Inflorescences of *Cliffortia* L. (Rosaceae) and related vegetative branching patterns

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ABSTRACT

The inflorescence construction of eight species, representative of the types found in the 119 species of the rosaceous genus *Cliffortia* L. is described, based on stereo microscopic examination of fresh and dried specimens, combined with extensive field observations. In its simplest form the inflorescence is a reduced short shoot, bearing a lateral ebracteate flower and a potentially viable apical bud. Variations in the basic structure can be in the number of flowers, the mix of the sexes of the flowers and the number and type of short shoots as primary, secondary and tertiary axes. A high incidence of structural plasticity of the inflorescence occurs. This can be either throughout the development of the inflorescence or only at the onset of the vegetative stage. These changes occur in the short shoot(s) constituting the axes of the inflorescence, causing either an increase in the length of the internodes, apical proliferation of the axes or a combination of these two effects. A specific combination of changes is linked to a specific inflorescence type. The vegetative elements of the inflorescence thus modified, are retained as an integral part of the vegetative branching system, with extensive influence on the branching pattern. This can also result in the predominance of one sex over the other over time, so that an individual, initially of the one sex, can become one of the opposite sex by the end of the season. Erroneous interpretation of a single point in the process of sex change as if it is a permanent state of sexuality, led to the prevalent acceptance of dioecy as the norm for the genus. Monoecy with dichogamy (or herkogamy at inflorescence level) was observed in this genus, as in many other wind-pollinated taxa.

CONTENTS

INTRODUCTION

Cliffortia L. includes 119 species of woody evergreen plants. The genus was last revised by Weimarck in 1934, and most of the publications since then have dealt with the description of occasional new species (Weimarck 1940, 1946, 1953, 1959; Oliver & Fellingham 1991, 1994; Fellingham 1993a, b, 1994, 1995), or developed the taxonomy to incorporate new species (Weimarck 1946, 1948). Koutnik (1987) listed the genus as being the largest genus of wind-pollinated plants in the Cape flora, but added the comment that many of these species might be apomictic. This has not yet been corroborated. Oliver & Fellingham (1994), in a detailed discussion of the inflorescence construction and phenology of section *Arborea* in *Cliffortia* hinted at the biological and morphological complexity found in the genus.

Cliffortia is a typical member of the temperate Cape Flora, and with ± 114 species in the southwestern tip of South Africa (Fellingham 2000). It is one of the 13 genera in the remarkably rich Cape Floral Region (CFR) with more than 100 species (Goldblatt & Manning, 2000). Although the genus is found from sea level to the highest mountain summits in the CFR, further north it is restricted to high altitude areas. At least eight species are found in the Drakensberg of Lesotho and KwaZulu-Natal (Jacot Guillarmod 1971; Hilliard & Burtt 1987). Only three species occur in Zimbabwe and Malawi (Mendes 1978), one of which reaches north to the East African highlands (Graham 1960).

Cliffortia is usually included in section *Sanguisorbeae*, on account of the reduced carpel numbers, predominantly uni-ovulate ovaries and missing petals (Melchior 1964; Takhtajan 1997). The entire section including *Cliffortia* is wind pollinated and has, therefore, unisexual and obscure flowers with stigmas or stamens as their most prominent parts, and the flowers are often variously aggregated into dense spikes or heads. Eriksson *et al.* (1998) found the elements of the section *Sanguisorbae* to have strong links with each other and not simply an artifact of convergent evolution. A phylogenetic analysis of this section, based on ITS sequence data (Helfgott *et al.* 2000), indicated that some species of a paraphyletic genus, *Sanguisorba* (a northern hemisphere genus), are the closest relatives of *Cliffortia*. These in turn are related to *Acaena* and *Polylepis*, both, like *Cliffortia*, southern genera. The other African wind-pol-

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linated genera, *Hagenia* and *Leucosidea*, are sisters to each other, but are rather more distantly related to *Cliffortia*. Furthermore, they differ morphologically by the presence of petals. Morphological data are thus consistent with the classifications proposed by Melchior (1964) and Takhtajan (1997).

Cliffortia is remarkably uniform in flower structure, but diverse in leaf morphology. *Aspalathus* (Fabaceae) and *Anthospermum* (Rubiaceae) exhibit morphological convergence in vegetative parts with *Cliffortia*. Nineteen species of *Aspalathus* are indistinguishable in the sterile state from as many species of *Cliffortia*, except for the absence of leaf sheaths and stipules (Dahlgren 1971). Several species of *Anthospermum*, sharing habitats with *Cliffortia* species, are indistinguishable from these species, but for their opposite leaves. The similarity extends beyond the presence of leaf sheaths and stipules to include flower morphology, both having small unisexual flowers, prominent calyx lobes and remarkably similar fruits.

To date, the inflorescences of *Cliffortia* have received scant attention. Weimarck's (1934) rather superficial descriptions of the inflorescences indicate that he misunderstood the basic construction of the inflorescences (not difficult, if working with limited material, especially if most of it is herbarium material, which has to be treated with great care). This lack of understanding of the inflorescence construction affected the interpretation of the patterns of sexuality in *Cliffortia*. Often only overtly male or overtly female plants are found in any population at any specific time, leading to suggestions that at least some of the species may be apomictic (Koutnik 1987), and the general impression that most species are dioecious. Weimarck (1934) noted that 'the distribution of male and female flowers has been shown to be very irregular so that, as far as is known, not less than 47 species out of 78 have been found at least capable of being monoecious'. Nevertheless, he still held the notion of dioecy as the rule for the genus.

These findings established the existence of a wide range of inflorescence types in *Cliffortia*, varying from solitary flowers to fascicled flowers and highly condensed cones containing large numbers of flowers. In this paper we wish to address several questions: (a) is there a common basic construction discernable in the different inflorescences of *Cliffortia*; (b) can these common units be used to compare different types of inflorescence construction; (c) how can this account for the apparent dioecy in the genus; and (d) how does the inflorescence type influence the branching pattern?

Terminology

The terminology we use is largely derived from Weberling (1983, 1989). Inflorescences refer to 'the shoot system which serves for the formation of flowers and which is modified accordingly' (Troll in Weberling 1989). On a single plant or branch system, separate inflorescences are separated by sets of vegetative branches. Short shoots [brachyblasts in Weimarck (1934)] are defined here by their short internodes. A short shoot is not, however, always a permanent element of the plant morphology but can disappear through abortion, or trans-

formation into a long shoot. Neither is it always a patently visible structure but can be completely and permanently hidden in the axil of its subtending leaf. The matrix for the flower-bearing short shoots is the long shoot, which is a vegetative shoot with long internodes. Ordinary vegetative leaves on the long shoots subtend these fertile short shoots. The main involvement of the short shoot is with flower bearing, with the flowers either bracteate or ebracteate but never subtended by ordinary vegetative leaves. Vegetative short shoots do occur, but only rarely and then they bear ordinary vegetative leaves, as long shoots do. A short shoot is thus a permanent or temporary, patent or obscure shoot with short internodes, has the main function of flower bearing and occurs in the axil of a vegetative leaf on a long shoot, or rarely on a vegetative short shoot. Such short shoots are then equivalent to 'florescences'. A group of florescences aggregated on a vegetative short or long shoot would constitute a 'synflorescence'. Where several florescences are adjacent, they form double racemes or a diplobotryum.

The inhibition zone lies directly below the inflorescence where the formation of florescences is inhibited, and which is therefore sterile. Axillary buds in the inhibition zone need to have at least the potential to make florescences, but are prevented from doing so by the actual inflorescence. By contrast the proliferation zone is above the synflorescence, and occurs where the florescence apex grows out and returns to vegetative growth (Weberling 1989).

Vegetative leaves are usually borne on long shoots, and never subtend flowers. Since floral bracts are recognized as being different from vegetative leaves, the correct identification of these is important. Floral bracts are defined as subtending flowers, but the loss of true bracts may lead to the first leaf below a flower being vegetative, thus making the application of the definition potentially misleading. It therefore seems more practical (though not typologically correct) to recognize bracts as being morphologically different from vegetative leaves. This identification is important, as florescences are defined as being subtended by vegetative leaves (rarely modified), and as containing floral bracts.

In spite of the fact that Weberling's (1989) new terminology had been used to describe the inflorescence in *C. conifera* (Oliver & Fellingham 1994), we have been reluctant to use it in this paper. His definition of a raceme or botrys (botryum?) as having 'clearly developed internodes' and 'stalked flowers', seems to preclude its application to the short shoot inflorescence typical in the genus *Cliffortia*. It would appear that Weberling's earlier (1983) definition of long shoots and short shoots in terms of their respective function is more appropriate to the subject of this paper.

MATERIALS AND METHODS

Observations on inflorescence structure were based on both fresh and dried specimens, and where possible, collections of fresh material were made repeatedly from the same populations, over a season or more. Fertile branches were dissected, examined and sketched with the aid of a stereo microscope fitted with a camera luci-

da. The dried material was softened, by boiling and soaking in diluted dishwashing solution before dissection. The majority of drawings were done using the camera lucida, but larger, fresh specimens were drawn free-hand.

Species were selected to reflect the diversity of inflorescence structure in the genus. The most specialized are the three cone-bearing species, *C. conifera, C. dichotoma* and *C. arborea*. A highly condensed inflorescence, though with an amazing plasticity, is found in *C. odorata*, which, furthermore, appears to have no short shoots. In *C. heterophylla* the inflorescence is clearly demarcated and initially condensed but extremely plastic and impermanent. The multiflowered form of the short shoot inflorescence, with bracteate flowers, is represented by *C. ruscifolia*. The apparent lack of short shoots (and flowers) in *C. crenata*, makes it an interesting and important subject. *C. nivenioides* is an exceptional and therefore very interesting species for two reasons. It has a preponderance of short shoots, the majority of which are vegetative and the rarer fertile ones appear to bear single flowers directly in the axils of ordinary vegetative leaves.

RESULTS

1. *Cliffortia nivenioides* Fellingham

This species is known from the type locality only: a very discrete locality on an open sunny marsh at an altitude of almost 2 000 m, north of Blesberg in the Swartberg Mountains. The general appearance of this small shrub is that of a compact bunch of long branches emerging from a central point. These long branches are themselves sparsely branched to totally unbranched. The leaves are arranged imbricately on short shoots to form flat, slightly elongated fans. The combined effect is that of a species of the genus *Nivenia* Vent. (Iridaceae) (Figure 1A), hence the derivation of the specific epithet.

Flowers occur on the apical short shoots only, or rarely also on one or two lateral short shoots just below the apex. Each flower appears to be subtended by an ordinary vegetative leaf. These subtending leaves are bilaterally flattened and closely arranged on the short shoots, with the leaf sheaths imbricate, completely obscuring the internodes of the short shoot (Figure 1A, C). As these subtending leaves are not modified in any way, they are not bracts. The male flowers occur together with the female flowers on the same short shoots, but in the lower, and therefore older leaf axils. The young female flowers are borne singly and totally hidden in the axils of the leaves, and fertile plants can easily be mistaken as sterile. Being more mature, and having larger calyx lobes and protruding stamens, the male flowers are more readily visible than the totally hidden, immature female flowers (Figure 1A, C). This difference in developmental stages between male and female flowers excludes the possibility of self-fertilization.

The fertile short shoot in the axil of a vegetative leaf, on a long shoot, appears to be the inflorescence (Figures 1A; 2A: i1). The presence of vegetative leaves on the short shoot, however, indicates that it is a vegetative shoot. This is confirmed by the lengthening, in ascending order, of the hitherto very short internodes of the short shoot with imbricate leaves, changing it into a long shoot with distant leaves at the time of fruiting. This change clearly reveals the true nature of this short shoot as equivalent to the vegetative long shoots supporting the inflorescences encountered in other species (Figures 1B; 2B).

At the end of the flowering season the male flowers and the fruits are shed and the vegetative stage (Figure 2C) is entered. This is marked by two events. The apical bud of the newly formed vegetative long shoot forms a new apical short shoot (na) and new lateral short shoots (nl) develop in the axils of the leaves which subtended the past season's flowers. Thus longitudinal growth occurred on the main
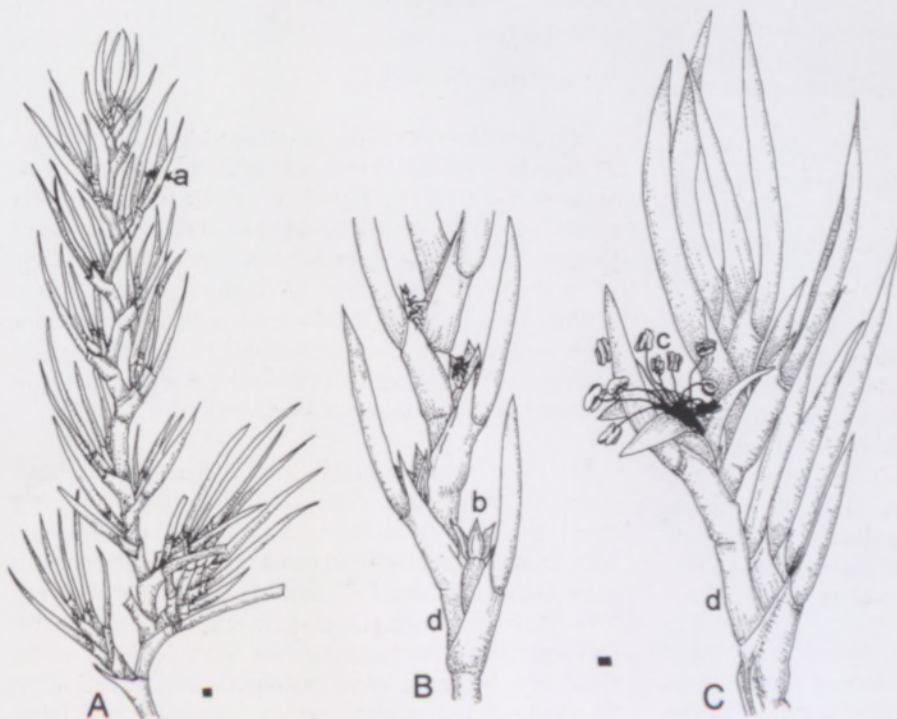

FIGURE 1.—*Cliffortia nivenioides, Viviers & Vlok 470* (BM, K, MO, NBG, P, PRE). A, long shoot bearing short shoots with female flowers in axils of leaves; B, fruit-bearing long shoot, developed out of short shoot; C, short shoot with lower node elongated and lower leaf axil bearing male flower. a, female flower; b, fruit; c, male flower; d, visible internodes. All copied from Inge Oliver's drawings. Scale bar: 1 mm.
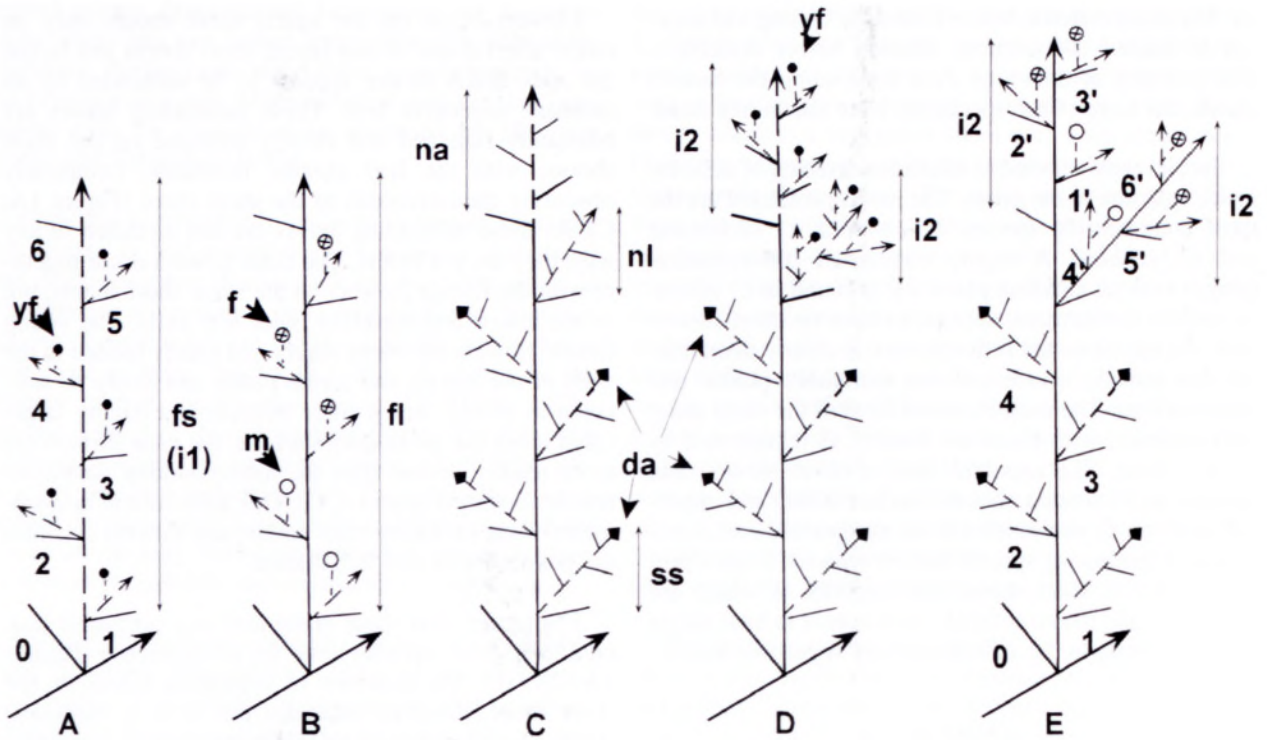
FIGURE 2.—*Cliffortia nivenioides*: longitudinal diagrams of inflorescence and branch development, covering two fertile seasons spanning a vegetative season. A, young fertile short shoot season with young single-flowered inflorescences; B, same as A, matured: a long shoot with mature flowers; C, same as B, vegetative stage: new short shoots developed out of remaining inflorescence; D, same as C, second season: the apical and one lateral short shoot bearing flowers; E, same as D, matured: apical and one lateral long shoot (lateral long shoot to become vegetative branch). O, subtending leaf on main branch; 1–6, subtending leaves of first season's inflorescence; 1'–6', subtending leaves of second season's inflorescences; da, dormant apical buds; f, female flower; fl, flowering long shoot; fs, fertile short shoot; i1, fertile short shoot in A becoming long shoot in B; i2, fertile short shoot in D becoming long shoot in E; m, male flower; na, new apical short shoot; nl, new lateral short shoot; ss, sterile short shoot; yf, young flower. Broken lines: expanded axes of short shoots.

stem and a new branch is formed. The short shoots thus formed, appear to replace the single flowers of the recent flowering season, but are in fact, proliferation shoots of minute, single-flowered inflorescences each with an ebracteate flower. Most of these newly formed, short shoots remain vegetative and do not undergo any further vegetative growth. Their apical buds have become dormant. Only a small number near the apex of the plant develop further, viz. the new apical short shoot (na) and the uppermost new lateral short shoot (nl) and become the new flowering short shoots of the second flowering season (Figure 2D: i2). Their imbricate leaves become the subtending leaves for the new single-flowered inflorescences (Figure 2C–E). As in the previous fertile stage (Figure 2A: fs (i1), B: fl), these fertile short shoot(s) change from short shoots with imbricate leaves, into long shoots with distant leaves as they mature (Figure 2D: i2, E: i2).

The number and positions of the long shoots thus formed, are determined by the number and positions of the short shoots involved in flower bearing. With only the apical short shoot and one lateral involved, the result will be one apical long shoot and one side branch (lateral long shoot) (Figure 2D, E). As before, the next stage of development is the shedding of the flowers leaving the new long shoots with their now no longer imbricate leaves (1'–6), ready to subtend a new generation of short shoots, some of which are destined to become future branches.

Branching occurs only where lateral long shoots develop. The sparse vegetative branching pattern in this species, is thus directly linked to the structure of the fer-

tile shoot (synflorescence) of the previous fertile season, limiting the development of long shoots. Where only the new apical short shoot (na) develops into the new fertile shoot (i2), no side branch will develop, so that solely longitudinal growth takes place. It is only when one (or more) of the lateral short shoots (nl) are also flower bearing, that one (or more) lateral long shoots develop and branching occurs (Figure 2D, E).

2. *Cliffortia crenata* L.f.

This species occurs on mountain slopes and plateaux at altitudes ranging from 1 300 m in the northern, drier areas of the CFR, to 300 m in the Montagu area. The plants appear to be totally without short shoots, being virgate, lanky shrubs up to 2 m tall, very sparsely branched in the upper parts only. At no time are any flowers visible. The two large leaflets are attached to the stem at an acute angle, completely enveloping it, so that, in order to examine the leaf axils for flowers, at least one of the leaflets has to be folded back or removed.

An immature (primordial) inflorescence (Figures 3G; 4A) consists of a pair of immature flowers, one slightly above the other, attached to a swollen basal structure, with an apical bud between the two flowers. The flowers are subtended by small but unmistakably leafy elements. The size of the immature flowers relative to that of the inflorescence axis, facilitates the interpretation of the structures. It is quite clear that the flowers are borne on the swollen basal structure and not adjacent to it. In terms

FIGURE 3.—*Cliffortia crenata*, *Oliver 10387* (NBG). A, portion of main branch with condensed inflorescence; B, proliferating inflorescence (branchlet from axil of a vegetative leaf), bearing one male flower and three fruits; C–E, subtending leaves, in ascending order, on branchlet B; F, apical growth point from axil of fourth leaf on branchlet B; G, primordial inflorescence (short shoot from axil of vegetative leaf near apex of a main branch), showing a basal contracted axis bearing two lateral flowers and a central apical growth point. Scale bars: 1 mm.

of the elements of a simple inflorescence consisting of a short shoot, the swollen basal structure is the inflorescence axis bearing two lateral, alternate flowers with the apical portion of the axis continuing beyond. In an inflorescence, condensed to such a degree as this, the subtending leafy elements can be expected to be bracts rather than vegetative leaves.

A primordial inflorescence can develop into one of two types of mature inflorescences: a condensed type or a proliferating type. The condensed type contains a single flower or a cluster of mature flowers, on a much condensed inflorescence axis without any apical proliferation. In a typical instance, three flowers, each laterally in the axil of a bract, are found in a cluster: the two lower female and upper male. These three mature flowers obscure the inflorescence axis and its ancillary vegetative parts viz. leaves or bracts. The two female flowers are much more advanced in development than the male. The one female is a fully developed fruit without calyx lobes, whereas the other is a younger fruit with the calyx still in place. The male flower is still in the bud stage and therefore, much younger than the female flowers (Figures 3A; 4B). In this type of inflorescence there is evidence of the presence of an apical bud but no proliferation takes place. The diminutive size of the subtending leaves suggests that these would not develop into vegetative leaves but rather into bracts, subtending flowers of both sexes.

The proliferating type of mature inflorescence presents not only clusters of fruit and flowers in a more open arrangement than those in the condensed type, but has a viable apical bud which proliferates into a young vegetative shoot, which eventually develops into a branch. The structure that originates in the leaf axil is the shoot and the flowers are borne laterally on the basal part of the shoot and not directly in the axil (Figures 3B; 4C). The lower two flowers are female and close to each other, with their small imbricate subtending modified leaves completely covering the very short internodes. The next slightly more distant flower is female and followed by younger male flower(s). The internodes separating the flowers become increasingly longer upward, but remain much shorter than those higher up on the vegetative part of the shoot (Figure 3B). The leaves subtending the basal female elements (fruits and/or flowers), show progressive development from the base upwards. The lowest are merely scale-like structures, consisting mainly of a narrow sheath without any stipules and with only the vestige of a blade attached directly to the sheath, without articulation (Figure 3C). Above these are leaves in progressive stages of development from very small and bract-like with just the indication of stipules and a single articulating leaf blade (Figure 3D), to almost normal, small vegetative leaves with two leaflets (Figure 3E). These small leaves subtend the male flower in Figure 3B. Above the male flowers, the shoot becomes a normal long shoot with vegetative leaves. In occasional leaf axils near the apices of these vegetative shoots, small buds which could develop into secondary primordial inflorescences, are found (Figures 3F; 4C: pi).

The proliferating inflorescence consists of a basal flower-bearing short shoot (ssh) in which the apical bud proliferates into a distal long shoot (lsh) which will lengthen to extend beyond the subtending leaf on the main stem to form the new branch (Figure 4C). This type of inflorescence occurs less frequently than the contracted type and usually near the apices of the branches. These then, are the only inflorescences that give rise to vegetative branches, as the formation of branches depends entirely on the occurrence of inflorescences with subsequent distal long shoot development. The sparseness of the branching pattern, resulting in the virgate growth form of this species, can thus be directly related to the small number of inflorescences that undergo the full range of changes. The positions of the branches are determined by the position of the proliferating inflorescences which is usually near the apices of existing branches.
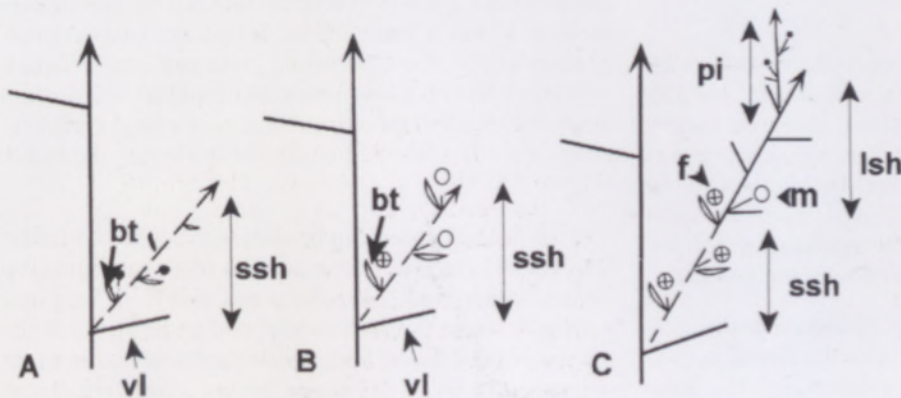

FIGURE 4.—*Cliffortia crenata*: longitudinal diagrams of inflorescences. A, primordial, with immature flowers; B, mature contracted, with mature male and female flowers; C, proliferating, with mature male and female flowers, apical proliferating branch/long shoot (lsh) with secondary primordial inflorescence (pi). bt, bract; f, female flower; m, male flower; ssh, short shoot; vl, vegetative leaf. Broken lines: expanded axes of short shoots.

FIGURE 5.—*Cliffortia ruscifolia.* A, well-developed inflorescence exhibiting male and female flowers subtended by tridentate bracts, overtopped by proliferating shoot with linear vegetative leaves; B, C, vegetative leaves from just below inflorescence in A, each successively shorter and broader than the one below; D–F, bracts subtending flowers in inflorescence A; G–K, leaves of proliferation zone in A; L, growth point of proliferating shoot; M, inflorescence with male and female flowers subtended by tridentate bracts and vegetative leaves below inflorescence, shed to form inhibition zone (i); N, rare single-flowered inflorescence (one fruit) subtended by a shortened vegetative leaf (no bract); i, inhibition zone; j, proliferation zone. A–L, *Oliver 10567* (NBG); M, *Oliver 10569* (NBG); N, *Oliver 10574* (NBG). Scale bars: 1 mm.

3. *Cliffortia ruscifolia* L.

This is a widespread and probably the most familiar species of *Cliffortia*, occurring in well-drained habitats over a wide range of altitudes. It occurs in a great variety of vegetative forms from low, sparse, sprawling plants with yellowish green leaves, to erect bushy plants up to 1.5 m tall and with grey-green leaves, from the same locality. The size and shape of the vegetative leaves are also very variable but always unifoliolate and pungent.

The inflorescence is generally bracteose and multi-flowered, rarely single-flowered with the flower apparently subtended by an ordinary vegetative leaf. The latter type could be mistaken for the immature form of the inflorescence if it was not for the fact that the female element in it was a mature fruit. In essence, the inflorescence is a short shoot, occurring in the axil of an ordinary vegetative leaf on a long shoot. Male and female flowers are borne singly in the axils of bracts, in a single inflorescence, usually with the female flowers below the males (Figure 5A, M).

Two distinct zones can be distinguished in the fertile short shoot. The lower zone consists of ± five vegetative leaves, which graduate in form and size from long and narrow (lowest) to much shorter and wider in the highest. All of these leaves are typical vegetative leaves, plain with slightly hairy edges and nerves and sharp apical spinelets. With the leaves diminishing in length upwards,
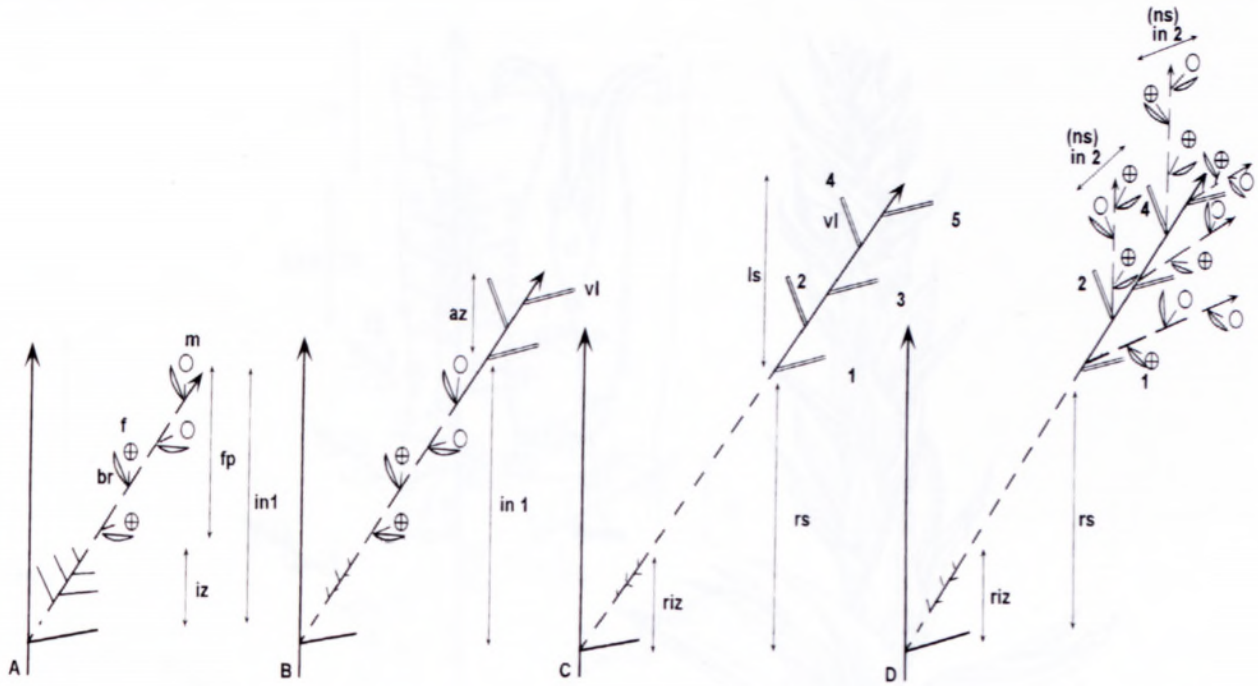
FIGURE 6.—*Cliffortia ruscifolia*: longitudinal diagrams of inflorescence development and related branches. A, young inflorescence in axil of vegetative leaf on long shoot; B, mature inflorescence with proliferation of apical bud; C, vegetative stage: new branch consisting of remains of the short shoot (rs) plus new long shoot (ls); D, new inflorescences in axils of vegetative leaves on long shoot, constituting potential new branches developing as illustrated in B and C. az, apical proliferation zone; br, bract; f, female flower; fp, fertile part of short shoot; in1, inflorescence of first season; in2, inflorescences of second season; iz, inhibition zone; ls, long shoot; m, male flower; ns, new short shoot; riz, remains of inhibition zone; rs, remains of short shoot; vl, vegetative leaf; 1–5, vegetative leaves on long shoot becoming subtending leaves for inflorescences of second season. Broken lines: expanded axes of short shoots.

this zone seems to fit the description for Troll's 'field of inhibition' (Weberling 1989). For such a small area of inhibition as is encountered here, the term inhibition zone seems appropriate. As seen in Figure 5M, the leaves of this area are shed to reveal the fertile part of the inflorescence, a zone of imbricate bracts, each subtending a flower. The bracts are much shorter and more hairy than the leaves of the inhibition zone, and dentate to trilobate. In some instances the apical bracts are immature. All multi-flowered inflorescences contain male and female flowers in equal proportions (Figures 5A–F, M; 6A).

The apical buds of the mature inflorescence proliferate to form comas of young vegetative leaves, some with minute buds in their axils, on a developing long shoot. The appearance of this vegetative long shoot marks the onset of the new vegetative stage. This phenomenon can be defined in terms of Weberling's (1989) concept of 'late proliferation', except that he sets the prerequisite of a frondose inflorescence for the use of this term. It does otherwise fit the requirement of marking the return of the 'inflorescence apex to the vegetative condition'. In spite of the bracteose character of the inflorescence, we propose the use of the term proliferation zone for the early stage of development of the long shoot (Figures 5A, G-K; 6B: az, 6C: ls).

With the appearance of the proliferation zone the vegetative stage is entered. At the same time, or in some instances, before this event, the leaves of the inhibition zone are shed, followed by the shedding of the flowers and their subtending bracts (Figures 5N; 6B, C). The short shoots are thus left bare with the short internodes (which do not elongate) permanently visible. The prolif-

eration zones are thus the entire source of vegetative growth. These then develop into long shoots with proximal zones of bare short internodes, as the only indications of the sites of the old inflorescences. Though these zones are a permanent feature of the basal (proximal) portions of all branches thus derived, they do not contribute any further to their development (Figure 6B–D). As the fertile stage is characterized by the development of short shoots, the vegetative stage is characterized by the development of long shoots proliferating out of the short shoots (Figure 6B, C). Potentially every short shoot could develop into a vegetative branch. Furthermore, all the leaves on a long shoot could become subtending leaves for the next fertile season's short shoots (Figure 6D). However, usually only a limited number of leaves develop short shoots in their axils. Of these short shoots only a limited number give rise to long shoots.

4. *Cliffortia heterophylla* Weim.

This species is locally common in sunny situations near streams in the Betty's Bay area. In the vegetative stage, the plants have the general appearance of saplings up to 3 m tall, with willow-like leaves and some secondary thickening of the main stems. In spring a single conspicuous cylindrical inflorescence develops on the apex of the main stem (Figure 7A). Plants under stress, as those from which the apical inflorescences have been removed or those having their main stems constricted by twiners, may develop multiple lateral inflorescences.

Inflorescences are initially female, then progress through a bisexual phase to the male stage. Only minimal traces of the fertile stage, in the form of amplexicaul

FIGURE 7.—*Cliffortia heterophyl-la, Fellingham 1640* (NBG). A, female inflorescence on apex of main stem; B, female flower in situ on node (bracts removed); a, bracteoles; b, calyx lobes; h, internode. Scale bar: 1 mm.

sheaths around the main axis of the plant, are left in the vegetative stage, after the shedding of the fugacious bracts (Figure 8: rb). With the secondary thickening of the main stem, these sheaths also disappear as they are stretched and broken.

In the bisexual phase, the inflorescence demonstrates all the different developmental stages in the form of recognizable zones, which are dealt with here in the chronological order of development, viz. female zone, male zone and the two vegetative zones: the inhibition zone and the proliferation zone. The longitudinal diagram (Figure 8) depicts all of these zones as one entity. It is, however, rare to find specimens showing all the stages: usually the proliferation of the apical bud takes place only after the shedding of all sexual elements.

The cylindrical, apical inflorescence is in essence a short shoot up to 240 mm long, the uppermost internodes about 1 mm long, gradually increasing in length to about 7 mm basally. All internodes of the short shoot are totally obscured by the lanceolate-acuminate bracts, which are up to 60×15 mm. In the apical part of the inflorescences, the female flowers occur singly on very short asymmetrical structures (Figure 7B). In the older (lower) part of the inflorescence, up to six female flowers are borne on lateral short shoots, totally hidden by the imbricate bracts. (Figure 8: ls). The flowers are lateral on these short shoots, and subtended by leafy elements that are much smaller than, and different in shape to the normal vegetative leaves, and therefore, bracts (bt). The short asymmetrical structures bearing the single flowers higher up on the same inflorescence, can thus be interpreted as primordial short shoots. Such a short shoot has a fully viable apical bud while only the lowest node is mature enough to sustain a fully developed flower, without the bract being in evidence yet. Already at this stage, the inflorescence can be described as a diplobotryum or double raceme, with a central short shoot bearing lateral short shoots in the axils of its bracts; the lateral short shoots bearing (female) flowers in the axils of their bracts.

Two events mark the onset of the development of the male zone. The hitherto short internodes of the apical
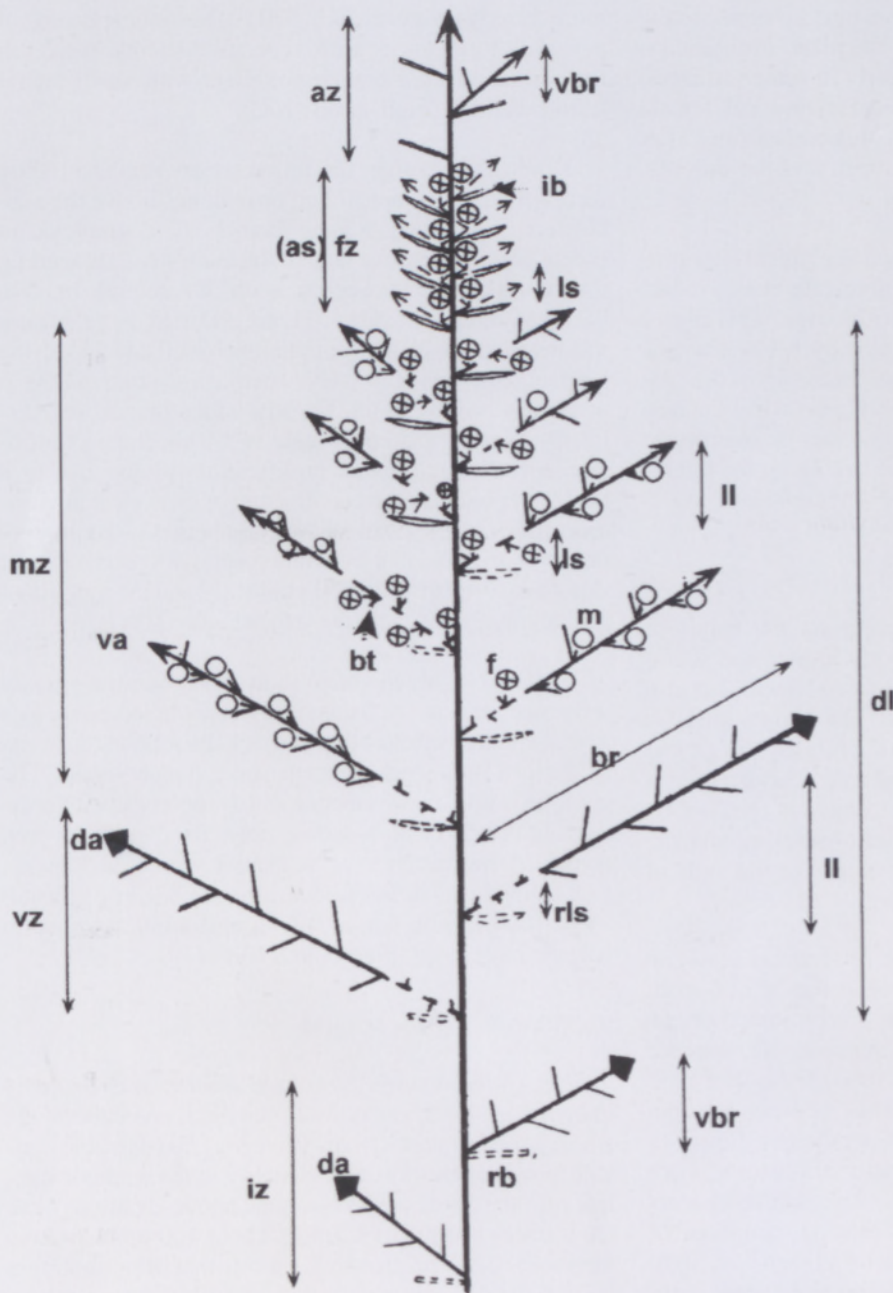
FIGURE 8.—*Cliffortia heterophylla*: longitudinal diagram of inflorescence. as, apical short shoot; az, apical zone; br, branch; bt, bract; da, dormant apical bud; dl, developing main axis long shoot; f, female flower; fz, female zone; ib, imbricate bract; iz, inhibition zone; ll, lateral long shoot; ls, lateral short shoot; m, male single-flowered inflorescence; mz, male zone; rb, remains of imbricate bract; rls, remains of lateral short shoot; va, viable apical bud; vbr, vegetative branch; vz, vegetative zone. Broken lines: expanded axes of short shoots.

short shoot of the main stem start lengthening, the lower ones first and then the others in sequence upwards. The result is the separation of the previously imbricate bracts to reveal the internodes, thus changing the short shoot into a long shoot (Figure 8: mz). At the same time, the apical buds on all lateral short shoots (ls) give rise to long shoots (ll), in sequence from below upwards. These lateral long shoots lengthen and male flowers (m) develop on their distal parts, whereas the female flowers (f) on the proximal part, (short shoot), mature into fruits before dropping off, starting with the lowest, then involving those higher up, again in ascending order (Figure 8: mz).

The formation of the vegetative zone is initiated by the shedding of the male flowers as well as any fruits that might still be present. This leaves the remains of the lateral short shoot (rls) in the form of a region of short internodes, interspersed with ridged nodes, on the proximal part of the branch (br). This is accompanied by the loss of the bracts (ib) on the main stem, leaving their remains (b) in the form of the leaf sheaths which are

eventually destroyed by secondary thickening of the main stem. Thus the vegetative zone (vz) comes into being, and develops upwards as the fruit and flowers mature and are shed. With the shedding of the last flower, the vegetative zone spreads to envelop the whole of the inflorescence, reducing it to a framework of newly formed vegetative branches on an apical extention of the original main stem. With this, the vegetative stage has been entered (Figure 8: vz).

The vegetative stage is completed by the development of the apical proliferation zone (az). This is achieved by the proliferation of the apical bud of the main inflorescence axil, which is just a highly condensed portion of the main stem, giving rise to an apical long shoot with vegetative leaves. In the axils of the vegetative leaves of this zone, purely vegetative branches (vbr) develop. These consist of long shoots only, without any remains of lateral short shoots on them as in the case of the branches originating in the inflorescence and are shorter than the side branches originating in the inflorescence (Figure

8: az). The apical proliferation zone thus gives rise to the only purely vegetative growth of the plant. Proliferation of the apical bud can take place early in some instances, producing a coma above the apical cylindrical female zone (Figure 8: az, fz). Normally this occurs only after the vegetative zone is fully developed and the inflorescence has disappeared completely.

The vegetative stage ends when the apical bud produces the new apical cylinder of imbricate bracts, marking the onset of the following fertile stage. This places the old apical proliferation zone directly below the new inflorescence. The youngest (apical) branches of the proliferation zone, will still be relatively short when the new inflorescence starts developing. This can be interpreted as the old apical proliferation zone becoming the inhibition zone of the new inflorescence (Figure 8: iz).

5. *Cliffortia odorata* L.f.

Dense mats of this species occur on the banks of rivers and dams in the southwestern, southern and southeastern coastal districts, usually at low altitudes but also up to 1 000 m on Table Mountain. The upright shrub is up to 2 m tall with the main stems slightly zig-zagging at the nodes, where the branches originate. This irregularity develops as a result of the displacement of the stem by the enlarging highly condensed inflorescences and the subsequent development of the branches in the axils of the amplexicaul leaves at these nodes.

The young inflorescence first appears as a single flower in the axil of a young leaf near the tip of a main stem or branch. This single flower is soon joined on the broad flower base, which is the primordial inflorescence axis, by small clusters of much younger flowers with their bracts and bracteoles developing between the first flower and its bracteoles, thus causing the first flower to appear ebracteate (Figure 9A). These inflorescences are subtended by vegetative leaves, and develop into clusters of flowers of both sexes. Each cluster is composed of several subclusters, each subtended by a bract-like, highly modified and extended membranous leaf sheath without a leaf blade. The individual flowers are interspersed with membranous bracts in varying states of development, with an occasional ebracteate flower. The subclusters are implanted onto a flattened disc, the condensed inflorescence axis, by means of short stalks. Removal of the subclusters reveals the discreet implantation sites left on the disc. In the centre of an occasional inflorescence in this stage of development, a small raised area in the shape of a pyramid occurs. This pyramid is the apical bud of the condensed inflorescence axis, starting to proliferate (Figures 9E; 10A).

In a significant proportion of inflorescences, further changes follow, culminating in production of a central branch in each inflorescence. In some cases, the central pyramidal section of the initially much-condensed inflorescence axis, develops into a very short vegetative shoot with one or two of the subclusters attached to it, thus separating these subclusters somewhat from the rest of the inflorescence. At the same time, vegetative leaf blades develop on the sheaths subtending the subclusters, thus marking the nodes in the condensed inflorescence axis

more clearly (Figures 9C; 10B). This interspersing of partial inflorescences with vegetative shoots, results in the formation of a branch complete with small lateral inflorescences. (Figures 9B; 10C).

More often though, the inflorescence remains tightly compact when the apical bud proliferates above the subclusters, generating a new branch. The amplexicaul sheath of the vegetative leaf on the main stem, subtending this compact inflorescence with its central branch, becomes much extended (Figure 9D). In large mature inflorescences with the central branch well developed, the implantation sites of the subclusters are so numerous as to be closely packed around the base of the branch, in a distinctly spiraling pattern (Figure 9F). This compact inflorescence with the apical proliferation, giving rise to a branch, represents the basic structure of the typical inflorescence. It exhibits a clear distinction between the production of short shoots, or as in this species, a system of short shoots, associated with the fertile stage and the long shoot formation of the vegetative stage (Figure 10A).

With two highly modified short shoots viz. the primary inflorescence axis as a flattened disc and the secondary axis as the stalk to a subcluster of flowers, the inflorescence can be defined as a double raceme or a diplobotryum. The arrangement of these subclusters (diplobotrya) within the total inflorescence is, however, not a fixed state. As seen above, in the instance of vegetative shoots and leaves developing in the inflorescence, a certain degree of plasticity exists, allowing the initially compact inflorescence to become more open (Figures 9C; 10B).

6. *Cliffortia arborea* Marloth

For a considerable time this species was the only known 'tree' in the genus. Marloth (1905) noted the height as occasionally up to 10 m. There was considerable variability in growth form and sexuality in the studied population in the Nuweveld Mountains above Beaufort West. On terraces against rock ledges about 100 m away from the sheer cliffs, the growth form was that of upright trees up to 4 m tall, with main trunks up to 150 mm in diameter and with reddish brown, flaking bark, and mostly female cones. On the edge of the cliffs, the population was smaller and the growth form more stunted and compact, and the plants were almost totally covered in male flowers from just below the occasional apical female cones to the lowest branches brushing the ground.

Female cones appear as apical thickenings on the ends of main branches. On older plants, the female inflorescence cones can be clearly seen to occur in series, from the older ones below to the one of the current season above (Figure 11A). Occasionally cones are also found on side branches originating from older cones lower down on main branches (Figure 12A).

The female inflorescence forms an oblong cone-like polytelic synflorescence (Figure 12A, B: SN) consisting of an aggregated and spirally arranged condensed lateral double racemes (homothetic diplobotrya). In the young (current season's) cone, each diplobotryum culminates in a coma of vegetative leaves forming a star-shaped rosette. Together, the rosettes cover the cone in a shroud

FIGURE 9.—*Cliffortia odorata, Fellingham 1660* (NBG). A, young, apparently single-flowered, inflorescence with central female flower and two lateral clusters of immature flowers in axils of its bracteoles; B, main stem with three well-developed vegetative leaves, each subtending a discrete inflorescence containing flowers of both sexes; C, proximal side of inflorescence with two pairs of subclusters separated by short vegetative shoot; D, main stem with compact inflorescence of three clusters (flowers and bracts removed, leaving subtending leaf sheaths) enveloping base of side branch originating within uppermost leaf sheath; E, semischematic drawing of young condensed inflorescence axis in leaf axil on main stem with three implantation sites of flower clusters and central raised pyramid marking onset of branch proliferation; F, mature form of E with well-developed central branch surrounded by numerous spirally arranged implantation sites of flower clusters. Scale bars: 1 mm.

of neatly arranged stars, from which the common name for this species viz. *sterboom* (= star tree) is derived.

On the main axis of the cone, trifoliolate primary cone leaves with broadened curved sheaths with or without pungent stipules, are spirally arranged (Figures 11B; 12B: pcl). Each primary cone leaf subtends and surrounds a diplobotryum (DB). A diplobotryum consists of

a number of co-florescences (CoF) on a secondary axis, which is basally much condensed but apically proliferates into a vegetative shoot, bearing the star-like coma of vegetative leaves. The co-florescences (botrya) are arranged on the basal condensed part of the axis and surrounded by involucre-like groups of unifoliolate secondary cone leaves (scl), which form the firm part of the cone underneath the shroud of comas (Figures 11C; 12B:
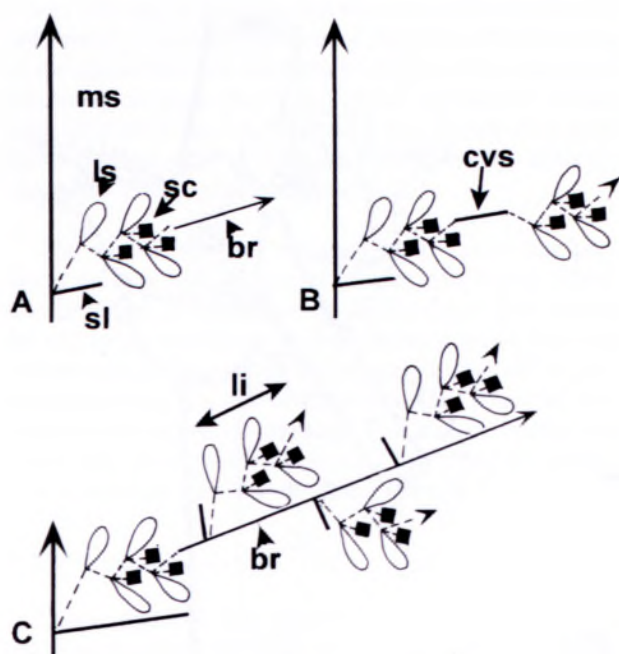
FIGURE 10.—*Cliffortia odorata*: longitudinal diagrams of inflorescences in different stages of development. A, compact mature inflorescence with apical branch; B, open inflorescence separated into two parts by central vegetative short shoot; C, later developmental stage with three lateral inflorescences. br, branch; cvs, central vegetative short shoot; li, lateral inflorescence; ls, leaf sheath subtending subcluster; ms, main stem; sc, subcluster; sl, subtending leaf. Broken lines: considerably expanded axes of short shoots.

scl). The botrya (co-florescences) are highly condensed with the axes not more than a slightly raised flattened area bearing a number of tiny flowers in a capitulum-like arrangement. The flowers are almost completely hidden by the secondary cone leaves with not much more than the strap-shaped styles and stigmas showing.

Mature cones proliferate apically into a vegetative continuation of the main axis, which will give rise to the following season's cone. Furthermore, the star-like comas of vegetative leaves marking the apices of the diplobotrya, proliferate into vegetative side branches. These can bear female cones, male flowers or eventually thicken and continue the vegetative development of the plant (Figures 11A; 12A: VB). Old cones are retained on main stems for a number of years but eventually disintegrate. This happens in stages. Firstly, after three or four years, abscission of the secondary cone leaves takes place at the top of the sheaths, leaving the woody bases on the main branches for several years (Figure 11A). Eventually the clusters of secondary leaf bases get separated from each other, as the main branches bearing them undergo longitudinal growth and secondary thickening. By that time, the leaf bases will have been reduced to a few scattered scales on the main stem and will be hardly recognizable as the remains of the original cone.

Male inflorescences are simple clusters of a few ebracteate flowers in the axils of vegetative leaves on lateral branches. These are borne below the female cones but on the same main branches (e.g. *Acocks 18625*, *Fellingham 1625*, *Marloth 9730*). Occasionally male flowers also occur on the thin side branches originating from older female cones (*Fellingham 1625*), but always

lower down on the plant than the female inflorescences of the same season. While distinctly monoecious, this species never has the male and female flowers occurring in the same inflorescence. Where male flowers do occur on the thin vegetative side branches of the occasional older female cones, as seen in *Fellingham 1625*, they are more than a year younger than these female cones and borne on vegetative shoots, and not on the female cones themselves.

7. *Cliffortia dichotoma* Fellingham

This new species of *Cliffortia* section *Arboreae*, from near Nieuwoudtville, Namaqualand, is closely related to *C. arborea*. It occurs on rocky ledges, on slight northern and southern slopes on the Oorlogskloof escarpment, south of the Oorlogskloof Nature Reserve. The whole population is old and moribund, with part of every plant dead and dry. No seedlings have been found for at least 25 years.

The plants appear more tree-like than any other species in the genus and are up to 5 m tall. The main trunks are buttressed and therefore irregular in shape, up to 500×300 mm in cross section, and bare for the lower 0.5 m. Branching is dichotomous from below a cone, with the new season's cones at the tips of the new branches (Figure 14A). This branching pattern results in a tree with a spreading canopy.

In spring female cones are initiated as swellings covered by imbricate, hard, spiky, tridentate leaves with broad, amplexicaul sheaths, at the tips of some of the branches (Figure 13A). By early summer these are fully developed young female cones with numerous circles of long, maroon, strap-shaped stigmas marking rosettes of conical, hairy and pointed modified leaves, the centres of which soon become raised and punctuated by 'stars' of about 5 vegetative leaves. The two lateral branches directly below the cone, start to thicken and curve upward in preparation for the production of the following season's pair of apical cones (Figure 13C). By the following spring the old female inflorescence cones are shrouded in numerous upwardly curving vegetative branchlets, having originated from the 'stars' of the previous spring, plus one apical, straight and slightly more robust, branchlet. The two branches just below the cone are close together and clearly more robust than the ones lower down (Figure 13B).

The female inflorescence cones consist of a number of lateral condensed double racemes (homothetic diplobotrya) (Figure 14B: DB), each consisting of a few sessile capitulum-like co-florescences (botrya) (CoF). These are aggregated and spirally arranged on a condensed main axis to form an oblong, cone-like, polytelic synflorescence on the end of a main branch, originating as one of a pair from below a cone of the previous season (Figures 13C; 14A–D). Each diplobotryum is subtended by a primary cone leaf (pcl) with a grossly extended sheath segregating the individual diplobotrya from each other, and a tridentate, often stipulate, woody blade just emerging between the involucres of secondary cone leaves (Figures 13E; 14B–D). The secondary cone leaves have thickened woody sheaths without stipules and swollen trifoliolate blades, with the leaflets of each
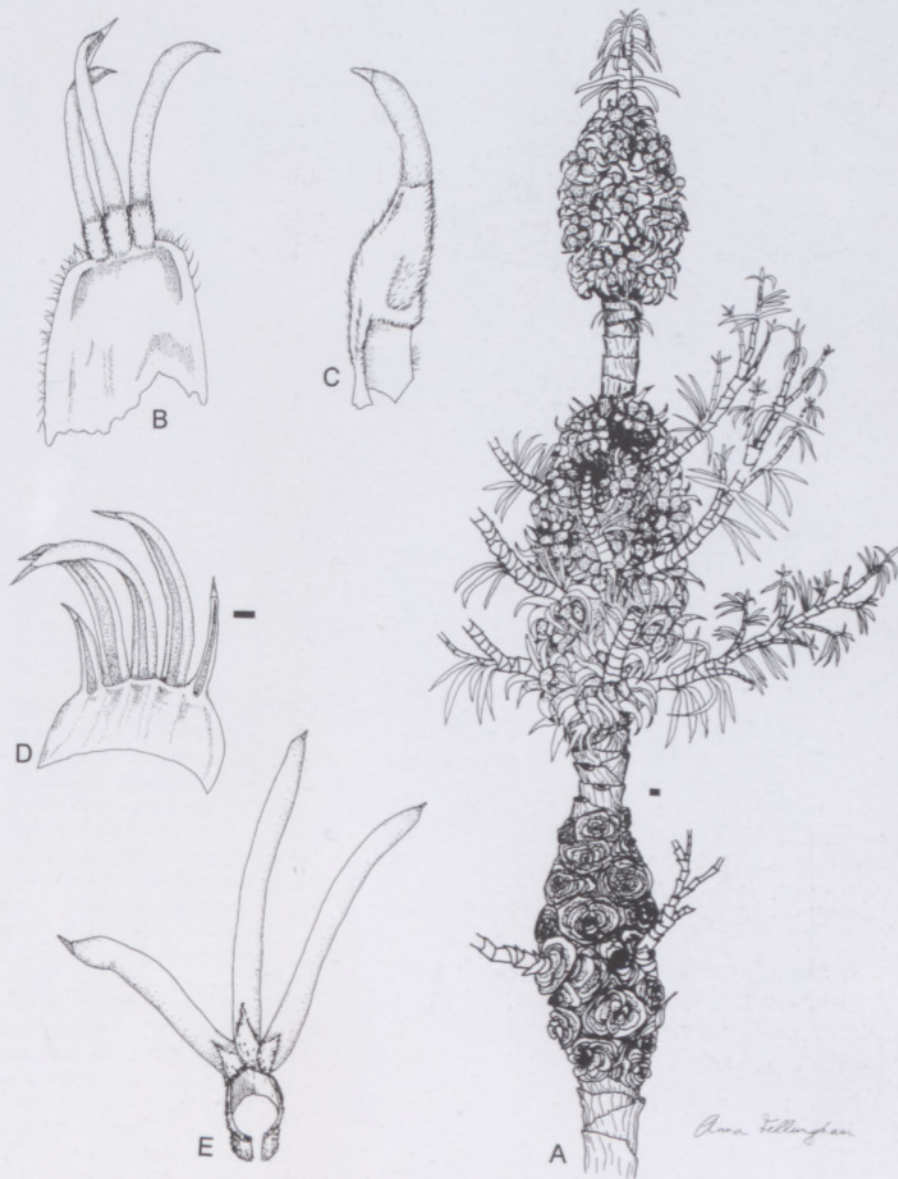
FIGURE 11.—*Cliffortia arborea*. A, apical portion of main stem with three female inflorescences (cones) in situ, oldest one lowest, weathered to basal portions of primary and secondary cone leaves and the remains of two lateral branches; B, primary cone leaf, astipulate type, adaxial view; C, secondary cone leaf, lateral-adaxial view; D, leaf from region of stem directly below female cone, abaxial view; E, vegetative leaf, adaxial view. A, *Fellingham 1624*; B–E, *Oliver 10054*. Scale bars: 1 mm.

leaf arranged in triangles (Figures 13D; 14B, C, D: scl). Both the primary and secondary cone leaves differ from the ordinary vegetative leaves, which are small, unifoliolate and ligulate in shape (Figure 13G). Each secondary cone leaf subtends a capitulum-like botrys, bearing up to 12 flowers on minute pedicels, subtended by greatly modified bracts (Figure 13F). The flowers, each with three or four calyx lobes, are totally hidden amongst the secondary cone leaves with only their ligulate styles protruding (Figure 13C). The fully developed fruits are irregularly angular and closely packed in the concavity in the adaxial side of the sheath of the secondary cone leaf, which subtends the capitulum-like flower-bearing structure, the co-florescence (Figure 13D). In the mature young cone in which proliferation of the apical bud has already given rise to a conspicuous vegetative continuation of the main stem, spirally arranged circles of long maroon stigmas—each circle with a tridentate, woody, primary leaf below it—demarcate the double racemes (diplobotrya) (Figure 13C).

In the slightly more mature cone with withered stigmas, the centres of these circles are raised as the second order axes proliferate, and each circle becomes crowned with a star-like arrangement of vegetative leaves. The appearance of the 'stars' that are to develop into the shroud of side shoots, seems to coincide with fertilization, as at that point the styles begin to dry and shrivel. As the second order axes elongate in the more mature cone, the 'stars' are replaced by a shroud of vegetative side shoots (Figure 13B). These side shoots as well as the apical proliferation of the main stem, are shed in the older cones. It seems that the shrouds of shoots are in place during the development of the fruits, which is the rest of the current season and the following one.

The male inflorescences are in the axils of ordinary vegetative leaves on branchlets lower down on the main branches bearing the female cones, and consist of solitary male flowers or small groups of very shortly pedicelate male flowers with much reduced bracteoles (Figure 13G).

8. *Cliffortia conifera* E.G.H.Oliv. & Fellingham

The only known population of this species is on an east-facing cliff edge, on the Anysberg. The small group of tree-like shrubs up to 4 m tall and with the main trunks up to 150 mm in diameter, resemble conifers in their upright growth form, as well as in their cone-like inflorescences, each terminally on a short lateral branchlet.
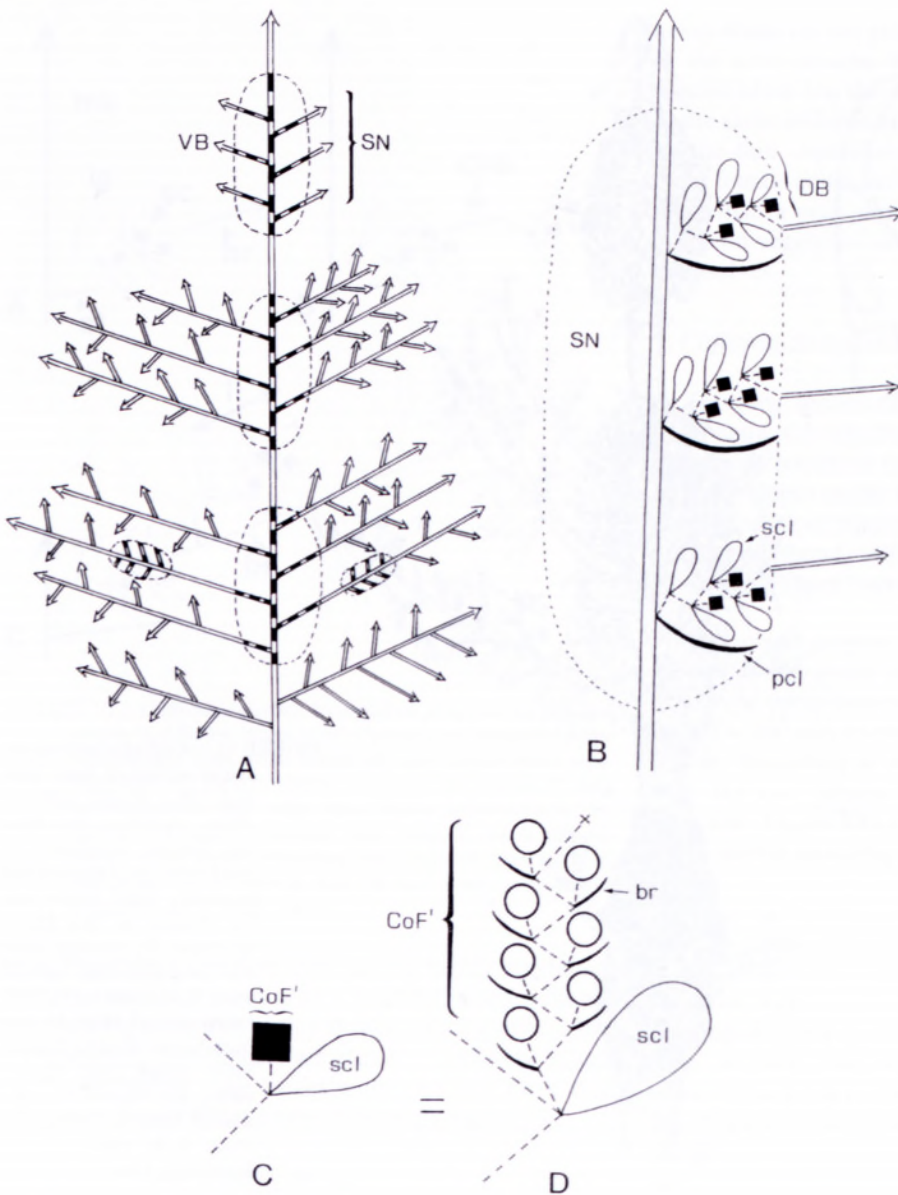
FIGURE 12.—*Cliffortia arborea*: longitudinal diagrams of inflorescences. A, three female cones on main branch and two on lateral branches; B, part of cone showing three dibotrya with vegetative branches; C, D, single botryum or co-florescence (solid square), expanded to show individual flowers (circles). br, bract of single flower; CoF, co-florescence or botryum; DB, diplobotryum; pcl, primary cone leaf; scl, secondary cone leaf; SN, synflorescense; VB, vegetative secondary branch. Broken lines: considerably expanded axes of short shoots.

These cone-bearing branchlets occur in groups of up to 10, in subterminal zones on main branches; rarely on secondary branches. Older branches have several zones of cones interspersed with vegetative regions consisting of well-developed, leaf-bearing lateral branches.

The obovoid or occasionally spheroid female cone consists of many condensed double racemes (homothetic diplobotrya) aggregated on a shortened main axis, which is the condensed end of a lateral branchlet. The cone is devoid of proliferating shoots, either from the ends of the double racemes or the apex of the cone (Figures 15A; 16A, B). The cone can be interpreted as a polytelic synflorescence composed of numerous (up to 50), condensed, sessile racemes (botrya), the co-florescences, grouped together in highly condensed, double racemes (diplobotrya). The co-florescences resemble capitula with up to 16 flowers all arising at the same level from the truncated end of the very short, 3rd order, florescence axis. The flowers are interspersed with long erect hairs from which the variously modified and reduced bracts just emerge. Except for the protruding stigmas and occasionally the small calyx lobes, the flowers (and eventualy the fruit) are concealed by the bulbous secondary cone leaves on the 2nd order cone axes, which are involucrally arranged and form the matrix of the cone. The sec-

ondary cone leaves are unifoliolate, lack both stipules and sheaths but have a demarcation between the upper bulbous part with velvety indumentum, and the basal flattened glabrous part (Figures 15C, D; 16B: scl). The primary cone leaves originate on the main cone axis, subtend the lateral second order diplobotrya and are also concealed by the secondary cone leaves. The primary cone leaves differ from the secondary cone leaves in having extended leaf sheaths with stipules and, being uni- or trifoliolate (Figures 15E; 16B: pcl). Both the primary and secondary cone leaves differ from the ordinary vegetative leaves which are trifoliolate, the leaflets flat with rolled edges and plain to tridentate and the sheath amplexicaul and stipulate (Figure 15A, B).

The male inflorescence is a much simpler structure, consisting of a cluster of 3 or 4, occasionally 5 flowers, on a highly reduced short shoot, in the axil of a subapical vegetative leaf, on lower lateral branches, well below zones of female cones (Figure 15B).

DISCUSSION

Although only eight species of the 119 in *Cliffortia* were included in this study, they are representative of the
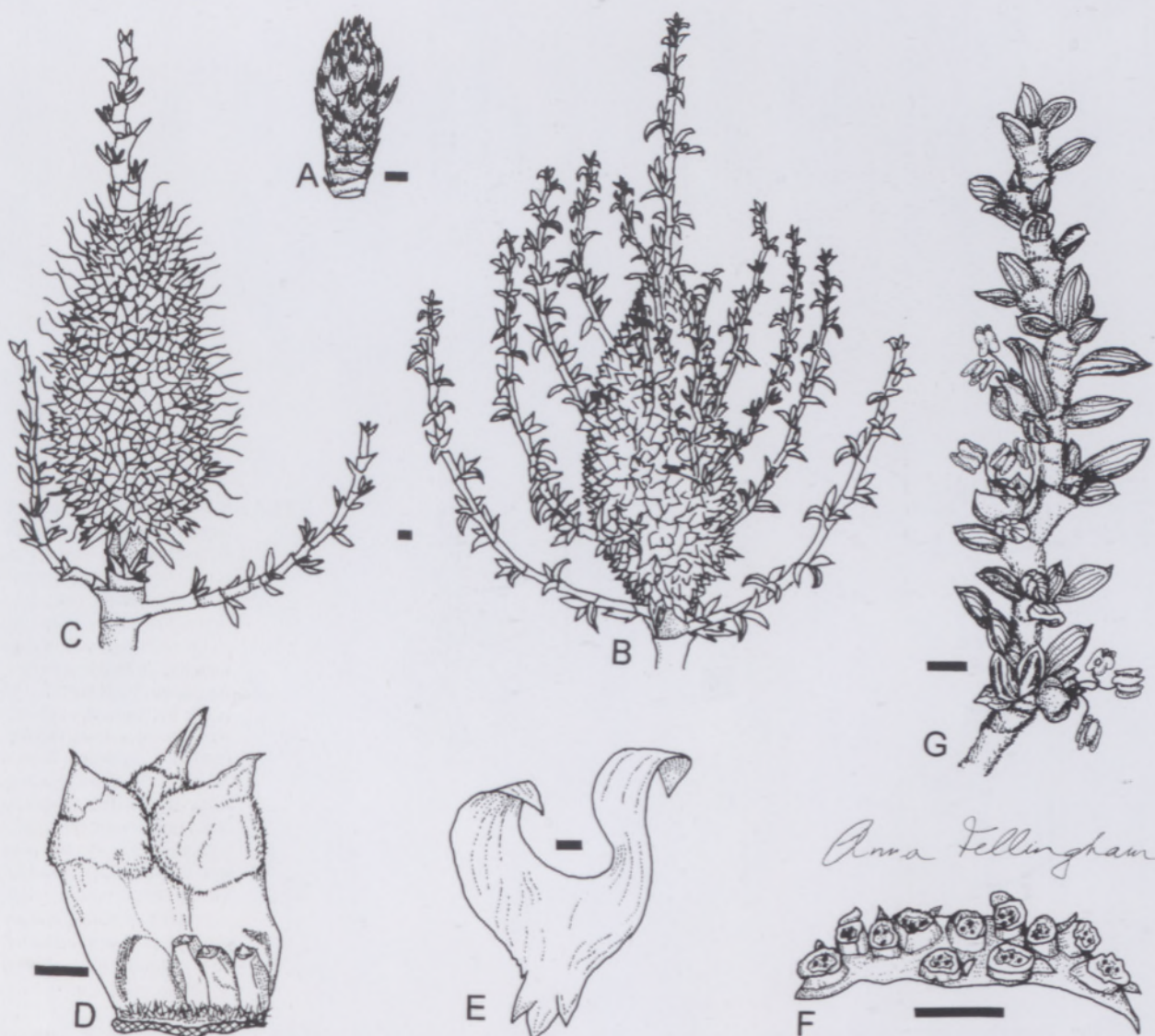
FIGURE 13.—*Cliffortia dichotoma*. A, apical swelling on main stem; B, mature inflorescence cone shrouded in vegetative lateral branchlets and apical continuation of main stem; C, young female inflorescence cone with numerous circles of strap-shaped stigmas; D, secondary trifoliolate cone leaf with exstipulate wooden sheath, subtending capitulum-like botrys bearing three remaining fruits; E, primary cone leaf with extended curved sheath; F, capitulum-like botrys, flowers and surrounding hairs removed exposing pedicels, each with subtending modified bract; G, vegetative branch with male flowers. A, B, D, F, *Fellingham 1684* (BOL, NBG); C, E, G, *Fellingham 1689* (BOL, NBG). Scale bars: 1 mm.

types of inflorescences in the genus, covering the range from the single-flowered inflorescence in *C. nivenioides*, to the highly condensed and discrete female cone in *C. conifera*. There is no hypothesis of the phylogenetic relationships in *Cliffortia*, so our sampling could not be based on the phylogenetic patterns in the genus. Nonetheless, it seems likely that the sampling captured most of the variation in the inflorescence morphology in the genus.

Basic inflorescence construction

The basic inflorescence unit in *Cliffortia* is a short shoot with one or more internodes, bearing one or several lateral, unisexual flowers, which may be bracteate or ebracteate. This is therefore an indefinite polytelic florescence (Weberling 1989). The short shoot itself is borne in the axil of a vegetative leaf. In its most common form, the shoot is single-flowered, and this misled Weimarck (1934) into interpreting them as 'solitary flowers in the axils of ordinary vegetative leaves'. There

are a number of ways in which this can be modified to generate the diversity of inflorescences observed in *Cliffortia*: these are detailed below.

Given that all inflorescences are basically racemose short shoots, there are a number of parameters that vary among species in the genus, and that are to some extent responsible for the variability in the inflorescence constructions:

1, number of flowers per inflorescence. These vary from one (probably the most common situation in the genus), to several as in *C. ruscifolia*, to numerous as in *C. heterophylla, C. odorata* and the three coniferous species of the section *Arboreae*. In some cases, initially only one or a few flowers are formed (usually female). When these flowers have matured, growth resumes in the florescence, to form a further set of usually male flowers. In *C. heterophylla*, though, the female florescence continues growth as a long shoot, which then bears single-flowered lateral male florescences;
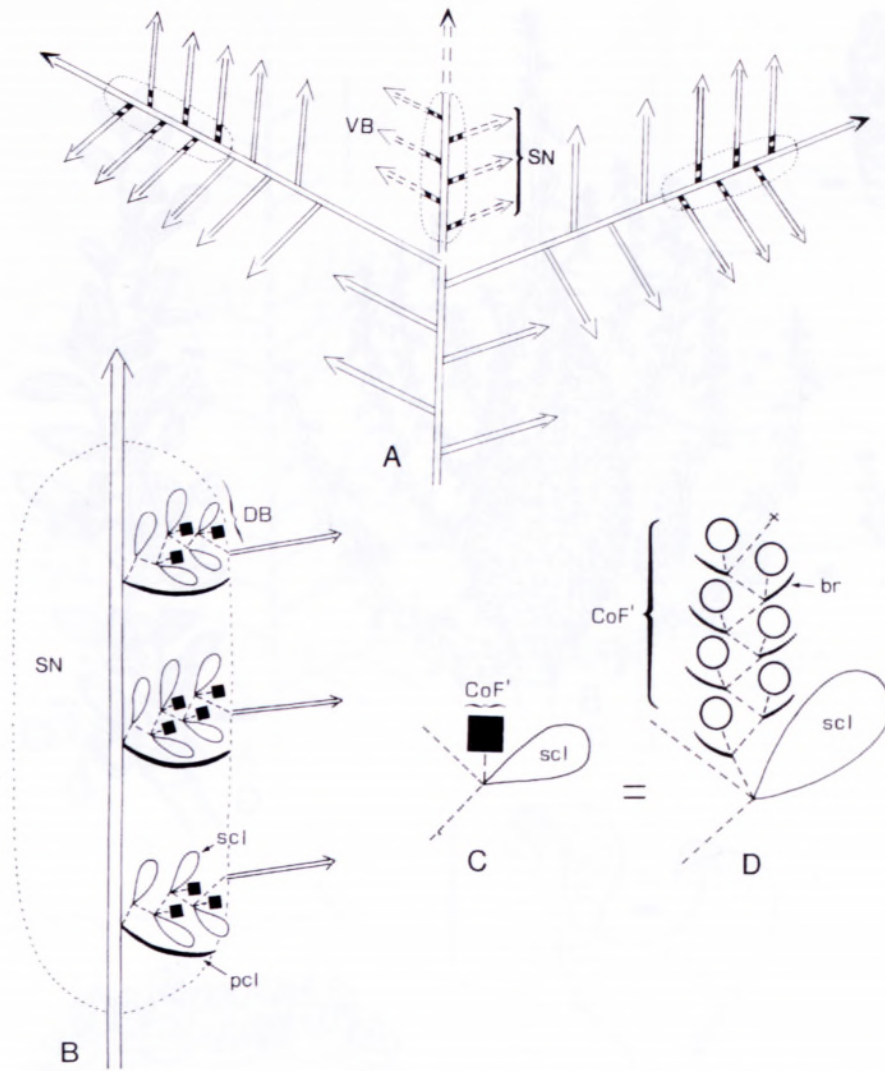
FIGURE 14.—*Cliffortia dichotoma*: longitudinal diagrams of inflorescences. A, three female cones, two on dichotomous branches, central one older, having lost its apical and lateral branches; B, part of cone showing three dibotrya with vegetative branches; C, D, single botryum or co-florescence (solid square), expanded to show individual flowers (open circles). br, bract of single flower CoF, co-florescence or botryum; DB, diplobotryum; pcl, primary cone leaf; scl, secondary cone leaf; SN, synflorescence; VB, vegetative secondary branches. Broken lines: considerably expanded axes of short shoots.

2, the short shoot internodes are generally about equal in length. This is so in most primary short shoots, secondary short shoots and even in systems containing tertiary short shoots as well. In *C. odorata*, however, the axis of the primary short shoot is very condensed, forming a flattened disc borne in the axil of a vegetative leaf. This disc-like short shoot retains its viable apical bud and bears secondary short shoots in the form of stalked discs as the ultimate flower-bearing short shoots. Disc-like ultimate flower-bearing short shoots also occur in *C. arborea*, *C. conifera* and *C. dichotoma*, but in these species as the tertiary short shoots;

3, aggregation of short shoots can be variously developed. In some cases, the florescences are borne solitary, although generally in distinct zones on the plant. However, they may be aggregated into clusters (in *C. odorata*), elongated synflorescences (in *C. heterophylla*), or aggregated into dense cone-like structures (in *C. arborea*, *C. dichotoma* and *C. conifera*). Some of these synflorescences can be remarkably complex, and diverse in structure, while exhibiting great plasticity;

4, short shoots transforming into long shoots. After the flowers on the short shoot have matured, the internodes elongate, thus transforming the short shoot into a long shoot, as seen in *C. nivenioides* and *C. heterophylla;*

5, viability of the apical bud of short shoot. In *C. conifera* all apical buds of short shoots have lost their viability. In the other species, continued growth from at least some of these apical buds variously affects the synflorescence, and often the whole plant architecture. Firstly, continuing the growth of the florescence generally leads to the bearing of a later generation of male flowers after the initial generation of female flowers. This was observed in a number of species, such as *C. crenata*, *C. heterophylla* and *C. odorata*. This extends the period of time over which the florescence unit remains productive, and allows for the evolution of herkogamy at an inflorescence (rather than flower) level. Secondly, this continued growth may lead to the formation of new vegetative shoots, thus true proliferation, where the reproductive apical bud transforms to a sterile (vegetative) bud. This is common in the genus, and is discussed in more detail below.

The approach of searching for a basic pattern in the inflorescence, and then establishing how the inflorescence can be modified to produce a remarkable diversity of apparently different types, can be very productive. Weber (1995) used this approach to show that in *Phyllagathis* superficial description of inflorescences can be quite misleading, and that this can be revealed by searching for the basic pattern (in this case a monotelic homocladic thyrse). Here we attempt to account for the variation in inflorescences in *Cliffortia* by finding 'switches', simple 'on or off' devices. Modifications in the behaviour of the apical buds of the inflorescences,
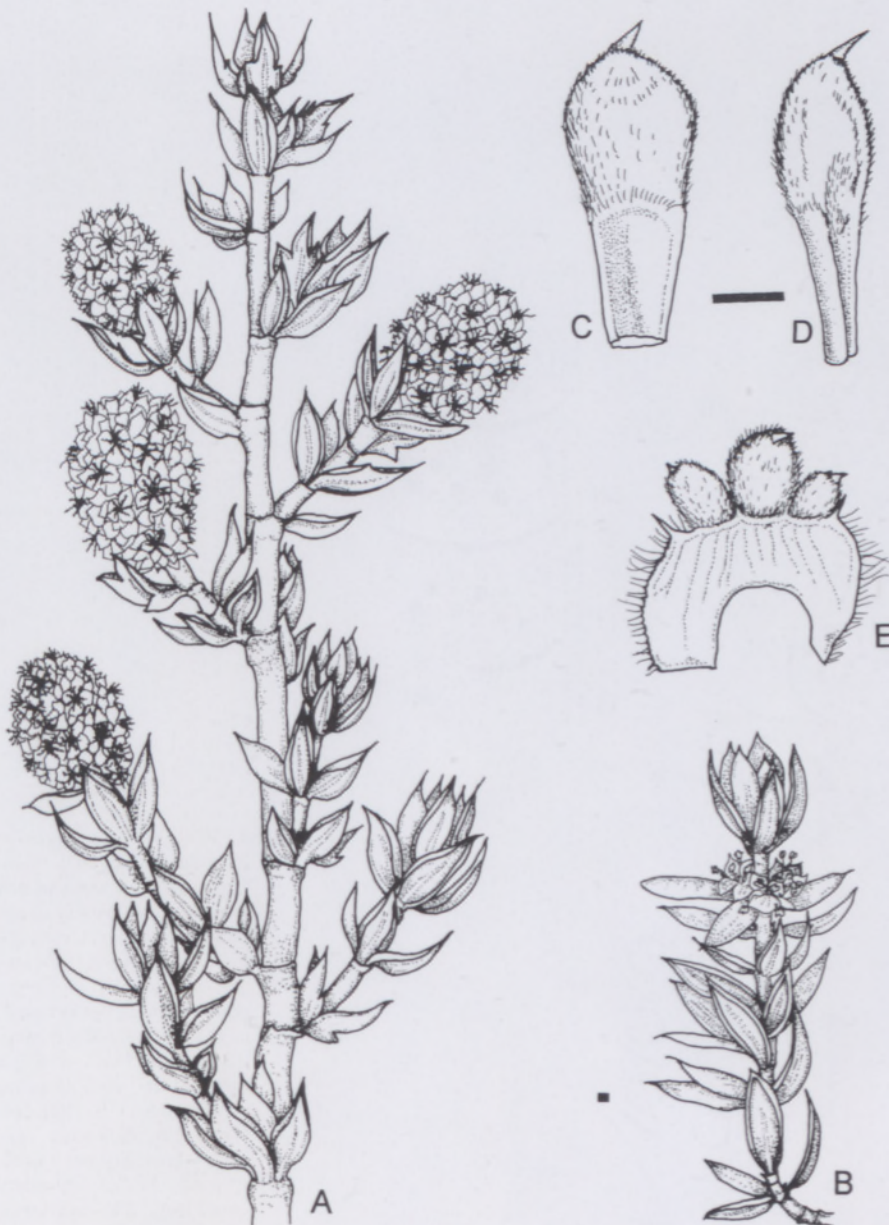
FIGURE 15.—*Cliffortia conifera, Oliver 10055* (NBG). A, branch bearing female cones; B, branchlet bearing male flowers. C, D, secondary cone leaf: C, adaxial view; D, lateral view. E, primary cone leaf, adaxial view. A, B, copied from Inge Oliver's drawings. Scale bar: 1 mm.

and the timing of internode elongation of the synflorescence and florescence axes, should be adequate. Such modifications have also been used to explain the variation in the inflorescences of the legume tribes Ingeae and Acacieae (Grimes 1999). These 'switches' could then be used as characters for a cladistic analysis. This could lead to a much better set of inflorescence homologies, than using descriptive terms directly, since using the switches allows for more intermediate conditions.

The possible characters that could be used are listed below. We have not attempted to score these for the species, since our sample of species is too small to be able to interpret the result: 1, florescence number of flowers: one/several; 2, florescence flower arrangement: protogynous/mixed; 3, florescence growth: continuous (all flowers formed more or less at the same time)/ interrupted (leading to sex changes); 4, florescence short shoot: permanent/later elongating into long shoots; 5, florescence apical bud: terminating/proliferating; 6, synflorescence apical bud: terminating/proliferating; 7, florescences: solitary/aggregated/forming cones; 8, male and female florescences: in the same synflorescence/in separate synflorescences.

Sexuality

The flowers are always unisexual, and there are several ways in which the male and female flowers can be combined to form a monoecious species. The following three patterns were observed:

Firstly, the male and female flowers may be found in separate synflorescences, and would therefore be spatially separated. This is exemplified by the cone-bearing species, *C. arborea, C. dichotoma* and *C. conifera*, in which the female florescences are many-flowered and are aggregated into cone-like synflorescences which are completely female. Male florescences are borne in separate, very different looking synflorescences with very few flowers. This situation is comparable to that found in most conifers.

Secondly, single-flowered florescences where the male and female florescences are combined into a common synflorescence. The only species with this pattern investigated is *C. nivenioides*. Male florescences mature first, followed by a time lag before the females mature.
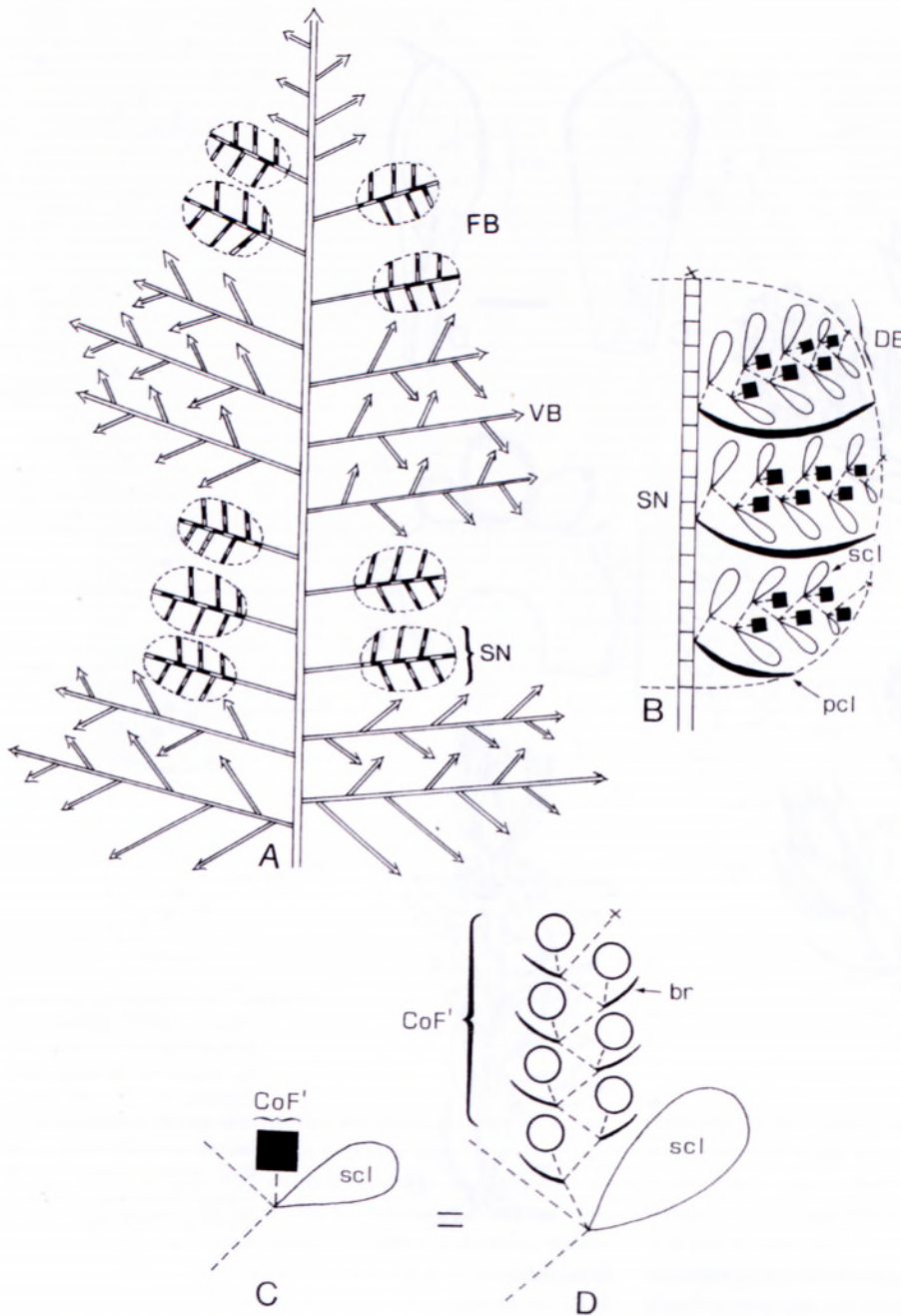
FIGURE 16.—*Cliffortia conifera*: longitudinal diagrams of inflorescences. A, main branch with two cone-bearing zones; B, part of female cone showing three dibotrya; C, D, single botryum or co-florescence, (solid square) expanded to show individual flowers (circles). br, bract of single flower; CoF', co-florescence or botryum; DB, diplobotryum; FB, flowering secondary branches; pcl, primary cone leaf; scl, secondary cone leaf; SN, synflorescence; VB, vegetative secondary branches. Broken lines: considerably expanded axes of short shoots.

Thirdly, male and female flowers are found in the same florescence (raceme), the flowers are separated usually with the female flowers borne below the male flowers (thus on the older parts). In general, the females then flower before the males, so that there is no overlap in the flowering time between male and female flowers. Thus the inflorescences are dichogamous. This has been referred to as sex changes or sequential hermaphrodism of the individual (Freeman *et al.* 1980), and is particularly well illustrated by *C. heterophylla*. The individual always starts out as overtly female, then becomes bisexual, and eventually is overtly male. Single observations would suggest that the species is dioecious, and bisexual individuals could be taken to be anomalous. This sequential hermaphrodism is only possible because of the morphological plasticity of the inflorescences, and in particular because the apical buds retain viability. Sex changing (or sequential hermaphroditism) as 'a phenomenon of at least some dioecious species', has more recently been based on findings in 66 species in 25 families, doc-

umented from as early as 1910 (Freeman *et al.* 1980). 'Apparent dioecy' in any one season, masking the true labile nature of the sex of the plant which can change with changes in the physiological state, which in turn depends on external factors, was described in *Arisaema triphyllum* (Araceae) by Bierzychudek (1982). She also found that all *Arisaema* species change sex, though only some change from male to female without any hermaphrodites. Similar findings of sex changes were reported in *Myrica gale* (Myricaceae) (Proctor *et al.* 1996).

Two of the species investigated here have bisexual florescences, but show no segregation of the sexes either in time or space. In *C. ruscifolia* the female flowers were in the fruit stage when the males still had good anthers [*Oliver 10387* (NBG)]. The same phenomenon is seen in *C. odorata* [*Fellingham 1664* (BOL), *1678* (BOL)].

It appears as if all species of *Cliffortia* may be monoecious. Previously it had been suggested that the

standard condition in *Cliffortia* is that the plants are dioecious, and Weimarck (1934) suggested that ± 60% of the species in the genus are 'capable of being monoecious'. This could be a misinterpretation based on single samples of species exhibiting sex changes, such as *C. heterophylla*. Oliver & Fellingham (1991) described *C. burgersii* as dioecious, but this might reflect yet another example of the possible erroneous interpretations of morphologically different stages of a monoecious plant, as morphologically different plants of a dioecious species. It seems essential to follow a plant through its flowering sequence to uncover sequential female and male phases.

Wind pollination

Many of the specializations in the inflorescences of *Cliffortia* can be interpreted as adaptations to wind pollination. The genus as a whole shows typical wind-pollinated flowers: a reduced, dull perianth, and unisexual flowers (Faegri & Van der Pijl 1979; Proctor *et al.* 1996; Linder 1998). Since most species and genera in the Sanguisorbae are wind pollinated, the anemophilous syndrome was mostly inherited by *Cliffortia*, and indeed many of the typical wind-pollination features of *Cliffortia* are also found in the related genera *Acaena, Sanguisorba*, and others. Wind pollination is generally seen as a common alternative to biotic pollination in species-poor or cool habitats where the survival of biotic pollinators would be difficult (Whitehead 1969, 1983). Yet, wind pollination has frequently evolved in the species-rich and structurally dense Fynbos of the Cape Floral Kingdom, and is found in the Ericaceae, Proteaceae, Asteraceae (*Tarchonanthus*), Rubiaceae (*Anthochortus*) and Rosaceae (*Cliffortia*) (Koutnik 1987; Le Maitre & Midgley 1992). Accepted as a primitive condition in the gymnosperms, it had been confirmed in the Cape genera *Podocarpus* and *Widdringtonia* (Koutnik 1987). Within *Cliffortia*, most inflorescences appear to separate male and female flowers either in time (through sequential hermaphroditism) or spatially (in the species with cones, where female and male synflorescences are separated). However, the coniferous species of *Cliffortia* have a rare reversal of the location on the plant of the male and female elements, with the male below the female. This rare condition is shared with only one evergreen gymnosperm, viz. *Pinus sylvestris* (Proctor *et al.* 1996).

Impact on vegetative branching

In *Cliffortia* the florescences generally proliferate, that is, the apical bud transforms to a vegetative bud, and growth continues into the next season as a vegetative shoot. This can be a major source of vegetative branching to the plant, and as such have a major impact on the plant architecture. The degree of involvement of the various orders of short shoots, determines the abundance and positions of long shoots produced.

A sparsely branched, lanky growth form is produced where flower bearing is limited to a few apical vegetative short shoots. These are the only short shoots that eventually develop into long shoots (vegetative branches) by the lengthening of their internodes (e.g. *C. nivenioides*). By contrast, the rich and random branching pattern in *C. ruscifolia* originates from its numerous inflorescences. Most of these proliferate into vegetative long shoots. A sparse and virgate branching pattern results from the small percentage of inflorescences, all near the apex of the main stem, that proliferate. This is seen in *C. crenata*. The monopodial branching in *C. odorata* is the result of proliferation of the primary short shoots of numerous axillary inflorescences on main stems, which themselves grow vegetatively only. The monopodial branching of *C. heterophylla*, however, is the result of a combination of two factors. The fast-growing main stem gains from the lengthening of the primary short shoot of the apical inflorescence as well as the eventual apical proliferation. The limited linear increase in the lateral branches, originating from the proliferation of the second order short shoots, enhances this effect. Similarly, in the young plant of *C. arborea*, the monopodial branching is regulated by the proliferation of the first order short shoot, which is the main stem of the plant. As the plant ages and side branches become involved in flower bearing, the branching pattern is obscured. A peculiar involvement of the position of the inflorescence determining the branching pattern is found in *C. dichotoma*. With the abortion of all initial proliferation shoots, two vegetative branches, close to each other and just below the terminal inflorescence, take over the function of continuing linear growth. These develop into a pair of thick main branches, one on each side of the central apical inflorescence. This results in the dichotomous branching pattern, unique in the genus. It is only in *C. conifera*, the species that exhibits no morphological plasticity of the inflorescence, that there is no effect of the inflorescence on the branching pattern, other than that a zone of branches are dedicated exclusively to the bearing of the female cones. In this aspect, it approaches the condition in the gymnosperms.

In inflorescences consisting of a system of short shoots of primary and secondary or primary, secondary and tertiary short shoots, it is always only the ultimate short shoots that are dedicated to flower bearing, to the extent to which the viability of their apical buds is lost. The apical buds of the lower order short shoots, forming the matrix of the inflorescence, however, retain their viability. These are the short shoots that can undergo one of two changes, or a combination of these two, at the onset of the vegetative stage or, in some instances, during the development of the inflorescence. The changes to the short shoot are the lengthening of the internodes rendering it a long shoot, or the proliferation of the apical bud into an apical long shoot, or a combination of the two processes. With the lengthening of the internodes, it becomes a long shoot without leaving a trace of the original short shoot. With the addition of apical proliferation to the lengthened shoot, the ensuing long shoot would gain greatly in longitudinal growth. It is only in the case of apical proliferation without any lengthening of the internodes, that the original short shoot can still be discerned. It is this inherent morphological plasticity of the matrix of the inflorescence that renders it capable of contributing to the vegetative growth both in substance and pattern.

SPECIMENS EXAMINED

Fresh material

Notes

1. Fresh specimens of *Cliffortia heterophylla* (4): *Karin Behr sub Fellingham 1638; Jane Forrester sub Fellingham 1640* (4) NBG, BOL,

were examined in the early Spring of 1994. Six field trips were undertaken between the 3-01-1995 and the 22-06-1995 to the Harold Porter Nature Reserve in Betty's Bay, to study this species in situ. Sketches are from *Forrester sub Fellingham 1640* (4) NBG, BOL.

2. Field work was done on the two populations of *C. arborea* (6) on the Nieuweveldberg escarpment, at Beaufort West and fresh material taken for study were *Fellingham 1624* female (6) MO, NBG, PRE; *1625* male & female (6) BM, NBG, PRE.

3. Field work on *C. dichotoma* (7) was done in September 1995, November 1995, November 1996, and October 1997, on the Farm Papkuilsfontein in the Lokenberg area of Namaqualand. Specimens were collected on all of these occasions. The fresh specimens studied and sketched were *Fellingham 1684* (7) BOL, K, NBG, PRE and *Fellingham 1689* (7) BOL, K, NBG, collected on 27-09-1995 and 16-11-1995 respectively.

4. Fresh material of the type specimen of *C. conifera* (8), *Oliver 10055* male & female (8) BOL, K, NBG, PRE, was examined and sketched. The type locality, the eastern end of the Anysberg in the Ladismith District, was visited and more fresh material, *Fellingham 1531* female (8) NBG, collected for examination in the herbarium.

Other fresh material

Fellingham 1647–1652, 1654–1658, 1663, 1668, 1673, 1675, 1677 (4) NBG; *1660, 1664, 1678* (5) NBG; *1662, 1674, 1676* (4) BOL. *Fellingham & Vlok 1588* (1) NBG.

Oliver 10387 (2) NBG; *10567, 10569, 10574* (3) NBG.

Viviers & Vlok 470 (1) NBG.

Herbarium specimens

Acocks 18621 male & female (6) BOL; male & female (6) K; male (6) NBG; *19280* (2) NBG.

Barker 5593 (3) BOL; *8263* (2) NBG. *Barnes s.n.* (3) BOL. *Bean & Trinder-Smith 2733* (2) BOL. *Bolus 2754* (2) NBG, *7600* (2) BOL, NBG; *10603, 12674* (3) BOL; *19854, 19855* (5) BOL. *Bond 1754* (1) NBG, PRE. *W.Bond 1511* (2) BOL. *Boucher 209* (4) NBG, PRE; *502* (3) NBG, PRE; *4193, 5019* (2) NBG. *Burman 895* (3) BOL.

Compton 3039, 9492 (3) BOL; *3040, 3459, 3920* (2) BOL, *5685, 7412, 8662, 10830, 11831, 18425, 18523, 22216, 22247, 22843* (2) NBG; *14374, 51589* (5) BOL. *Cooper 1451* (5) BOL.

De Villiers s.n. immature female (6) NBG. *De Vos 624, 1213* (4) NBG. *Dickin 83* (5) BOL. *Durand 263* (3) NBG, PRE.

Ebersohn 15/68 (4) NBG. *Ecklon & Zeyher 1720* (3) BOL. *Esterhuysen 3447, 5139, 5263a, 10346, 13959, 25911, 27596* (2) BOL; *5241a* (2) NBG; *s.n., 3030, 3443, 9540, 29097* (3) BOL; *13677* (4) BOL; *29003* (4) BOL, NBG; *1831, 15311, 19430, 23890, 29064, 30049, 33509, 33759* (5) BOL.

Fellingham 1533 (2) NBG; *1702* male & female (7) BOL, NBG, male (7) PRE, K; *1705, 1709* (7) BOL, NBG, PRE; *1706, 1707, 1708, 1710, 1711, 1712* (7) BOL. *Fourcade 24* (5) BOL; *3089* (3) BOL.

Gillett 1908 (2) BOL, NBG; *4244* (3) BOL. *Goldblatt 2162* (2) NBG. *Grobler 20181* (4) NBG.

Haynes 362 (3) NBG, PRE. *Hennecart 54* (3) BOL. *Hugo 911* (2) NBG. *Hutchinson 1123* (2) BOL.

Kerfoot 5397 (3) NBG, PRE. *Kruger 801* (4) NBG; *1204, 1346* (2) NBG, PRE.

Leighton 12 (3) BOL; *13* (4) BOL; *2977* (5) BOL. *Levyns 482, 2918, 3016, 4061, 4091, 4776, 7938, 8056, 9141, 11634* (3) BOL; *2051, 2460, 6167, 6444, 6511, 8010, 8975, 9210, 11194* (2) BOL; *6466* (5) BOL; *7789, 7795, 8095* (4) BOL; *Lewis 6065* (2) NBG. *Loubser 825* (5) BOL.

Maguire 155 (3) BOL. *Manson 130* (3) NBG, PRE. *Marloth 1977* (2) NBG, *9089* (2) BOL; *3907* female (6) BOL, male (6) K; *9730* male & female (6) NBG; *9770* female (6) NBG, PRE; *14106* (4) NBG; *Mauve, Van Wyk & Pare 28* (2) NBG. *McDonald 1688, 1732* (2) NBG. *McOwan STEU13375* (2) NBG. *Michell BOL16091* (5) BOL. *Moffett & Steensma 4067* male (6) NBG.

Nel & Boucher 73 (5) BOL, K, NBG, PRE.

Oliver 4252, s.n. (2) NBG; *9730* female (8) NBG, PRE, S; *10054* female (6) BOL, K, MO, NBG, PRE, S.

Parker 3663 (5) BOL; *3717* (3) BOL. *Paterson 2015* (5) BOL. *Pillans s.n.* (2) BOL; *7358, 9292* (3) BOL. *Pretorius 396* (7) BOL, K, MO, NBG, PRE.

Rehmann 2716 (2) BOL. *Rodin 3091* (3) BOL.

Salter 6335 (2) BOL. *Schoncken 269* (2) NBG. *Shearing 893* female (6) PRE. *Simpson 93* (2) NBG. *Sims 2514* (5) BOL. *Stephens 7125* (3) BOL. *Stokoe 405* (4) BOL, PRE, SAM; *7260* (3) BOL; *7264, 9048, 17238* (4) BOL; *SAM61486, SAM59988* (4) NBG, SAM; *s.n.* (5) BOL.

Taylor 4728, 8023, 9517 (2) NBG. *Thode 4818* (2) NBG. *Thompson 176* (3) NBG, PRE; *2275* (1) NBG, PRE. *Tyson 766* (2) BOL, NBG.

Van der Merwe 847 (4) NBG. *Van Niekerk 763* (2) BOL; *787* (3) BOL. *Van Wilgen 162* (3) NBG, PRE. *Van Wyk 536* (2) NBG; *1072* female (8) NBG. *Yvette Van Wyk 626* (7) NBG. *Van Zyl 3363* (2) NBG. *Vlok 1326* (1) NBG, PRE. *Von Willard s.n.* (7) NBG.

Walters 1741 (2) NBG. *Whitman s.n.* (3) BOL. *Wolley Dod 5* (3) BOL. *Wurts 1366* (2) BOL, NBG.

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