Bot., 22: 303 (1886); ≡ *Calymperes africanum* (Mitt.) Paris, Index Bryol. 227 (1894); ≡ *Calymperopsis africana* (Mitt.) Broth., Nat. Pflanzenfam. ed. 2, 10: 235 (1924).

Type citation: 'Usagara Mountains, *Mr. Last.*'

Holotype: [**Tanzania**] 'Central Africa', Usagara Mountains, *leg.* Last *s.n.* (NY —00919813!); *isotypes*: (BM —Hb. Dixon, BM000663239 !; S —Hb. Möller — B179446!); *probable isotype*: (NY —02225216 !)

Taxonomic notes: *S. africanus* (Mitt.) Paris was described in detail and illustrated by Ellis (2007), but the features of the sporophyte mentioned in that treatment were based on material from NW Africa herein recognised as *S. spuriodisciformis*. Sporophytes were not present in the available material of *S. africanus* itself.

Features distinguishing *S. africanus* from *S. spuriodisciformis* are well exemplified in their normal leaves. In *S. africanus*, these leaves are: (1) lingulate, 2–4(–5) mm long, with a broadly pointed (–obtuse), apiculate apex (Figure 2A) (as opposed to lanceolate with an acute (–acuminate apex); (2) the costa is subpercurrent to percurrent (Figure 2B) (never shortly excurrent); (3) the cells forming the ventral surface of the costa in the hyaline leaf base appear distinctly differentiated from those of the adjacent hyaline lamina. Unlike in *S. spuriodisciformis*, they do not resemble small hyaline cells, but are relatively thick-walled, and in cross-sections of the costa, appear smaller than the adjacent guide cells (Figure 2G–I). (4) The cells of the chlorophyllose lamina reach a slightly larger size (7.5–15(–17.5) × 7.5–10(–12.5) μm) than those in *S. spuriodisciformis* ((5–)7–12.5(–15) × (5–)7–8(–10) μm), but are similarly pluripapillose dorsally and ventrally (Figure 2C, D). (5) In most leaves, the marginal stereome fails short of the leaf apex, which consequently is formed by cells of the chlorophyllose lamina, and is crenulate or papillose crenulate to irregularly denticulate (Figure 2B) (in *S. spuriodisciformis* the marginal stereome often reaches the leaf apex).

Modified leaves in S. *africanus* are broadly triangular-lingulate and form gemmiferous comae at the tips of some shoots. These comae are similar to those in *S. spuriodisciformis*, but often less obviously visible, being only slightly emergent above the normal leaves. As in the latter, the modified leaves have a broadly pointed (–obtuse), apiculate apex, a subpercurrent costa, and a marginal stereome failing short of the leaf apex.

Habitat and distribution: *S. africanus* is known from eastern and central Africa, where it occurs on twigs, branches and trunks of trees in high-altitude forest (1460–1650 m a.s.l.). Reports of *S. africanus* from lowland areas of Réunion Island (below 300 m a.s.l) were based on three specimens collected by T. Arts (see Wilbraham & Ellis, 2010). The cells forming the chlorophyllose lamina in these specimens were similar to those in *S. mandrakensis*, but otherwise the leaves possessed features closer to those in *S. africanus*. Discovering the true affinities of Arts' collections will require the examination of further well-developed local material. More typical of *S. africanus*, was a collection from Réunion by T. Hedderson (occurring on *Pandanus* at 850 m a.s.l.), which confirms the presence of this species on the island.

Specimens examined: Democratic Republic of the Congo: Penghe, forêt aux bords de l'Ituri, 3 February 1914, *leg.* Bequeart *s.n.* (BM —BM000677677). **Uganda:** Bwindi National Park, Rukubira, 1650 m a.s.l., 2 February 1996, *leg.* R. D. Porley *269a* (BM —BM001226507); Bushenyi, Kalinzu Forest Reserve, near Nkombe sawmill, 0°23′S 30°5′E, 1460 m a.s.l., 4 February 1997, *leg.* N. G. Hodgetts *U4557a* (BM— BM001226509); Bushenyi, Kalinzu Forest, near Forest Department Offices, 0°22′S 30°6′E, 1500 m a.s.l., 4 February 1997, *leg.* M. J. Wigginton *U8080d* (BM— BM001226508). **Réunion Island:** Tremblet, *ca* 230 m a.s.l., 8 November 1998, *leg.* T. Arts *RÉU92/28* (BM— BM000678107); Commune Plaine des Palmistes, just outside village of Plaine des Palmistes, 850 m a.s.l., 7 October 2006, *leg*. T. A. J. Hedderson, C. Ah-Peng & D. Strasbourg *16346* (BM —BM000976257).

3. ***S. graminicola*** R.S.Williams, Bull. Torrey Bot. Club, 47: 379 (1920). (Figure 3)

≡ *Syrrhopodon africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese, Bryologist, 98: 141 (1995).

Type citation: Jamaica, Woodstock, Westmoreland Hills, 'growing on bamboo joints', September 1907, *E. G. Britton 579* (NY).

Holotype: Jamaica. Westmoreland Hills, New Market, Woodstock, near Beaufort, 21 September 1907, *leg.* E. G. Britton *579* (NY —00635579 !); isotype: (NY —00635578!).

= *Calymperes disciforme* Müll.Hal., Linnaea, 21: 183 (1848) ≡ *Calymperopsis disciformis* (Müll.Hal.) Tixier, *hom. illeg.*, Rev. Bryol. Lichenol., 35: 290 (1967) ≡ *Syrrhopodon parasiticus* var. *disciformis* (Müll.Hal.) Florsch.

Type citation [Suriname], Bei *Paramáribo*. .. Aug. 1844. Hb. Kegel. No. 505.

Holotype: Suriname, bei *Paramáribo, leg.* Kegel *505* (GOET —GOET013649!).

= *Syrrhopodon schiffneri* Broth., Ergebn. Bot. Exped. Südbras., Musci, 281 (1924). [reprinted: Akad, Wiss. Wien, Math.-Naturwiss. Kl. Denkschr., 83: 281 (1927)].

Type citation: [Brazil], Sao Paulo. In silvis litor. prope Conceição de Itanhaen. 5–50 *m* s. m. [V. Schiffner] (226).

Holotype: Brazil, Sao Paulo. 'In silvis litor. prope Conceição de Itanhaen. 5–50 *m* s. m .', 3 July 1901, *leg.* V. Schiffner *226* (H-BR); isotype: BM — BM000664458 !).

Nomenclature: Tixier (1967) published the combination '*Calymperopsis disciformis* (Müll.Hal.) Tixier', which proved to be an illegitimate homonym owing to the prior existence of *Calymperopsis disciformis* (Dusén) M.Fleisch. Incidentally, the specimens that Tixier examined and cited in support of his new combination belonged to three different entities: *Syrrhopodon africanus* (Mitt.) Paris from East Africa, *S. spuriodisciformis* Dusén from NW Africa, and *S. graminicola* R.S.Williams from the Neotropics. However, Tixier's basionym for his illegitimate combination, *Calymperes disciforme* Müll.Hal., was validly described from Suriname (Müller, 1848), and transferred into *Syrrhopodon* by Florschütz (1964) as *Syrrhopodon parasiticus* var. *disciformis* (Müll.Hal.) Florsch. Reese (1993b) later recognised *C. disciforme* within *Syrrhopodon* at the species level, but as the combination '*Syrrhopodon disciformis* Dusén' already existed for another species, he used the next earliest valid heterotypic synonym within the genus, *Syrrhopodon graminicola* R.S.Williams, to replace '*disciformis*', Müller's specific epithet. Subsequently, Reese (1995) revised *S. graminicola*, with its solely Neotropical distribution, as *S. africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese. However, an examination of the type and other collections of *S. graminicola* indicate that the entity is completely distinct from *S. africanus* and has some features in common with *S. spuriodisciformis.*

Taxonomic notes: In *S. graminicola*, the ventral surface of the costa in the hyaline leaf base is formed by small hyaline cells (Figure 3G). Such a hyaline epidermis does not occur in the leaves of *S. africanus*, but is characteristic of those in *S. spuriodisciformis* and some other otherwise distinct taxa within the subgenus *Pseudocalymperes* (e.g. *S. flexifolius* ssp. *reunionensis*

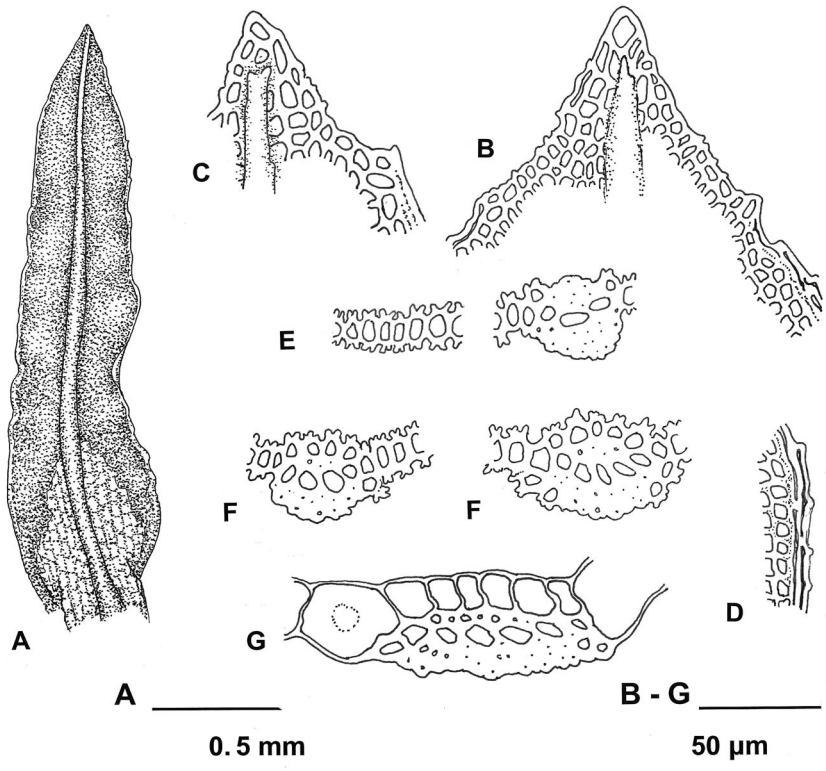

Figure 3 ***Syrrhopodon graminicola*** **Williams. (A) Leaf in dorsal view, with (B, C) detail of apex in dorsal view. (D) Marginal stereome in proximal chlorophyllose limb. (E, F) Chlorophyllose limb in cross-section: (E) costa and lamina through distal limb, (F) costa through mid-chlorophyllose limb. (G) Leaf base in cross-section through costa. (A, C, E, G) Drawn from Schiffner *226* (BM000664458); (B, D) from Buck *33122* (NY— 00227109); (F) from Buck *2791* (NY —01102647).**

L.T.Ellis, see Wilbraham & Ellis, 2010). This feature distances *S. graminicola* from *S. africanus*, but on its own, does not necessarily imply a close relationship between *S. spuriodisciformis* and *S. graminicola*.

Plants of *S. graminicola* appear to be generally smaller than those of *S. spuriodisciformis,* with shoots (often well-branched above) rarely exceeding 0.5–1.0 cm high, and their longest leaves rarely exceeding 3 mm long, about 1 mm shorter than those in *S. spuriodisciformis*. The most common leaf shape in *S. graminicola* is closer to that in *S. africanus*, the normal leaves being lingulate with a broadly acute (–obtuse) apiculate apex (Figure 3A) and a subpercurrent to percurrent costa (Figure 3B, C). However, a degree of variability is evident; for example, in 'Curtis *45'* (NY —00607216) from Haiti many leaves are broadly lanceolate, whereas in 'Steere *E-77'* (NY —01102649) from Ecuador, they are very broadly lingulate.

The costa, aside from often being excurrent in *S. spuriodisciformis* and subpercurrent to percurrent in *S. graminicola*, differs between these species in other details. In most collections of *S. graminicola*, the dorsal surface of the costa above the hyaline base has scattered minute teeth, which project from the distal end of many cells (becoming larger towards leaf apex), and the ventral surface of the costa from above the hyaline base to beyond mid-leaf often has an extensive cortex of small chlorophyllose, pluripapillose cells (Figure 3F) (nearer leaf apex surface formed by stereids (Figure 3E) and often bearing small teeth,). In both *S. spuriodisciformis* and *S. africanus*, minute teeth on the dorsal surface of the costa are extremely sparse or absent, and in normal leaves of these species, small chlorophyllose cells on the ventral surface of the costa are absent or form only a broken layer restricted largely to a region just above the apex of the hyaline lamina (most of the ventral costa surface being formed by stereids).

S. graminicola has cells in the chlorophyllose lamina that resemble those in *S. spuriodisciformis* in being dorsally and ventrally pluripapillose (Figure 3E), and at (5–)7.5–12.5(–15) × 7–10(–12.5) μm are not significantly larger than those in the latter species.

In most collections of *S. graminicola*, the notably undulate leaf margin is bordered by a narrow stereome that usually fails short of the leaf apex (Figure 3B, C). As in *S. africanus*, the apical margin, formed by laminal cells, varies from regularly papillose-crenulate to irregularly denticulate. From around mid-hyaline base to its distal limit, the stereome is often well endowed with remote, small (sometimes double) teeth, and the cells on its outer edge often bear two or three small, simple papillae (Figure 3D). Although such marginal teeth and papillae occur in *S. africanus* and *S. spuriodisciformis*, they are generally less numerous, and in the latter species, the marginal stereome usually reaches the leaf apex.

Consistent differences (but seen in few examples) appear to exist between the sporophytes in *S. graminicola* and *S. spuriodisciformis*. Plants of both taxa exhibit polysety, but in *S. spuriodisciformis*, the capsule is erect, narrowly cylindrical and 2–2.5 mm long, while the seta is 3.5–4 mm long. Slightly smaller, the sporophyte in *S. graminicola* has an erect to suberect, cylindrical to slightly asymmetric, ellipsoid capsule, 1–1.5 mm long, and the seta reaches a length of 3 mm. In either species, a calyptra was not located by the present author, but that in *S. graminicola* was reported by Reese (1993b) as being '2.5 mm long, divided into several narrow segments from base to rostrum'.

Typical leaves of *S. spuriodisciformis*, with their lanceolate chlorophyllose limb, slightly excurrent costa, and a marginal stereome that reaches an acute leaf apex, are easily distinguishable from typical leaves of *S. graminicola*. However, properly evaluating the consistency of the relatively conspicuous differences (in both the gametophyte and sporophyte) between these two geographically remote taxa will require examination of more, well-developed material. Presently, their apparent differences are sufficient to suggest that they should be regarded as distinct species.

Habitat and distribution: *S. graminicola* was cited by Reese (1993b) as occurring in Panama, Cuba, Jamaica, Haiti, Dominican Republic, Colombia, Guiana, Suriname, French Guiana, Ecuador and Brazil. The type collection of *S. graminicola* occurred on the joints of bamboo shoots, hence the specific epithet '*graminicola*', but like *S. spuriodisciformis*, the species occurs on tree trunks and twigs at relatively low altitudes (mostly 5–550 m a.s.l.). This contrasts with *Syrrhopodon africanus* and *S. mandrakensis* (see below), which appear to flourish at higher altitudes.

Specimens examined: Brazil: Utinga Forest, near Para, 16 December 1923, *leg.* N. Fraser-Tytler *162* (BM000665028); Serra do Cachimbo: Base Aérea do Cachimbo and vicinity, km 780–820 on Cuibá-Santarém highway (BR 163), *ca* 9°22′S 54°54′W, 430–480 m a.s.l., 25–30 April 1983, *leg.* W. D. Reese *16352* (NY —01102650), *16437* (NY —01102652); Serra Maze and vicinity, 1208–1229 km N of Cuiaba along Cuibá-Santarém highway (BR 163), *ca* 5°55′S 55°40′W, 100–200 m a.s.l., *leg.* W. D. Reese *16774* [*pro parte*] (NY —01102651); Along Rio Uatumã just E of Igarape Tucumanduba, campina, 02°15′S 59°04′W, 12 August 1979, *leg.* W. R. Buck 2791 (NY —01102647). **Ecuador:** Province Napo, near Santa Clara, between Puyo and Puerto Napo, 11 January 1981, leg. W. C. Steere E-77 (NY —01102649). **Colombia:** Comisaria Amazonas, Comunidad de

Vilazul, E of Araracuara. Isla Mariname in river Caquetá, 0°45′S 72°06′W, 240 m a.s.l., 1 November 1988, *leg.* H. Sipman & J. Duivenvoorden 28153 (NY —01102648). **French Guiana:** St-Laurent-du-Maroni, Canton de Maripasoula, Commune de Saül: *ca* 6 km N of Saül along road to Bélizon, vicinity of Eaux Claires, 3°37′N 53°12′W, *ca* 200 m a.s.l., 30 August 1994, *leg.* W. R. Buck *25303* (NY —00435514), *25300* (NY —00435515); 7–12 November 1990, *leg.* W. R. Buck *18344* (NY —00435517), *leg.* W. R. Buck *18653* (NY —00435518); *leg.* W. R. Buck *18435* (NY —00435519); vicinity of Eaux Claires, along Sentier Botanique at ridge, 3°37′N 53°12′W, *ca* 400 m a.s.l., 15–17 November 1990, *leg.* W. R. Buck *18840* (NY —00435520); Mont Galbao, *ca* 3°36′N 53°16′W, 225–525 m a.s.l., 9 September 1994, *leg.* W. R. Buck *25601* (NY —00435516); Crique Saint-Eloi at Route de Bélizon, *ca* 10 km N of Eaux Claires, 3°35′N 53°12′W, *ca* 200 m a.s.l., 8–9 November 1997, *leg.* W. R. Buck *33122* (NY —00227109). **Puerto Rico:** Caribbean National Forest, Luquillo Division, trail from Highway 186, 0.2 miles SE of junction of Highway 960, 1.9 miles S of entrance to El Verde Biol. Station, 400–500 m a.s.l., *leg.* W. D. Reese *14873 B* (NY —00631591). **Cuba:** Sierra Nipe, near Woodfred, Oriente, 400–550 m a.s.l., December 1909, *leg.* J. A. Schafer *3732a* (NY —00607220). **Dominican Republic:** Province of La Vega, vicinity of Piedra Blanca, 200–500 m a.s.l.: 17 December 1947, *leg.* H. A. Allard *17992a* (NY —00607218), *18000* (NY —00607219); 9 January 1948, *leg.* H. A. Allard *18899* (NY —00607217). **Haiti:** Camp Perrin, Jeremie Road, 5 May 1944, *leg.* J. T. Curtis *45* (NY —00607216).

4. ***Syrrhopodon mandrakensis*** (Tixier) L.T.Ellis, *comb. & stat. nov.* (Figure 4)

≡ *Calymperopsis mandrakensis* Tixier, Bryologist, 95: 284–286.

≡ *Syrrhopodon africanus* ssp. *mandrakensis* (Tixier) W.D.Reese, Bryologist, 98: 141 (1995), *syn. nov.*

Type citation: Madagascar. Tananarive: Forêt de la Mandraka, formation dégradée, corticole, 1,250 m, *Tixier '11355'* [*11335*] (Holotype PC).

Holotype: Madagascar, Antananarivo, La Mandraka, 1250 m, en forêt dense, 23 February 1978, *leg*. P. Tixier *11335* (PC, Herb. Tixier — PC101529!).

Taxonomic notes: Reese (1995) reduced *Calymperopsis mandrakensis* Tixier to a subspecies of *Syrrhopodon africanus* (Mitt.) Paris. However, there is some justification for considering the entity as a distinct species within *Syrrhopodon*. With shoots up to 1 cm high and leaves mostly 2–4 mm long, plants of *S. mandrakensis* reach similar dimensions to those of *S. africanus*. The leaves in both taxa have a percurrent (–subpercurrent) costa, ending in a short apical cusp, and the dorsal and ventral surfaces of the costa are largely smooth and formed by stereids (Figure 4H), (although in *S. mandrakensis*, the dorsal surface near the leaf apex often has one or two teeth, and the ventral surface sometimes has a few generally scattered small teeth).

As in related taxa, the two entities share a similar distantly toothed marginal stereome that mostly fails short of the leaf apex, and in *S. mandrakensis*, the margin at the leaf apex can range from being uneven, subcrenulate to irregularly papillose-crenulate (Figure 4C, D), as variable as that in the leaves of *S. africanus*.

Aside from these general similarities, there are some consistent features of the leaves in *S. mandrakensis* that contrast strongly with those of *S. africanus*. These are: (1) Where well-developed 'normal' leaves are lingulate (exceeding 4 times longer than broad) in the latter species, in *S. mandrakensis*, they tend to be ligulate, i.e. narrower in relation to their length (some reaching 6–8 times longer than broad) (Figure 4A). (2) In *S. mandrakensis*, the cells of the chlorophyllose lamina are relatively small (mostly 5–10(–15) × 5–8(–12.5) μm); dorsally, each has a multifid papilla, and ventrally are pluripapillose (in surface view papillae appear at the edge of the lumina, protruding over the cell walls (Figure 4E, F, G)). In contrast, the chlorophyllose cells in *S. africanus* are larger on average (mostly 7.5–15(–17.5) × 7.5–10(–12.5) μm), and pluripapillose on both dorsal and ventral surfaces. (3) In *S. africanus*, the well-defined apex of the hyaline lamina is acute, whereas that in *S. mandrakensis* is usually obtuse (Figure 4A) (sometimes broadly acute or truncate). (4) In *S. mandrakensis*, the cells forming the ventral surface of the costa in the leaf base are usually not, or only barely differentiated (contrary to Tixier, 1992, Figure 7), i.e. the ventral surface is formed by stereids (Figure 4I, J, K), whereas in *S. africanus*, these superficial cells are usually differentiated, having broader lumina than the underlying stereids (Figure 2G, H, I).

These differences from *S. africanus* in leaf shape and cell structure indicate that Tixier (1992) was more than likely correct in regarding *S. mandrakensis* as a distinct species. Unfortunately, further evidence in support of his proposal from the asexual or sporophytic features of these taxa is sparse. Gemmiferous comae and gemmae in *S. mandrakensis* are not dissimilar to those in *S. africanus*, and for this present study, sporophytes and gametangia were not found in material of the latter, making comparison with those of *S. mandrakensis* impossible.

Most available specimens of *S. mandrakensis* (including the holotype) are small and fragmentary (especially epiphyllous collections, see Geissler *19864/4*, *19859/6*), their tiny underdeveloped shoots

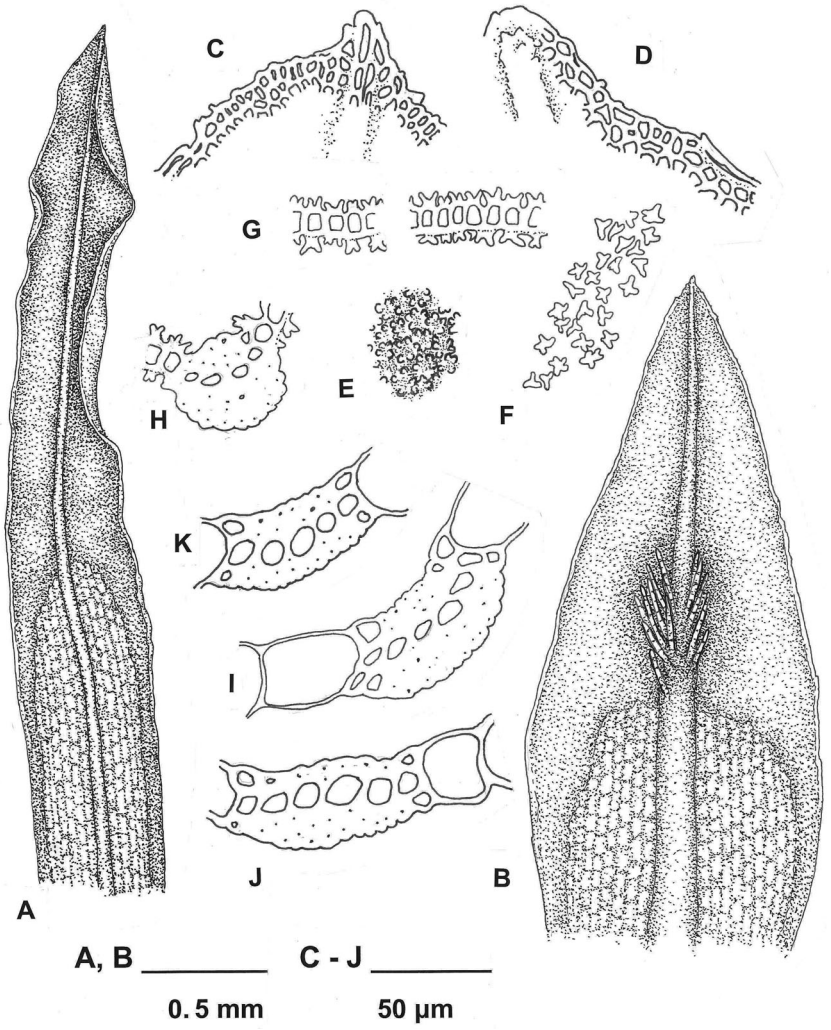

Figure 4 ***Syrrhopodon mandrakensis*** **(Tixier) L.T.Ellis. (A) Normal leaf in ventral view. (B) Modified leaf in ventral view. (C, D) Margin at leaf apex. (E, F, G) Cells of chlorophyllose lamina: (E) papillae on ventral surface, (F) multifid papillae on dorsal surface, (G) in cross-section. (H–K) Cross-section of costa: (H) through chlorophyllose limb, (I–K) through hyaline leaf base. (A, E – I) Drawn from Madagascar, Pócs *et al. 90103/BC* (G00111129); (B, C, J) from Madagascar, Tixier *12468* (PC0101530); (D) from Madagascar, Tixier *11335* (PC101529, holotype of *S. mandrakensis*); (K) from Madagascar, Geissler *19857/2* (G00111124).**

unlikely to show the full complement of the plants' potential features, such as gemmiferous comae. Fortunately, some better developed material does exist and was present in a paratype of *S. mandrakensis* (Tixier *12486*, cited below). Some shoots in this collection possessed apical comae, albeit slightly obscured behind over-topping normal leaves. The comae were formed by small, modified, broadly triangular-lingulate leaves (<2–3 mm long) (Figure 4B), and filamentous gemmae, characteristic of the subgenus *Pseudocalymperes*, were produced from the lateral cells on the ventral surface of the costa along the middle third of the leaf (Figure 4B).

Like most fertile species in the Calymperaceae, *S. mandrakensis* is apparently dioicous, terminal perigonia were present in Pócs *et al. 90103* (G00111128), and terminal perichaetia in Pócs *et al. 90103/BC* (G00111129), while Geissler *19857/2* (G00111124) included immature sporophytes. The perichaetia in the latter were unisetous, with smooth, red setae, 3.5 mm long. One developing sporophyte retained a calyptra, which was 3 mm long, very narrowly mitriform and split into narrow segments from the base to around mid-calyptra, dull straw-coloured below, and very dark red and densely scabrid in the upper third.

Habitat and distribution: *S. mandrakensis* has been recorded on bark, branches, twigs, and leaves in high altitude forest (920–1200 m a.s.l.) in northern and central-western Madagascar. Collections from Zaire and Rwanda, identified as *S. mandrakensis* by Tixier (1995), could not be located in Tixier's herbarium (PC) and consequently, have not been examined by the present author.

Specimens examined: Madagascar. Tamatave, piste de Lakato, 12 May 1978, P. *leg.* P. Tixier *12486* (PC-PC0101530, paratype of *C. mandrakensis*); Reserve Forestiere Andasibe, 100 km E of Antananarivo, E of the 'Station de Pisciculture', 920–990 m a.s.l., 15–

16 March 1990, *leg*. T. Pócs, C. Lafarge & R. E. Magill *90103* (G —G00111128); *90103/BC* (G— G00111129); Antsiranana (Diego Suarez), Reserve special de Manongarivo Ambahatra, cours supérieur, 13°59′S 48°26′E, 1200 m a.s.l., *leg.* P. Geissler *19864/4* (G —G00111127); Antsiranana (Diego Suarez), Reserve special de Manongarivo Ambahatra, cours supérieur, 13°59′S 48°26′E, 1200 m a.s.l., *leg.* P. Geissler *19857/2* (G — 00111124); 19859/6 (G— G00111126); 720 m a.s.l., 19576/22 (G— G00111125).

Uncertain Species

Syrrhopodon obuduensis Egunyomi & Olar., Bryologist, 85(3): 312–314 (1982).

Type Citation: 'NIGERIA. CROSS RIVER STATE: Obudu Cattle Ranch; on small branches of a shrub in a forested valley, elev. 1420 m, 18 September, 1975, *Egunyomi 388* (holotype —UIH [=UCI]; isotype —personal herbarium of the late Prof. W. Bizot [PC].'

Syrrhopodon obuduensis Egunyomi & Olar., another species in subg. *Pseudocalymperes*, was described from NW Africa (Egunyomi & Olarinmoye, 1982), but Reese (1995) suggested it was probably conspecific with *S. africanus* (Mitt.) Paris.

The holotype of *S. obuduensis* (Egunyomi *388*), cited as held in the University of Ibaden in Nigeria (see above), has been inaccessible, and an isotype said to be in the herbarium of M. Bizot (PC) could not be located. Without an examination of type or authentic material, it is not possible to be certain of the status of *S. obuduensis*. Illustrations with the protologue (Egunyomi & Olarinmoye, 1982; Figures 1–15) show a polysetous moss not dissimilar to *S. spuriodisciformis* Dusén. However, the latter, also a NW African species, occurs at lower altitudes than the type locality of *S. obuduensis*. Moreover, two major features of the leaves in *S. obuduensis,* as described and illustrated by its authors, differ significantly from those in *S. spuriodisciformis*. Cross-sections through the leaf base drawn from *S. obuduensis* (Egunyomi & Olarinmoye, 1982; Figures 12–15) show a ventral costa surface apparently formed by stereids (as in *S. mandrakensis*) rather than small hyaline cells; in addition, cells with large lumina (rather than stereids) were said to form the ventral surface of the costa at the leaf apex. This apparently unique feature, if only observed in surface view (as illustrated in the protologue (Egunyomi & Olarinmoye, 1982; Figure 7) was possibly illusory. These apparently superficial costal cells may have been a median layer of guide cells, brought into focus under the microscope through a very thin (unistratose) ventral superficial layer of stereids (evident in cross-section at the leaf apex in *S. spuriodisciformis* (Figure 1G)).

A further distinctive feature reported in the protologue for *S. obuduensis* was that the cells of the chlorophyllose lamina were 'multipapillose on [the] adaxial [ventral] surface only'. The abaxial [dorsal] surface was not explicitly described, but if without papillae, it would be very unusual within the subgroup of the subgenus *Pseudocalymperes* covered herein. Be that as it may, until original material of *S. obuduensis* is rediscovered, its affinities and status will remain obscure.

Acknowledgements

This work was supported by The Natural History Museum, London (BM). I am grateful to the curators of G, GOET, H-BR, NY, PC, and S for the loan of specimens, and to Jo Wilbraham (BM) and two anonymous reviewers for constructive comments on the draft manuscript for this article.

Taxonomic Additions and Changes: *Syrrhopodon spuriodisciformis* Dusén (*S. guineensis* Broth. & Paris in Paris, *syn. nov.*); *Syrrhopodon mandrakensis* (Tixier) L.T.Ellis, *comb. & stat. nov.* (*S. africanus* ssp. *mandrakensis* (Tixier) W.D.Reese, *syn. nov.*); *Syrrhopodon graminicola* R.S.Williams, *stat. nov.* (≡ *S. africanus* ssp. *graminicola* (R.S.Williams) W.D.Reese).

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