THE LIVING COLLECTION AT THE ROYAL BOTANIC GARDEN EDINBURGH ILLUSTRATES THE FLORAL DIVERSITY IN *STREPTOCARPUS* (GESNERIACEAE)

Michael Möller[1], Sadie Barber[2], Hannah J. Atkins[3] & David A. Purvis[4]

ABSTRACT

A visual summary of the floral types present in the diverse genus *Streptocarpus* is given along with descriptions of the different categories. We categorised the species and defined seven types and six sub-types. The use of a comprehensive and well-curated living collection for the study of floral diversification is presented and its use for interpretation and education discussed.

INTRODUCTION

As outlined in its Collections Policy (Rae *et al*., 2006), the living collection of the Royal Botanic Garden Edinburgh (RBGE) underpins much of its scientific research. Living plants provide essential material for taxonomic, cytological, developmental and genetic studies.

With c. 490 species, RBGE holds one of the world's largest living collections of paleotropical Gesneriaceae. Scientists use this collection for studies into genome evolution, vegetative and floral development, systematics and new species descriptions. Living collections play a key part in this research, helping to unravel the mechanisms by which plant diversity is established.

Flowers vary dramatically in plants, which led Darwin (1862) to comment on the remarkable co-evolution of plants and their animal pollinators. Many forms appear to have evolved in synchrony with pollinators, with an estimated 90 per cent of flowering plants depending on animal pollinators (Ollerton *et al*., 2011).

In Gesneriaceae some genera exhibit a rather conserved floral morphology where the flower shape and colour hardly vary, such as *Aeschynanthus* (~ 166 species, Möller *et*

1. Michael Möller is Molecular Systematist and Cytologist in the Science Department at the Royal Botanic Garden Edinburgh.
Address: 20A Inverleith Row, Edinburgh EH3 5LR, UK.
Email: mmoeller@rbge.org.uk
2. Sadie Barber is Senior Horticulturist at the Royal Botanic Garden Edinburgh and currently a Longwood Fellow at Longwood Gardens.
Address: Longwood Gardens, PO Box 501, Kennett Square, PA 19348, USA.
Email: sbarber@longwoodgardens.org
3. Hannah J. Atkins is Gesneriaceae Taxonomist in the Science Department at the Royal Botanic Garden Edinburgh.
Address: 20A Inverleith Row, Edinburgh EH3 5LR, UK.
Email: hatkins@rbge.org.uk
4. David A. Purvis is Herbarium Assistant in the Science Department at the Royal Botanic Garden Edinburgh.
Address: as above
Email: dpurvis@rbge.org.uk

al., 2017) or *Agalmyla* (96 species, Hilliard, 2002). Others show a remarkable diversity in flower shape, such as the Asian *Oreocharis* (115 species, Möller *et al*., 2011, 2018) and *Streptocarpus*.

The RBGE *Streptocarpus* collection (c. 115 species) contributes to fundamental taxonomic work by providing living plant materials; these exhibit a whole suite of characters that may be lacking in preserved material, such as colour, texture, scent and three-dimensional form. A living collection also allows for observations over time, recording developmental characteristics of flowers from bud to bloom and fruits.

AIMS

In the following we illustrate the floral diversity observed in *Streptocarpus*, building on the categorisation first developed by Harrison *et al*. (1999) and later modified by Hughes *et al*. (2006) and Nishii *et al*. (2015), amended by current knowledge of the pollination mechanisms and observations involved and new species discovered. Since the basic types do not fully capture the diversity that can be observed between the species, particularly for the open flower type, we also define sub-types.

The categorisation into floral types by Harrison *et al*. (1999) and Hughes *et al*. (2006) for *Streptocarpus* flowers included the small-pouch, open-tube, keyhole, personate, flat-faced *Saintpaulia* and bird-pollination types. The open-tube type was further subdivided into sub-types that included two types distinguished by Nishii *et al*. (2015), namely the Acanth type and the Labellanthus type. The *Streptocarpus acicularis* type is introduced here and is based on a recently described species from Mozambique (Darbyshire & Massingue, 2014).

METHODS

Images were taken with a Canon Powershot G12 or a Coolpix 4500 digital camera, or were provided by Prof. D.U. Bellstedt, Stellenbosch University, Cape Province, South Africa (*Streptocarpus lilliputana*). Images were processed and plates assembled in Photoshop version CC (Adobe Systems Inc., San Jose, US).

The categorisation of species into types was based on observations on the >100 species growing in the living collection, combined with the descriptions and drawings given in Hilliard & Burtt (1971) and Humbert (1971), study of herbarium specimens and protologs of other species (Appendix). Observations were made on fully opened flowers, and species categorised primarily by shape and secondarily by size. The terminology used follows primarily that of Hilliard & Burtt (1971).

STREPTOCARPUS FLOWER MORPHOLOGY

Streptocarpus was recently expanded to include all African and Malagasy Gesneriaceae genera of subtribe Streptocarpinae, in tribe Trichosporeae, subfamily Didymocarpoideae and now contains around 179 species including those newly described (Darbyshire & Massingue, 2014; Nishii *et al*., 2015; Randrianasolo *et al*., 2018).

In this delineation, *Streptocarpus* species show a particularly wide range of floral sizes, shapes and colours (Harrison *et al*., 1999; Hughes *et al*., 2006; Nishii *et al*., 2015). In the latter, flowers were roughly divided into eight types. Some of the types can be linked to pollination syndromes (Faegri & Van der Pijl, 1966; Dafni, 1992; Ollerton *et al*., 2009). Blue, purple and pink flowers with wide openings and a wide tube-like corolla are often linked to bee pollination (melittophily). Moth- and butterfly-pollinated (psychophilous) flowers often have broad ventral and lateral petals providing landing platforms and have long narrow tubes. Red, tubular corollas suggest pollination by birds (ornithophily). Actual pollination observations in the genus *Streptocarpus*, however, are few and far between, and published data are only available for pollination by long-tongued flies (myophily) in *S. formosus* of section *Streptocarpus*, and buzz pollination in *S. teitensis* by bees of section *Saintpaulia* (Potgieter & Edwards, 2005; Martins, 2008).

Martins (2008) further noted that "*Amegilla* spp. were common visitors to other forest floor flowers, primarily Lamiaceae, and were seen visiting *Streptocarpus* spp., the genus within which *Saintpaulia* is embedded (Möller & Cronk, 1997a,b), in the Taita Hills forest, Mount Kasigau and in the Aberdares (pers. obs.)". Unfortunately, the author did not provide the identities of the other *Streptocarpus* species. These hills contain at least five species with three different floral types, the keyhole type (*S. saxorum*), personate type (*S. caulescens*, *S. glandulosissimus*) and pouch type (*S. kirkii*, *S. montanus*), and thus it is unclear which type the bee visited, or indeed whether it visited all types.

An investigation into the evolution of floral form found that, at least on the African continent, the plesiomorphic, i.e. ancestral, floral form is the small-pouch type (7–10 mm long), prone to selfing, from which larger forms evolved (Harrison *et al*., 1999; Hughes *et al*., 2005, 2006). A distinct enlargement in flower size can be observed alongside a north–south migration and speciation in section *Streptocarpus* (Möller *et al*., 2001), culminating in the huge 70 mm long and 55 mm wide *S. formosus* in the Eastern Cape of South Africa. In Madagascar and the Comoro Islands, flowers are generally small (7–10 mm long), with the only exception being *S. hilsenbergii* with a corolla length of up to 45 mm. The distinct keyhole type, putatively butterfly- or moth-pollinated, evolved independently in the two subgenera and half a dozen times in section *Streptocarpus* (Hughes *et al*., 2006).

A typical *Streptocarpus* flower can be described as zygomorphic, more or less strongly two-lipped, with two upper and three lower lobes. In *S. actinoflorus* the corolla is almost regular, and in *S. betsiliensis*, the corolla is actinomorphic. In *Streptocarpus* the flowers are usually chasmogamous, except for *S. itremensis* and *S. nobilis* that additionally produce cleistogamous flowers. The flowers in *Streptocarpus* have in general two anterior fertile stamens, with absent (perhaps only in *S. peltatus*), one or three staminodes. The inclusion of *Acanthonema* into *Streptocarpus* expanded the fertile stamens to four with usually only the anterior pair fertile. The anthers usually cohere face to face and are only free in the woody caulescent species of section *Lignostreptocarpus* and the recently described *S. peltatus*. Pollen release is by apically confluent dehiscence lines, and sometimes by arcuate confluent slits. All species have single pollen grains, except for *S. daviesii* and species in section *Parasaintpaulia*, which produce tetrads (Weigend & Edwards, 1996; Möller, 2018). In section *Saintpaulia* the anthers are exserted, bright yellow to attract insects, and large and robust to tolerate buzz pollination. Enantiostyly, the deflection of the style either to the left or right side of the floral axis, perhaps to prevent autogamy, can be observed in species in sections *Caulescentes* and *Saintpaulia* and in *S. nobilis*. In the other species, the position of the anthers can vary from some distance behind the style (in the majority of species to prevent autogamy) to close or touching the stigma (in autogamous species) or in front of the stigma (in keyhole flowers). Nectaries are predominantly present and only sometimes lacking, as in section *Saintpaulia*. Thus, pollinator rewards involve nectar and pollen.

FLORAL TYPES

In this article, the floral types are arranged by their putative pollination mechanisms (from selfing to more specialised) and do not reflect evolutionary trends (*cf*. Hughes *et al.*, 2006).

I Small-pouch type (~ 51 spp., e.g. *Streptocarpus beampingaratrensis* subsp. *beampingaratrensis*, Fig. 1A; *S. montanus*, Fig. 1B)

The small-pouch type represents the 'primitive' form among the floral types in *Streptocarpus* (Harrison *et al*., 1999; Hughes *et al*., 2006). They occur in most sections, but are widespread in sections *Hova* (11 out of 13 spp.), and include all of section *Parasaintpaulia* in subgenus *Streptocarpella*. In subgenus *Streptocarpus* they include most of section *Colpogyne* (3 out of 5), and all of sections *Lignostreptocarpus* and *Protostreptocarpus*, all basal lineages. Only a few species of section *Streptocarpus* (8 out of 85) belong here, often residing on basal lineages in this section.

The flowers are predominantly small, mostly around 7–10(–15) mm long with short limbs and short tubes (4–8 mm) with the anthers placed often close behind the stigma. The corollas are unscented, mostly entirely white, sometimes with markings, or occasionally pale violet, rarely dark pink. The darker colours and markings may indicate the involvement of pollinators, but no observations are available yet. The corolla mouth is mostly between 2 and 8 mm wide and may often allow pollinators to fully enter the corolla. Some species, such as *Streptocarpus beampingaratrensis*, *S. levis*, *S. muscosus*, *S. oliganthus* and *S. thompsonii*, set seeds readily in cultivation in the absence of pollinators. Others, however, like *S. papangae* and *S. suffruticosus*, never set seeds even after artificial self- and cross-pollination (while most other species in the genus set seed readily with forced pollination). The latter two species have free anthers with short filaments, which is not promoting autogamy, and may represent an adaptation to, as yet unidentified, pollinators or pollination mechanism.

II(1) Open cylindrical tube

II(1a) With narrow tube (~ 31 spp., e.g. *Streptocarpus kentaniensis*, Fig. 1C)

This type predominantly includes species from sections *Plantaginei* and *Streptocarpus*. Those of the former are often smaller (8–20 mm corolla length) than those of the latter (10–40 mm) and anthers are placed behind the stigma in species of both sections. This type has predominantly straight and narrow cylindrical tubes with distinct lobes. The flowers are often white or pale violet in section *Streptocarpus*, or violet in section *Plantaginei*. The rather long tubes have 2–5(–10) mm narrow corolla mouths which might suggest that long-tongued pollinators are involved in pollen transfer. However, there is at present no pollination information on any of the species in this group, other than from observations in cultivation: *Streptocarpus perrieri* and *S. variabilis* set seeds readily while *S. kentaniensis*, *S. meyeri*, *S. modestus* and *S. trabeculatus* only set seed after artificial pollen transfer. *Streptocarpus itremensis* is an exception in that it produces cleistogamous flowers and ensures seed set this way. In the field the fruits can be found pressed in the moss with germinating seedlings emerging from them (Michael Möller, pers. obs.). This mechanism might explain the rather short fruit with few seeds that this species produces.

II(1b) With broad tube (10 spp., e.g. *Streptocarpus grandis*, Fig. 2A)

This type occurs in section *Streptocarpus* only. It is characterised by mostly straight, wide cylindrical tubes of 7–12 mm width and 17–45 mm length with anthers placed behind the stigma, and corolla colours of white, pale violet to medium violet. The wide corolla openings could suggest that pollinating insects may fully enter the corolla tube. This type includes the only three members of *Streptocarpus* with scent: *S. candidus*, *S. fanniniae* and *S. wilmsii*. The features overall suggest insects as pollinators. The stamens are inserted and to trigger the mechanism, the pollinators are required to enter the tube. The cylindrical broad tube would allow insects with short proboscises to reach the nectar and trigger the pollen release, and it would be deposited dorsally on the thorax. No pollination observations are available.

II(2) Open tube with pollination chamber (~ 38 spp., e.g. *Streptocarpus pumilus*, Fig. 2B; *S. cyaneus* subsp. *longi-tommii*, Fig. 2C; *S. formosus*, Fig. 3A; *S. primulifolius*, Fig. 3B)

This type mostly comprises species from section *Streptocarpus*, with five from section *Trachystigma* and one from section *Hova*, which is *S. hilsenbergii*, the largest-flowered species in Madagascar. The flower colour ranges widely from deep to pale violet, blue, purple to purple-red, pink, with few being white.

This flower type is characterised by the partition of the corolla tube into an undilated proximal part (alignment channel *viz*. Westerkamp & Claßen-Bockhoff, 2007) and dilated distal part (pollination chamber) with openings ranging from 4 mm as in *S. bolusii* to 20 mm wide as in *S. floribundus* or *S. longi-tommii*, but often with the anthers placed some distance behind the stigma. The corolla length can vary in size from 12 mm

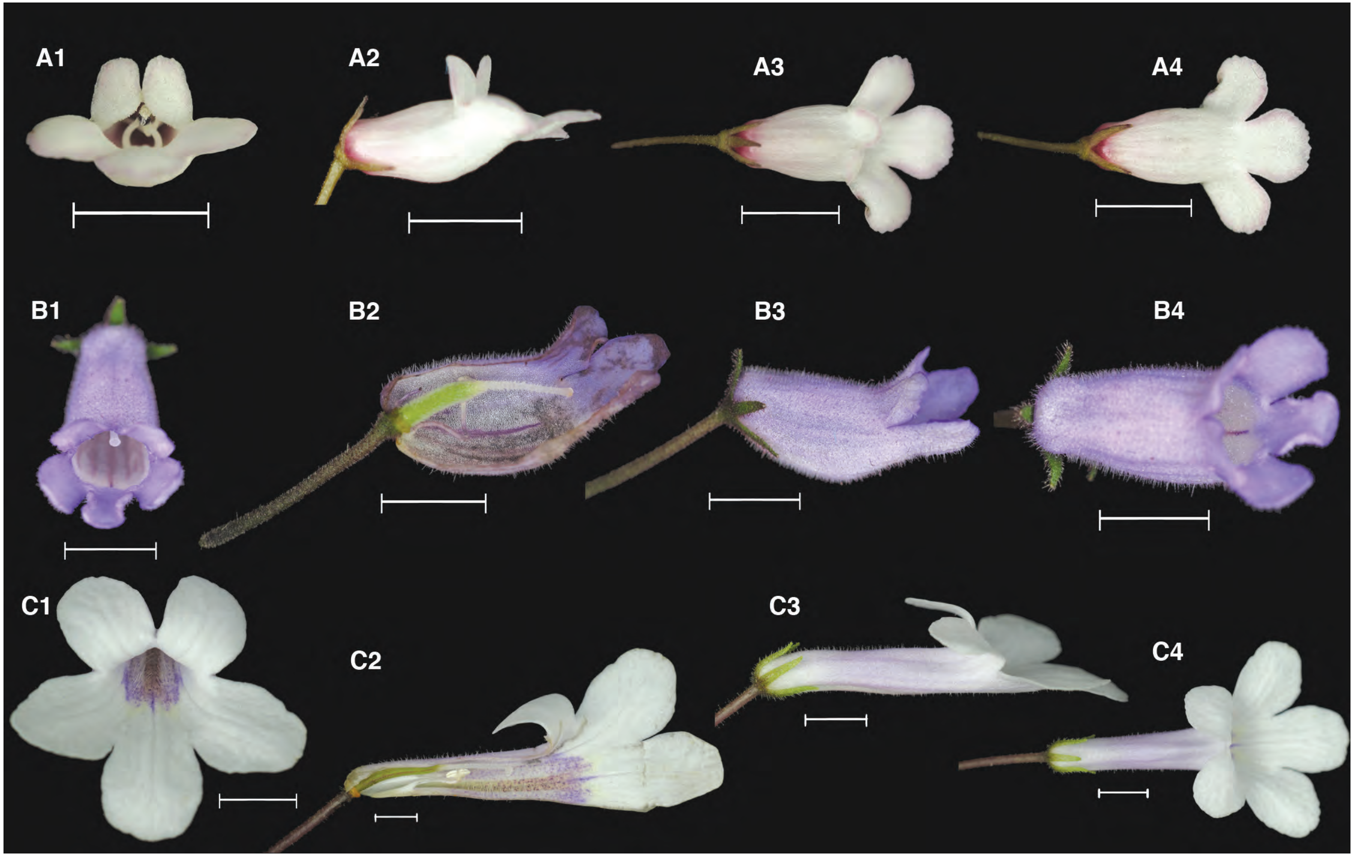

Fig. 1 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. beampingaratrensis* subsp. *beampingaratrensis* (type I): A1 front view; A2 side view; A3 top view; A4 bottom view. B: *S. montanus* (type I): B1 front view; B2 cut-open side view; B3 side view; B4 top view. C: *S. kentaniensis* (type II1a): C1 front view; C2 cut-open side view; C3 side view; C4 top view. Scale bars 5 mm. (All images taken and modified by D. Purvis.)

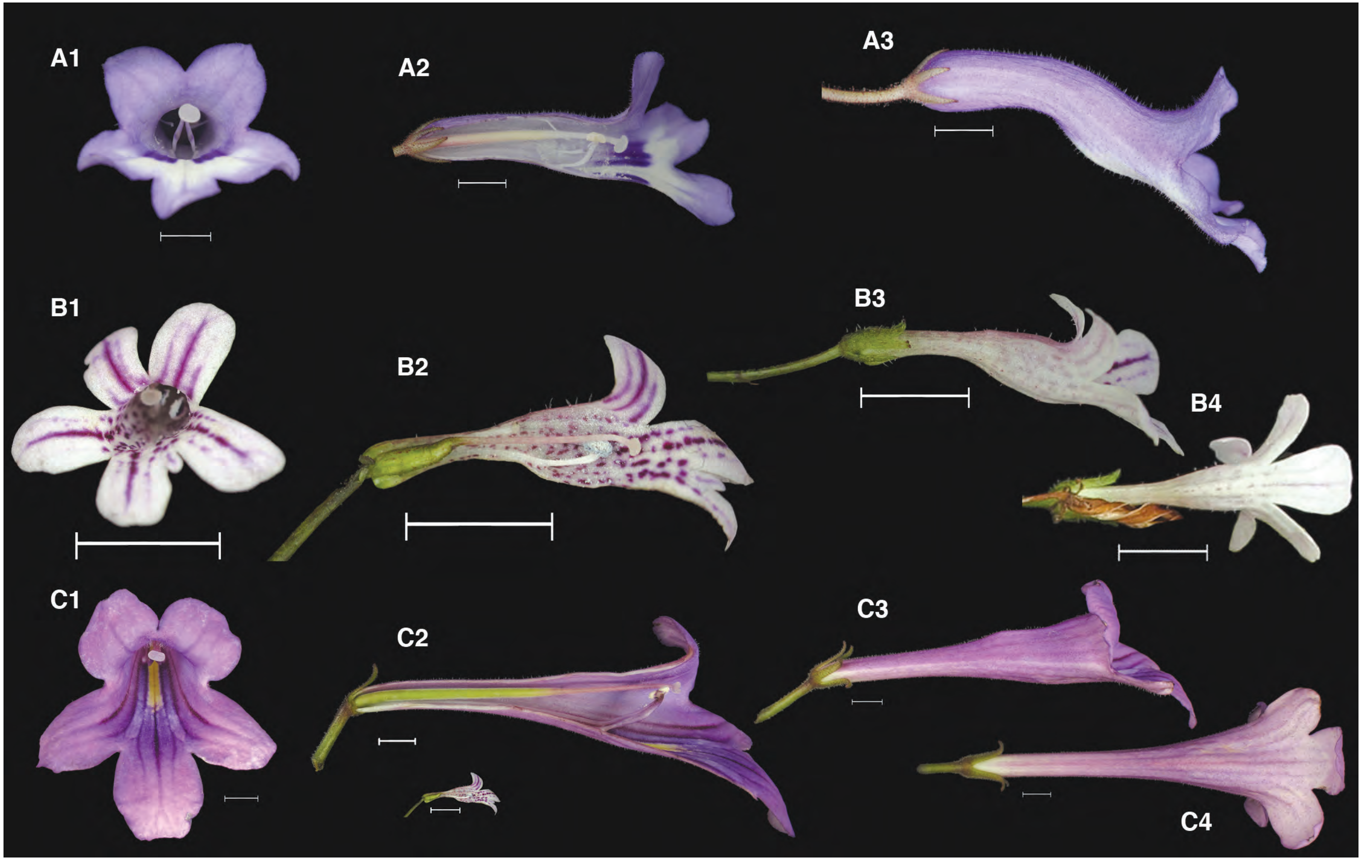

Fig. 2 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. grandis* (type II1b): A1 front view; A2 cut-open side view; A3 side view. B: *S. pumilus* (type II2): B1 front view; B2 cut-open side view; B3 side view; B4 bottom view. C: *S. cyaneus* subsp. *longi-tomii* (type II2): C1 front view; C2 cut-open side view (with *S. pumilus* below at same magnification); C3 side view; C4 bottom view. Scale bars 5 mm. (All images taken and modified by D. Purvis.)

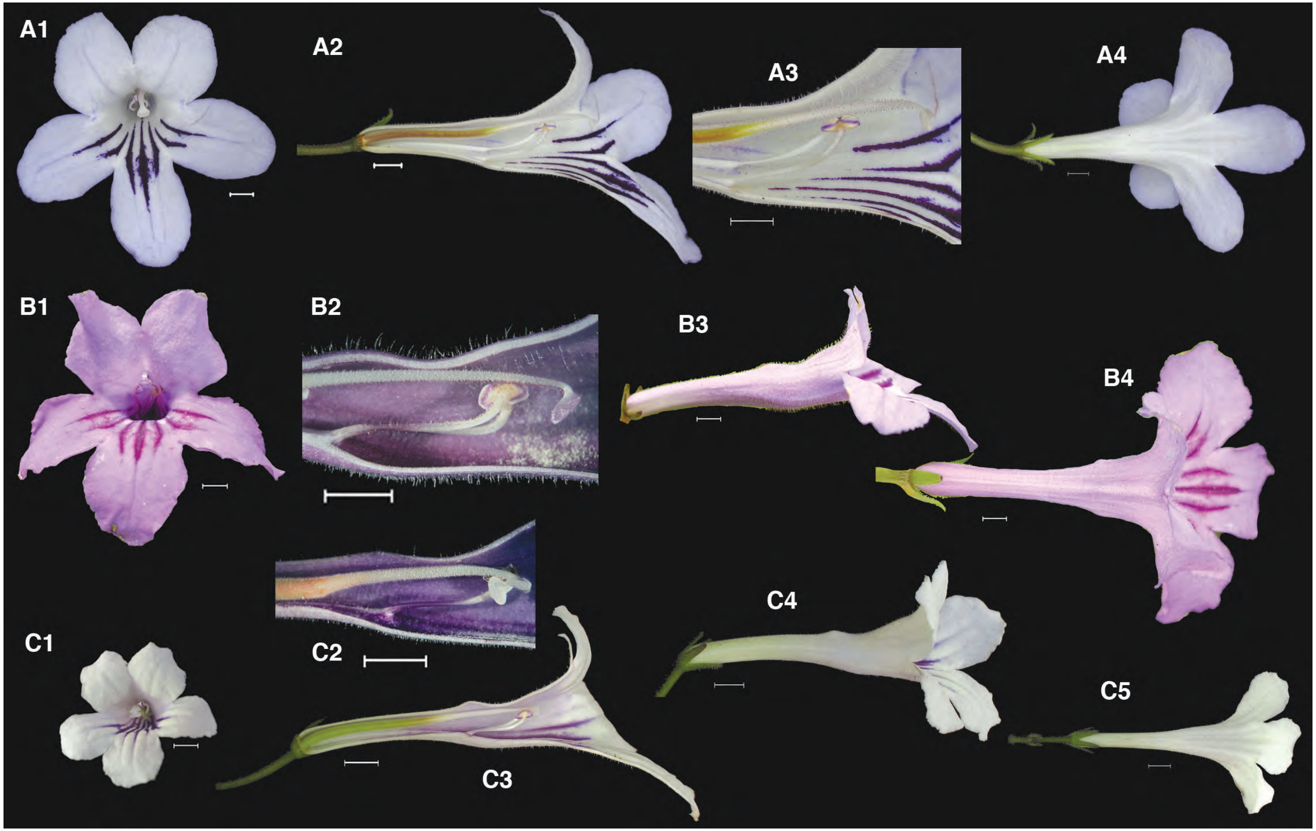

Fig. 3 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. formosus* (type II2): A1 front view; A2 cut-open side view, enlarged in A3; A4 bottom view. B: *S. primulifolius* (type II2): B1 front view; B2 enlarged cut-open side view; B3 side view; B4 top view. C: *S. rexii* (type II2 shift to selfing): C1 front view; C2 enlarged cut-open side view; C3 cut-open side view; C4 side view; C5 bottom view. Scale bars 5 mm. (B1–B4, C2 original photos by M. Möller, others by D. Purvis; all modified by D. Purvis.)

in *S. pumilus* to 105 mm in *S. formosus*. The species with the longest tube is *S. cyaneus* subsp. *longi-tommii* with 78 mm and an undilated tube length of up to 45 mm, as opposed to 5 mm in *S. pumilus*. Some species have a large corolla face, but a very short undilated tube, such as *S. caeruleus*, *S. galpinii* or *S. aylae*. The length of the undilated tube perhaps evolves in adaptation to the proboscis length of pollinating insects.

The pollen release from the coherent nototribic anthers in this type is triggered by an insect fully entering the corolla tube and pushing wide the filaments upon which pollen is deposited on the thorax of the insect. The flowers are optimised for a single flower visit. This was verified by field observations on *Streptocarpus primulifolius* where in a total of about one week of observations only two pollinator visits were observed of tabanid or nemistrinid long-proboscid flies (Dirk U. Bellstedt, Mark Hughes, Michael Möller, pers. obs.). The Nemistrininae species *Stenobasipteron wiedemanni* was found to pollinate the closely related *S. formosus*. This *Streptocarpus* species is part of a floral guild that covers nineteen species from six plant families that are pollinated by *S. wiedemanni* (Potgieter & Edwards, 2006).

II(3) Inverted V-type opening (3–6 spp., e.g. *Streptocarpus wendlandii*, Fig. 4A)

There are at least three species, *Streptocarpus compressus*, *S. goetzei* and *S. wendlandii,* described in Hilliard & Burtt (1971) which possess a dorsally laterally compressed corolla mouth to create an opening in an inverted V-shape, somewhat reminiscent of *S. stomandrus* and *S. trabeculatus* and perhaps *S. pole-evansii*. This may somewhat restrict the pollinator from fully entering the flower. The corollas are mostly violet in colour and of medium size (17–50 mm long) with the anthers placed behind the stigma. Nothing is known about the pollinators of any of these species, although in cultivation, *S. wendlandii* tends to self-pollination. The corolla appears to be suitable for any long-tongued insects, bees or butterflies.

II(4) Acanth type (1 sp., *Streptocarpus lilliputana*, Fig. 4B)

The Acanth type category was established for the relatively recently described *Streptocarpus lilliputana* Bellstedt & T.J.Edwards in section *Streptocarpus* that exhibits an extremely long 25–30 mm proximate alignment channel and a strongly developed pollination chamber with anthers placed some distance behind the stigma (Bellstedt & Edwards, 2004). The corolla is very similar in dimensions to the Acanthaceae species *Mackaya bella* and *Asystasia varia* that occur in the ravines in the Eastern Cape of South Africa where *S. lilliputana* also occurs (Dirk U. Bellstedt, pers. comm.). Perhaps this is a case of parallel adaptation to the same pollinator, though field observations are lacking at present. The pollinator may enter the 11–12 mm wide corolla entirely and pollen deposition here would be dorsally on the thorax, similar to *S. primulifolius* of flower type II(2).

II(5) Acicularis type (1 sp., *Streptocarpus acicularis*)

This type is newly established here and based on the recently described *Streptocarpus acicularis* (Darbyshire & Massingue, 2014). This species belonging to section

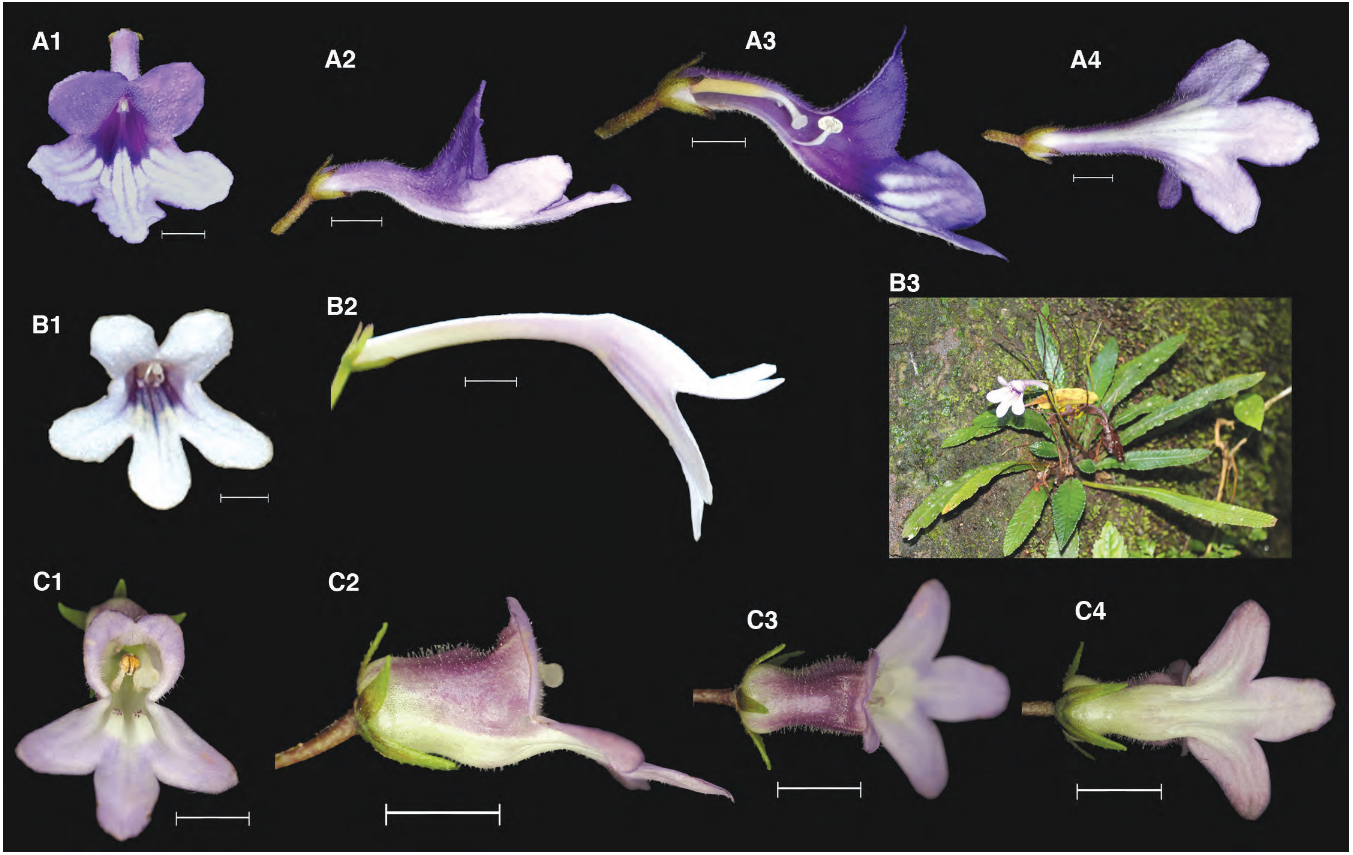

Fig. 4 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. wendlandii* (type II3): A1 front view; A2 side view; A3 cut-open side view; A4 bottom view. B: *S. lilliputana* (type II4): B1 front view; B2 side view; B3 habit in field. C: *S. thysanotus* (type III): C1 front view; C2 side view; C3 top view; C4 bottom view. Scale bars 5 mm. B1–B3 original photos from D.U. Bellstedt with permission; others by D. Purvis; all modified by D. Purvis.

Streptocarpus has the longest, most slender corolla, with anthers placed quite some distance behind the stigma, 70 mm in total length, with a 33–40 mm long and 2.5–3.5 mm delicately narrow alignment channel, 12–13 mm long and 10 mm wide pollination chamber. This would exclude all but those insects with an extremely long proboscis. The relatively short lobes of the limb do not immediately suggest that butterflies are involved as the landing platform seems inadequate. Perhaps hovering insects such as hawk moths or hovering long-tongued flies (Goldblatt & Manning, 2000; Johnson & Raguso, 2016) are possible candidates, entering the corolla only with their head, and pollen deposition would be on the forehead.

III Labellanthus type (~ 4 spp., e.g. *Streptocarpus thysanotus*, Fig. 4C)

This type has a corolla with a conspicuous forward-directed lower lip and a reduced upper lip, occurring only in section *Schizoboea*. The flowers are mostly white with small 7–8.5 mm long corollas and 4–6 mm tubes, and mouths 2–3.5 mm wide, except for the larger purple coloured *Streptocarpus thysanotus* (with 17 mm corolla length), with anthers placed behind the stigma. The corollas have straight and narrow cylindrical tubes, are not scented and, at least in *S. thysanotus*, are laterally somewhat compressed. No pollinator observations are available for this floral type. Altogether it is possible that pollinators of this type of flower do not enter the corolla tube and the lower lip serves as a landing platform for pollinators. Pollen is potentially deposited on the proboscis and/or head.

IV Keyhole type (~ 12 spp., e.g. *Streptocarpus johannis*, *S. saxorum*, Figs 5A, 5B)

Keyhole flowers, where the opening of the corolla is laterally strongly compressed to a 2–3 mm narrow vertical slit, occur in both subgenera of *Streptocarpus*, once in subgenus *Streptocarpella* in *S. saxorum*, but occur with ten species predominantly in section *Streptocarpus*. The flower sizes vary, with 15–50 mm corolla lengths and 5–20 mm tubes, with the anthers placed some distance in front of the stigma. The flowers are most often pale violet and not scented. The narrowed corolla mouth is accompanied by a more or less strongly S-shaped cylindrical corolla tube and a strongly oblique limb with spreading lobes, perhaps serving as a landing platform. It is interesting that the position of the coherent anthers is in front of the stigma (Fig. 5B3). This might prevent self-pollination; experiments with horse hairs suggest that entering the tube is best achieved by sliding it along the bottom into the keyhole and pulling it out in an upwards direction; this loads the hairs with ample sticky pollen (Georgiadis, 2005; Michael Möller, pers. obs.). Pollen is deposited on the proboscis.

V Personate type (6 spp., e.g. *Streptocarpus glandulosissimus*, Fig. 5C)

In this flower type, the lower lip is folded upward at a right angle so as to close the gap between the lips, as in snapdragon (*Antirrhinum*). The tube is usually cylindrical, 7–8 mm long and 2.5–3 mm wide, the corollas 15–30 mm long. The corollas in this group are mostly deep blue, violet to deep violet, and unscented. The personate corolla is associated with enantiostyly that predominantly affects anther displacement to the left

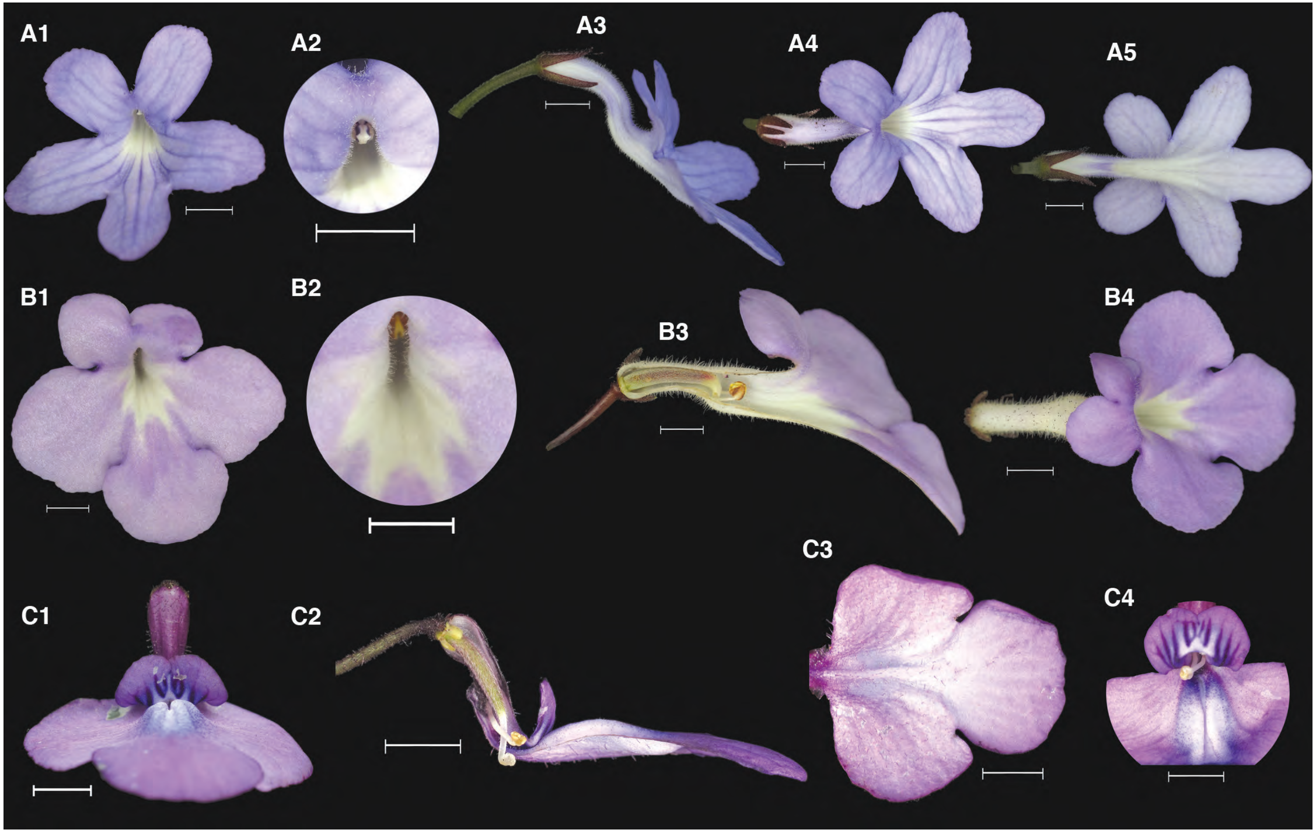

Fig. 5 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. johannis* (type IV): A1 front view; A2 enlarged keyhole view; A3 side view; A4 top view; A5 bottom view. B: *S. saxorum* (type IV): B1 front view; B2 enlarged keyhole view; B3 cut-open side view; B4 top view. C: *S. glandulosissimus* (type V): C1 front view; C2 cut-open side view; C3 bottom view; C4 enlarged enantiostyly view. Scale bars 5 mm. (All images taken and modified by D. Purvis.)

or right next to the stigma (Fig. 5C4). Observations at RBGE indicate that bumble bees can effectively pollinate *Streptocarpus glandulosissimus* (Michael Möller, pers. obs.): the bee hovers in front of the flower before settling on the lower lip, which folds down under the weight of the insect, allowing the insect to access the tube only with its long proboscis. Pollen is deposited laterally on the head of the insect.

VI Flat-faced *Saintpaulia* type (10 spp., e.g. *Streptocarpus shumensis*, Fig. 6A)
This is perhaps the most homogeneous section with respect to floral shape and it constitutes the previous genus *Saintpaulia*. Species in this section possess flat-faced corollas from white-violet bicoloured to dark violet colours. The corollas have very short tubes of 2–3 mm and have exserted robust, bright yellow anthers cohering face to face (Trapp, 1954 in Weberling, 1981, p. 131) and dehisce by arcuate confluent slits. All species exhibit enantiostyly whereby the longer style is more strongly deflected than the slightly shorter stamens. In *Streptocarpus teitensis* from Kenya, and in perhaps all species, it is heteromorphic, with the style placed either to the left or right of the floral axis. Harrison *et al.* (1999) reported previous suggestions that *Saintpaulia* is buzz-pollinated (Vogel, 1978; Dafni, 1992), and tested the release of pollen with tuning forks, which did indeed release pollen. Martins (2008) provided definite proof and observed at least four *Amegilla* species as pollinators of *S. teitensis*. The bees land on the flower holding on to the petals, and repeated 1–3 second vibrations release the pollen by buzz pollination, which is typical for this mechanism (Proctor, 1996). Pollen is deposited ventrally on the thorax of the insect.

VII Bird-pollination type (2 spp., e.g. *Streptocarpus dunnii*, Fig. 6B)
The tubular reddish or vermilion flowers of *Streptocarpus dunnii* and *S. myoporoides* (both section *Streptocarpus*) are strongly suggestive of pollination involving birds (Faegri & Pijl, 1980; Proctor *et al.*, 1996). The two species have very different flower sizes, up to 50 mm long and 10 mm wide in *S. dunnii* and up to 25 mm and 6 mm respectively for *S. myoporoides*, with the anthers placed some distance behind the stigma. The corollas, at least of *S. dunnii*, are comparatively sturdy, perhaps to withstand the ‘assaults’ from a pollinating bird. Pollination observations in 2004 in Verlooren Valei, Mpumalanga, South Africa, while only providing sight of one visit by the malachite sunbird (*Nectarinia famosa* L.) on a *S. dunnii* flower (Dirk U. Bellstedt, Mark Hughes, Michael Möller, pers. obs.), confirmed the involvement of birds in the pollination of this *Streptocarpus* species. Pollen deposition is on the forehead of the birds.

The compacted inflorescence of *Streptocarpus myoporoides* is very reminiscent of that found in other putatively bird-pollinated Gesneriaceae, such as *Petrocodon coccineus* (Weber *et al.*, 2011).

Additional specialisations

Cleistogamy (2 spp., e.g. *Streptocarpus nobilis*, Fig. 6C)
Streptocarpus nobilis from Tropical Africa has a large deep-violet corolla up to 33 mm

Fig. 6 Photographic images of *Streptocarpus* species displaying different floral types: A: *S. shumensis* (type VI): A1 front view; A2 top view; A3 side view; A4 cut-open side view. B: *S. dunnii*: B1 front view (male stage); B2 front view (female stage); B3 pre-pollination (left) and post-pollination flower in the field (right); B4 side view. C: *S. nobilis* (type II2 with added cleistogamy): C1 front view showing enantiostyly; C2 side view; C3 pistil with disc; C4 developing fruits of cleistogamic flowers just after pollination (bottom) and close to maturity (top), both showing persisting flower bud; C5 top view. Scale bars 5 mm. (B1–B4 original photos by M. Möller, others by D. Purvis; all modified by D. Purvis.)

long with a 13 mm long laterally flattened undilated proximal alignment channel and a prominent, large 12 mm long and 10 mm wide pollination chamber, in function perhaps similar to those chasmogamous flowers in other species in group II(2) to attract and accommodate long-tongued insect pollinators. However, it also produces additionally much smaller 3 mm long pallid coloured flowers that are cleistogamous and do not open and enable self-pollination (autogamy). It is worth noting that the chasmogamous flowers are often produced first and strongly show enantiostyly with the anthers and stigma some distance apart side by side aiding outbreeding; the cleistogamous ones develop later in the flowering period of the species, the latter perhaps as a safety strategy to ensure seeds set. Pollen deposition in chasmogamic flowers is likely dorsally on the thorax of insects.

The species is strongly short-day depending on flowering with a daylight cut-off length of 11–12.5 hours and flowering can be induced by as few as 2–4 short days (Lawrence, 1943; Nitsch, 1967; Handro, 1976).

The Madagascan *Streptocarpus itremensis* also produces cleistogamous flowers later in the flowering season in reduced inflorescences produced from the base of the primary ones. The chasmogamous flowers are 15 mm long and deep violet, the cleistogamous ones similar to those produced in *S. nobilis*.

Shift to selfing (1 sp., *S. rexii*, Fig. 3C)

The phylogenetically closest species to the classical outbreeding long-tongued fly-pollinated species *Streptocarpus primulifolius*, *S. rexii* has a similar corolla but differs by its smaller dimensions, a less pronounced pollination chamber, paler violet to white colour, less reflexed upper corolla lobes and its pair of anthers closer or in touch with the stigma (reduced herkogamy, Dole, 1992). The coherence of the anthers is also not as tight as in other species and 'leaks' pollen. This results in frequent self-pollination with, at least in cultivation, every flower setting seeds and developing fruits, as opposed to *S. primulifolius* that does not or only very rarely sets seed in cultivation in the absence of pollinators. As a consequence of the shift to selfing, the corollas of *S. rexii* are smaller and less attractive to pollinators (French *et al*., 2005). The shift may have been the consequence of the species distribution at higher altitudes or colder latitudes compared to *S. primulifolius* (Hughes *et al*., 2005), where the pollinator *Stenobasipteron wiedemanni* does not occur (Potgieter & Edwards, 2006).

Uncategorised species

Most of the floral diversity across the species could be categorised with only a few defying classification or being insufficiently known (e.g. *Streptocarpus hirsutissimus*, *S. katangensis*, *S. plantagineus*).

The large-flowered (40–55 mm long) Tanzanian species *Streptocarpus bambuseti* and *S. eunanthus* are described as having very oblique limbs, narrow cylindrical tubes, suggestive of butterfly pollination, but no information is available on the shape of the corolla mouth, whether it is laterally compressed or possesses a pollination chamber. The small-flowered (17 mm long) *S. semijunctus* from Madagascar has an oblique limb and a narrow, cylindrical, straight tube, also suggestive of butterfly pollination, but too little else is known to place it in a type. Perhaps these three species have found other less complex pathways to accommodate butterflies or exclude short-tongued pollinators. More studies are needed here.

USE OF THE COLLECTION FOR INTERPRETATION AND EDUCATION

A rich living collection of a genus, such as *Streptocarpus*, which has been the focus of taxonomic and phylogenetic research and displays a wide range of floral diversity, can be an ideal resource for both interpretation and education.

Many of the species listed above can be assigned, speculatively or following observation, to the various classic pollination syndromes first identified in the 1870s (Delpino, 1873–1874), though in the field their relationship with pollinators may be more complex (Ollerton *et al.*, 2009). However, they can still be an excellent, and very visual, way to inform the public and students about the relationship between plants and their pollinators in general. For example: *Streptocarpus dunnii* – bird pollination; *S. johannis* – butterfly pollination; *S. shumensis* – buzz pollination; *S. montanus* – self-pollination.

The genus *Streptocarpus* also includes an example of a recent radiation in the South African Cape flora where a large number of species evolved very rapidly about 1.5 million years ago (Möller & Cronk, 2001), to show a remarkable floral diversity in an array of very closely related taxa. For example, *S. kentaniensis* with narrow cylindrical tube; the fly-pollinated *S. primulifolius*; the putatively butterfly-pollinated *S. johannis*; the fly-pollinated turned selfer *S. rexii* and the extremely long and narrow-tubed *S. lilliputana* are all part of this Cape primrose clade (Möller & Cronk, 2001). This differentiation has most likely been driven by pollinator specialisation, a dramatic example of divergent evolution.

Streptocarpus also contains examples of parallel or convergent evolution where distinctive forms have evolved independently in the genus in response to pollinator preference, for example the two bird-pollinated species, *S. dunnii* and *S. myoporoides*, that possess tubular red corollas but very distinctly different inflorescence morphologies, or the keyhole-flowered putatively butterfly-pollinated *S. saxorum* and *S. johannis* that have evolved strikingly similar flowers but are not closely related (Nishii *et al.*, 2015).

CONCLUSIONS

Streptocarpus species exhibit a wide range of flower morphologies, suggesting the involvement of a wide range of pollinators. Our re-evaluation of corolla shapes for species in the genus *Streptocarpus* has resulted in a refinement of our types, particularly the open-tube type, which was formerly a very broadly defined group. The re-evaluation has resulted in the recognition of seven main types with the open-tube type further divided into six sub-types.

Some of the pollinators of *Streptocarpus* flowers proposed on the basis of floral shape and colour have now been confirmed in field studies, such as in the buzz pollination by bees in *Saintpaulia*, or the bird pollination of *S. dunnii*. The involvement of long-tongued flies in the pollination of species with chamber-carrying open-tube type was unexpected, since in earlier work it was suggested that it involved bees (Harrison *et al*., 1999). This demonstrated that both pollen and nectar are the rewards for pollinators. There is still no confirmation of butterfly pollination in *Streptocarpus* to date and clearly more field observations are needed. The recent discovery of hitherto unobserved floral diversity as seen by the new (sub)types established for the recently discovered *S. lilliputana*, and more recently *S. acicularis*, demonstrates that not all diversity has been discovered in the genus *Streptocarpus*, and perhaps more is to be found for 'those who dare to venture out'.

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APPENDIX

Species and references additionally used for the study of floral characters that are not grown at RBGE or listed in Hilliard & Burtt (1971).

Species	Reference
S. acicularis I.Darbysh. & Massingue	DARBYSHIRE, I. & MASSINGUE, A.O. (2014). Two new species of *Streptocarpus* (Gesneriaceae) from tropical Africa. *Edinburgh Journal of Botany*, 71(1): 3–13.
S. actinoflorus T.J.Edwards & M.Hughes	EDWARDS, T., HUGHES, M., MÖLLER, M. & BELLSTEDT, D.U. (2008). New *Streptocarpus* species (Gesneriaceae) from South Africa. *Botanical Journal of the Linnean Society*, 158: 743–748.
S. afroviola Christenh.	BURTT, B.L. (1958). Studies in the Gesneriaceae of the Old World XV. The genus *Saintpaulia*. *Notes from the Royal Botanic Garden Edinburgh*, 22(6): 547–568.
S. albus (E.A. Bruce) I.Darbysh.	WEIGEND, M. (2000). A synopsis of the genus *Linnaeopsis* (Gesneriaceae), an 'Uluguru Streptocarpus'. *Flora (Jena)*, 195: 45–50.
S. arcuatus Hilliard & B.L.Burtt	HILLIARD, O.M. & BURTT, B.L. (1986). Studies in the Gesneriaceae of the Old World XLIX. Additions and amendments to *Streptocarpus*. *Notes from the Royal Botanic Garden Edinburgh*, 43(2): 229–232.
S. aylae T.J.Edwards	EDWARDS, T., HUGHES, M., MÖLLER, M. & BELLSTEDT, D.U. (2008). New *Streptocarpus* species (Gesneriaceae) from South Africa. *Botanical Journal of the Linnean Society*, 158(4): 743–748.
S. burttianus T.Pocs	PÓCS, T. (1991). Two new phanerogam species from the Nguru Mountains of Tanzania, East Africa. *Fragmenta Floristica et Geobotanica*, 35(1–2): 40.
S. diandra (Engler) Nishii & Mich. Möller	BURTT, B.L. (1981). New Gesneriaceae from tropical West Africa. *Bulletin du Muséum national d'Histoire naturelle*, sér. B, *Adansonia* 3 (sér. 4): 415–417.
S. heckmannianus (Engler) I.Darbysh.	WEIGEND, M. (2000). A synopsis of the genus *Linnaeopsis* (Gesneriaceae), an 'Uluguru Streptocarpus'. *Flora (Jena)*, 195: 45–50.
S. hilburtianus T.J.Edwards	EDWARDS, T.J. (2003). Two new species of *Streptocarpus* (Gesneriaceae) from South Africa. *Novon* 13(2): 185–188.
S. huamboensis B.L.Burtt	BURTT, B.L. (1999). Old World Gesneriaceae: VI. Six miscellaneous notes. *Edinburgh Journal of Botany*, 56(3): 371–379.

Species	Reference
S. inconspicuus (Burtt) Christenh.	BURTT, B.L. (1958). Studies in the Gesneriaceae of the Old World XV. The genus *Saintpaulia*. *Notes from the Royal Botanic Garden Edinburgh*, 22(6): 547–568.
S. kamerunensis (Engler) B.L.Burtt	BURTT, B.L. (1974). Studies in the Gesneriaceae of the Old World XXXVII. *Schizoboea*, the erstwhile African *Didymocarpus*. *Notes from the Royal Botanic Garden Edinburgh*, 33(2): 265–267.
S. kunhardtii T.J.Edwards	EDWARDS, T.J. (2003). Two new species of *Streptocarpus* (Gesneriaceae) from South Africa. *Novon* 13(2): 185–188.
S. lilliputana D.U.Bellstedt & T.J.Edwards	BELLSTEDT, D.U. & EDWARDS, T.J. (2004). A new species of *Streptocarpus* (Gesneriaceae) from the Pondoland coast, South Africa. *Edinburgh Journal of Botany*, 60(3): 409–414.
S. lineatus (B.L.Burtt) Mich.Möller & M.Hughes	BURTT, B.L. (1981). New Gesneriaceae from tropical West Africa. *Bulletin du Muséum national d'Histoire naturelle*, sér. B, *Adansonia* 3 (sér. 4): 415–417.
S. makabengensis Hilliard	HILLIARD, O.M. (1992). Two new species of *Streptocarpus* from southern Africa. *Edinburgh Journal of Botan*, 49(1): 75.
S. mannii (C.B.Clarke) Nishii & Mich. Möller	CLARKE, C.B. (1883). *Cyrtandreae*. In: DE CANDOLLE, A. & C., *Monographie Phanerogamarum*, *vol. 5*. G. Masson, Paris.
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S. montis-bingae Hilliard & B.L.Burtt	HILLIARD, O.M. & BURTT, B.L. (1990). Studies in the Gesneriaceae of the Old World LI. A new *Streptocarpus* from Mozambique. *Notes from the Royal Botanic Garden Edinburgh*, 46(3): 321–322.
S. occultus Hilliard	HILLIARD, O.M. (1992). Two new species of *Streptocarpus* from southern Africa. *Edinburgh Journal of Botany* 49(1): 75.
S. strigosus (Hook.f.) Nishii & Mich. Möller	HOOKER, J.D. (1862). *Acanthonema strigosum*. Strigose *Acanthonema*. *Botanical Magazine*, 88(3/18), plate 5339.
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S. thysanotus Hilliard & B.L.Burtt	HILLIARD, O.M. & BURTT, B.L. (1975). Studies in the Gesneriaceae of the Old World XXXVIII. A new species of *Streptocarpus* from East Africa. *Notes from the Royal Botanic Garden Edinburgh*, 33: 467–469.