

ANATOMY AND EVOLUTION IN THE MACARONESIAN SONCHUS SUBGENUS DENDROSONCHUS (COMPOSITAE - LACTUCEAE). NODAL AND PETIOLAR VASCULAR PATTERNS.

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RESUMEN

Sugerencias previas referidas a la evolución de las especies Macaronésicas de *Sonchus* (Compositae - Lactuceae) subgénero *Dendrosonchus* dentro de las dos tendencias básicas se completan con investigaciones de los modelos vasculares nodal y peciolar. El número de lagunas en el nudo varía de tres a diez y los vasos peciolares también exhiben una amplia variación de tipos. Como estos modelos de vasos peciolares no han sido descritos previamente para ningún otro Angiosperma, se sugiere una nueva terminología. Los cuatro tipos básicos son denominados el U-type, el U-plus-phloem-type, el O-by-phloem-type y el O-by-xylem-and-phloem-type. El número primitivo de lagunas en el nudo se considera que es tres y la condición vascular peciolar primitiva es el U-plus-phloem-type.

CONTENTS

Introduction	41
Material and Methods	42
Results	42
Discussion	49
Acknowledgements	57
References	57

INTRODUCTION

The subgenus *Dendrosonchus* Webb ex Schultz Bip. comprises the woody, pachycaulous members of the genus *Sonchus* L. which are endemic to the islands of the Canaries, Madeira and Cape Verdes with one species also occurring in Western Morocco. Two sections are recognised within the subgenus, being *Dendrosonchus* with fourteen species and five subspecies and *Atalanthus* (D. Don) DC. with three species and five subspecies (Aldridge, 1976b). The morphological characteristics of the group have previously been described (Aldridge, 1976a, 1976b) and using this information in

conjunction with that of anatomy the evolution of the members may be elucidated. It has been shown (Aldridge, 1977) that two major trends of evolution, one within each of the two sections, can be interpreted from the quantitative and qualitative observations of the tracheary elements. The present study of the nodal and petiolar vascular patterns is used to clarify, within the two sections, the evolutionary situation of the species.

MATERIALS AND METHODS

Fresh material was found to give the best results but when this was unobtainable herbarium specimens were used after 'reviving' the appropriate parts in boiling water. Voucher specimens of the material used for this study are preserved in the herbarium, Reading University. Many samples were examined and several nodes were serially sectioned from each sample, the series being cut from the region below the node to that above it. Where a leaf was still attached to the stem, that is in the higher or younger regions of the stem, the serial sections were taken from below the node and into the petiolar region up to 30 mm along its length. Several petioles were sectioned to determine the constancy or variability of the vascular patterns.

Howard (1974) stated that to obtain the nodal and petiolar vascular patterns in three dimensions it is necessary to make sections progressively from the internode, through the node and into the petiole. Initially, sections were taken at wide intervals through these regions to determine where the critical areas of pattern change occur. As this method of investigation entailed very large numbers of sections the staining used was the rapid, temporary, microchemical test for lignin by phloroglucinol and concentrated hydrochloric acid. Free-hand diagrams were made of each section and interpretations of the three-dimensional vascular structures were made. The interpretation of vascular patterns in herbarium material proved to be more difficult, especially when the leaves had become detached from the stem in the process of drying. It was at this junction that petiole vascular patterns were found to be most critical in fresh material.

RESULTS

The nodal and petiolar vasculatures of *Dendrosonchus* s.l. are extremely variable from species to species. The numbers of

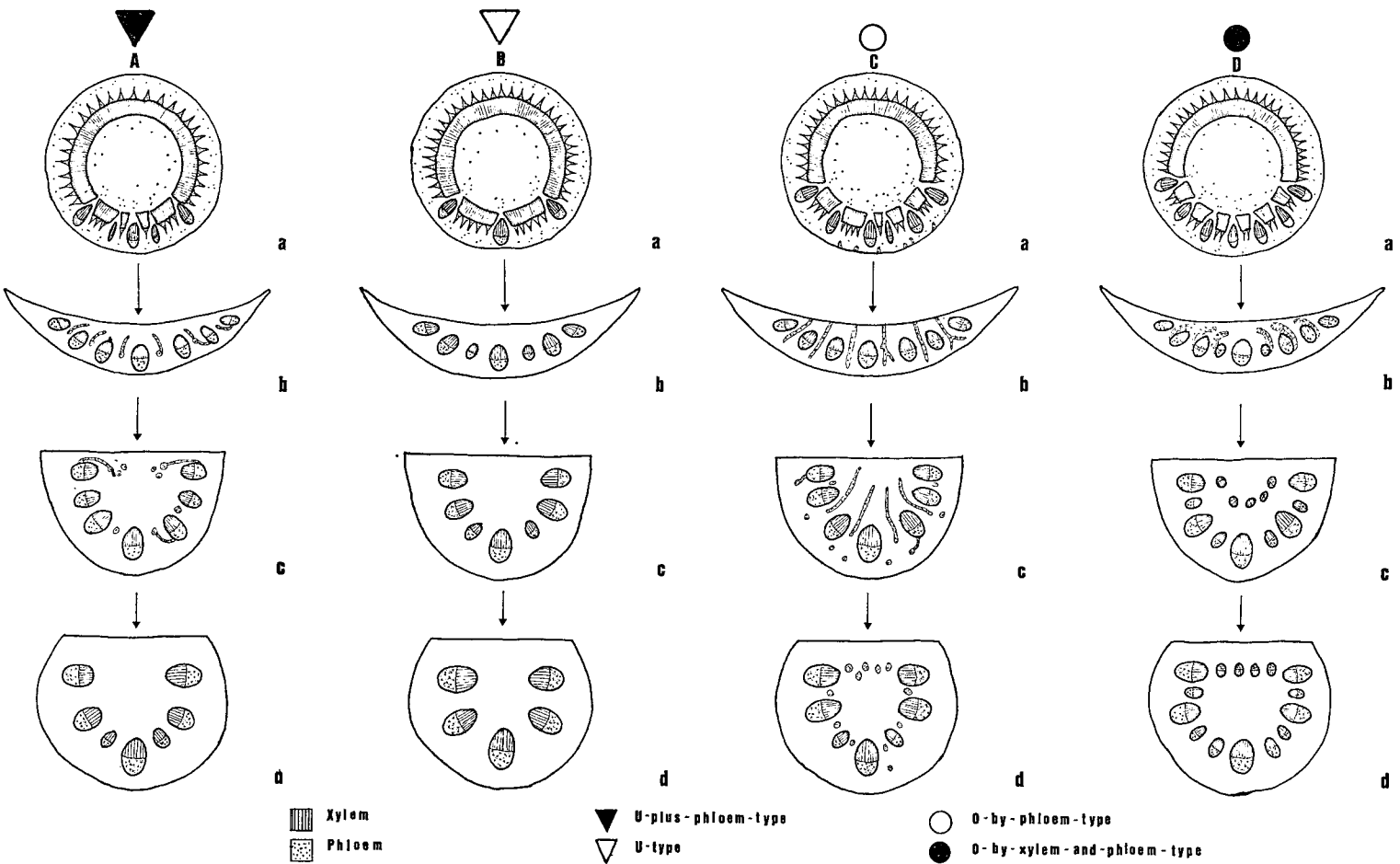


Figure 1. Nodal and petiolar vascular patterns (see text for details).

lacunae at the node range from three to ten. Each lacuna is formed by the departure from the stele of one leaf trace which may remain discrete throughout the length of the petiole, or it may divide into two or more traces before or after it has entered the petiole.

There are four basic types of petiolar vascular supply in the subgenus *Dendrosonchus* and these are illustrated in Figure 1. Using the typology of Hare (1942-3), the simplest petiolar vasculature is the U-type as shown in Figure 1B. For purposes of describing the three-dimensional structures of the nodes and petioles from two-dimensional diagrams of the sections, movements of bundles to new situations from section to section are given. These 'movements' are, however, not intended as interpretations of directions of development. Figure 1 Ba shows the departure of the leaf traces from the stele. There are usually three lacunae but in some species with this type, one or two minor, lateral lacunae have been seen. Figure 1 Bb, the proximal portion of the petiole as it departs from the stem, shows that the leaf traces have divided to form subsidiary, lateral vascular bundles. In the central region along the petiole, as shown in Figure 1 Bc, these vascular bundles remain undivided and are positioned in the petiole in a U-shape. This shape continues through the petiole to the distal position, as seen in Figure 1 Bd, but the minor, lateral traces have fused.

A modification of Hare's system is required to describe the other basic types of petiolar vascular supply found in *Dendrosonchus*. These types have not previously been described for any angiosperm and, therefore, a new terminology is proposed. The second type is here called the U-plus-phloem-type as illustrated in Figure 1. Figure 1 Aa shows the leaf traces departing from the stele. The numbers of lacunae found in the species with this type are either three, three with one or two minor laterals, five, five with one lateral, six or seven. After the vascular bundles have moved into the proximal position of the petiole, as shown in Figure 1 Ab, small phloem strands depart from the phloem regions of the bundles to positions between them. Some of these phloem strands may then move towards the adaxial position of the petiole. Figure 1 Ac shows the situation in the central region along the petiole where the adaxial phloem strands are beginning to fuse with one another and to move to fuse with the phloem of the extreme lateral bundles. Also the phloem strands remaining on the abaxial side show a tendency to fuse back into the phloem of the abaxial vascular bundles. Figure 1 Ad shows the situation in the distal region of the petiole where there are no longer any signs of phloem strands. The pattern at this level in the petiole is practically identical to that in the U-type.

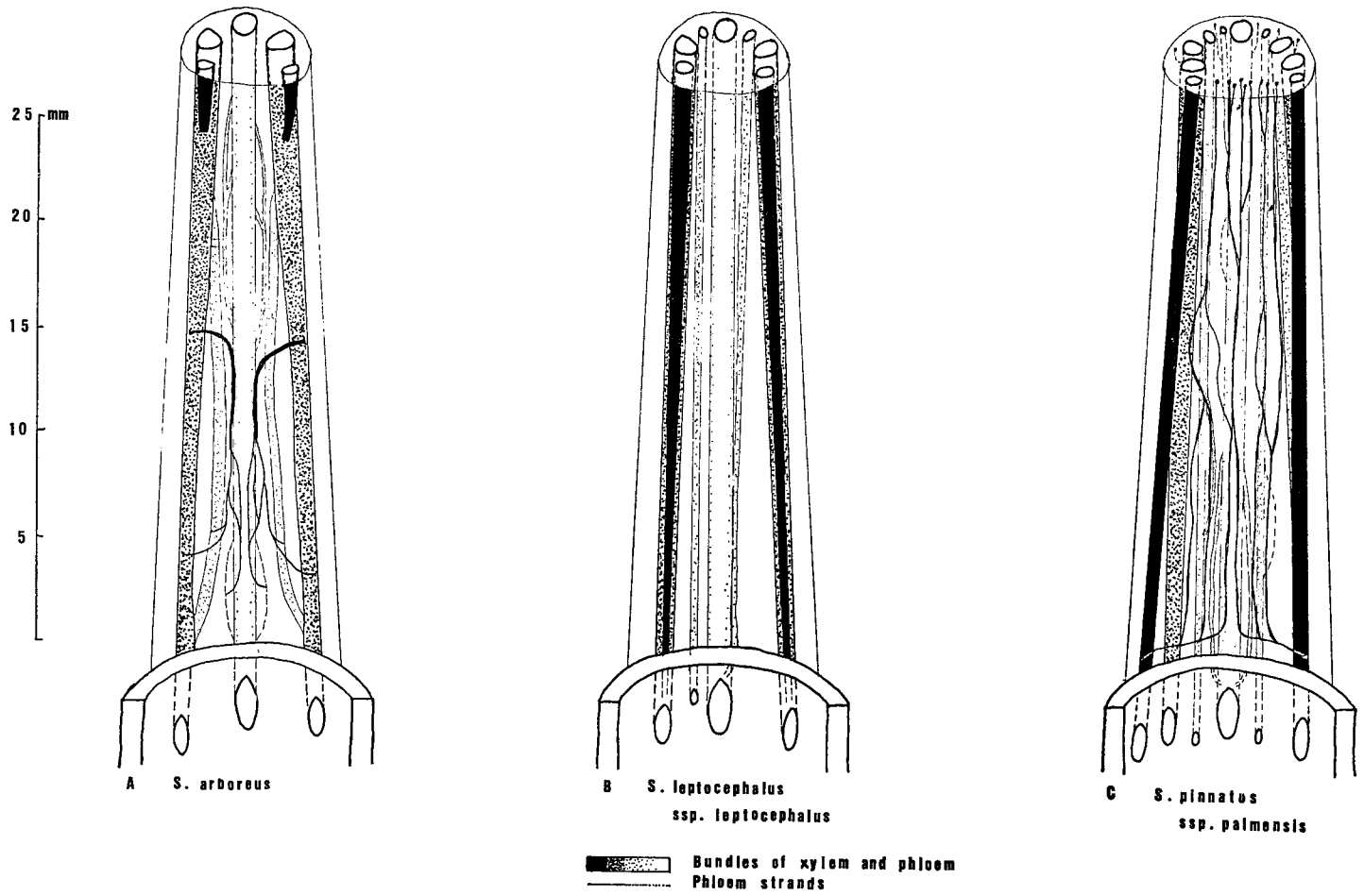


Figure 2. Nodal and petiolar vasculares of section *Alanthus* (see text for details).

The third type of petiolar vascular supply is here termed the O-by-phloem-type and is illustrated in Figure 1 C. As in the previous type, phloem strands only are involved in a course through the medullary region of the petiole. Figure 1 Ca shows that many more leaf traces leave the stele and also that the cortical phloem strands take part in the vascular supply of the petiole. Six or seven lacunae are formed in species with this type. The proximal region of the petiole, as shown in Figure 1 Cb, has these cortical phloem strands moving across the petiole to the abaxial position. Some strands move from this phloem into the abaxial, cortical region of the petiole, while almost immediately the remainder begin to move back across the medullary region to the abaxial position as shown in Figure 1 Cc. In the distal region, these phloem strands are in an adaxial position. The arrangement of the vascular supply then appears as a ring as seen in Figure 1 Cd.

The fourth type of petiolar vascular supply is here called the O-by-xylem-and-phloem-type. In this situation movement of complete vascular bundles with both xylem and phloem tissue through the medullary region of the petiole produces an extremely complex pattern. This is the most common type of vascular pattern within the section *Dendrosonchus*, but is only found in one subspecies of the section *Atalanthus*. This type of petiolar vasculature is shown in Figure 1 D. The numbers of lacunae in the stele of this type range from three with one minor lateral, to ten. Immediately after the leaf traces have entered the petiole and moved into an abaxial position, minor lateral bundles depart from them as shown in Figures 1 Da and 1 Db. These minor traces then move across the medullary region and in so doing turn around within the petiole until their xylem faces the abaxial side of the petiole i.e. they are completely inverted. Figure 1 Dc shows these medullary bundles attaining this new orientation. They continue to move across the cortex until they reach the adaxial position where they remain to form a complete ring of bundles. This situation is seen in the distal region of the petiole as illustrated in Figure 1 Dd.

An intermediate situation between the U-plus-phloem-type and the O-by-xylem-and-phloem-type was consistently found in one species, *S platylepis*. One or a few strands of xylem and phloem move from an abaxial vascular bundle to the adaxial position, but almost immediately return to their original position. This could be termed the U-plus-xylem-and-phloem-type. This species is also interesting in that strands of cortical phloem move from the stem to the abaxial position in the petiole and, therefore, could be considered as intermediate between the U-type and the O-by-phloem-

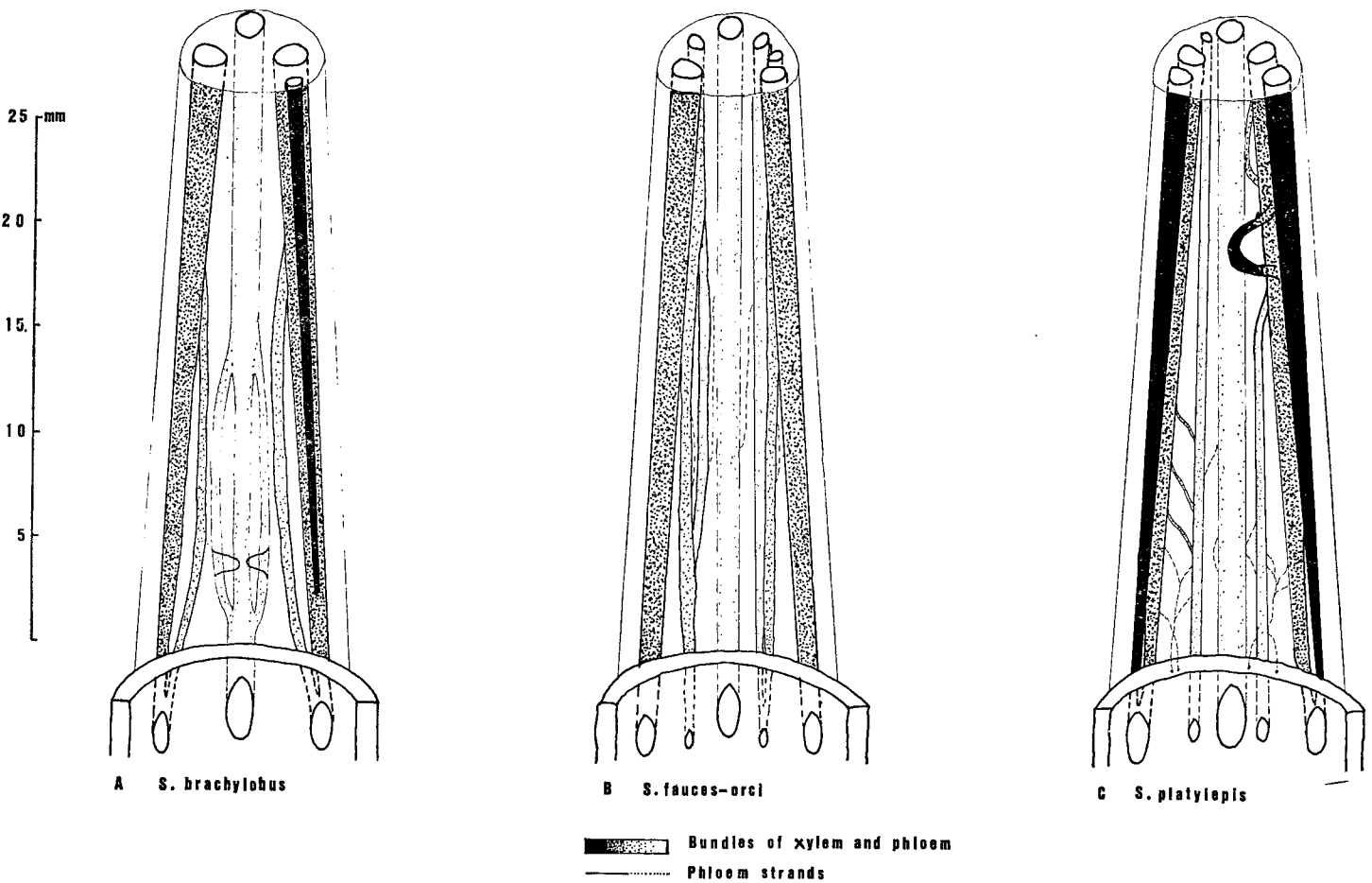


Figure 3. Nodal and petiolar vasculares of section *Dendrosonchus* (see text of details).

type. These abaxial phloem strands do not move towards the adaxial position, as in the O-by-phloem-type, but fuse with the abaxial vascular bundles.

Table 1 gives a list of species with their type of petiolar vascular pattern and the numbers of lacunae that have been found. The species are listed in the order of their average, vessel length to width ratios (as explained in Aldridge, 1977). *Sonchus brachylobus* var. *canariae* and *S. daltonii* have been added to this list and placed in the positions where they are thought to fit best on morphological evidence (cf. Aldridge, 1976a, 1976b). *Sonchus daltonii* is a caudex (or short, woody-stemmed) perennial species which closely resembles *S. acaulis*, and it was placed near the end of the list in the section *Dendrosonchus*.

To illustrate the complex nature of the nodal and petiolar vasculature within the two sections of *Dendrosonchus*, Figures 2, 3 and 4 show three-dimensional drawings of stems and petioles of 30 mm of selected species. For simplicity the stems are shown as cross sections through the vascular tissue. The phloem strands can be distinguished as they are represented by simple lines (dotted when on the adaxial surface), whereas xylem and phloem strands are solid lines. Figure 2 A is the nodal and petiolar vascular supply found in *S. arboreus* which has three lacunae and the U-plus-phloem-type of petiolar vasculature. The U-type in section *Atalanthus* is illustrated by *S. leptocephalus* subsp. *leptocephalus* in Figure 2 B. Here a minor, lateral strand, making its own small lacuna, is shown. The O-by-phloem-type of vasculature in section *Atalanthus* is found in *S. pinnatus* subsp. *palmensis* and is illustrated in Figure 2 C.

Figures 3 and 4 show the types of vasculature in species of section *Dendrosonchus*. Figure 3 A represents the U-plus-phloem-type found in *S. brachylobus*. Only a minute amount of phloem was seen to supply the adaxial position for a very short distance in the proximal region of the petiole. The U-type is illustrated by *S. fauces-orci* in Figure 3 B. The intermediate type of petiolar vascular supply between the U-plus-phloem and the O-by-xylem-and-phloem types is shown in Figure 3 C. This situation, the U-plus-xylem-and-phloem-type, is surprisingly asymmetrical and is found in *S. platylepis*, as discussed above. Figure 4 A shows the O-by-phloem-type as seen in *S. congestus*. Figures 4 B and 4 C depict the vascular patterns of the nodes and petioles of *S. radicans* and *S. acaulis*, respectively. The, both have the O-by-xylem-and-phloem-type of petiolar vasculature.

Sections through the distal end of the petioles of *Dendro-*

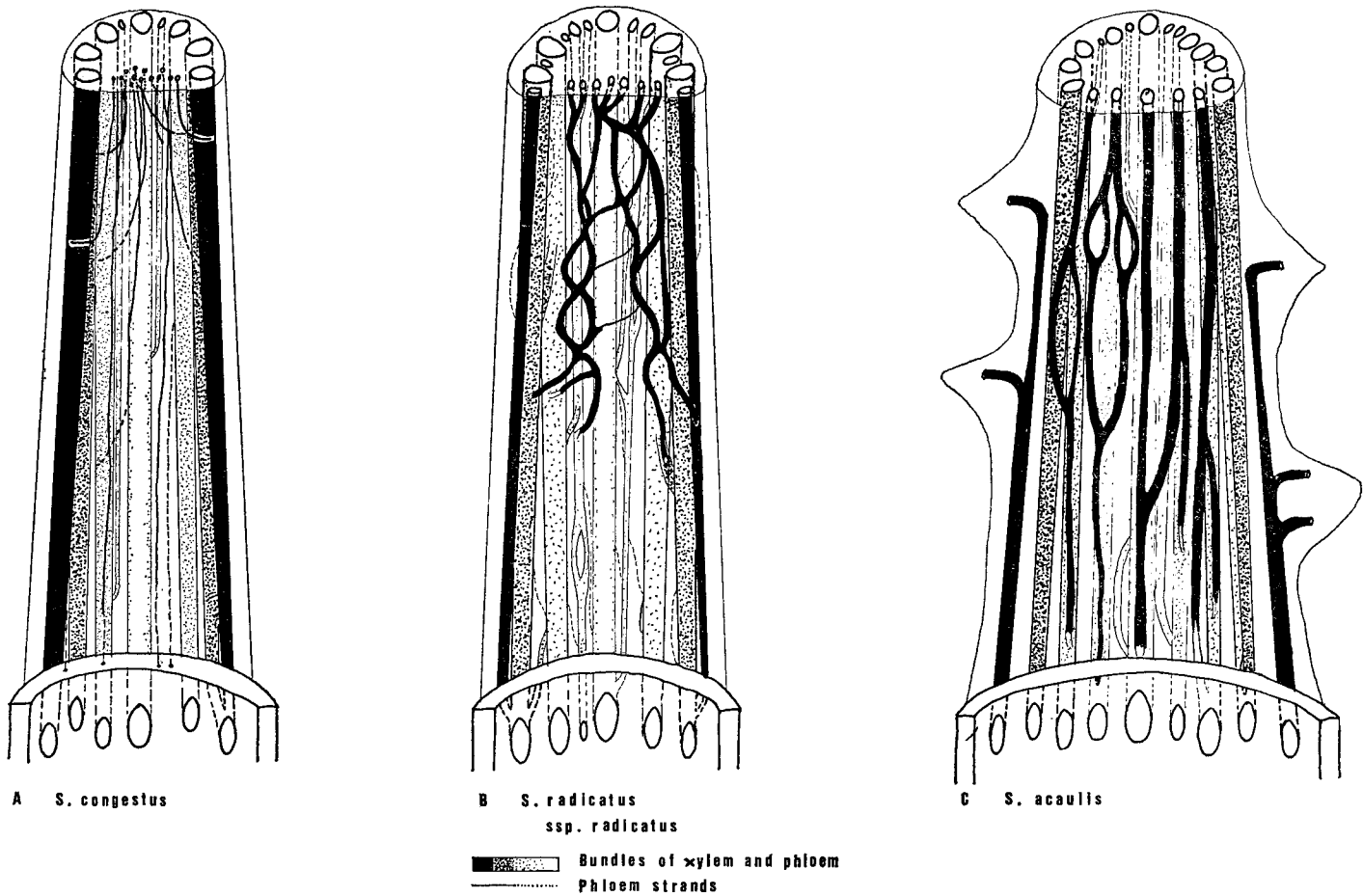


Figure 4. Nodal and petiolar vasculares of section *Dendrosonchus* (see text of details).

sonchus show a simple arc or a ring of separate bundles. All are provided with a peripheral zone of chlorenchyma, but no other strengthening tissue. The medullary region is composed of large, thin-walled parenchyma which is distinguishable from the cortical parenchyma. Fibres commonly occur on the inner side only of the vascular bundles as in *S. radicans* subsp. *tectifolius* and *S. brachylobus*, on both the inner and outer edges as in *S. arboreus*, *S. hierrensis* and *S. bornmuelleri* or they are entirely absent as in *S. congestus* and *S. platylepis*.

DISCUSSION

The anatomy of the region of the node has generally been considered as conservative. Sinnott (1914a) investigated the nodal structures of many angiosperms with the view of determining broad areas of relationship. The angiosperm node typically has an odd number of leaf traces, each departing from a distinct gap in the vascular ring. According to Sinnott the number of bundles and gaps is usually constant among related groups and every family has a relatively invariable characteristic nodal formula. Sinnott considered that the ancient type of node among the dicotyledons had three bundles, each leaving an individual gap in the stem cylinder. He termed this condition trilacunar and as it is widespread in many unrelated families he suggested that it may represent the ancestral condition. He envisaged the trilacunar condition as having been modified both by reduction and by amplification. The unilacunar type of nodal structure has a single or multiple foliar supply arising from a single gap and Sinnott considered it to be derived from the trilacunar by reduction and gave evidence from a few transitional families. Alternatively the multilacunar condition was considered to have been derived from the trilacunar by amplification.

The type of nodal structure was found by Sinnott to be generally independent of the size, shape or mode of attachment of the leaf. Several instances were encountered in which the leaf was so reduced by adaptation to xerophytic or hydrophytic conditions that it was only supplied by a single bundle instead of by the higher number which normally characterized the other members of its family. These cases were considered to be comparatively rare and their nodal anatomy to be of little taxonomic value above the species level. Sinnott (1914b) examined the nodal structure of 164 families in 35 orders of angiosperms. He found the majority of plants with a trilacunar node to be stipulate, although entire-leaved

families which had the trilacunar condition generally lacked stipules. The family Compositae was found to be trilacunar or, in a few members, multilacunar and he concluded that the trilacunar node may frequently have become expanded into a multilacunar one within the same family or even in the same genus. This family comprises genera with and genera without stipules. In almost all plants with a unilacunar condition stipules were absent and the leaves of those plants with the multilacunar condition all had a more or less sheathing base. Sinnott rarely found the trilacunar and unilacunar types occurring in closely related groups. Sinnott's suggestions, elaborated from work at the family level, do not apply to *Dendrosonchus*. All members of section *Atalanthus* are petiolate without sheathing bases or stipules but, as has been shown, both the trilacunar and multilacunar conditions are present. In section *Dendrosonchus* two of the three species which have the trilacunar condition have petiolate leaves without sheathing bases or stipules. The third species, *S. brachylobus*, has sheathing leaf bases and, therefore, also does not conform to Sinnott's findings.

Howard (1962) introduced a system of classifying the main pattern of vascular structure in the petioles of woody Dicotyledons. He analysed over 160 families, examining serial sections through the petioles to reconstruct a three-dimensional vascular pattern. He considered the vascular structure of the petiole to be most useful at the generic level and in a few cases at the family level. Where it appears to be useful at the specific level he suggested that this may indicate generic segregations. He examined the variability of the petiolar patterns in different plants, in plants of different ages and conditions of growth, in different regions of the same plant, in plants from different habitats and in fresh or dried plant material. He found very little variation and the three-dimensional pattern of vascular structure in the petiole was considered to be a character of great taxonomic value. Howard (1974), in revising his previous classification of nodal types, mentioned that generic variations have subsequently been found. He considered the vascular pattern of the petiole to be of value as a taxonomic character. The systematic level of the taxonomic value was thought to vary from one group to another. Families could be recognised in some cases, an genera, species or varieties could be distinguished in others on the basis of their petiolar vascular patterns.

Howard (1962, 1974) recognised thirty-nine patterns of nodal and petiolar vasculature of woody Dicotyledons. These covered the origin of traces from the stem and their various changes through the petiole until the position became stable in the geometrical

centre of the petiole. According to Howard's system of classification, subgenus *Dendrosonchus* has the 'Miconia' and the 'Ricinus' types, both of which are equivalent to the U-type here. Howard's system does not accommodate the other types found in this group. The distinguishing feature between the 'Miconia' and 'Ricinus' types is the trilacunar node in the former and the multilacunar node in the latter. A similar criticism of Howard's classification was made by Drury (1973). He examined the Australasian, shrubby Senecioneae and recognised two categories of petiole-node vasculature, simple and complex. The nodes ranged from five- to nine-lacunar. The complex types possessed medullary bundles which arose from the lateral leaf trace bundles. These medullary bundles either formed a U-V shape in the petiole (cf. Hare, 1942-3), or fused to form a single strand. The simple condition was found in species with three or five (to six) lacunae. The departing traces remained discrete along the entire length of the petiole in the U-V-shaped configuration. Drury also found that species with sessile leaves exhibited a range of nodal configurations similar to those with petioles but the vascular pattern in the basal portion of the midrib was of the simple type. The simple condition, as described by Drury, has also been reported for other Compositae by Petit (1888) and Metcalfe & Chalk (1950). In Howard's scheme this simple condition is the 'node 3-3, bundles free' and also 'node multilacunar, many traces from equal numbers of gaps' (Howard, 1962). Drury stated that species with five- to nine-lacunar nodes and a complex petiolar anatomy are not properly covered by Howard's classification.

In considering the phylogenetic sequences variously proposed by different authors, Howard (1974) stated that the ancestral form of the modern leaf are either lacking or have not been recognised and, therefore, any attempts to determine the primitive type of node are considered to be futile. The primitive node, from the trace-gap point of view, has been proposed as trilacunar with single traces (Sinnott, 1914a), trilacunar with a double trace in the median gap (Takhtajan, 1969), unilacunar with a single trace (Benzing, 1967), unilacunar with a double trace (Marsden & Bailey, 1955) or multilacunar (Ozenda, 1948). Attempts to place in a single phylogenetic sequence the nodal trace-gap area are considered by Howard to be fundamentally useless as such characteristics of modern plants must be recognised as mid-points in the evolution of the modern leaf. He stated that such expressions are probably parallel developments from a simple ancestral type. It can, however, be argued that for those small groups of plants which are in a recent state of rapid evolution, the changes in the patterns of nodal gap-

trace area will be very informative. Howard's statement was based essentially upon the assumption made by previous authors concerning the evolution of the whole of the angiosperms. I agree with Howard that the primitive condition of the nodal gap-trace area for the angiosperms probably will not be discovered since the use of fresh material is almost essential to this type of investigation.

Carlquist (1967) examined the shoot vascularization of *Dendroseris* in great detail. This genus, of the family Compositae tribe Lactuceae, comprises pachycaulous plants from the Juan Fernandez Islands and is considered by Jeffrey (1966) to be taxonomically related to *Dendrosonchus*. This study, therefore, is of some value for comparisons with the morphologically similar, insular subgenus *Dendrosonchus* which is discussed in the present work. The nodes of all species of *Dendroseris* were found to be multilacunar. In some species the medullary phloem strands were reported to take part in the vascularization of the petioles. The leaf traces departed as a simple arc but further along the petiole formed a ring of bundles. Carlquist explained the presence of the adaxial bundles by the formation of an adaxial meristem which he found during ontogenetic studies of apical meristems of leaf primordia. He called these adaxial bundles 'supernumeraries' and stated that they may be either phloem strands or xylem and phloem strands. The medullary phloem strands of the stem entering the petiole became aligned on the adaxial faces of the main vascular bundles, thus making these bundles bicollateral. Other phloem strands in the petiole were considered by Carlquist to have arisen 'de novo'. The petiolar vascular supply of the members of *Dendrosonchus* differs from those given for *Dendroseris* by Carlquist in the following features: the phloem strands in the outer cortices of the stems of *Dendrosonchus* species contribute, in a few species, to the vasculature of the petiole; the medullary phloem strands, present in all species, have not been seen to take any part in the vascular supply of the petiole; and the bundles of xylem and phloem in the petiole are collateral, as opposed to bicollateral in *Dendroseris*. The adaxial bundles in the petioles of *Dendrosonchus* do not originate from the apical meristem of the leaf, as reported for *Dendroseris* by Carlquist, but arise by movements of bundles from the abaxial side across the medullary region as described above.

In the section *Dendrosonchus* the complexity of the petiolar vasculature does not always correlate with leaf-lamina area. The species *S. platylepis*, which has the less complex U-plus-xylem-and-phloem condition, has larger leaf-surface areas than do the subspecies of *S. radicans*, all of which possess the O-by-xylem-and-phloem-type of petiolar vasculature. In this section the U-type is

found only in *S. fauces-orci* which has larger leaf, surface areas than *S. brachylobus* having extra phloem strands in the petiole. In the section *Atalanthus* the size of the leaf surface areas of each species does not appear to relate with their petiolar vascular condition, except in the subspecies of *S. leptocephalus* which have the smallest leaf-surface areas and the reduced U-type vasculature.

In Table 1 the species are listed in the order of their average vessel length to width ratios, as explained above. The numbers of lacunae can be seen to increase from three in the most primitive member of section *Atalanthus* (based on vessel anatomy in Aldridge, 1977) to six or seven in *S. pinnatus* subsp. *palmensis*, considered to be the most derived member of this section. Where minor, lateral traces were found these have been given as '+1' or '+2' added to the number of major lacunae with which they are associated. *Sonchus leptocephalus* subsp. *capillaris* again appears to be more primitive than subsp. *leptocephalus*, if the trend in increasing lacuna numbers is considered as showing an evolutionary pathway. This situation in subsp. *capillaris* may result directly from its having more reduced leaves. This correlation with leaf area does not apply in all cases, since *S. arboreus* has much broader leaf lobes than either subspecies of *S. leptocephalus* and yet has three lacunae which is considered to be more primitive. *Sonchus pinnatus* subspecies *pinnatus* and *canariensis* have fewer lacunae than subsp. *palmensis*, indicating once more that the latter, on this particular piece of evidence, is more derived.

In section *Dendrosonchus* the same trend in increase of lacuna numbers was repeated. *Sonchus brachylobus*, the species regarded as most primitive on grounds of vessel anatomy, has three (or three plus two minor) lacunae, and *S. acaulis*, the most derived species, has nine or ten lacunae. In many cases the different numbers of lacunae given for each species were found in one individual sample. In this section the number of lacunae is again not always correlated with the area of leaf-lamina. For example, *S. radicans* subsp. *tectifolius* has pinnatisect leaves with small lobes but has the same range of lacuna numbers as *S. congestus* which has larger, slightly pinnatifid leaves. Increases in the area of leaf-lamina (regardless of the extent to which the leaf is divided), in the diameter of the petiole and in the pulvinus area of the sheathing leaf bases, which are present in some species, generally, however, tend to correlate with an increase in the number of lacunae. Those species within section *Dendrosonchus* with the primitive number of three leaf gaps are *S. brachylobus*, *S. fauces-orci* and *S. pinnatifidus*. The latter two species may, therefore, be considered on this evidence to be the earliest departures from the ancestral line.

The species which were found to have the minor lateral lacuna probably represent intermediate stages between the primitively low numbered condition and the more derived condition of higher numbers. These minor lacunae probably arose by the retardation of the time of departure of the leaf traces from the stele. A study of the ontogenetic development of the vascular supply to the leaf may be required here, but even then the sequence of the evolutionary change, as proposed here, would not be established. In many species, after a major leaf trace has moved away from the stele into the cortex of the stem this trace begins to divide into two or more traces before entering the petiole. If these secondary leaf traces were delayed in their departure from the stele then small lateral leaf traces would be seen at the node. This is in fact the case. In those species with minor, lateral leaf traces these traces were in some samples, extremely close to the major, median trace and separated from it only by a negligible amount of vascular tissue. In other samples of the same species this distance between the lateral and the median trace was much greater. I suggest that this has been the mode of the evolutionary trend in the increasing number of lacunae in *Dendrosonchus* s.l.

In section *Atalanthus* all types of petiolar vascular supply but the U-plus-xylem-and-phloem-type were found. In the most primitive member, *S. arboreus*, the condition is the U-plus-phloem-type. If the trends for the vessel length to width ratios and for the lacuna numbers are considered as valid, then the U-type, the O-by-phloem-type and the O-by-xylem-and-phloem-type are derived from the U-plus-phloem-type. In section *Dendrosonchus* the most primitive member, *S. brachylobus*, also has his U-plus-phloem-type of petiolar vascular supply and, therefore, the above consideration is strengthened. The movement of the phloem strands from the phloem of the abaxial vascular bundles to the adaxial position has been retarded in *S. leptcephalus* subspecies *leptocephalus* and *capillaris*, possibly because the leaf area is more reduced in these two subspecies than in *S. arboreus*, as discussed above. This is one pathway of evolution that the species appear to have taken in section *Atalanthus*. The second is to a more complex situation in *S. pinnatus* subsp. *pinnatus*, where the phloem strands are accompanied by elements of the xylem from their respective abaxial bundles. The movement of these, subsequently adaxial, bundles to the point of fusion with the lateral bundles, as in the U-plus-phloem-type, has been retarded, thus giving the O-by-xylem-and-phloem-type. *Sonchus pinnatus* subsp. *canariensis* has lost this complex pattern and possesses the U-type. The O-by-phloem-type of petiolar vascular supply is quite unusual for the subgenus and was found only in *S.*

congestus of section *Dendrosonchus* and *S. pinnatus* subsp. *palmensis* of section *Atalanthus*. Although phloem strands from the cortex of the stem are seen to move into the petiole with the leaf traces in one other species, *S. platylepis*, it is only in the former taxa that these strands play an important part in supplying the adaxial bundles of the O-type condition. This condition may have arisen first by the retardation of the phloem strands in the U-plus-phloem-type to give the U-type, as explained for *S. pinnatus* subsp. *canariensis*. Subsequently the role of these phloem strands was replaced by cortical phloem strands. This must have been a secondary accomplishment in the evolutionary development of the species as the O-by-xylem-type which does not involve cortical phloem probably developed from the U- or the U-plus-phloem-type. This has been the conclusion to the second branch of petiolar evolution within the section *Atalanthus*. It is obvious from this account that the evolution of the patterns of petiolar vasculature, although constant for a species or subspecies, has occurred by the simple conversion of one type to another. The cause of these changes is unknown but it is clear that an increase or decrease in leaf area is not of prime importance, as exemplified by *S. pinnatus* subsp. *palmensis* which has much broader leaf-lobes and larger leaves than *S. pinnatus* subsp. *pinnatus*. The petiolar vascular pattern constitutes a reliable, specific and subspecific character.

The retardation of the phloem strands in the U-plus-phloem-type to form the U-type has occurred only once in section *Dendrosonchus*. This has been in the derivation of *S. fauces-orci*, considered above to be one of the earliest departures from the ancestral line on evidence from numbers of nodal lacunae. More than half of the species examined in this section have the O-by-xylem-and-phloem-type and these are considered to be the most derived species. *Sonchus congestus* has the O-by-phloem-type vascular condition the probable derivation of which has been discussed above. This species has a relatively primitive position in the section *Dendrosonchus*, based on vessel anatomy. The intermediate situation in *S. platylepis*, where the cortical phloem strands enter the petiole but do not move to the adaxial position, also suggests that this sequence of events is plausible.

In conclusion, four basic types of petiolar vascular supply, one intermediate type and from three to ten lacunae are present in the species of the subgenus *Dendrosonchus*. The differences between the species and subspecies, with respect to these features, are generally constant and could be useful taxonomically if this is considered to be practical. It is unusual to find such a wide range of petiolar and nodal conditions within a small, closely related

	TYPE OF PETIOLAR VASCULATURE	NUMBERS OF NODAL LACUNAE
SECTION <i>ATALANTHUS</i>		
<i>Sonchus arboreus</i>	U + Ph	3
<i>S. leptcephalus</i> subsp. <i>capillaris</i>	U	3
<i>S. pinnatus</i> subsp. <i>pinnatus</i>	O-by-X+Ph	3+1, 5
<i>S. leptcephalus</i> subsp. <i>leptcephalus</i>	U	3, 3+1
<i>S. pinnatus</i> subsp. <i>canariensis</i>	U	3+2
<i>S. pinnatus</i> subsp. <i>palmensis</i>	O-by-Ph	6, 7
SECTION <i>DENDROSONCHUS</i>		
<i>S. brachylobus</i>	U + Ph	3, 3+2
<i>S. brachylobus</i> var. <i>canariae</i>	U + Ph	5+1
<i>S. fauces-orci</i>	U	3, 3+1, 3+2
<i>S. congestus</i>	O-by-Ph	5, 5+1, 5+2, 6
<i>S. fruticosus</i>	O-by-X+Ph	5, 6
<i>S. pinnatifidus</i>	U + Ph	3, 3+1, 3+2
<i>S. platylepis</i>	U + X+Ph	5, 5+1
<i>S. radicans</i> subsp. <i>gummifer</i>	O-by-X+Ph	5, 6+1, 7, 7+1
<i>S. radicans</i> subsp. <i>radicans</i>	O-by-X+Ph	5, 5+1, 5+2
<i>S. radicans</i> subsp. <i>tectifolius</i>	O-by-X+Ph	5+1, 6, 7
<i>S. hierrensis</i>	O-by-X+Ph	6, 7, 7+2, 8
<i>S. daltonii</i>	O-by-X+Ph	7
<i>S. bornmuelleri</i>	O-by-X+Ph	7+1
<i>S. acaulis</i>	O-by-X+Ph	9, 10

TABLE 1. The types of petiolar vasculature and numbers of nodal lacunae in the species of subgenus *Dendrosanchus* s.l.

U = U-type; U + Ph = U-plus-phloem-type; U + X+Ph = U-plus-xylem-and-phloem; O-by-Ph = O-by-phloem-type; O-by-X+Ph = O-by-xylem-and-phloem-type (see text for details).

group of plants. The diversity of vascular patterns at the subgeneric level may reflect the rapid and recent evolution of *Dendrosonchus*. On the basis of the evolutionary trends in vessel anatomy, as proposed in an earlier paper (Aldridge, 1977), the primitive number of lacunae at the node for the subgenus is suggested to be three, and the primitive petiolar vascular conditions to be the U-plus-phloem-type. From these primitive conditions evolutionary trends towards more complex situations such as the O-by-xylem-and-phloem-type petiolar vasculature and the multilacunar nodal condition have occurred. The proposed evolutionary trends within petiolar and nodal vasculatures are based on the evidence provided by vessel anatomy. As stated previously (Aldridge, 1977), two major lines of evolution are proposed, one within each of the two sections *Dendrosonchus* and *Atalanthus*. The trends in petiolar and nodal vasculatures are considered to be useful for the interpretation of directions, within each of the two sections, in which different species have evolved.

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