PHYLLOMORPHIC ORGANISATION IN ROSULATE STREPTOCARPUS

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ABSTRACT. The vegetative architecture of certain rosulate species of *Streptocarpus* (Gesneriaceae) has been investigated, in particular *S. gardenii*, *S. kentaniensis*, and *S. primulifolius*. At least two distinct rosulate patterns, distinguished by the nature of the axis—whether vertical or horizontal—and by the phyllotactic arrangement, have been identified. The axis in each case is terminated by an apical meristem derived from a much delayed plumule.

Although there is some resemblance to an ordinary basal rosette, the rosulate form of these species is far from straightforward. The structural units comprising the "rosettes" exhibit a mixture of leaf and stem characteristics not normally found in conventional foliage leaves. These units conform instead to a phyllomorphic organisation in which shoot-like and leaf-like properties are intimately combined in an integrated novel structure—the phyllomorph. Recognition of the phyllomorphic constitution in rosulate species paves the way for a more meaningful study of form diversity and inter-relationships in *Streptocarpus*.

The subgenus *Streptocarpus* of *Streptocarpus* Lindley comprises a wide variety of species of unusual vegetative architecture, the most spectacular of which are those that form only a single foliar organ (of cotyledonary derivation) throughout the individual's life. Such unifoliate plants are monocarpic, producing inflorescences at maturity from the base of the midrib, and the whole plant dying after flowering and seeding. Other species are perennial and have a more elaborate structure composed of few to many leaves. Those that produce a cluster of numerous leaves arranged in more or less a rosette pattern are referred to as rosulates.

S. rexii (Hook.) Lindl. and *S. gardenii* Hook. were among the earliest of rosulate forms in the genus to claim the attention of botanists. The structural innovations and variations present in these forms, however, have largely escaped notice. The intrinsic interest that rosulate species held was eclipsed by the more overtly peculiar morphology of unifoliate and near unifoliate forms (such as *S. wendlandii* Sprenger and *S. polyanthus* Hook.) and by the problem of anisocotyly which proved irresistible to experimentalists. Much of the early investigations suffered from several limitations: an inadequate knowledge of the genus as a whole; the tendency to treat anomalous growth forms as monstrosities (with attendant imputations); the constraints imposed by a rigid classical morphological framework in which these forms were seen, often in isolation.

Indeed the vegetative structure of these plants is not amenable to satisfactory analysis in terms of the standard morphological categories stem and leaf. It has been demonstrated particularly clearly in *S. fanniniae* C. B. Clarke that the plant body consists of recurring units called *phyllomorphs*, units of mixed stem and leaf nature (Jong 1970, 1973; Jong & Burtt 1975). The application of the phyllomorph concept to rosulate species of *Streptocarpus* (referred to briefly in Jong & Burtt 1975) is here considered in greater detail.

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First I digress to add that my first earnest encounter with *Streptocarpus* was in fact through *S. fanniniae*, *a plurifoliate species of remarkable complexity and morphological unorthodoxy from South Africa, a developmental account of which has been given by Jong & Burtt (1975). Its open and diffuse habit of growth facilitated analysis and helped lay the foundation of the phyllomorph concept, a concept which provided the basis for a meaningful comparative approach to the study of form diversification in *Streptocarpus*.

PHYLLOMORPH TERMINOLOGY

Each phyllomorph is composed of a *petiolode* (stalk) which exhibits a mixture of leaf-like and stem-like properties, and a *lamina* that has the power of continued growth. The petiolode frequently roots at its base, or along the lower surface if creeping, and can form vegetative buds on its upper surface. In certain species such as *S. fanniniae* and *S. hirtinervis* C.B.Cl. there is a marked elongation of the petiolode associated with flowering. Continued growth of the lamina is achieved through the activity of a *basal meristem* at the base of each laminal lobe. A *petiolode meristem* which is located at a point where the petiolode merges into the midrib (i.e. at the transitional zone) contributes to the intercalary growth of the midrib as the lamina enlarges and also of the petiolode. A *groove meristem* whose function resembles in many respects that of an ordinary shoot apical or axillary meristem occurs in a depression on the adaxial surface at this point of junction. The ultimate destiny of this groove meristem is its transformation into the first of a series of inflorescence primordia.

The lamina may shed a large part of its distal surface through abscission under unfavourable conditions, a remarkable phenomenon unknown in other flowering plants (see Hilliard & Burtt 1971 p. 29; Noel & van Staden 1975). Growth can resume from the remaining basal region of the lamina on the return of favourable conditions. A phyllomorph therefore is an integrated structure exhibiting a combination of stem and leaf attributes as a hallmark of morphological innovation. Diagrams summarising the general morphology of a phyllomorph are given in Jong & Burtt (1975).

It is useful to distinguish between the first phyllomorph of the plant and subsequent ones. The first is derived from an accrescent cotyledon, named the *cotyledonary phyllomorph*, which is frequently the largest and the first to flower. Subsequent ones produced by an apical meristem resemble the form of the first and are called *primary phyllomorphs*.

THE ROSULATE SPECIES

The outward resemblance to a familiar basal rosette, such as that of a primrose, shown by many rosulate species is rather deceptive for it masks a host of interesting morphological and developmental features not generally

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* It was an undoubted reflection of insight that led Mr Burtt to introduce me in 1965 to the fascination of *Streptocarpus* morphology with *S. fanniniae*. The investigations on which the present paper is partially based (Jong, 1970) were carried out at the Royal Botanic Garden, Edinburgh, where I had the privilege of working in close collaboration with him for several years as a Senior Research Fellow.

found in ordinary plants. The distinction between leaf and stem is as blurred in rosulate species as it is in *S. fanniniae*. The structural units composing a rosette typically possess a number of characteristics in common: continued growth of the lamina, production of inflorescences from the base of the midrib, regular formation of roots and vegetative buds on the petiolode, laminal abscission. These units thus conform in all important respects to a phyllomorphic organisation instead of to a conventional foliar one. The application of phyllomorph terminology to these units is therefore considered appropriate.

With regard to the rosulate habit itself, it is represented not by a single pattern of growth, but by at least two. Among the 13 rosulate species examined (see Table I), the two distinct patterns recognised are: the *centric pattern*, in which the phyllomorphs are arranged in a spiral (rarely opposite) phyllotactic sequence on a short vertical axis; and the *excentric pattern*, in which the phyllomorphs are arranged in two ranks on the upper surface of a horizontal rhizomatous axis.

TABLE I

A subgrouping of 13 Rosulate species of *Streptocarpus* according to structure of "rosette"

Centric	*Excentric*
S. baudertii L. L. Britten	S. hirtinervis C. B. Clarke
S. candidus Hilliard	S. johannis L. L. Britten (predominantly excentric)
S. gardenii W. J. Hooker	S. modestus L. L. Britten
S. kentaniensis Britten & Story	S. primulifolius Gandoger subsp. formosus Hilliard & Burtt
S. meyeri B. L. Burtt	S. parviflorus J. D. Hooker
S. montigena L. L. Britten	S. rexii (Hook.) Lindley
S. cyaneus S. S. Moore	

The terms rosulate and rosette normally refer to plants with a cluster of leaves arranged around a central unextended axis and are clearly applicable to centric rosulates without much difficulty. However, in conformity with past usage for *Streptocarpus*, the terms will be extended to cover also the excentric forms. For brevity, plants that conform to the centric pattern of development are referred to as centric rosulates and similarly those that follow the excentric pattern as excentric rosulates.

The horizontal axis in excentric rosulates is normally above ground or at least partially so, and is composed of an aggregation of petiolode bases which are often pigmented and supplied with groups of stomata and with roots. The resemblance to a rhizome (an underground creeping stem with scale leaves that often subtend axillary buds) is largely superficial, hence the terms rhizomatous stock or "rhizome" are adopted for the description of such an axis.

One of the characteristic features of a phyllomorph is the occurrence of vegetative buds on the petiolode. These buds vary in number, prominence, and disposition in different species; they generally occur some distance above the axillary position. It is from these buds that lateral rosettes or branch "rhizomes" develop.

Individual phyllomorphs of the main rosette regularly form roots at the base of the petiolode, from the lower surface as well as from its flanks. This property, normally absent in ordinary intact foliage leaves, provides each phyllomorph with its own root system.

As stated earlier, rosulate species are perennial plants, although like a unifoliate plant, individual phyllomorphs perish after flowering and are thus monocarpic. The cotyledonary phyllomorph being the oldest phyllomorph of the rosette is normally the first to flower. In an adult plant, several phyllomorphs often flower at the same time. Each flowering phyllomorph bears a series of inflorescences, the first in the series emerging close to the base of the lamina. New inflorescences appear in acropetal succession.

The base of the lamina of a phyllomorph that has been flowering for some time becomes spread out, an indication that growth of the blade has ceased. By contrast, the laminal lobes are erect, either conduplicate or involute in a developing phyllomorph.

Intercalary growth often continuing well after the initiation of the final inflorescence primordium results in the formation of a petiolar region between this primordium and the lamina base. The late development of such a petiole is a common feature of many rosulate species and is particularly prominent in *S. primulifolius* Gandoger, *S. johannis* Britten, and *S. hirtinervis* C. B. Clarke, but is inconspicuous in *S. kentaniensis* Britten & Story.

The two rosulate patterns mentioned earlier are now considered separately, with particular reference to three of the species: *S. gardenii* and *S. kentaniensis* as representatives of the centric pattern, and *S. primulifolius* subsp. *formosus* as an example of the excentric pattern.

CENTRIC PATTERN

Six of the 13 species listed in Table I have been observed to follow regularly the centric pattern of growth. All are typically non-rhizomatous, with the possible exception of some plants of *S. candidus* from Nhlazatsche, Zululand, which sometimes develop a short horizontal stock when growing on a steep rock face (Hilliard, pers. comm.). All bear a general resemblance to ordinary rosette plants in that the phyllomorphs are radially clustered around a short central axis terminated by an apical meristem.

Although sharing a common structural theme, the six centric rosulate species show a certain degree of variation in length of the petiolodes and in size, shape, venation pattern and texture of the lamina of the phyllomorphs, and hence in the configuration of the rosettes. It is possible to recognize two types of configurations which may be loosely described as "broad-leafed" and "narrow-leafed"; on this basis, the six species (all South African) can be divided into two groups:—

a. "Broad-leafed" Rosettes:	*S. baudertii* (plate 5A) *S. meyeri*, *S. montigena*
b. "Narrow-leafed" Rosettes:	*S. gardenii*, *S. candidus* *S. kentaniensis* (plate 5B)

This subgrouping has no taxonomic significance as is clearly demonstrated for example by the contrasting rosette configurations produced by the two related species *S. meyeri* and *S. kentaniensis*.

The "broad-leafed" type of rosette is characterised by firm, subsessile (longest petiolode less than 1 cm), broad elliptic to ovate phyllomorphs, lamina 2 to 3 times longer than broad; rosettes neat with 8–10 prostrate phyllomorphs.

The "narrow-leafed" type has ovate to oblong phyllomorphs, lamina 3–10 times as long as wide, often with conspicuous petiolodes 0·4–1·5 cm long, more than 3 cm in odd individual phyllomorphs, as for example in *S. candidus*. Wild specimens of this species from the Ngome Forest, Natal have phyllomorphs up to 60 × 20 cm, with much longer petiolodes up to 7 cm (Hilliard 1964). In adult flowering specimens of *S. gardenii* and *S. kentaniensis*, the rosettes generally consist of 14–17, sometimes 20 phyllomorphs.

S. johannis, a close relative of *S. baudertii*, is normally an excentric rosulate species, but one specimen from Mt Ngeli, N Natal (*C.* 4952) developed into a centric rosette. It is not known how widespread this variation is in the field.

The arrangement of the phyllomorphs has been determined by observations made directly on adult specimens of 4 species (*S. baudertii*, *S. meyeri*, *S. gardenii*, *S. kentaniensis*). Except for two plants of *S. baudertii* which had an opposite and decussate arrangement, all four species conform to a spiral phyllotaxis usually 3 + 5, sometimes 2 + 3. The rudimentary central axis, 0·7–0·8 cm long and seldom exceeding 1 cm, is highly compact and lacking internodes (fig. 1A).

VEGETATIVE BUDS. All the species possess vegetative buds which normally occur along the median plane on the upper surface of the petiolodes. The position these buds occupy varies somewhat from species to species, from being apparently axillary, that is, close to the base of the petiolode as in *S. kentaniensis*, to near the base of the first floral scape as in *S. gardenii*; they are frequently located somewhere between these two points. Buds sometimes develop in between the petiolode bases of two adjacent phyllomorphs, as in *S. gardenii* and *S. kentaniensis* (Plate 5C).

In most species, each phyllomorph of the plant bears only a single vegetative bud (fig. 1 B & C), but in certain species such as *S. kentaniensis*, only a few of the outer phyllomorphs of a rosette seem to possess a bud. More than one bud, usually in acropetal series (fig. 1D), occur in phyllomorphs of *S. baudertii*, *S. candidus* and *S. gardenii* (up to four). Buds that are clearly floral are sometimes intermixed with the vegetative ones on the same petiolode. This has been encountered only in *S. gardenii* (fig. 1E).

Streptocarpus gardenii

This occurs in forest, and is the commonest species of *Streptocarpus* over much of its area of distribution—the Transkei districts of the Eastern Cape Province and Natal (Hilliard & Burtt 1971).

GENERAL MORPHOLOGY. Plants for the present study were raised from two different seed sources, one from Natal, Qudeni (*C.* 5945) and the other from the Eastern Cape (x 66/406 G. Gray, locality unknown); all conformed to the centric pattern of growth. The typically wrinkled elliptic to ovate primary phyllomorphs are arranged in either a clockwise or a counter-clockwise 3 + 5 spiral phyllotactic pattern. An adult plant is composed of 14–16 phyllomorphs (including visible primordia), the largest of which being usually the cotyledonary phyllomorph.

Flowering of the first inflorescence occurs 8–8½ months from seed. The first to flower is the cotyledonary phyllomorph followed successively by the first up to the 5th primary phyllomorph. As in other acaulescent species, the inflorescences arise in acropetal succession from the junction of midrib and petiolode (fig. 3A; see also fig. 1C). With the development and subsequent enlargement of successive scapes, the older ones whose basal regions are often much swollen are frequently displaced from their point of origin, thus imparting the misleading impression of having been initiated well below the lamina (fig. 1F; see also fig. 1C).

The petiolode of a flowering phyllomorph varies in length from 3·5–6 mm and in diameter from 2·5–3·5 mm. It is often distinctly erect to suberect with the lamina held at an angle to it (fig. 1F), a feature not normally noticeable in the vegetative phase. Although it is somewhat reminiscent of the erect elongated petiolodes associated with flowering in *S. fanniniae*, it is uncertain whether the phenomenon in the two species is exactly comparable without detailed analysis.

DETAILED MORPHOLOGY OF A PHYLLOMORPH. Each young phyllomorph has a groove meristem situated in a shallow despresion at the midrib-petiolode junction. Also in this transition zone is located the petiolode meristem. It is usual to find a close association between these meristems and a deeper coloration of surrounding tissues. Fig. 2 A-C shows that the rim of this depression, extending in an arc to the laminal insertions, and sometimes a collar corresponding to the position of the petiolode meristem, appears darker in colour than the rest of the petiolode which is typically dull brownish red.

The whole phyllomorph is adorned with predominantly long multicellular eglandular trichomes. Narrow green spots 0·5–2 mm long representing groups of stomata occur scattered on the petiolode as well as inflorescence scapes.

On the adaxial surface of a petiolode of a young developing phyllomorph, there occurs a narrow *translucent tract* (normally obscured by long multicellular hairs), more or less 1 mm long, directly below the groove meristem (fig. 2A). A number of bud primordia or meristematic mounds later originate in this tract (fig. 2 B & C).

These buds remain dormant even in phyllomorphs already in fruit but lateral rosettes do develop on some of the first formed phyllomorphs, and they are probably derived from such buds released from dormancy. The properties of the translucent tract in *S. gardenii* appear to be comparable to the detached meristems of *S. fanniniae*, and it seems reasonable to treat the two as of a similar nature.

There are, however, certain obvious points of difference. The translucent tracts in relatively young phyllomorphs of *S. gardenii* are difficult to detect by mere inspection due to the absence of differential pigmentation, which is characteristic of the detached meristems of *S. fanniniae*. They become faintly visible on wetting, but are best seen by carefully removing obscuring hairs from surrounding areas, an operation that is also necessary for revealing the presence of bud primordia. These primordia, variable in number (1–4), are disposed in a single longitudinal row instead of transversely as in *S. fanniniae*;

they are extremely small and seldom develop beyond 1 mm in length even in a phyllomorph already in flower (fig. 1E). In any given phyllomorph, however, they are not all necessarily vegetative. Occasionally an aborted floral bud is found directly at the base of the first flowering scape (fig. 1F); in this case, it is not possible to decide whether the bud belongs to the normal serial order of inflorescences or whether it originated from a detached meristem.

In an actively growing phyllomorph, the basal lobes of the lamina are folded together lengthwise along the midrib, highly convoluted and dense with hairs. The lateral veins in this region are close together. The basal meristem resident here is intensely stained with the usual histological dyes such as haematoxylin and safranin O. These features indicate that the basal meristem is in an active state of growth forming new laminal tissue. After flowering, the laminal lobes become spreading, and their points of insertion, which at an earlier stage of growth are in continuity with the groove meristem, become separated from the youngest floral bud by a short petiolar region 1–3 mm long. Transverse sections through the lamina base at this stage show that the basal meristem has lost much of its avidity for the stains and is in the process of differentiating into mature laminal tissues. These features are regarded as indicative of a decline or cessation in laminal growth. A groove meristem is no longer present at this stage.

The petiolar region resembles anatomically and morphologically a conventional petiole. The delayed formation of the petiole, like the marked elongation of the petiolode of a flowering phyllomorph in for instance *S. fanniniae*, is yet another feature frequently associated with flowering. Such a petiole occurs also in many other rosulate species already mentioned, and it would be interesting to ascertain its mode of growth..

ANATOMICAL FEATURES. Transverse sections (TS) taken at different levels of a young phyllomorph (fig. 2A), from the base upwards, reveal a histological pattern that is basically similar to that observed in *S. fanniniae*. The vascular system at the base of the petiolode is composed of three major bundles arranged in an arc while a few minor bundles often occur on the adaxial side to complete the vascular ring (fig. 2D). At higher levels, the two lateral major bundles and in certain cases, the median bundle as well, split up into numerous smaller strands (fig. 2E). Other minor bundles comprising usually only phloem tissue also regularly occur on either side of the median bundle. The stele is completely or only partially encircled by a true endodermis (i.e., one with distinct Casparian strips) or by an endodermoid layer—the starch sheath. Both cortical and pith tissues are full of compound starch granules while the endodermis or starch sheath contain fewer but larger ones.

Sections through the petiolode at the level of the translucent tract show that there is a zone of small cells extending some distance into the pith (fig. 2F and 2G). These cells are slightly denser staining than those of neighbouring tissues and appear to be meristematic. Other cortical cells, especially those immediately next to the arms of the horseshoe-shaped vascular cylinder and those next to the endodermis are in active division. Note the interruption of the endodermis on the adaxial side of the stele.

The groove meristem, initially flat and soon changing to a low raised dome, is situated in a shallow depression which deepens slightly distally (fig. 2H & I).

Cells smaller and denser in cytoplasm than other cortical cells occur on either side of and immediately underneath the meristem.

The petiolode meristem occurs in the transition zone as a diffuse region of narrow cambial-like cells which grades into the progressively larger cells on either side of it. Epidermal cells in this zone are often noticeably smaller than in neighbouring areas. In preserved material, both the groove and petiolode meristem, as well as the translucent tract, are easily distinguished by their darker colour.

An incipient vegetative bud primordium appears in T.S. as a dome of meristematic tissue opposite a parenchymatous gap. Procambial strands depart towards the bud from the arms of the pear-shaped vascular arc. Active cell division occurs both in the central region of the pith and inner cortex. This association of active cell division in mature parenchyma tissue with the occurrence of vegetative or floral primordia is a recurrent feature observed also in *S. fanniniae* and in the rosulate species.

FLOWERING PHYLLOMORPH. The vascular system at the base of the petiolode is a closed cylinder, completely surrounded by an endodermis thus resembling a stem structure; the dorsiventrality observed in a young petiolode is now further emphasized by the unequal distribution of secondary xylem and lignified pericycle fibres (fig. 3B). Sections through the base of a flowering scape show intense pigmentation in the outer cortex, the intensity decreasing inwards. The U-shaped stele of the petiolode itself (fig. 3D) surrounded by a starch sheath, is composed of numerous primary vascular bundles. By contrast, secondary xylem is well developed in the peduncle (pe). There are two distinct cortical bundles at the insertion of the scape (peduncle), each surrounded by a starch sheath.

The anatomical structure at the base of a petiolode is thus stem-like with an asymmetric but complete vascular cylinder bounded by an unbroken endodermis. The vascular ring tends to be broken distally and becomes more petiole-like near the insertion of the peduncle (fig. 3C).

STRUCTURE OF THE PETIOLE. An example of a phyllomorph with a distinct petiole is illustrated in fig. 4A, the region below the inhibited floral buds is the petiolode. A series of transverse sections of the petiole near its base towards the lamina is represented in fig. 4C, D (cf. fig. 4B). The petiole has a U-shaped vascular arc which extends well into the midrib where it assumes a more crescentic form (fig. 4F). There is no evidence of a groove meristem at the base of the lamina (fig. 4D). Anatomically there is a close similarity to the petiole structure of a caulescent species such as *S. nobilis* C. B. Clarke.

There is a consistent anatomical difference between the petiole and petiolode—the vascular configuration of the petiole is typically U-shaped whereas that of the petiolode tends to be a complete ring surrounded by an endodermis, i.e. it is more stem-like. Nevertheless the vascular cylinder of the petiolode is distinctly asymmetrical and this becomes more obvious when the endodermis (or starch sheath) is interrupted on the adaxial side, forming a gap. A distinction between petiole and petiolode based on purely anatomical criteria therefore must be treated with caution.

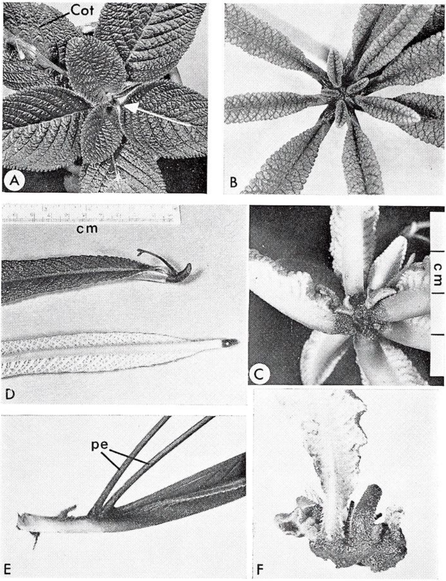

PLATE 5. A-D, centric rosulates. A, *S. baudertii*, adult plant with spirally arranged broad phyllomorphs; arrow indicating involute base of lamina (× $\frac{1}{3}$). B-D, *S. kentaniensis*: B, rosette of narrow phyllomorphs in a 3 + 5 spiral phyllotaxis (× $\frac{2}{3}$); C, 10-month old plant viewed from below, cotyledon removed to reveal two vegetative buds in between adjacent primary phyllomorphs; D, detached phyllomorphs, upper and lower surface views. E-F, excentric rosulates: E, *S. johannis*, vegetative bud with single secondary phyllomorph on petiolode of a detached phyllomorph (× 1); F, *S. primulifolius*, "rhizome" in wild specimen (× $\frac{3}{5}$). Cot, cotyledonary phyllomorph with inflorescence; pe, peduncles.

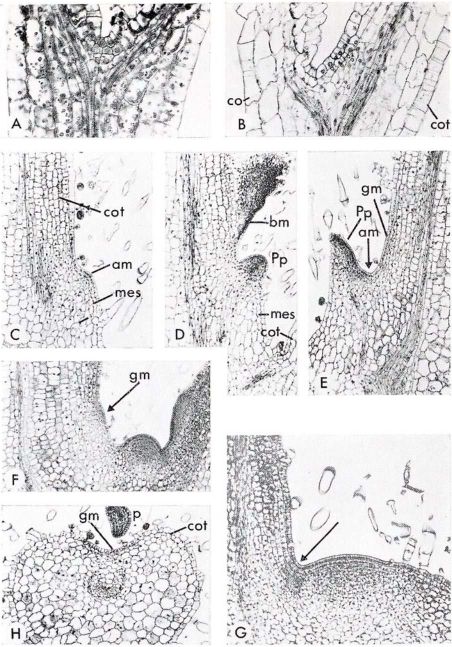

PLATE 6. Centric rosulates. A-F, *S. gardenii*: A, M.L.S. 3–4-day old seedling—meristematic group in fork of cotyledons (× 260); B, M.L.S. displaced embryonic meristem in 25-day old seedling (× 200); C-E, L.S. 35-day old seedling (× 75), C-D are neighbouring sections; E, L.S. in plane of primary phyllomorph primordium. F, M.L.S. apical meristem in ± 53-day old seedling (× 75). G, *S. kentaniensis*, M.L.S. apical meristem in mature plant—arrow indicating axillary meristem (× 100). H, T.S. macrocotyledon of 35-day old seedling (× 75).

am, apical meristem; bm, basal meristem; co, smaller cotyledon; cot, macrocotyledon; gm, groove meristem; mes, mesocotyl; p, densely stained 1st primary phyllomorph; Pp, phyllomorph primordium.

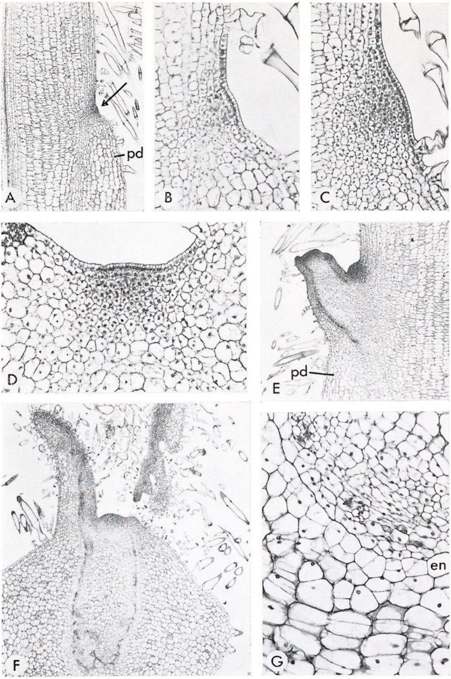

PLATE 7. *S. kentaniensis.* A-E, a series of phyllomorphs in L.S., illustrating developmental changes in the groove meristem: A, M.L.S. groove meristem (arrow) in primary phyllomorph (× 35); B, M.L.S. groove meristem—close-up view of A (× 150); C, M.L.S. much enlarged dome-shaped groove meristem in older phyllomorph (× 150); D, T.S. groove meristem in shallow groove (× 150); E, L.S. first inflorescence primordium and incipient second primordium present as a meristematic mound (× 40). F, L.S. apical meristem and axis of a 4½-month old plant (× 35). G, close-up of portion of axis in F. Note variations in orientation of new cell walls in endodermis and seriation of cortical cells (× 220). en, endodermis; pd, petiolode.

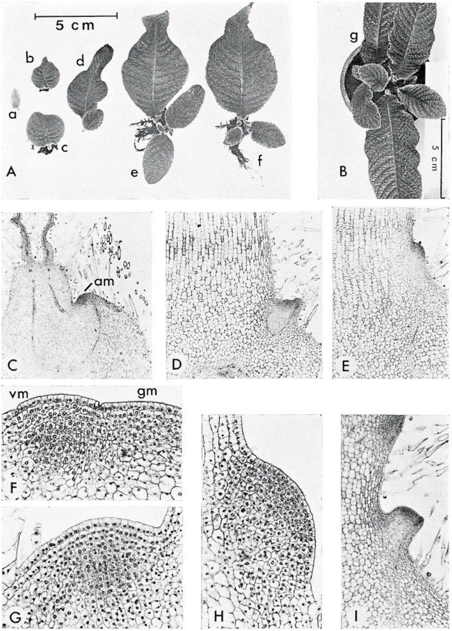

PLATE 8. *S. primulifolius*, excentric rosulate. A-B, plants of different ages, macrocotyledon uppermost: a-b, young seedlings with enlarging macrocotyledon; c, appearance of the first primary phyllomorph; d-g, older plants. Note variation in orientation of the first phyllomorph in relation to macrocotyledon; c-g are schematically represented in Fig. 7. B, 6½-month old, already with floral primordia. C, M.L.S. apical meristem (deeply stained) at growing tip of a 5½–6-month old plant (× 20). D & E, L.S. of primary phyllomorph: D, vegetative bud with secondary phyllomorph primordium (× 20); E, groove meristem in M.L.S. above the bud primordium shown in D of the same phyllomorph (× 20). F, T.L.S. of petiolode parallel to plane of lamina: two meristematic mounds—one on the right probably groove meristem; the other a bud meristem (× 150). G, M.L.S. apical meristem at growing tip of 5½–6-month old plant, close-up view to show histological details (× 150). H, M.L.S. dome-shaped groove meristem approaching reproductive phase (× 150). I, L.S. first inflorescence primordium (× 40). am, apical meristem; gm, groove meristem; vm, bud meristem.

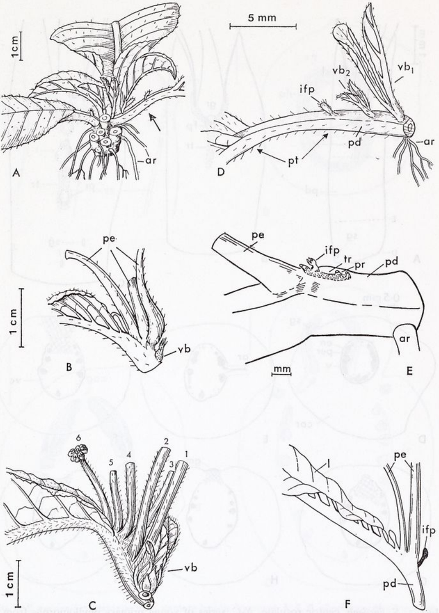

FIG. 1. Centric rosulates. A, *S. baudertii*, adult plant with certain phyllomorphs removed to reveal axis (arrow: phyllomorph shown enlarged in D). B,C, *S. meyeri*, detached phyllomorphs; B, flowering phyllomorph with inhibited vegetative bud; C, much older phyllomorph with 6 peduncles and 1 developing vegetative bud. D, primary phyllomorph arrowed in A. E,F, *S. gardenii*: E, camera lucida drawing of basal region of detached phyllomorph (translucent tract stippled) bearing 3 bud primordia and 1 floral primordium at base of peduncle; F, detached flowering phyllomorph showing aborted floral primordium (black) and sub-erect petiolode.

ar, roots from base of petiolode; ifp, inhibited inflorescence primordium; l, lamina; pd, petiolode; pe, peduncle; pr. bud primordium; pt, long petiole; tr, translucent tract; vb, vegetative buds; vb1, vb2, vegetative buds in acropetal sequence.

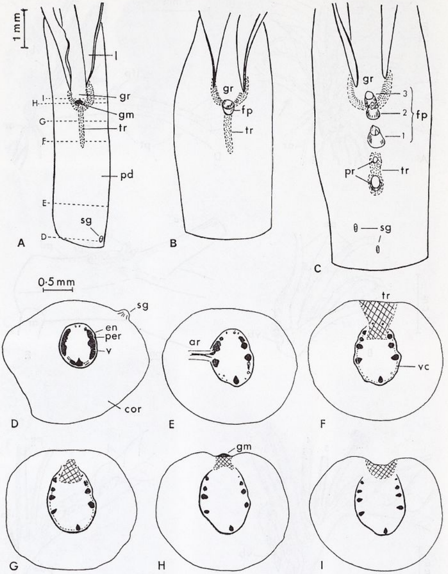

FIG. 2. *S. gardenii*, centric rosulate. A-C, series of young primary phyllomorphs from a 10-month old plant: A, youngest phyllomorph with translucent tract (D-I, indicate position from which transverse sections are taken); B, phyllomorph with a single primordium; C, older phyllomorph with 2 vegetative bud primordia on detached translucent tract and 3 inflorescence primordia in acropetal sequence (stippling indicates areas of darker pigmentation); D-I, camera lucida drawings of T.S. taken from positions indicated by the dotted lines in A, (cross-hatching indicates regions of small cells in the translucent tract). ar, part of root; cor, wide cortex; en, endodermis; fp, inflorescence primordia; gm, groove meristem; gr, groove; l, lamina; pd, petiolode; per, pericycle; pr, bud primordia; sg, stomatal group; tr, translucent tract; v, vascular tissue; vc, vascular cambium.

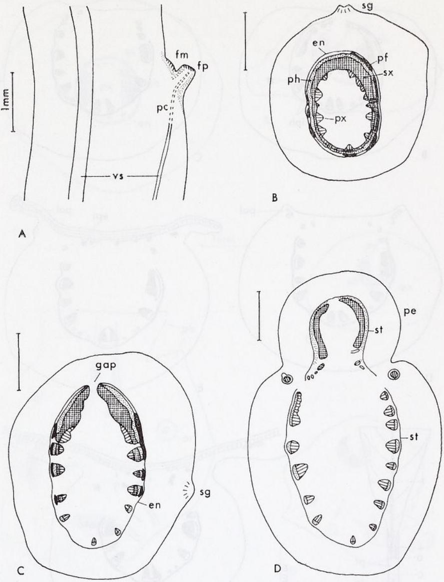

FIG. 3. *S. gardenii*, centric rosulate, camera lucida drawings. A, L.S. of primary phyllomorph with first inflorescence primordium and floral meristem (area bounded by broken lines darker red in colour). B-D, T.S. of petiolode of flowering phyllomorph: B, base of petiolode; C, close to base of first peduncle; D, at level of second peduncle, xylem in peduncle seen in oblique view.

en, endodermis; fm, floral meristem; fp, inflorescence primordium; pc, procambium; pe, peduncle; pf, pericyclic fibres; ph, phloem; px, primary xylem; sg, stomatal group; st, starch sheath; sx secondary xylem; vs, vascular strands.

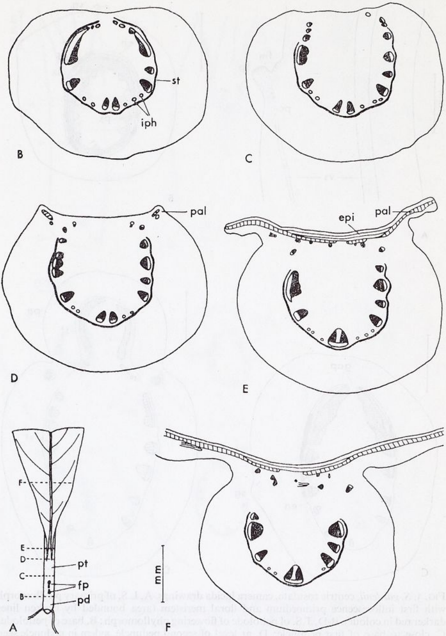

FIG. 4. *S. gardenii*, centric rosulate. A, primary phyllomorph with distinct petiole (semi-diagrammatic). B-F, camera lucida drawings of transverse sections which correspond to points indicated in A.
epi, epidermis; fp, arrested floral primordia; iph, phloem strands; pal, palisade; pd, petiolode; pt, petiole; st, starch sheath.

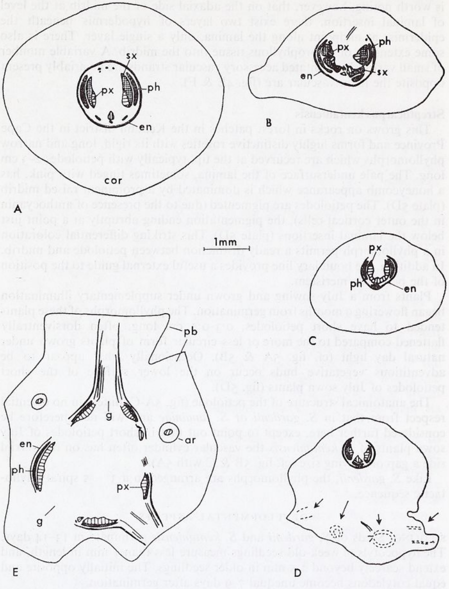

FIG. 5. *S. kentaniensis*, centric rosulate, camera lucida drawings. A, T.S. of petiolode from plant grown in daylight. B-E, transverse sections from 9-month old plant grown for 4 months under supplementary lighting: B, base of petiolode of cotyledonary phyllomorph; C, near base of 1st primary phyllomorph; D, base of 4th primary phyllomorph—arrows indicate apparently adventitious buds on lower surface of petiolode; E, mid-point of adult axis.
ar, roots in oblique section; cor, wide cortex; en, endodermis; g, gap; pb, petiolode base; ph, phloem; px, primary xylem; sx, secondary xylem.

STRUCTURE OF THE LAMINA. The structure of the lamina is unexceptional. It is worth noting, however, that on the adaxial side of the midrib at the level of laminal insertion, there exist two layers of hypodermis beneath the epidermis; at midpoint along the lamina, only a single layer. There is also some extension of chlorophyllous tissue into the midrib. A variable number of small variously orientated accessory vascular strands are invariably present opposite the main vascular arc (fig. 4E & F).

Streptocarpus kentaniensis

This grows on rocks in forest patches in the Kentani district in the Cape Province and forms highly distinctive rosettes with its rigid, long and narrow phyllomorphs which are recurved at the tip, typically with petiolodes 2–3 cm long. The pale undersurface of the lamina, sometimes tinged with pink, has a honeycomb appearance which is dominated by a prominent raised midrib (plate 5D). The petiolodes are pigmented (due to the presence of anthocyanin in the outer cortical cells), the pigmentation ending abruptly at a point just below the laminal insertions (plate 5D). This striking differential coloration in a phyllomorph permits a ready distinction between petiolode and midrib. In addition, the boundary line provides a useful external guide to the position of the petiolode meristem.

Plants from a July sowing and grown under supplementary illumination began flowering 9 months from germination. The phyllomorphs of these plants tended to have short petiolodes, 0·3–0·5 cm long, often dorsiventrally flattened compared to the more or less circular form of plants grown under natural day light (cf. fig. 5A & 5B). Occasionally what appear to be adventitious vegetative buds occur on the lower surface of the short petiolodes of July sown plants (fig. 5D).

The anatomical structure of the petiolode (fig. 5A-C) differs in no essential respect from that in *S. gardenii* or *S. fanniniae* and will not therefore be considered further here, except to point out that in short petiolodes of July sown plants of *S. kentaniensis* the vascular cylinder often has on its adaxial side a gap of varying size (cf. fig. 5B & C with 5A).

Like *S. gardenii*, the phyllomorphs are arranged in a 3 + 5 spiral phyllotactic sequence.

DEVELOPMENTAL ASPECTS

SEEDLING. Seeds of *S. gardenii* and *S. kentaniensis* germinate in 13–14 days. The hypocotyls of week-old seedlings measure less than 1 mm in length, and extend scarcely beyond 2·5 mm in older seedlings. The initially opposite and equal cotyledons become unequal 7–9 days after germination.

The first primary phyllomorph, on emergence 1½–2 months after germination, usually faces the enlarged cotyledon (macrocotyledon) but orientations at oblique or right angles to it, either to the left or the right, are quite common. At the microscopic level, it is already discernible as a small primordium in 30–35 day old seedlings (plate 6D). A mesocotyl averaging 0·5 mm and seldom exceeding 1 mm in length is sometimes present at 1–2 months. The mesocotyl is an intercalated region that elevates the macrocotyledon above the smaller cotyledon. This structure is a notable feature of many caulescent species e.g. *S. caulescens* Vatke and *S. nobilis*, but is not strongly developed among rosulate species.

The first and successive primary phyllomorphs originate in a more or less conventional apical meristem in an orderly spiral sequence. The ontogeny of such a meristem is traceable from early seedling development.

ONTOGENY OF APICAL MERISTEM. In seedlings less than one week old, an embryonic meristem—a small group of meristematic cells about two layers deep, with prominent nuclei and denser cytoplasm than surrounding cells—is discernible in the fork of the two cotyledons (plate 6A). In some 9-day old seedlings, the laminal base of the macrocotyledon is stained more intensely than the embryonic apical meristem. It is the meristematic activity of this basal meristem that leads to continued growth of the cotyledonary lamina.

At a later stage, in seedlings 20–25 days old, changes in size and position of the apical meristem become evident. As shown in plate 6B the outermost layer has increased in longitudinal extent and the apical meristem has been displaced to the base of the distinctly larger cotyledon. The meristem undergoes a period of enlargement in this lateral position as it is being carried upwards (with the cotyledonary lamina) by a mesocotyl of variable size (plate 6C). Longitudinal sections of the seedling at this point of ontogeny are virtually indistinguishable from those of other acaulescent *Streptocarpus*. This stage might appropriately be called the *juvenile unifoliate phase*.

During this phase the embryonic meristem constitutes temporarily a groove meristem of the macrocotyledon. The meristem later bulges out to form a low dome which is inclined at 40–45° to the vertical plane; a small indistinct group of cells at its upper flank is left behind in the axil of the macrocotyledon, while the opposite flank continues into the slope of the mesocotyl (plate 6C). Thus the eventual transformation of the embryonic meristem (=groove meristem) into a more or less conventional apical meristem represents a delay in plumular development rather than its suppression.

Formation of the first primary phyllomorph primordium appears to involve virtually the whole of the young apical meristem (plate 6E). The original rounded apex of the meristem then persists as a flat to concave structure 40 μm wide and about as deep at the foot of the primordium. Note in median longitudinal sections of older (50–57 days old) seedlings, the reappearance of the rounded form of the apical meristem, and the presence of an axillary meristem at the point of insertion of the young first primary phyllomorph (plate 6F). This means that after initiation of the first primary phyllomorph, the apical meristem undergoes a period of enlargement before initiation of the next phyllomorph primordium. Subsequent phyllomorphs involve a relatively small part of the apex. These observations confirm those of Schenk (1942) on *S. rexii*.

Histologically the apical meristem, which at this time is $\pm$ 140μm broad and 60 μm high and almost vertically orientated, has a clear outer tunica and a less distinct inner tunica layer overlying a substantial corpus in which there is no clear zonation. A third tunica-like layer is sometimes discernible in the central region of the apex. While some periclinal divisions occur in the second tunica layer, divisions in the outer layer are exclusively anticlinal. It is therefore reasonable to infer that inception of a phyllomorph primordium is subepidermal.

A notable feature of the apical meristem in both *S. gardenii* and *S. kentaniensis* is its tendency towards asymmetry as a result of vacuolation on the side next to the cotyledonary petiolode. In older apices a central cambium-like zone below the corpus (plate 6G) is discernible, but this varies in extent and distinctness in different apices of roughly comparable age. Note that the apical region of the older plant (plate 6G) is broader in radial extent than that of the younger apex (plate 6F).

MESOCOTYL. In *S. fanniniae*, the mesocotyl of the seedling constitutes a permanent petiolode of the cotyledonary phyllomorph. In the case of *S. gardenii* and *S. kentaniensis* the mesocotyl acts only temporarily as a petiolode of the enlarging cotyledon. During later ontogeny the mesocotyl becomes incorporated into the main axis of the plant, while the cotyledonary phyllomorph later acquires its own new petiolode.

GROOVE MERISTEM. The axillary meristem of the cotyledonary phyllomorph of a 35-day old seedling is composed of 2–3 layers of superficial meristematic tissue (plate 6 E & H). It constitutes the new groove meristem of the phyllomorph and bears at this point of ontogeny some resemblance to the displaced embryonic apical meristem of a 25-day old seedling (plate 6B). The new groove meristem is therefore of axillary origin. Further stages in the ontogeny of this meristem are exemplified by *S. kentaniensis*; plate 7 A & C illustrate the progressive increase in its size in successively older phyllomorphs This developmental series strongly parallels that in *S. fanniniae*.

Active cell division in the upper and lower margins of the groove meristem provides new tissues for longitudinal growth on the adaxial side of the midrib and petiolode respectively. The activity of the petiolode meristem in the transition zone is largely responsible for elongation of the rest of the petiolode and the midrib.

Transverse sections of the petiolode through the groove meristem, but for minor details, are virtually indistinguishable from those of *S. fanniniae* (plate 7D). The one obvious difference is in the depth of the groove, which is consistently much shallower in *S. kentaniensis* and other rosulate species than in *S. fanniniae*.

The first of the phyllomorphs to flower is the cotyledonary phyllomorph. As the groove meristem develops into the first inflorescence primordium, a residuum of meristematic tissue at its base is left behind to grow into a second inflorescence primordium, and so the process is repeated with subsequent primordia, always in an acropetal direction (plate 7E).

It is clear from its ontogeny that the ultimate destiny of the groove meristem is flowering, but whether it is earlier involved at all in the formation of detached meristems as found in *S. fanniniae* requires further study. The presence of a translucent tract leading to the groove meristem on petiolodes of *S. gardenii* is suggestive of such an involvement but a similar feature is not detectable in *S. kentaniensis*.

THE PRIMARY AXIS. The primary axis formed by the apical meristem is a morphologically complex structure in which enlarged bases of phyllomorphs and cortex are inextricably merged. Transverse sections at midpoint of an adult axis of *S. kentaniensis* show a poorly developed vascular system interrupted by numerous gaps associated with departure of trace supplies to the primary phyllomorphs (pb) (fig. 5E). The young axis (plate 7F) of a 4½ month old plant consists of an extensive cortex and a narrow vascular cylinder surrounding a relatively large pith area. Radial expansion of the axis appears to be accomplished mainly through active cell division and vacuolation in the cortex, part of which is derived from meristematic activity of the endodermis and repeated periclinal divisions of its derivatives (plate 7G). All the parenchymatous tissues are rich in starch granules.

EXCENTRIC PATTERN

All of the seven rosulate species listed in Table I conform to the excentric pattern of growth.

Excentric rosulates are characterized by a horizontal rhizomatous axis and arrangement of the phyllomorphs in two ranks on the upper side of the axis (fig. 6A). Most of the species have erect to semi-erect phyllomorphs which give the plants a more or less tufted appearance. The phyllomorphs of *S. hirtinervis* and *S. modestus* tend to be prostrate. In cultivation more than one active growing point such as the one illustrated in fig. 6B often occur in a single plant.

VEGETATIVE BUDS. Most of the excentric rosulates normally have only one vegetative bud per phyllomorph. It is from such a bud that a branch axis can develop. The position of the bud on the petiolode varies, most frequently it is either to the left or right of the median plane (figs 6A, 7 A & B). When the bud is located well above the base of a long petiolode, it gives the impression of being an adventitious structure (plate 5E).

RHIZOMATOUS STOCK. The horizontal axis of the different excentric rosulate species vary in size and extent of development. *S. rexii*, *S. parviflorus*, *S. cyaneus*, *S. modestus*, *S. johannis* and *S. hirtinervis* (all South African excepting the last mentioned, which is from Malawi) have feebly developed rhizomatous stocks which appear to be composed of a loose association of adjacent petiolode bases.

The stoutest stock is developed by *S. primulifolius* but it is nowhere nearly as robust as in wild specimens (plate 5F). Apparently the extent and sturdiness of the "rhizome" varies with habitat and may therefore be ecologically controlled (Hilliard & Burtt 1971). According to Hilliard (1966), the closely related *S. cyaneus* also habitually develops a long stout stock. The stock of this species and of *S. primulifolius* is often branched.

In one specimen of *S. primulifolius* brought back from the wild by Mr Burtt, the longest piece of rhizomatous stock measured 7·5 cm and had a diameter of c. 1·7 cm. The growing end bore a tuft of several phyllomorphs which were arranged in two alternate rows. Prominent groups of stomata and roots occur on the abaxial surface of the petiolodes as well as on the flanks of such a "rhizome". Neighbouring phyllomorphs are sometimes separated by a short region resembling an "internode". Laminal abscission occurs regularly in this species, even under cultivation. The older part of the stock is composed of the swollen petiolode bases and corky scars of fallen phyllomorphs.

Transverse sections of such an older region reveal a weakly developed vascular system in which very little secondary tissue is formed. Most of the sections present a large proportion of the vascular tissue in oblique view. As in the central axis of the centric rosulate species, growth in diameter of the rhizomatous stock appears to be largely through increase in the amount of parenchymatous tissue, which is similarly densely packed with starch granules.

Fig. 6C represents a section from the extremity opposite to the growing tip; it shows an asymmetric vascular cylinder which recalls that normally seen in the basal region of the primary petiolode. The two petiolode scars (pds) are separated from the parenchyma tissue below by a corky layer which continues round to the upper surface (shaded portion) of the axis.

Fig. 6D is a section through an "internodal" region of another but stouter "rhizome". Asymmetry of the stele is again clearly evident and there is feebly developed primary xylem on the side proximal to a scar (not shown in this section.) A small amount of secondary xylem occurs on the opposite side.

Most of the sections obtained, however, have the typical appearance of the one represented in fig. 6E, showing a large gap and continuity of the vascular tissue and pith with the petiolode scar.

FLOWERING PHYLLOMORPH. In common with the majority of acaulescent species, the inflorescences originate in acropetal succession from the junction of the petiolode and midrib. Each phyllomorph is monocarpic but may after flowering persist on the plant for more than one season.

A distinct petiole is generally present in the flowering phyllomorphs of most representatives of this group of rosulates (fig. 6A).

An event of special interest is frequently seen in *S. hirtinervis*, in which the initially short petiolode undergoes marked elongation at flowering. Petiolode elongation associated with flowering is most clearly seen in *S. fanniniae* (other examples are cited in Hilliard & Burtt 1971) but appears to be uncommon among rosulate species.

DEVELOPMENTAL ASPECTS

The pattern of development of the excentric rosulate habit is much more complex than that of the centric. It is best to illustrate the essential features using *S. primulifolius* as a representative.

Streptocarpus primulifolius

This species extends from Pietermaritzburg, Natal to East London in the Eastern Cape. It is usually found on rocks or rocky banks in forest (usually near margins), sometimes on shaded stream banks. For further details see Hilliard & Burtt (1971). The seeds used in this investigation come from Dumisa, Natal and are of *S. primulifolius* subsp. *formosus* Hilliard & Burtt. Since it is vegetatively indistinguishable from *S. primulifolius* subsp. *primulifolius*, further reference will not include the subspecific epithet.

Plate 8A shows plants of different ages forming a developmental series ranging from the juvenile unifoliate seedling phase to the more or less rosulate form at 6½ months (plate 8B). At this age floral primordia already occur in the cotyledonary and three of the primary phyllomorphs. The arrangement and successive formation of primary phyllomorphs are represented schematically in fig. 7 D-H, each diagram corresponding to the plants in plate 8 A,c-f & B. Fig. 7B is a semi-diagrammatic drawing, with certain features deliberately exaggerated, depicting the relationship of vegetative bud to parent phyllomorph and the growing tip.

The diagrams clearly illustrate the fact that each phyllomorph, including the cotyledonary phyllomorph, possesses a vegetative bud which is normally situated well above the base, and usually on one or the other side of the median plane of the adaxial surface of the petiolode. Buds occurring in pairs are sometimes found on a single phyllomorph (fig. 7A, see also fig. 7 Ga & Gb). In its early ontogeny, a bud consists of only a single phyllomorph that is most frequently orientated at an obtuse angle to the parent phyllomorph.

Fig. 7 Ga & Gb represent two successive stages in the development of a single plant; they show the formation of the second phyllomorph in each of the two vegetative buds on the cotyledonary phyllomorph. In older plants, one or more buds may become active centres of growth (fig. 7H and plate 8B) and these may ultimately form lateral branches. The pattern of development of primary phyllomorphs is repeated in the secondary phyllomorphs of such buds.

The question naturally arises whether or not these buds are adventitious, a question reminiscent of the problem presented by *S. fanniniae*. This will be discussed later, but first, attention is directed to the formation of the "rhizome".

FORMATION OF THE RHIZOMATOUS STOCK. The pattern of seedling development conforms to the standard pattern for acaulescent *Streptocarpus*; the early ontogeny and cytohistological configuration of the apical and the groove meristem are closely similar to *S. gardenii* and *S. kentaniensis*.

During the organization of the embryonic apex into a rounded dome, and in some cases during the formation of the first primary phyllomorph primordium the mesocotyl undergoes marked unilateral distension (fig. 6G cf. fig. 6F).

The first primary phyllomorph primordium is initiated in the apical meristem 40–50 days after germination, becoming macroscopically visible at 2½–3 months. Its orientation with respect to the cotyledonary phyllomorph is variable. Subsequent primary phyllomorphs originate in regular succession in the apex, forming two alternate rows on a horizontal axis (fig. 7H and 7C). The cellular organisation of the apex is basically similar to that of *S. kentaniensis* (plate 8G).

The apical meristem is not strictly terminal, for it occupies a position adaxial to the distended base of the preceding phyllomorph (plate 8C). With the development of each successive phyllomorph, the meristem is thus carried forward (fig. 7C), resulting in the formation of the rhizomatous stock. Morphologically the stock is composed of a series of concrescent petiolode bases, sometimes noticeably separated by intervening regions that resemble "internodes", but as with the vertical axis of centric rosulates, the delimitation between petiolode base and axial tissue is problematical.

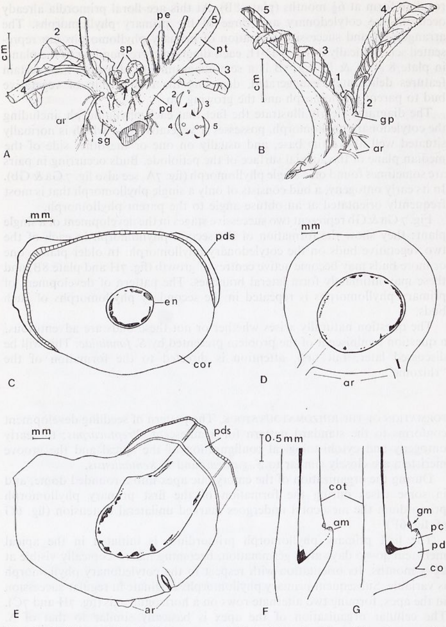

FIG. 6. Excentric rosulates. A, *S. cyaneus*, part of plant showing disposition of vegetative buds (each with a secondary phyllomorph) on petiolodes of primary phyllomorphs. Inset: diagrammatic representation: black caps—secondary phyllomorphs; white caps—primary phyllomorphs; open circles—peduncles. B, *S. johannis*, young branch axis and growing tip. C-G, *S. primulifolius*, camera lucida drawings: C, T.S. of rhizomatous stock (shading—corky layer); D, T.S. "internodal" region; E, T.S. of stock with gap in vascular cylinder; F,G, M.L.S. of apical meristems in c. 45-day old seedlings (solid black—vascular tissue). am, apical meristem; ar, roots; co, small cotyledon; cor, wide cortex; cot, macrocotyledon; en, endodermis; gm, groove meristem; gp, growing tip; pc, procambium; pd, petiolode; pds, petiolode scars; pe, peduncle; pt, petiole; sg, stomatal groups; sp, secondary phyllomorph.

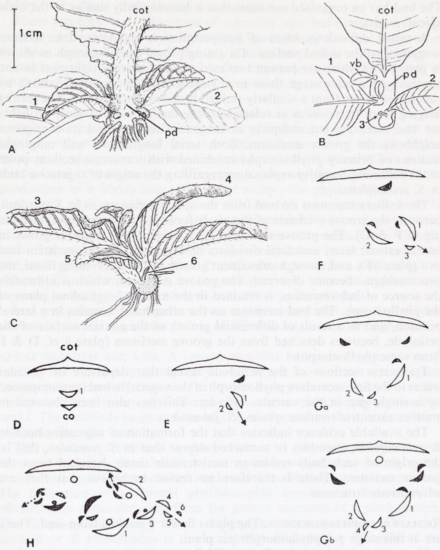

FIG. 7. *S. primulifolius*, excentric rosulate. A, part of a plant showing paired vegetative buds on macrocotyledon, viewed from rear. B, young plant (semidiagrammatic), illustrating relationship between vegetative buds, macrocotyledon and primary phyllomorphs (numbered in the order of formation). C, growing tip of plant depicted in Plate 8B (see also fig. 7H). Stippling in A and C denotes areas of stronger pigmentation. D-H, schematic representation of plants in Plates 8A, c-f and B. Note variations in orientation of several orders of phyllomorphs in relation to each other. Ga, Gb, represent two successive stages in the development of the same plant (cf Plate 8A, f).

Solid black caps, secondary phyllomorphs; white caps, primary phyllomorphs; striped caps, tertiary phyllomorphs; circles, floral primordia—arrows indicate the direction of growth; co, small cotyledon; cot, macrocotyledon; pd, petiolode; vb, vegetative bud.

ORIGIN OF VEGETATIVE BUDS. Plate 8D shows in longitudinal section a young vegetative bud in the process of forming the first secondary phyllomorph. The bud has an organised meristem that is histologically similar to the main apical meristem.

A rather difficult problem of interpretation is encountered in sections tangential to the dorsal surface of a young primary phyllomorph as shown in plate 8F in which are present two meristematic mounds right next to one another. At a later stage there is a more conical meristem separated by vacuolated tissue from a similarly stained broad smooth mound. The former judging from its position in relation to the lamina base, is most probably the bud meristem cut obliquely in tangential section, and its contiguous neighbour the groove meristem. Both serial longitudinal and tangential sections of primary phyllomorphs combined with transverse sections point to the following tentative explanation regarding the origin of vegetative buds in *S. primulifolius*.

The axillary meristem derived from the apical meristem, as in *S. gardenii*, becomes the groove meristem of the newly formed phyllomorph primordium (fig. 6 F & G). The groove meristem in *S. primulifolius* however grows in lateral extent; later, anticlinal divisions subdivide this broad meristem into two (plate 8F), and through subsequent growth of the intervening tissue, the two meristems become divorced. The groove meristem, which is ultimately the source of inflorescences, is retained in the median longitudinal plane of the phyllomorph. The bud meristem on the other hand, remains in a lateral position, and as a result of differential growth of the adaxial surface of the petiolode, becomes detached from the groove meristem (plate 8 cf. D & E from same phyllomorph).

Transverse sections of the petiolode reveal that departure of vascular traces to the first secondary phyllomorph of the vegetative bud is accompanied by a single gap in the vascular cylinder. This has also been observed in another excentric rosulate species, *S. johannis*.

The available evidence indicates that the formation of vegetative buds in *S. primulifolius* resembles to a marked degree that in *S. fanniniae*, that is, the origin of such buds resides in meristematic tissue detached from the groove meristem. There is therefore no reason to believe that they are adventitious structures.

FORMATION OF INFLORESCENCES. The plants flower 7 months from seed. There are at this stage 7–8 phyllomorphs per plant.

The groove meristem in *S. primulifolius*, as in *S. kentaniensis* and *S. gardenii*, is ultimately the source of inflorescences (plate 8 H & I).

DISCUSSION

Although it has been demonstrated that a greater diversity of growth patterns exist among rosulate species than previously recognised e.g. by Fritsch (1904), (for a general account of growth patterns in the subgenus *Streptocarpus* see Hilliard & Burtt, 1971, chapter 2), there occurs an underlying morphological unity in the vegetative architecture of the various patterns. The repetitive basic structural units comprising the rosettes of all the rosulate species examined have the following attributes in common:

continued growth of the lamina, production of inflorescences from the base of the midrib, formation of roots and vegetative buds on the petiolode, ability to shed part of the lamina by abscission.

These represent a combination of stem-like and leaf-like properties not normally encountered in ordinary foliage leaves, properties that do however fit those ascribed to a phyllomorph. Thus, the phyllomorph concept so valuable to the comprehension of the extraordinary morphology of *S. fanniniae* finds wider application in interpreting the vegetative organisation of rosulate species.

At the anatomical level, the meristematic organisation of the structural units is also consistent with a phyllomorphic theme. Each unit (as in the phyllomorph of *S. fanniniae*) has three intimately associated though distinct meristems—the groove, the basal and the petiolode meristem. Their characteristics and coordinated but differing roles already described result in the production of a highly integrated novel entity—the phyllomorph.

As each phyllomorph is supplied with its own root system, it is to be regarded as a semi-autonomous unit that is capable of independent existence, continued growth, and flowering if isolated from the parent plant. This has been demonstrated by Jong (1970) in *S. candidus*, and by Hollies (1959–60) and by Marston (1964, 1964–5) in *S.* x 'Constant Nymph', a rosulate hybrid cultivar. The rosulate habit in *Streptocarpus* may thus be appropriately regarded as an aggregation of unifoliate subunits (Burtt 1970).

In a more detailed comparison between rosulate forms and *S. fanniniae*, there arise several significant points of difference that require emphasis.

APICAL MERISTEM AND AXIS. A typical plumular bud is lacking in the early seedling but this is only a temporary deficiency. A more or less typical apical meristem is eventually organized from the embryonic meristem. From this meristem arise primary phyllomorphs either in a spiral sequence or in two ranks. The petiolode bases and the axial tissue formed by the apical meristem merge to form the axis.

This sequence of events is in sharp contrast to that in *S. fanniniae* where development of a plumular bud is completely suppressed, and a central meristematic apical dome of the kind found in rosulate species not organized. The formation of additional phyllomorphic members is dependent on meristematic zones detached from the groove meristem of a phyllomorph. The morphogenetic facility for developing an axis comparable to that of *S. gardenii* or *S. primulifolius* is not realised in *S. fanniniae*. The role of the main axis has been transferred instead to the cotyledonary petiolode.

A notable anatomical peculiarity of the main axis of rosulate species is the feeble development of vascular tissue. The limited radial expansion of the axis seems to occur largely through cell division and vacuolation of cortical tissue, including the endodermis.

GROOVE MERISTEM. As described earlier, the original groove meristem of the seedling of *S. gardenii*, *S. kentaniensis* and *S. primulifolius* resides temporarily only in the cotyledonary phyllomorph. It is later transformed into a dome-shaped more or less conventional apical meristem from which primary phyllomorphs develop. The cotyledonary phyllomorph, like the primary phyllomorphs, then acquires its own groove meristem of axillary origin.

Elevation of this meristem together with the basal meristem of the developing lamina above the axil is accomplished through intercalary growth.

The axillary nature of the groove meristem has also been demonstrated by Schenk (1942) in *S. rexii*. That the origin and later the shift in position of the groove meristem is now known need not detract from morphological novelty of the phyllomorph. It is not simply the displacement of a growth centre but constitutes also part of a developmental modification of a complex structure.

According to Schenk (1942) the "axillary product" in *S. rexii* is exclusively floral but this conclusion is not of general validity.

That the groove meristem is not initially committed to the formation of inflorescences has been clearly demonstrated in *S. fanniniae*. The inception of vegetative buds formed on the adaxial surface of a petiolode is traceable to the groove meristem (Jong 1970; Jong & Burtt 1975). In the case of rosulate species it is likely that the groove meristem is also a source of detached vegetative buds before its commitment to the production of inflorescences. The evidence for this is strongest in *S. primulifolius* and less so in *S. gardenii*. The situation in *S. kentaniensis* is uncertain.

Inflorescence primordia originate from the groove meristem in *S. fanniniae*, *S. grandis* (Jong 1970; Jong & Burtt 1975), in *S. rexii* (Schenk 1942), and in rosulate species examined in some detail, e.g. *S. kentaniensis*, *S. gardenii* and *S. primulifolius*. This appears to be a general feature of most acaulescent *Streptocarpus*.

PETIOLODE. The petiolode of individual phyllomorphs although resembling in external form a leaf petiole exhibits certain shoot characteristics: the production of buds on its adaxial surface; to a certain extent, its vascular structure; the formation of roots at its base; the formation of inflorescences from the groove meristem at its point of junction with the midrib.

Although in *S. fanniniae* there is little difficulty in homologising the cotyledonary petiolode (derived from mesocotyl) with the petiolodes of all subsequently formed phyllomorphs, the situation is more complicated in rosulate species.

Rosulates resemble caulescent forms of *Streptocarpus* and of certain other genera e.g. *Chirita* sect. *Michrochirita* and *Rhynchoglossum* (see also Hill 1938) in that the mesocotyl, if present, becomes incorporated as an integral part of the main axis of the plant, and in that epicotylar growth and organ formation results from the activity of an apical meristem of conventional organisation. Therefore the petiolode of an adult cotyledonary phyllomorph of a rosulate species is not a direct derivative of the mesocotyl; formation of the petiolode proceeds after the apical dome is organised.

There is at present no evidence to suggest that the petiolode (or mesocotyl) is a compound structure representing fusion of petiole and axial tissue. This of course does not necessarily deny the possibility that an organ now unitary in form may have been descended from predecessors that possessed it as separate elements. But not enough is known about the morphology of *Streptocarpus* and its allies to permit useful discussions along these lines.

Deliberations on the probable origin of the petiolode can hardly be considered in isolation of the phyllomorph as an integrated structural unit, and should encompass the problem of anisocotyly, the development of the mesocotyl, and the retardation or complete inhibition of plumule development. All these events occur separately or concomitantly to varying degrees in Old World members of the subfamily *Cyrtandroideae* in the Gesneriaceae, only a small fraction of which have been studied developmentally.

A more profitable approach has been to consider the problem in terms of ontogenetic processes, relating the development of form to centres of growth, their displacement and modification of activity. We have seen in *Streptocarpus* how intercalary meristems in combination with the groove meristem form a nexus of meristems new to the morphogenetic scheme of ordinary plants; their differing yet harmonious activity resulting in the production of the phyllomorph, a morphological novelty combining shoot and leaf characteristics. It is in terms of Sattler's (1974) new conception of the shoot, an intermediate organ.

BUD FORMATION. Both Goebel (1900) and Arber (1930) among others have drawn attention to the pitfalls of the indiscriminate use of the term "adventitious". Arber (1930) points out that just because botanists have labelled certain structures as "adventitious" they feel justified in dismissing them as of no morphological significance and this practice "is a typical example of the tyranny exercised by words over thought".

In their stimulating discussion on the interpretation of epiphylly, Dickinson & Sattler (1974) include a useful review of the various meanings attached to the term "adventitious". They point out that the term is used in either too wide a context with pejorative connotations or too restrictively. These authors suggest the abandonment of this term for ". . . it obscures the real organogenic potential of a tissue".

In morphogenetic studies however it is important to be able to discriminate between that which is and that which is not adventitious. An important element in this is a question of pattern recognition (see Burtt 1975); therefore by labelling a structure as adventitious before such recognition is achieved is indeed an obstacle to its elucidation.

Buds from which additional phyllomorphs or lateral rosettes develop occur as a regular feature in *S. fanniniae* and in certain rosulate species they appear at first sight to be adventitious, i.e., accidental or random events, especially if the organ on which they occur is regarded as an ordinary petiole. Such an interpretation has been found to be unhelpful, at least in those species in which a predictable and sequential pattern of bud ontogeny is consistently detectable.

What appear to be adventitious buds are occasionally found on certain phyllomorphs of *S. kentaniensis* grown under supplementary illumination but it is uncertain whether these buds are artefacts of cultivation.

Unusual distributional patterns of buds which are not of adventitious origin are now widely acknowledged and the inception, displacement and final disposition of such buds have in many instances been the subject of careful morphogenetic studies (summarized in Allsopp 1964; Cutter 1965; Wardlaw, 1952, 1965, 1968).

The unusual pattern of bud formation observed in rosulate species, in particular *S. primulifolius*, and as reported earlier for *S. fanniniae* is therefore not unique. The uniqueness lies however in their development into phyllomorphs or into lateral rosettes composed of phyllomorphs.

ROSETTE FORMATION. It is well known that members of the Gesneriaceae are easily propagated from cuttings taken from almost any vegetative part of the plant, and it is perhaps this property that misled Beuttel (1939–40), and Oehlkers (1940, 1962) into attributing rosette formation to regenerative processes, the leaves of the "rosette" arising adventitiously from the basal region of preceding leaves. These authors, including Hill (1938) and Fritsché (1946) also subscribed to the view that all acaulescent species of *Streptocarpus* lacked an apical meristem.

The present study and that of Schenk (1942) have however clearly demonstrated that their views cannot be sustained. For although plumule development in the seedlings of rosulate species is delayed, an apical meristem of more or less conventional structure is eventually organised. It is the activity of this meristem that leads to the formation of a rosette.

TAXONOMIC IMPLICATIONS. *S. rexii* and *S. gardenii*, two closely related and widespread species, the most familiar of rosulates known in cultivation since 1826 and 1855 respectively (Lawrence 1940; Hilliard & Burtt 1971), have been included in many early morphological and experimental studies (e.g. Pischinger 1902; Oehlkers 1940; Schenk 1942). Their differing method of rosette formation, however, have only recently been recognised (Jong 1970; Hilliard & Burtt 1971). Furthermore, although *S. rexii* has most frequently been offered as a representative of the rosulate species, its pattern of growth remained undefined until the publication of Schenk's detailed account.

The two different rosulate patterns can be readily distinguished in living plants. This in combination with variations within each pattern, notably in degree of development of the rhizomatous stock, and distinctive features of individual phyllomorphs, enhances the diagnostic value of habit. It is clear, however, that the two patterns cut across taxonomic boundaries, as the following example shows.

S. rexii, *S. parviflorus*, *S. cyaneus*, *S. primulifolius* and its subsp. *formosus*, and *S. gardenii* all form a natural taxonomic group (Hilliard & Burtt 1971). All except *S. gardenii* conform to the excentric pattern, *S. gardenii* having a centric pattern. However, the excentric pattern provides a unity in vegetative structure to the other four species that constitute the *Streptocarpus rexii* aggregate.

CONCLUSIONS

The present study directs attention to the unusual vegetative structure of rosulate species of *Streptocarpus* which do not conform to the standard pattern of stem, leaf and axillary shoot of classical morphology. Departures from this classical pattern appear to be many and complex in *Streptocarpus* as well as in some other genera of the Old World Gesneriaceae. There exists, nevertheless, a central theme of organization in all the species studied from the subgenus *Streptocarpus* which is common to a wide range of growth patterns: the phyllomorphic constitution of the plant body. Variations on this theme can range from the unifoliate condition of *S. grandis* to the much more complex pattern of *S. fanniniae*. The distinction between stem and leaf presenting no less difficulty in the one than the other.

Thus, in addition to the inherent interest of the vegetative architecture of the rosulate forms considered here and of other growth forms of the subgenus *Streptocarpus*, the variety of unorthodoxy exhibited allows a deeper appreciation of the morphogenetic potential of plants. It also appeals for a more flexible approach to morphological interpretations (e.g. Sattler 1966, 1974; Jong & Burtt 1975). Such an approach, as Sattler (1974) points out, is not a denial of the value of classical morphological categories; it does require rather a readiness to accept innovative morphological modifications where they occur (Jong & Burtt 1975).

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