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PRELIMINARY OBSERVATIONS ON KORTHALSELLA (VISCACEAE) WITH SPECIAL REFERENCE TO VASCULAR PATTERNS

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SUMMARY

Sixty-two specimens covering the range of morphological variation in *Korthalsella* were examined to determine the arrangement, number, and taxonomic significance of their vascular bundles. Vascular anatomy is described in some detail. It was found that the vascular patterns fall into two major groups: between 2 to 6, usually 4, bundles or between 8 to 16, usually 8 to 10. These two groups do not coincide with the previous infrageneric classification, therefore the characters used in the previous classifications and the difficulties associated with them are discussed.

INTRODUCTION

Korthalsella Van Tiegh. (Viscaceae) is a genus of squamate monoecious mistletoes with highly reduced flowers. The genus is distributed throughout the higher islands of the Pacific, in Australasia, Malesia, north to Japan, and across the Himalayas to parts of Ethiopia and Madagascar (Danser, 1937: 119).

Specimens of this genus were first described from Malesia, under *Viscum geminatum*, by the Dutch botanist Korthals (1839). In 1896 Van Tieghem recognized the group as a separate genus and named it after his predecessor. The last monographer, Danser (1937 and 1940), divided the genus into 3 sections with a total of 23 species and 11 varieties.

Since reduction has made observation of floral and fruit characters difficult, infrageneric sections are distinguished on the basis of presence or absence of specialized inflorescence branches*, and distichous or decussate branch insertion. Species are distinguished mainly by phyllotaxy, arrangement of the flowers within the inflorescence, and shape of the branches and internodes. Other characters which have been used at the specific or varietal level include shape of flower cushions and of the collar-like ring of reduced fused leaves subtending the cushions, and plant size and colour (Danser, 1937).

* 'Branch', as used here, refers to individual vegetative or flowering axes on a plant; internode refers to the individual joints or articulations of a branch. See, for example, the habit drawing of *Korthalsella dacrydii* in figure 2.

An examination of vascular patterns within the genus has been undertaken to add information on the validity of the currently accepted taxa. The relation between vascular patterns and the three major characters mentioned above (specialization of inflorescence branches, branch insertion, and arrangement of the flowers) are considered in the Discussion section of this paper.

There has been little previous work on anatomy in *Korthalsella*. Stevenson (1934) studied the anatomy in detail but on a limited scale, using only New Zealand plants.

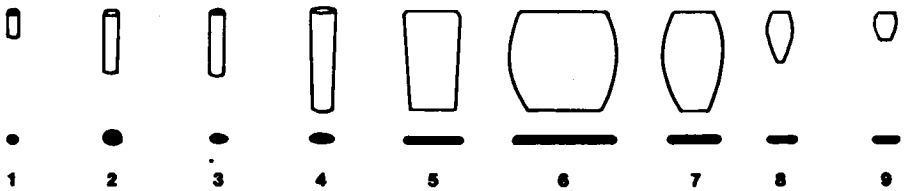


Fig. 1. Internode shape classes.

METHODS

The specimens selected for study cover the range of morphological variation within the genus and include representatives from all three currently recognized sections. The specimens are arbitrarily arranged according to the shape of the internodes, a character which has been widely used for specific delimitation. Shapes vary from narrow-cylindrical, through large, flat and more or less rectangular, to small, flat and constricted at the nodes. (See figures 2, 20–29 for drawings of actual internodes.)

Cross sections were made of mature flowering internodes (except as noted on the diagram in figures 20–29) which are representative of the specimens concerned. Attempts to sample internodes from a specific position on different specimens, such as the seventh from the apex, were obstructed by the often disarticulated condition of the specimens. A list of specimens examined is provided at the end of this paper. (The names cited are in accord with Danser's (1937, 1940) treatment.* However, my preliminary research indicates that the number of taxa may have to be considerably reduced.)

Material for study was prepared as follows. Dried herbarium specimens were soaked in concentrated ammonia until they appeared fully rehydrated, followed by 70% ethanol. Only a few specimens (the Touw, Palmer & Obata, and Kores collections) were preserved in FAA and did not require soaking. The rehydrated material was then either hand sectioned and stained with aqueous phloroglucinol and HCl to demonstrate the presence of lignin, or it was embedded, sectioned on a rotary microtome, and stained with lacmoid. Some internodes were cleared and stained with

* Barlow (1983: 48) points out that the correct name for the most widespread taxon, formerly *K. opuntia*, is *K. japonica*.

safranin, but this method is less than satisfactory since the material stains so readily in safranin that all but the largest bundles are obscured. Specimens in both the 2–6 bundle and 8–16 bundle groups were macerated by boiling in chromic acid in order to see whether both vessels and tracheids are present and to check the pattern of the secondary walls of the xylem. Figures were drawn with the aid of a *camera lucida.*

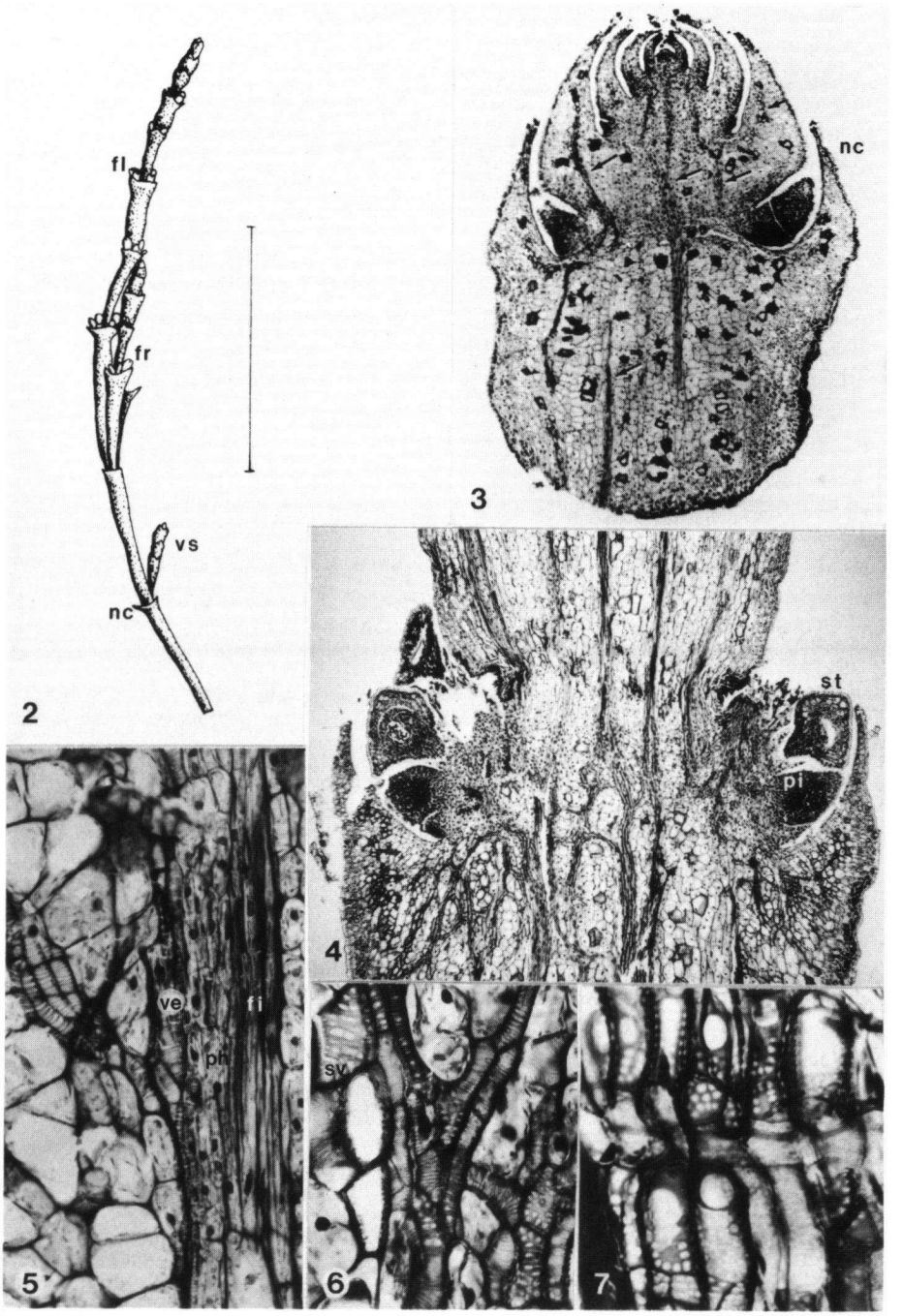
DESCRIPTION OF ANATOMY

A short description of the general anatomy is given below to provide a background for the discussion on the vasculature of the internodes. The various cell types found in the genus are shown in figures 5–7, 11, 12, 14, and 15. Following the general anatomy a more detailed description of the composition and pathways of the vascular bundles is provided.

Stevenson described in detail the anatomy of three New Zealand taxa of *Korthalsella, K. salicornioides, K. lindsayi*, and *K. clavata*. These taxa are currently distributed among two sections of the genus but include only very small 4-bundle plants. The larger sample included in this study confirms Stevenson's (1934: 177–178) results in some particulars: tracheids are short, vascular bundles often fuse at the node (figs. 4, 13, 14), sclereids are present in various parts of the plant, and a subepidermal layer is present containing inclusions which are probably resinous (figs. 3, 4, 8–10, 13–15). Stevenson (1934: 178) reported that phloem was absent from her specimens. However, Lamoureux (pers. comm.) identified callose plugs in lacmoid stained sections of *K. platycaula* and *K. complanata*, and I have seen them in all subsequently viewed embedded material prepared from fresh specimens. The phloem cells retain their nuclei and may therefore be difficult to recognize unless appropriate stains are used. Alternatively, study of fresh 2–6 bundle plants may show that they actually lack phloem.

Korthalsella branches vary in shape from tiny terete branchlets 1 mm in diameter and 2 cm long to tough flat structures well over 3 cm wide and 30 cm long. The anatomy, however, as indicated above, is surprisingly uniform. The surface layers of the plants are somewhat similar to those in other Viscaceae. The cuticle is quite thick (fig. 14), becoming somewhat more so in older internodes. The stomata are scattered over the whole epidermis, without differentiation between upper and lower surfaces of the branch (if the branch was oriented so as to have such surfaces). As in other Viscaceae, the stomata tend to be transversely oriented to the longitudinal axis of the branch. The subepidermal layer contains chloroplasts and inclusions which range in colour from light to dark green to very dark reddish black. The inclusions influence the colour of the plant. Stevenson (1934: 177) found that these inclusions were not tannin and suggests that they are probably resinous. Similar-looking inclusions are found in the trichomes of the floral cushions in many specimens (figs. 4, 13).

The deeper layers of the plants contain sclereids, parenchyma, and vascular bundles. Parenchyma cell walls vary in thickness in different specimens (see figs. 14, 15). In some the parenchyma appears to be very soft and may expand beyond normal when soaked in liquid. More commonly it is rigid and may even have walls which are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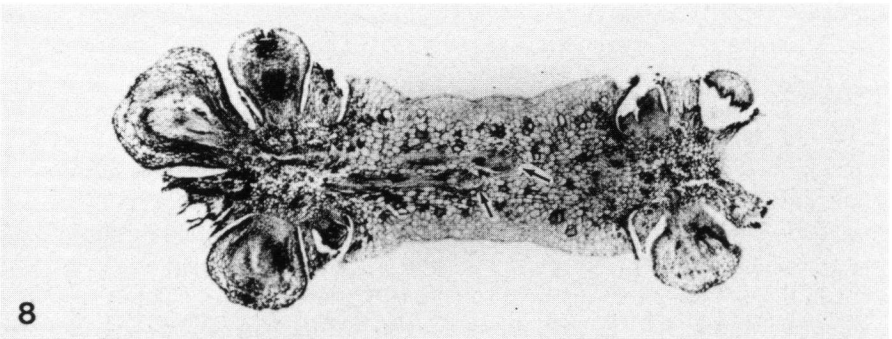
lignified or almost as thick (but unlignified) as those found in some sclerified cells (see *K. rubescens*, fig. 15). Bodies, which are similar in appearance to those presumed to be resinous in the subepidermal layer and the trichomes, occur in the parenchyma in a few specimens. Potassium iodide stain did not show starch storage anywhere within the parenchyma. Lignified sclerified cells occur singly or in aggregations of up to ten or, rarely, more. The walls may grow so thick in some sclereids as to completely obscure the lumen, and, especially in these very thick-walled cells, cross sections show the walls to be composed of numerous thin layers. Sclereid position varies: they can be buried in the subepidermal layer, or cluster around vascular bundles, or occur in the central 'pith', or simply be randomly scattered. They are very numerous in some plants or in older internodes, so much so that the parenchyma may no longer be discernible between the mass of sclereids.

The composition of the vascular bundles varies somewhat. The xylem is made up of short tracheids and even shorter vessels (figs. 5–7). The tracheids have helical secondary walls and no pits in all macerated specimens observed. However, some vessels of 8–16 bundle taxa have simple pits (see fig. 6), while those of the 2–6 bundle taxa have helical thickenings without pits like the tracheids. The helical thickenings are so closely spaced in a few of the 2–6 bundle specimens that the spaces between the strands resemble simple pits. There is always a dark area of phloem adjacent to a bundle of xylem and peripheral to it (figs. 5, 11, 12). Stevenson (1934: 178) describes this as an area of 'elongated cells with rich cytoplasmic contents and conspicuous nuclei.' If phloem proves to be absent from the taxa she studied, the dark area may represent a degenerate remnant of phloem tissue in those taxa. Fibre bundles are usually present peripheral to the phloem. These aggregations of xylem, phloem, and fibres are basically V-shaped, with the apex oriented toward the centre of the branch. Since fibres do not accompany minor vascular bundles or reticulations, they serve as a convenient marker to indicate major vascular bundles. Fibre bundles are not developed in young internodes in juvenile plants, as will be discussed

Fig. 2. Habit drawing of *Korthalsella dacrydii (van Steenis 11494)*. This is one of the smallest plants in the genus, but it is otherwise typical. nc: nodal collar of fused, reduced leaves; vs: young vegetative shoot; fr: fruit; fl: flower, staminate and pistillate flowers are not distinguishable on this scale. Bar × 1 cm. — Fig. 3. Apex of *K. complanata (Touw 159)*, longitudinal section, × 30. Note that development of the central bundle is already marked in the first, apical, internode; and that development of the vasculature is largely complete in the third internode. Arrows point to 5 bundles visible in this plane of the section. The scattered black bodies are sclereids. nc: nodal collar. — Fig. 4. Mature node of *K. platycaula (Touw 160)*, longitudinal section, × 30. Five discrete vascular bundles are visible above the node. Note anastomoses and branching at and below the node. st: staminate flower; pi: pistillate flower. — Fig. 5. Vascular bundle of *K. platycaula (Touw 160)*, longitudinal section, × 160. Note that the minor vascular bundle branching off the major one does not have accompanying phloem or fibre elements. ve: vessel; ph: phloem; fi: fibre. — Fig. 6. Detail of vessels, *K. platycaula (Touw 160)*, longitudinal section, × 160. The pits and helical thickenings of the xylem vessel elements are visible, as well as a few of the relatively common large, swollen vessels (sv). — Fig. 7. Detail of vessels, *K complanata (Touw 159)*, enlargement of a portion of figure 12, × 250. Large simple perforations and pits are visible.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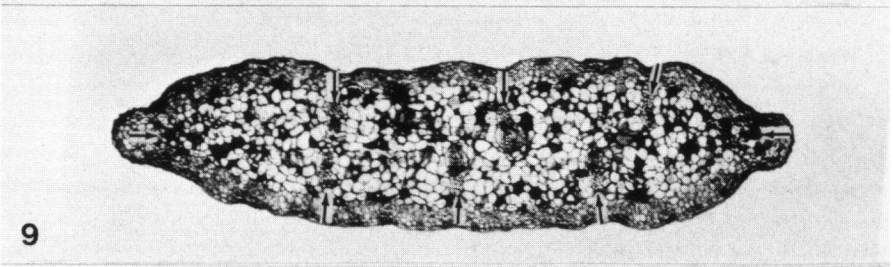
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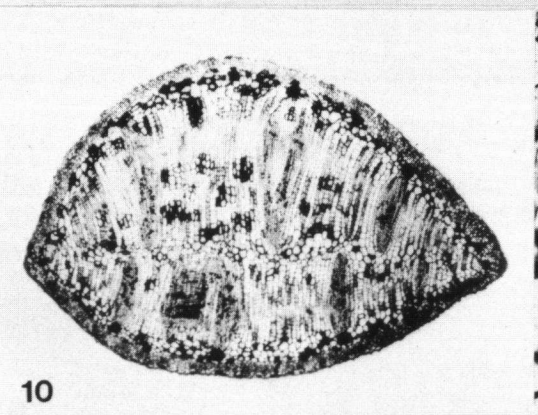
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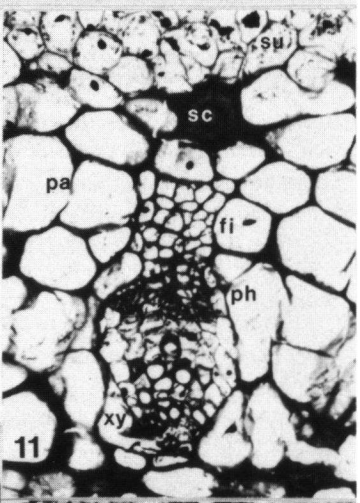
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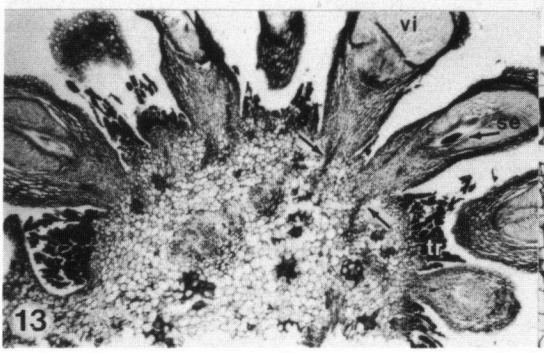
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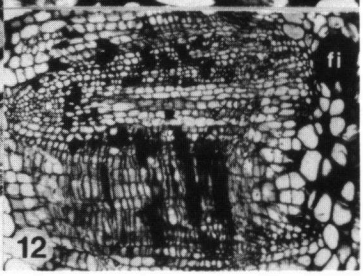
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at greater length later in the paper. Intraxylary fibres occur (e.g., see *K. complanata* in fig. 23), and on occasion fibres may be central to the xylem rather than peripheral (see *K. cylindrica* in fig. 21).

Major vascular bundles are well organized and distinct in the internodal area (figs. 4, 9). Within approximately one millimetre of the node, the fibre bundles usually end and the xylem elements branch out (figs. 3, 4, 8, 13). The rounder plants form an ill-defined central column of vascular tissue with interspersed parenchyma (figs. 13, 14); the flatter plants usually retain the two central bundles intact, but most or all of the lateral bundles break up (fig. 8). Elements from the bundles anastomose, or branch toward the flower cushions and vegetative side shoots. Fibre bundles can pass right through the nodes together with the xylem in old, especially basal, joints. Large percurrent fibre bundles were found in an old and exceptionally tough specimen of *K. latissima (Touw 214)*. The vascular elements are reorganized into the characteristic number of bundles for the given plant within 1 or 2 mm after passing through the node and reacquire accompanying fibres if these were lost.

A large number of xylem elements supply the flower cushions. Individual flowers are supplied with 3 strands which terminate in the tepals (figs. 16–19); there is no visible vasculature to the fused stamens or to the gynoecium. Once the embryo develops, 2 well-marked xylem bundles develop and branch to surround the embryo at the level of its viscin coat. Interestingly, the flower seems to enlarge somewhat and begins to develop this vasculature even when no embryo is present (fig. 17). The eventual abscission zone is visible as a thickening in the vasculature directly below the embryo (fig. 18).

The general vascular pattern in *Korthalsella* is somewhat similar to that described for other squamate mistletoes. Kuijt (1969: 218–219) notes that *Ixocactus* has accompanying fibre bundles peripheral to the vasculature, and *Dendrophthora flagelliformis* has an 'extremely intricate vascular reticulum' at the inflorescence internodes, which resembles the situation in *Korthalsella.*

Fig. 8. Cross section at the node of *Korthalsella complanata (Touw 159)*, × 18. Arrows point to the two central vascular bundles, elements branching toward the flower cushions can be seen to the left of the bundles. There are fruits on the two flower cushions. — Fig. 9. Internodal cross section of *K. complanata (Touw 159)*, × 23. Arrows point to major vascular bundles. — Fig. 10. Internodal cross section of a basal joint of *K. complanata (Touw 159)*, × 13. Vascular bundles are enlarged compared to ordinary mature internodes; two bundles beginning to fuse are visible in the lower left quadrant of this section. — Fig. 11. Detail of a major vascular bundle, *K. complanata (Touw 159)*, × 125. xy: xylem; ph: phloem; fi: fibres (slightly lignified); sc: sclereid; pa: parenchyma; su: subepidermal layer, cells containing nuclei, chloroplasts and some inclusions are visible. — Fig. 12. Detail of two bundles anastomosing prior to fusing in a basal node of *K. complanata (Touw 159)*, × 40. Highly lignified fibres are visible as black patches and bands interspersed through the xylem, as well as in a bundle peripheral to it (fi). — Fig. 13. Cross section at the node of *K. remyana (Touw 170)*, × 20. Two bands of vasculature form an 'ellipse' within the round node. Arrows point to two bundles of xylem elements branching toward two of the fruits at the narrow end of the 'ellipse'. vi: viscin layer surrounding the seed; se: small portion of a seed; tr: trichomes of the flower cushion.

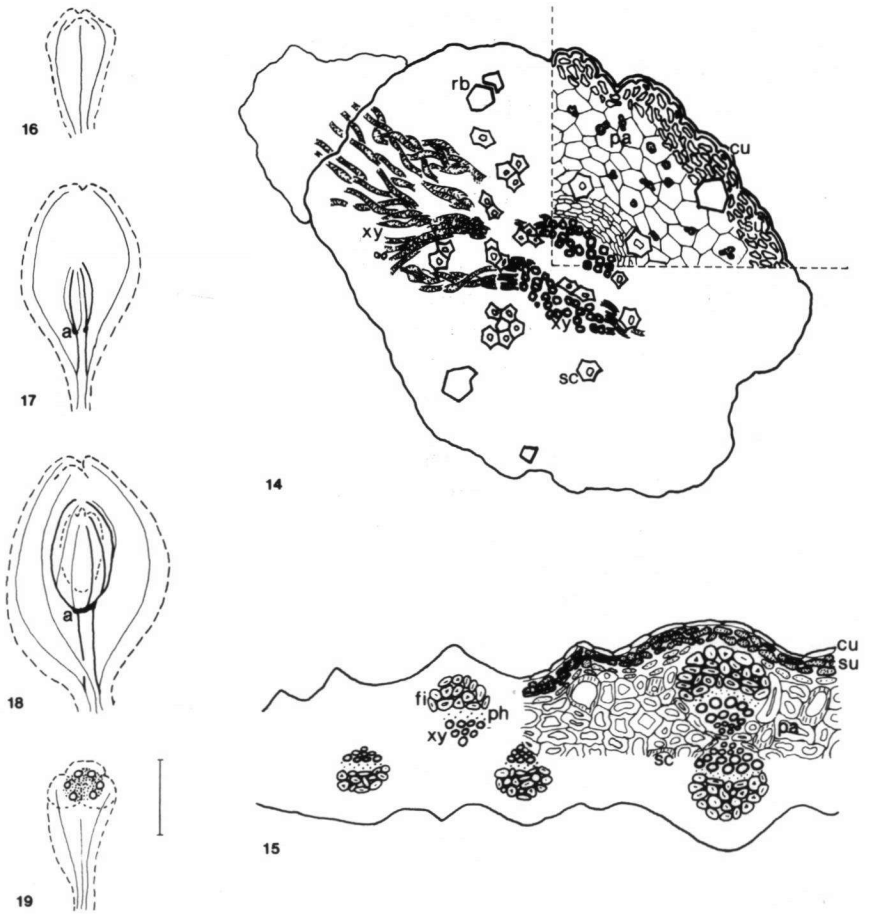

Fig. 14. Cross section at the node of *Korthalsella salicornioides (Bartlett s.n.)*, × 100. Note the two bands of vasculature forming a central column, and the vascular elements supplying a side branch. This is a juvenile (pre-flowering) specimen with thin-walled parenchyma and complete absence of fibres at the node. cu: cuticle; su: subepidermal layer; pa: parenchyma; rb: resin bodies; xy: xylem; sc: sclereid. — Fig. 15. Internodal cross section of a mature specimen of *K. rubescens (Grant 4070)*, × 100. Parenchyma is exceptionally thick-walled; diagonal stripes are used to distinguish sclereids from surrounding cells. fi: fibres; ph: phloem; for other abbreviations see figure 14. — Fig. 16–19. Flowers and fruit of *K. cylindrica (Kores s.n.)*, all to the same scale, bar × 1 mm. Flowers in all the taxa I have seen do not differ from these. a: abscission zone. Fig. 16. Pistillate flower with three small vascular bundles, one to each tepal. The small opening between the tepals allows access to the flat stigmatic surface (not shown). Fig. 17. Young 'fruit' which lacks an embryo but which is developing the vasculature that normally surrounds the seed. Fig. 18. Fruit, with seed (inner dashed line) surrounded by fully formed seed coat vasculature. The persistent tepals retain their vascular bundles. Fig. 19. Staminate flower bud with three bundles supplying the tepals and six separate anther thecae fused into one stamen (shown as a stippled area). Dehiscence is through a central pore (not shown).

RESULTS AND DISCUSSION

The classical characters used to delimit taxa (see paragraphs following discussion of anatomy) are often difficult and confusing to use, therefore anatomical characters have been studied here to see whether they would yield a more reliable differentiation. In one respect there is a consistent difference which may prove taxonomically useful: specimens either had less than 6 major vascular bundles or more than 8. The number can vary on one plant: broader internodes can have a larger number of bundles than young internodes close to the apex. The number also varies within a population and varies widely among plants not of the same population, even when they have the same general shape. However, there were no specimens which bridged the gap between a maximum of 6 bundles or a minimum of 8. This difference is discussed at greater length after table 1 and figures 20–29, together with the taxonomically insignificant variations in other aspects of the anatomy. Table 1 lists the specimens in the two groups, those with 8–16 bundles and those with 2–6 bundles. Figures 20–29 include diagrams of representative specimens covering the range of pattern found.

Table 1. Distribution of specimens examined among the two groups.
(See Appendix for specimens associated with the names, except where listed below.)

Group I : 8–16 bundles	*Number of vascular bundles*
(2) (= internode shape class)	
Korthalsella remyana	8
K. cylindrica	8
(3)	
K. aoraiensis	8
K. horneana	8
K. degeneri	10–11
(4)	
K. opuntia var. *fasciculata*	
Kajewski 1490 Queensland	8
K. platycaula	8–10
K. rubescens	8–12
(5)	
K. remyana var. *wawrae*	9–10
K. dichotoma	
Buchholz 1531 New Caledonia	8
Franc A24 New Caledonia	8–10
Franc 1218 New Caledonia	8–10
K. complanata (except St. John 15118)	8–12

Group I : 8–16 bundles *(continued)*	*Number of vascular bundles*
(5, *continued*)	
K. opuntia	
Brass 28379 Louisiades	8
African specimens	8
Clemens s.n. Queensland	8
K. platycaula var. *vitiensis*	8–14
(6)	
K. latissima	8–14
K. latissima var. *crassa*	12–16
K. opuntia McComish 18a Lord Howe Island	8–12
(7)	
K. opuntia	
Green 1641 Lord Howe Island	8–9
McComish 18 Lord Howe Island	8
K. complanata St. John 15118 Henderson Island	10–16
K. disticha	10–12
K. geminata	10–12
(8)	
K. papuana	8 or more
Group II : 2–6 bundles	
(1)	
K. salicornioides	4
K. dacrydii	4(–6)
(5)	
K. opuntia	
Jacobs 7196 Luzon	4
Hooker & Thomson s.n. Assam	2–5
Hooker & Thomson s.n. Khasia	4–6
Wilson s.n. Japan	4
Wilson s.n. Japan	4
K. dichotoma	
Virot 1398 New Caledonia	4–6
McPherson 3732 New Caledonia	4–5
McPherson 1927 New Caledonia	6(–7)
(8)	
K. opuntia Furuse s.n.	4
(9)	
K. lindsayi	4
K. clavata	4

General explanation regarding Figures 20–29: Diagrams of vascular patterns in cross section, and of details of vascular bundles: a) internode form; b) cross section taken at level of dashed line in a; c) bundle detail. Bar × 1 mm throughout and refers to the scale of the cross section. Conventions used in b) are as follows:

⓪ fibre ▼ xylem × phloem ⁘ sclereids ⎯ ⎯ ⎯ subepidermis

Figures 20–25: Group I, 8–16 bundles. Figures 26–29: Group II, 2–6 bundles.

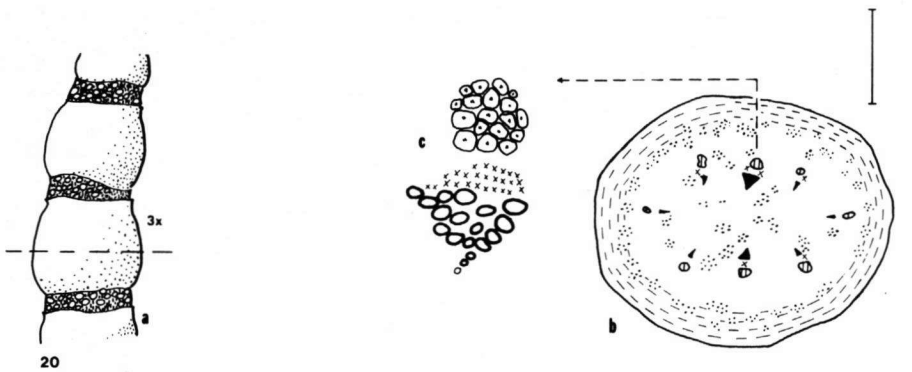

Fig. 20. *Korthalsella remyana (Touw 170).* Mature specimen. See also general explanation above.

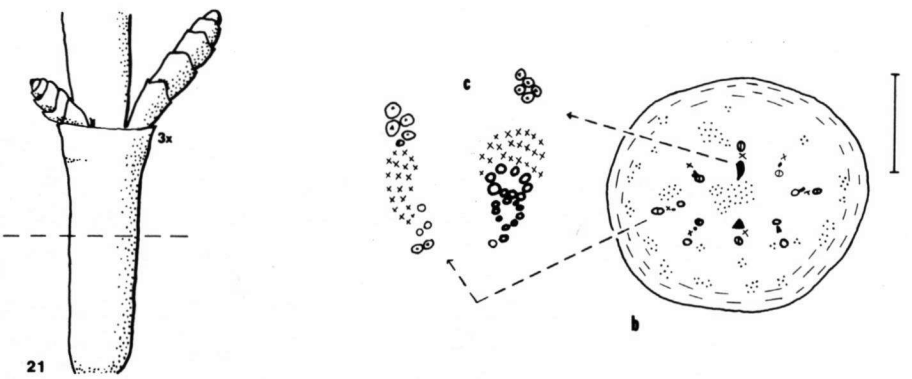

Fig. 21. *Korthalsella cylindrica (Touw 184).* Young specimen with very few flowering branches. Note small fibre bundles in c. See also general explanation above.

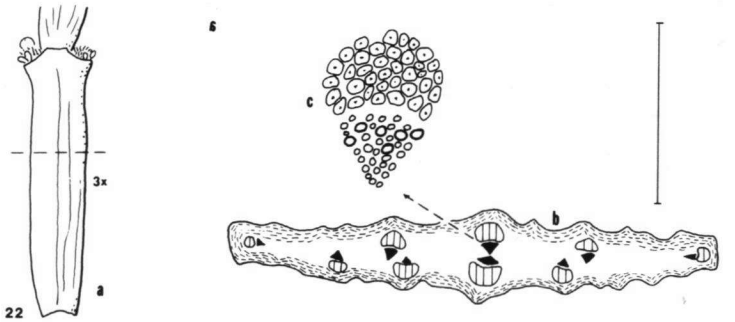

Fig. 22. *Korthalsella rubescens (Grant 4070)*. Young internode on a mature plant. Note abundance and organization of fibers in c. See also general explanation on p. 535.

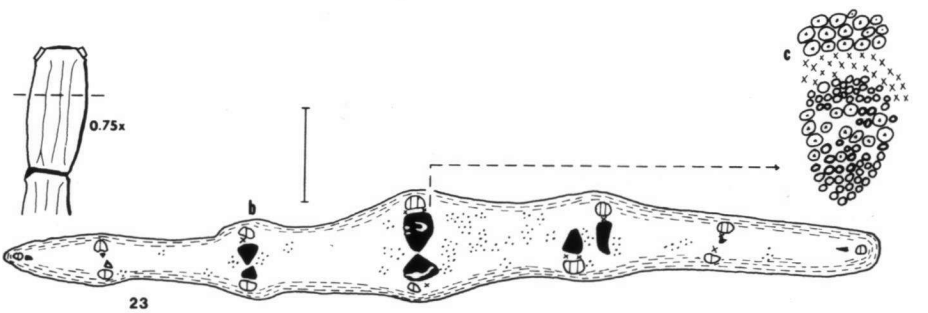

Fig. 23. *Korthalsella complanata (Remy 504; type)*. Note fibres included within the xylem in b and c. See also general explanation on p. 535.

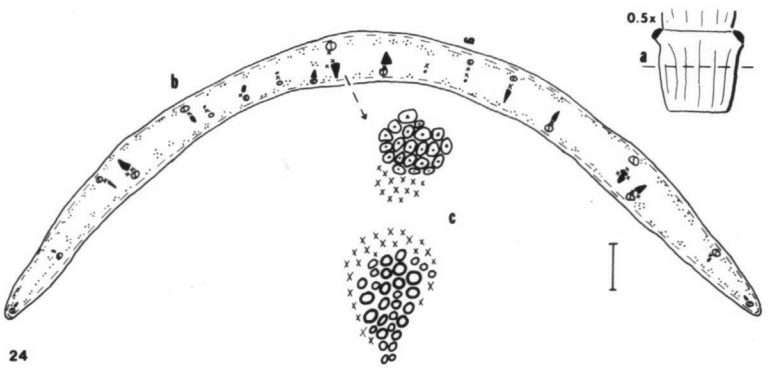

Fig. 24. *Korthalsella latissima (Touw 214)*. Curvature in b is not an artefact, but occurs in many of the broader Hawaiian mistletoes. See also general explanation on p. 535.

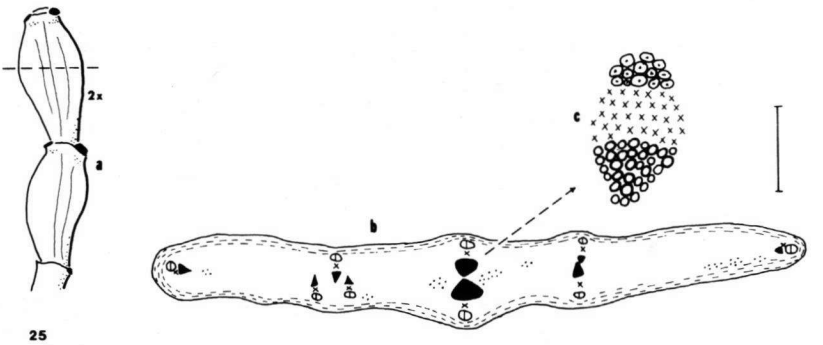

Fig. 25. *Korthalsella opuntia (Green 1641).* See also general explanation on p. 535.

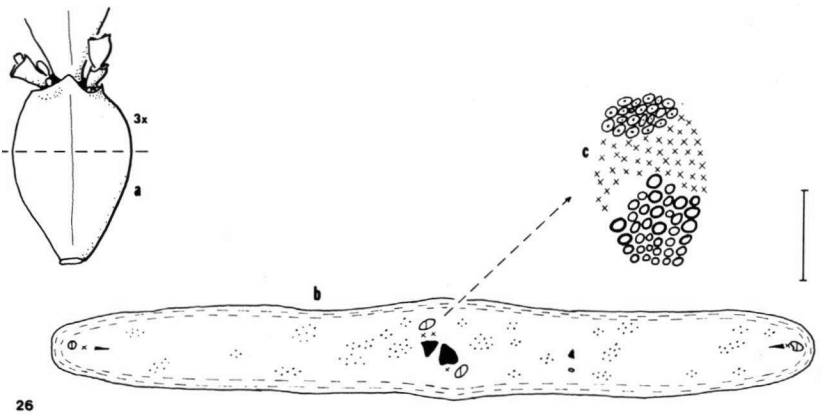

Fig. 26. *Korthalsella opuntia (Furuse s.n.).* See also general explanation on p. 535.

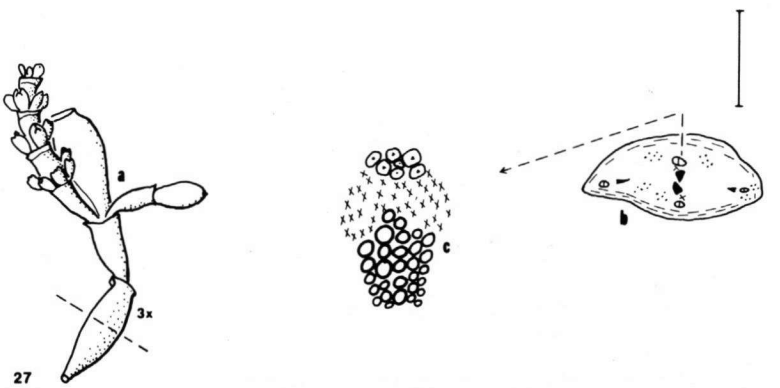

Fig. 27. *Korthalsella lindsayi (Anderson 85).* Nodal collars, visible directly below the fruit in a, are unusually well defined in this specimen. See also general explanation on p. 535.

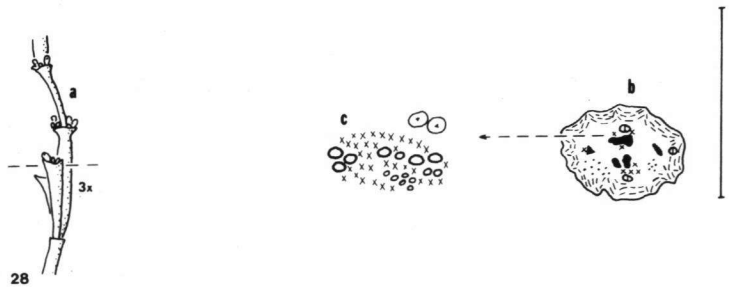

Fig. 28. *Korthalsella dacrydii (van Steenis 11494).* In c note that phloem and xylem are interspersed, and that there are few fibres. See also general explanation on p. 535.

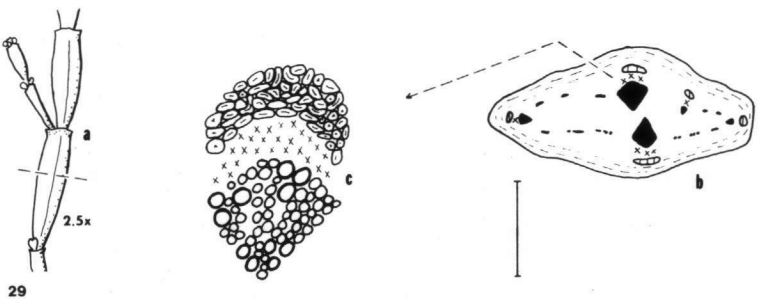

Fig. 29. *Korthalsella opuntia* var. *fasciculata (Hooker & Thomson s.n.).* Note subsidiary xylem bundles in b. See also general explanation on p. 535.

Fibres serve to distinguish between major vascular bundles and subsidiary ones, since size alone is not sufficiently reliable. The smaller reticulations are distinctly different in size, but there are intermediate bundles which can cause confusion, especially in the *fasciculata* group of specimens discussed below (e.g., see fig. 29). Since the number of bundles accompanied by fibres is constant within certain limits in a given plant, and since these are almost always the largest bundles in a given cross section, I have used the presence of fibres to define 'major vascular bundle' as the term used in this paper.

Quantity, and even presence, of fibres changes with age, so some qualification of the above definitions is necessary. Plants in seedling stage (when the plant is only a few internodes long) and the youngest internodes on all plants do not have fibres. Seedlings and juveniles of flat 8–16 bundle plants have 8 discrete fibreless bundles in the earliest stages, but in round plants the number of major bundles may be very unclear. In the juvenile stage (from seedling to first flowering) fibres start to develop but not on all bundles equally. The two central bundles are the first to acquire fibres.

(At this stage some 8–16 bundle plants, especially the rounder ones, can look deceptively similar to mature 2–6 bundle plants.) Later the other bundles acquire fibres more or less simultaneously, starting with a few fibres (see *K. cylindrica* in fig. 21) and gradually increasing to a sizable mass. Since juvenile plants tend to have few fibres even in basal internodes, the plants tend to be more lax. Conversely, older internodes, which are found low on the plant, have an exceptionally high number of fibres (fig. 15), as well as many xylem elements. The latter can cause the boundaries of bundles to become indistinguishable (fig. 12). Since fibres are used to define major bundles, only mature internodes can be used to distinguish reliably between 8–16 and 2–6 bundle taxa. Using over-mature basal internodes, apices, and juveniles can lead to confusion.

The complex of plants usually identified as *K. opuntia* var. *fasciculata* are an interesting intermediate case. Though they have 6 bundles of fibres or less, they have regions of intermediate size xylary strands connecting the bundles marked by fibres (see *K. opuntia* var. *fasciculata* in fig. 29). The two central bundles are larger than the subsidiary ones, but as one progresses toward the basal internodes in these plants, some of the subsidiary bundles may acquire fibres. In the equivalent ssituation in 8–16 bundle taxa, there is so much xylem and fibre in the bundles that these run together and/or form a large column of lignified tissue. However, basal internodes in the var. *fasciculata* type of specimens can cause confusion if their overmature nature is ignored.

There is a correlation between size of the internodes and, therefore, of the plant to some extent and number of vascular bundles. Most of the 2–6 bundle taxa have very small internodes, though some of the flattened internodes are as large as those found in medium-sized 8–16 bundle taxa, such as *K. complanata*. On the other hand, the minute internodes found in the flowering branches of *K. geminata*, an 8–10 bundle taxon, which are as small as some of the smallest internodes found in 2–6 bundle taxa, have the full complement of 8 to 10 bundles. Aside from these exceptions, however, the correlation between size of internode and number of vascular bundles is quite close.

Other aspects of the anatomy proved to be inconsistently variable or dependent on various factors. Age and certain environmental conditions seem to have a similar effect on anatomy. Plants known to have grown in drier, more exposed habitats (e.g., *Touw 170*) develop thicker parenchymal cell walls or increased numbers of sclereids throughout the plant; other plants may develop these characters only in rather old internodes or not at all. Number of sclereids seems to vary almost randomly, but there is some correlation with age; some older internodes may have so many that parenchyma cell walls are no longer visible. Their distribution varies, too, but longitudinal sections show that this depends at least partly on where the internode happens to be cross sectioned. Number of fibres within a bundle varies together with parenchymal wall thickness to some extent.

Colour and density of the subepithelial inclusions varies between plants from dark red-black to brown, yellowish, or greenish; but this variation is difficult to interpret. In the *K. rubescens* specimen (fig. 15), the layer is extremely dense and reddish black.

The specimen collected by St. John on Henderson Island and called *K. complanata*, shows precisely the same sort of layer. Perhaps the conditions under which these two plants grew caused the exceptional development of this layer. (However, it seems unlikely that a plant growing at 970 feet in the Society Islands and one found on an uplifted coral reef like minute Henderson Island, which is nowhere higher than about 100 feet, would be growing under the same general environmental conditions.) There are pink to orange to red to reddish black inclusions within the multicellular trichomes on flower cushions of almost all taxa in the genus. When these inclusions are absent, the trichomes appear white. Like the subepithelial inclusions, they show no reaction to the chemicals used in clearing.

Turning now to a discussion of the classical infrageneric characters, the genus was divided into three sections by Danser (1937) on the basis of presence of specialized inflorescence branches, or absence of the same and distichous versus decussate branch insertion. The first section contains only 5 species, *K. geminata, K. papuana, K. lindsayi, K. clavata*, and *K. amentacea.* The rest of the taxa, those considered to lack specialized branches, are almost evenly divided between the remaining two sections based on distichous or decussate phyllotaxy.

A perusal of the list of specimens at the end of this paper quickly shows how little correlation there is between Danser's infrageneric groups and vascular bundle number. Not only are the sections heterogeneous in this regard, but even some species, notably *K. opuntia*, include both vascular types. One possible explanation is that reduction (or increase) in bundle number was a repeated event. But the change would have had to occur several times to fit into Danser's classification. Furthermore, the 2–6 bundle taxa are distributed in two belts, one extending from New Zealand to Australia (and perhaps to Madagascar – material from there was not available), the other going from temperate and tropical Asia through the Philippines, south to New Caledonia. Possibly these two belts could have arisen independently because they differ slightly from each other in that the northern plants are more robust and tend to have more subsidiary bundles. But it seems to make matters unnecessarily complicated to split both these regions among different generic sections and then to postulate the evolution of multiple convergences. Another possible source of the discrepancy between bundle numbers and Danser's classification is that the characters on which the latter is based are not always satisfactory.

It is difficult to understand how phyllotaxy could have been construed as such a central character. Phyllotaxy can vary on one plant or be neither distichous nor decussate but 'oblique'. Even at the apices, though most plants are clearly either distichous or decussate there, some specimens show the undeveloped internodes at various intermediate angles relative to each other. Phyllotaxy is often consistent in a given population but is not therefore easily definable as either distichous or decussate. Some populations show a marked tendency to develop whorled branches by means of multiple young shoots on older nodes. Such variability would imply that phyllotaxy cannot be used as a distinguishing character above the varietal level. The unavailability of live plants may explain why this character was weighted so heavily.

Specialized inflorescence branches are branches devoted exclusively to flower

bearing and differ markedly in shape from the other, purely vegetative branches of the plant (e.g., *K. lindsayi*, fig. 27). In order to understand the significance of specialized inflorescence branches it is necessary to consider the phased growth pattern in *Korthalsella*. Vegetative buds elongate rapidly into branches, but growth almost stops once flowers develop at their nodes. There can follow a period of continued vegetative growth at the apex of the branch and of continued flowering on all sufficiently matured nodes of the branch. Then a quiescent period occurs and vegetative buds develop in the flower cushions. When these buds elongate, the formerly flowering branches become largely vegetative branches supporting the new flowering ones. (They may still bear some flowers in the cushions at the base of the new branches.) The older an internode is, the less likely it is to bear flowers. In some plants, the loss of ability to flower is complete after a given growth phase (usually the first), rather than gradual, which causes there to be vegetative* (old) or flowering (young) branches without intermediates.

Only *K. geminata, K. papuana, K. lindsayi, K. clavata*, and *K. amentacea* are supposed to have specialized branches. *Korthalsella geminata* and *K. papuana* do have remarkable, long, terete inflorescence branches which contrast sharply with the broad flat vegetative internodes. The terete inflorescence branches of *K. lindsayi* (fig. 25) are much shorter than those of the previous two taxa but are distinct from the flat vegetative branches. However, there is no discernible difference between *K. lindsayi* and *K. salicornoides*, both from New Zealand, except in the flattened vegetative internodes of the former. *Korthalsella clavata*, with slightly flattened vegetative internodes, shows a range of shapes intermediate between the terete internodes of *K. salicornioides* and the broad flat ones of *K. lindsayi*. In other words, *K. lindsayi* may have specialized vegetative branches rather than specialized inflorescence branches. No authenticated specimen of *K. amentacea* was available but, judging by descriptions (Danser, 1937; Kores, pers. comm.), the 'inflorescence branches' in *K. amentacea* might simply be the youngest branches on the plant, which, of course, always bear the most flowers. I have seen specimens, usually identified as *K. opuntia* var. *fasciculata*, which show heavily flowering young branches. These, precisely because they are young, are short and elliptical rather than flat in cross section. (*Korthalsella* internodes change shape with age to some extent, because their initially 'chubby' shape is followed by expansion first in breadth and last in length.) In this case, internodes are present which are intermediate in shape between young and old internodes. These 'medium' internodes often do not bear flowers at their nodes because they are past their first growth phase. Thus one is left with the impression that flowers are borne only on short, more or less terete, branches. On occasion, misinterpretation of the nature of such branches has led to misidentifications. The last case is one where young internodes assume the shape of older ones very rapidly and therefore do not differ from them significantly in shape but which do bear most of the flowers. There has been insufficient distinction between flower-bearing branches of a very different

* Vegetative is used here to mean branches or internodes which do not bear flowers at their nodes, though they may bear other branches which do flower.

shape, and branches which bear most or all of the flowers but differ in shape only because they are young, and branches shaped like all others on the plant but simply bearing more flowers. All may seem to be specialized inflorescence branches, but in some, for instance *K. geminata* and *K. papuana*, it seems to be a true specialization of the branch, whereas in the others it seems to be a restriction of the age at which a branch will bear flowers or the speed with which it assumes an 'old' shape.

Arrangement of flowers in the individual inflorescences has been considered an important character, but it seems to be age-dependent. *Korthalsella geminata* is unique in having a structural inflorescence with only 3 flowers per axil, even when fully mature. But *K. lindsayi*, which is reported to have only five flowers per axil (Stevenson, 1934), shows encircling rings of numerous fruits with no particular pattern at maturity, which is more similar to the unpatterned arrangement common on flower cushions of all other taxa. Very young inflorescences have the same organization in all the specimens I have seen: a central staminate flower emerges first, flanked by two (almost always) pistillate flowers. Later two more (usually) pistillate flowers emerge which flank the original triad of flowers. After this initial sequence, the pattern of the flowers on the enlarging cushion becomes disorganized. The arrangement of the inflorescences is almost perfectly correlated with the flatness of the branch. The initial triads are always in two separate lateral groups; in the flat specimens the inflorescences stay in two groups regardless of how large the flower cushion becomes through the continued formation of flowers at its base. The rounder the specimen, the likelier it is that growth of the cushions will eventually allow them to meet in the centre. One Hawaiian population of *K. remyana* in Niu Valley takes this process one step further and has perfectly encircling inflorescences (see *K. remyana* in fig. 20).

CONCLUSION

Vascular patterns divide *Korthalsella* into two major groups. These groups cut across currently accepted infrageneric lines based on phyllotaxy and the presence of specialized inflorescence branches. However, they are closely associated with other, more consistently varying, characters. The 2–6 bundle, Group II, plants tend to have markedly smaller internodes and are usually smaller plants than those in Group I. However, the *K. opuntia* var. *fasciculata* specimens proved to be somewhat intermediate. Not only do they have a large number of subsidiary xylem bundles, but they are also the largest plants in the 2–6 bundle group and exceed some 8–16 bundle plants in size. Group II plants also have their inflorescences on branches with short terete internodes, which allows the inflorescence to encircle the node at maturity. This also causes the flower-bearing branch to look congested with fruits when these are ripe. But short-internode terete flower-bearing branches are also found in *K. geminata* from Malesia and *K. papuana* from New Guinea and Queensland, which have at least 8 bundles.

The presence of small internodes and of inflorescences on terete branches bear a reasonably close relation to the presence of 2–6 vascular bundles in the specimens

studied. Although there is some correlation between size and number of vascular bundles, it is not necessarily a functional correlation because bundle number can be independent of size. Furthermore, the number does not vary beyond certain limits within one plant or population of plants. Number of vascular bundles may therefore be a factor in a future infrageneric realignment of *Korthalsella.*

APPENDIX – SPECIMENS EXAMINED

Specimens with an asterisk used in figures; the capital letters after collectors' numbers refer to Danser's three major sections (A: with specialized inflorescence branches, B: with decussate phyllotaxy, C: with distichous phyllotaxy); numbers following that refer to bundle number.

(1) (= branch shape class)			
Korthalsella salicornioides (Cunn.) Van Tiegh.*	Auckland	Bartlett s.n.	B 4
K. salicornioides	Auckland	Cheeseman s.n.	B 4
K. salicornioides	Ruahine	Allan s.n.	B 4
K. dacrydii (Ridley) Danser*	Java	van Steenis 11494	B 5
(2)			
K. remyana Van Tiegh.*	Oahu	Touw et al. 170	B 8
K. remyana	Oahu	Touw et al. 171	B 8
K. cylindrica (Van Tiegh.) Engl.*	Molokai	Touw et al. 184	C 8
*K. cylindrica**	Molokai	Kores s.n.	C 8
(3)			
K. horneana Van Tiegh.	Fiji	Horne 894 – Type	B 8
K. horneana	Fiji	Smith 4228	B 8
K. horneana	Fiji	Greenwood 840	B 8
K. degeneri Danser	Oahu	Degener 11870 – Type	C 10–11
K. aoraiensis (Nad.) Engl.	Tahiti	Gagne 1599	C 8
K. aoraiensis	Tahiti	van Balgooy 1786	C 8
K. binii Pichi Sermolli	Ethiopia	Pichi Sermolli 2488	C 8
(4)			
K. platycaula (Van Tiegh.) Engl.	Kauai	Degener 20594	C 8(–10)
*K. platycaula**	Oahu	Touw 160	C 8
K. platycaula	Oahu	Palmer & Obata s.n.	C 10(11)
K. rubescens (Van Tiegh.) Lec.*	Tahiti	Grant 4070	C 8–12
K. rubescens	Raiatea	Moore 685	C 8
K. dichotoma (Van Tiegh.) Engl.	New Caledonia	Buchholz 1531	C 8
(5)			
K. remyana var. *wawrae* Danser	Kauai	Degener 12661	B 8(10)
K. dichotoma (Van Tiegh.) Engl.	New Caledonia	Franc A24	C 8–10
K. dichotoma	New Caledonia	Franc 1218	C 8–10
K. dichotoma	New Caledonia	Virot 1398	C 2–4
K. dichotoma	New Caledonia	McPherson 3732	C 4–5
K. dichotoma	New Caledonia	McPherson 1927	C 6(–7)
K. complanata (Van Tiegh.) Engl.*	Maui	Remy 504 – Type	C 8–12
K. complanata	Oahu	Touw et al. 179	C 8–10
*K. complanata**	Oahu	Touw 159	C 10?
K. opuntia (Thunb.) Merr.	Louisiades	Brass 28379	C 8

(Appendix continued)

(5, *continued*)			
K. opuntia	Réunion	Lorence R19	C 8
K. opuntia	Mauritius	Lorence 1122	C 8
K. opuntia	Mauritius	Lorence 1967	C 8
K. opuntia	Mauritius	Lorence M7	C 8
K. opuntia	Queensland	Clemens s.n.	C 8
K. platycaula var. *vitiensis* (Van Tiegh.) Danser	Fiji	Smith 7888	C 8–14
K. opuntia	Japanese Islands	Wilson s.n.	C 4
K. opuntia	Luzon	Jacobs 7196	C 4
K. opuntia var. *fasciculata* (Van Tiegh.) Danser*	Assam	Hooker & Thomson s.n.	C 2–5
K. opuntia	Kashmir	Stewart 17462	C 4
K. opuntia var. *fasciculata*	Queensland	Kajewski 1490	C 8
K. opuntia	New South Wales	Johnson & Constable 32027	C 8
K. opuntia	New South Wales	Hadley 20557	C 8
(6)			
K. latissima (Van Tiegh.) Danser	Hawaii?	Remy 504 – Type	C 8–14
K. latissima	Oahu	Touw et al. 188	C 8–12
K. latissima	Oahu	Palmer & Obata s.n.	C 8–12
*K. latissima**	Kauai	Touw et al. 214	C 8–16
K. latissima var. *crassa* (Van Tiegh.) Danser	Hawaii	Faurie 981	C 12–16
K. opuntia	Lord Howe	McComish 18a	C 8–12
(7)			
*K. opuntia**	Lord Howe	Green 1641	C 8–9
K. opuntia	Lord Howe	McComish 18	C 8
K. complanata	Henderson	St. John 15118	C 10–16
K. disticha	Norfolk	Green 1420	C 10–12
K. geminata (Korth.) Engl.	Borneo	Clemens 33902	A 10
K. geminata	Sumatra	van Steenis 10051	A 10–12
(8)			
K. papuana Danser	Papua New Guinea	Carr 15120 – Type	A 8+
*K. opuntia**	Japanese Islands	Furuse s.n.	C 4
(9)			
K. lindsayi (Hook. f.) Engl.*	New Zealand, South Island	Anderson 85	A 4
K. lindsayi	New Zealand, South Island	Kirk s.n.	A 4
K. clavata (Kirk) Cheeseman	New Zealand, South Island	Kirk s.n.	A 4

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