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MORPHOLOGY AND VASCULAR SYSTEM OF THE INFLORESCENCES OF MOLLUGO NUDICAULIS LAM. AND HYPERTELIS BOWKERIANA SOND. (MOLLUGINACEAE)

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SUMMARY

The variation in build and vascular anatomy of the inflorescences of *Mollugo nudicaulis* Lam. and *Hypertelis bowkeriana* Sond. is examined, in living and herbarium material and in serial transverse sections. The 'umbel' of *H. bowkeriana* may be thought to be derived from an inflorescence like that of *M. nudicaulis* (a primitive type within the Molluginaceae) by suppression of internodes and reduction. Whereas the inflorescential structure of both species is rather constant, the vasculature of the younger inflorescential branchings (*H. bowkeriana*), or that of the younger basal ramification and the branchings in the partial inflorescences (*M. nudicaulis*), shows a certain amount of plasticity, the general idea being that of a system of distribution of a limited amount of material. 'Opportunism' *vs.* 'conservatism' of vascular bundles is discussed.

1. INTRODUCTION

The vascular system of inflorescences has attracted little attention as compared with that of both vegetative parts and flowers. HOFMANN (1973) examined the inflorescential structure of sixteen molluginacean species, not including *Mollugo nudicaulis* and *Hypertelis bowkeriana.* The inflorescential vasculature of Molluginaceae has not been studied so far; the inflorescential morphology of the two species under consideration has not adequately been dealt with. The variation in build and vascular anatomy of the inflorescences of *M. nudicaulis* and *H. bowkeriana* is subject of this study.

2. MATERIAL AND METHOD

Mollugo nudicaulis and *Hypertelis bowkeriana* are cultivated at Haren (Gn), in the Hortus Botanicus 'de Wolf' of the State University of Groningen. In addition to living material some specimens of *M. nudicaulis* stored in the Groningen University Herbarium were examined. Fresh inflorescences at various stages of maturity were fixed in FPA and, via TBA-dehydration, embedded in paraplast, according to the standard technique. Serial 10 μm thick transverse sections were stained with astra-blue – auramine – saffranine (MAÁCZ & VÁGÁS 1963).

3. OBSERVATIONS

3.1. Mollugo nudicaulis Lam.

3.1.1. Inflorescential structure

Mollugo nudicaulis (*fig. 1*) is a small annual pantropical and pansubtropical weed. The leaves are in a rosette; primary axis and shoots show a two-fifth phyllotaxy. Inflorescences are terminal at the primary stem and one or two subsequent orders of shoots. The pedicellate flowers have quincuncial perigon. Although the mature tepals constitute a whorl, organogeny and vasculature indicate an arrangement in a spiral (BATENBURG & MOELIONO 1982). The perianth members will be numbered here according to their relative position in the aestivation.

The long inflorescential stalk bears usually three bracts nearly at the same level and a terminal flower. The bracts follow up the spirals of both the leaves and the tepals, tepal 2 thus being in the median plane of the upper leaf. The partial inflorescence in the axil of the lower bract is generally slightly shifted towards the median plane of tepal 1 (*fig. 3*). Usually this partial inflorescence is the best developed one; that in the axil of the upper bract usually shows the least development. The primary axis of the former shows a homodrome, that of the latter and that of the partial inflorescence in the axil of the middle bract mostly show an antidrome phyllotaxy in relation to that of the parent axis. In the partial inflorescences each axis has a stretched first internode, two bracts nearly at the same level and a terminal flower. Tepal 2 faces the respective parent axis. The bracts, following up the spiral of the perianth members, are in the median planes of tepal 5 and 4. The axillary branch system of the upper bract is further developed than that of the lower one. The primary axis of the former shows an antidrome, that of the latter a homodrome phyllotaxy as compared with that of the respective parent axis.

The sequence of flowering follows that of the initiation, but in the dichasial ramifications the upper one of the two branches flowers first. Pedicels and peduncular axes are straight, thin, cylindrical and glabrous, apart from some papillae. The inflorescential stalk is usually somewhat pushed aside by the axillary shoot of the upper leaf; the pedicels are slightly pushed aside by the patulous branches. Deviations from the scheme – unstretched first internodes, missing or abortive flowers and branches – occur (e.g., at x in *fig. 1*). The basal ramification may be di- instead of trichasial; tepal 3 of the primary flower is, then, in the median plane of the upper leaf. These inflorescences are entirely comparable wih a partial inflorescence as described above.

3.1.2. Vascular system

Mature peduncular axes of the first and second order contain ten collateral vascular bundles (*fig. 5a*). Those of the inflorescential stalk, approaching the basal branching, fuse into continuous sheaths of phloem and xylem. The bract traces, one per bract, each leave a narrow and short gap just beneath the wider but equally short one left by the vascular sheath of the axillary branch. Each branch

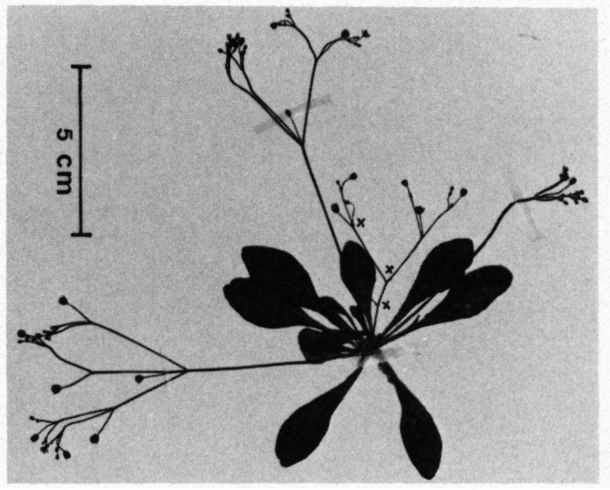

Fig. 1. *Mollugo nudicaulis* from Simla (India), Groningen University Herbarium D2730.

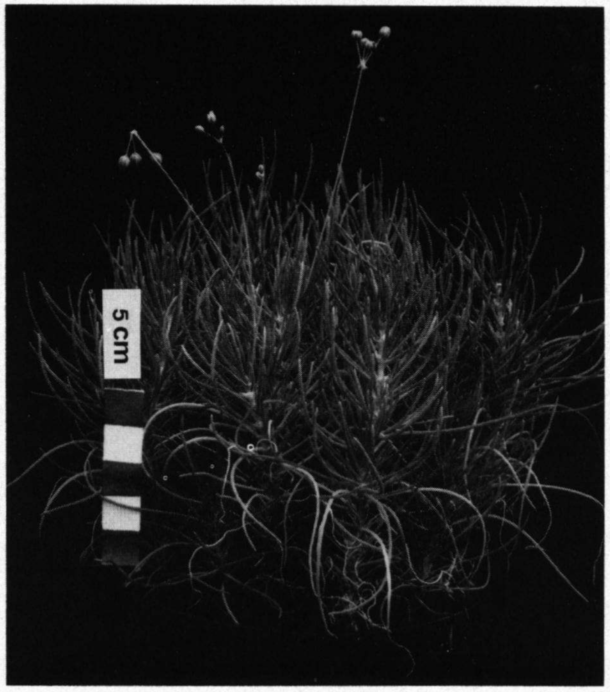

Fig. 2. *Hypertelis bowkeriana*, cultivated, ca. 3 months old.

cylinder splits up into the ten individual peduncular bundles immediately above the point at which it is tied off. The centrally remaining vascular sheath falls apart into five or more individual pedicellar bundles somewhat above the ramifi-

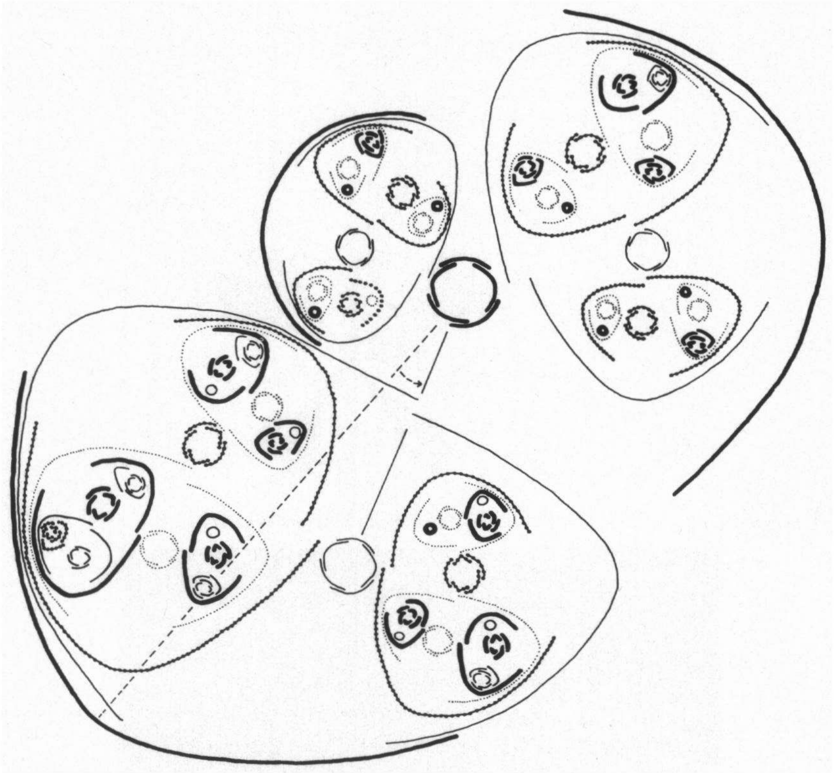

Fig. 3. *Mollugo nudicaulis*, inflorescential diagram (example).

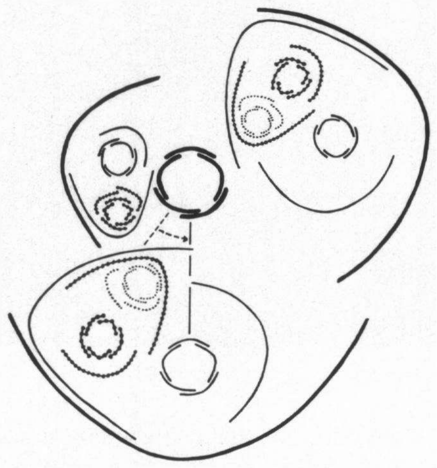

Fig. 4. *Hypertelis bowkeriana*, inflorescential diagram (example).

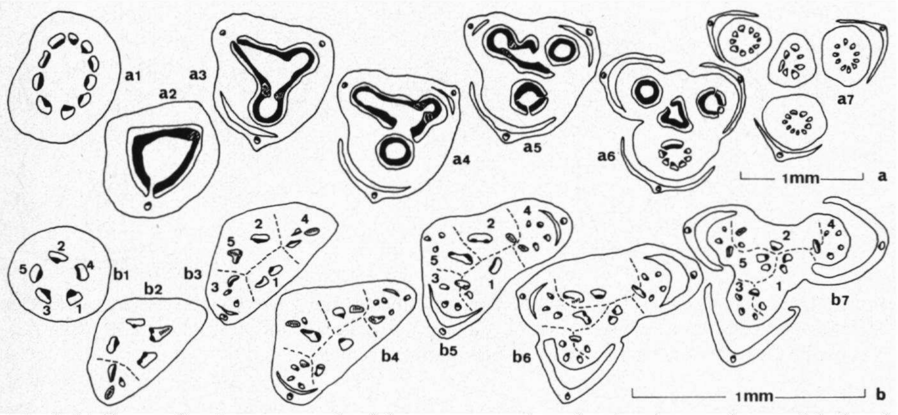

Fig. 5. *Mollugo nudicaulis*, two sets of serial transverse sections showing the vasculature of the basal inflorescential branching (a: mature; b: young; lignified xylem black when transversely, and striped when longitudinally cut).

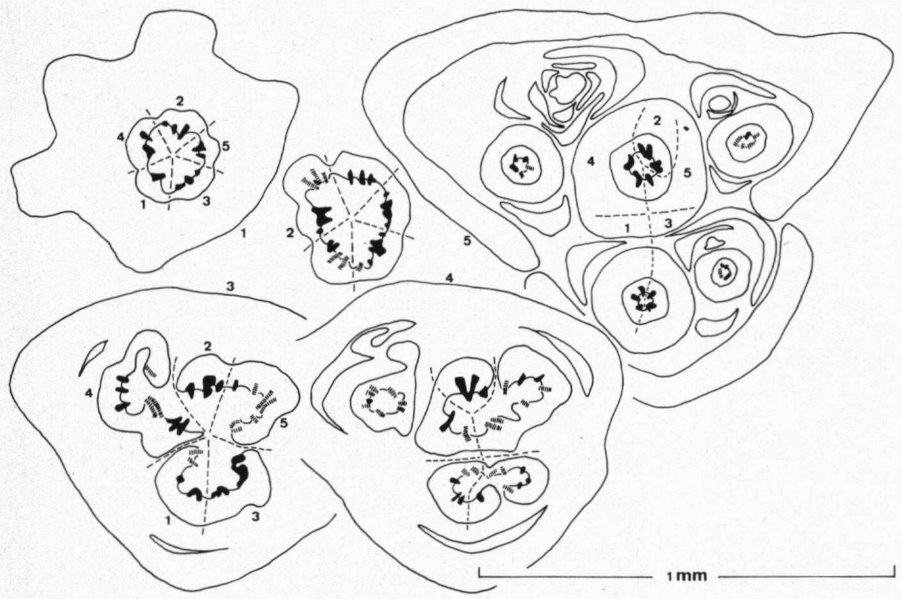

Fig. 6. *Hypertelis bowkeriana*, serial transverse sections showing the vasculature of the inflorescential branchings at an early age (lignified xylem black when transversely, and striped when longitudinally cut).

cation. If six or more, they reorganize into five strands slightly higher up.

According to BAKSHI & KAPIL (1952) the vascular tissue in the stem (read, as appears from their context: inflorescential axes) is in the form of an unbroken sheath of phloem with numerous separate xylem strands abutting into the pith. A continuous pedicellar vascular cylinder was observed by SHARMA (1963). Neither condition was met with in the present material, which may be due to cultivation factors.

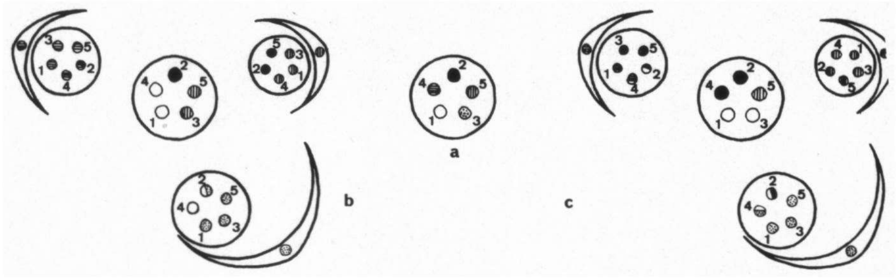

Fig. 7. *Mollugo nudicaulis*, diagrammatic representations of the origin of the vascular bundles in the primary bracts, branches and pedicel of young inflorescences (a: inflorescential stalk; a/b corresponds with the case shown in *fig. 5b*; a/c reflects another example).

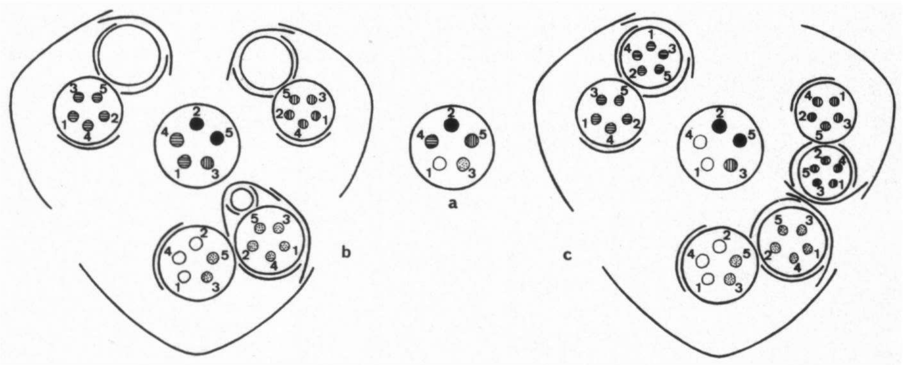

Fig. 8. *Hypertelis bowkeriana*, diagrammatic representations of the origin of the (groups of) xylary strands in the pedicels of young inflorescences (a: peduncle; a/b corresponds with the case shown in *fig. 6*, the usual case; a/c reflects another example).

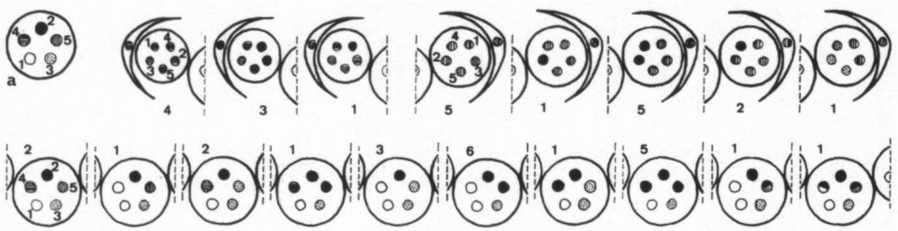

Fig. 9. *Mollugo nudicaulis*, diagrammatic representations of the origin of the vascular bundles in the bracts and branches (above) and pedicels (below) of the partial inflorescences; number of cases observed (a: peduncular axis below the ramification; cases in which the flower shows a sinistrorse aestivation are included in reverse).

At an earlier age the primary and secondary peduncular axes, like the branches of higher orders and the pedicels, normally contain five collateral vascular bundles in the median planes of the tepals of the respective terminal flowers (*fig.*

5b). The numbering of the peduncular and pedicellar bundles (PB and Pb, resp.) as used below follows that of the perianth members. Since a continuous vascular sheath is absent at the branchings of the partial inflorescences and at the younger basal inflorescential ramification, the vascular anatomy of these parts cannot be described in terms of stelar gaps.

The traces of the primary bracts and PB 1 and 3 of the primary branches arise from the facing bundle in the parent stele (*figs. 5b* and *7*). The same may apply to PB 2, 4 and 5, but these bundles, most frequently PB 2, may spring entirely or partially from one or both neighbour bundles in the inflorescential stalk as well. Pb 1, 2 and 5 of the primary flower are the continuations of the accordingly numbered bundles in the stalk. Pb 3 and 4 each originate from one of the respective two neighbour bundles.

In the partial inflorescences (and in the younger inflorescence as a whole, if it is basally di- instead of trichasial) the bract traces and PB 1, 3 and – with one observed exception – PB 5 of the branches arise from the facing bundle in the parent stele (*fig. 9*). The same may apply to PB 2 and 4, but these bundles may equally spring from PB 2 in the parent axis. In one case it was observed that PB 2 and 5 arose from PB 3 in the parent stele. Pb 1, 2 and 3 of the flowers are the continuations of the accordingly numbered bundles in the peduncular branch underneath. The same may apply to Pb 4 and 5, but these bundles usually originate from one or both of the respective two neighbour bundles: Pb 4 mostly from PB 1; Pb 5 mostly from PB 2.

Occasionally, six or more bundles are produced in a branch or pedicel, *i.e.* one or more bundles (most frequently PB 2) are double. The 'normal' situation is restored higher up. Equally, the level of arisal of a bundle may be shifted upwards, e.g., Pb 5 springs from Pb 3 halfway up the pedicel. With the aging of the inflorescence the number of bundles in the basal parts tends to double, and the individual bundles in these parts tend to fuse into a continuous sheath at the ramifications (see above).

3.2. Hypertelis bowkeriana Sond.

3.2.1. Inflorescential structure

Hypertelis bowkeriana (*fig. 2*) is a perennial South and East African and Malagasian shrubby herb. The basally crowded leaves of the primary axis are in a two-fifth spiral. From the primary stem, at a later stage also from other axes, with a similar phyllotaxy, sympodia arise. The sympodial members consist of a stretched first internode, two non-opposite leaves nearly at the same level and a terminal inflorescence. The sympodium continues from the axil of the upper leaf. The terminal inflorescences of the parent stems are usually abortive, as may be those of the basal members of the sympodia. The pedicellate flowers have a quincuncial perigon. Although the mature perianth members constitute a whorl and inter-tepal vascular internodes are absent, the organogeny suggests an arrangement in a spiral. The tepals will be numbered here according to their relative position in the aestivation.

The long peduncle bears three bracts nearly at the same level and a terminal flower. The bracts follow up the spiral of the perianth members, but the lower one has a position halfway between the median planes of tepal 3 and 1 (*fig. 4*). At an early age tepal 2 is in the median plane of the upper, tepal 3 in that of the lower leaf. Later, the peduncle undergoes some torsion (connected with the dorsiventrality of the sympodia and the order of flowering within the inflorescence) in the direction of the bract- and tepal-spiral. The axillary branch of the lower bract shows a homodrome, that of the middle bract an antidrome phyllotaxy in relation to that of the parent axis; the phyllotaxy of the one of the upper bract is homo- or antidrome. These primary branches, and branches of subsequent orders, have an unstretched first internode, two bracts nearly at the same level and a terminal flower. Tepal 2 faces the respective parent axis. The bracts, following up the spiral of the perianth members, are in the median planes of tepal 5 and 4. Most inflorescences are, initially, seven-flowered: each primary branch has a secondary one in the axil of its upper bract. In six-flowered 'umbels' the upper secondary branch is missing. If eight or nine flowers are present the lower secondary branch bears a tertiary one in the axil of the upper bract; in nine-flowered inflorescences either the same applies to the middle secondary branch (*fig. 4*), or the lower primary branch has an additional secondary one in the axil of its lower bract. The phyllotaxy of secondary branches is homodrome, that of tertiary ones usually antidrome as compared with that of their respective parent axes. Tertiary, secondary or even primary branches may be stunted; in some inflorescences only three flowers develop.

The order of flowering follows that of the initiation. Pedicels and peduncle are straight, thin, cylindrical and papillose. The peduncle is pushed aside by the subsequent sympodial member; in some cases a complete or partial concaulescence of the first internode of the latter with the peduncle was observed. The pedicel of the primary flower is slightly pushed aside by the patulous branches. Immediately after flowering each flower recurves.

3.2.2. Vascular system

The inflorescential axes contain a continuous vascular sheath (*fig. 6*). Bract traces are absent. The tying off of the vascular cylinder of each branch leaves a short gap in the peduncular stele. Nearly at the same level the vascular sheath of the secondary branch is tied off, leaving a short gap in that of the primary one, *etc.* In the mature peduncle, inflorescential branchings and lower parts of the pedicels both phloem and xylem are in the form of unbroken sheaths, apart from the branch gaps. At an earlier age the xylem is, like in the upper parts of the mature pedicels, in the form of separate strands abutting into the pith (*fig. 6*). The xylary strands of the peduncle are more or less arranged in five groups. These groups, and the usually five xylem strands or groups of strands in the pedicels, are in the median planes of the tepals of the respective terminal flowers. This enables us to describe the vascular anatomy of the younger inflorescential ramifications of *Hypertelis bowkeriana* in the same terms as used in the description of that of the younger basal inflorescential branching of *Mollugo nudicaulis*, on the understanding that in the following 'PB' and 'Pb' refer to (groups of) xylem strands rather than to peduncular and pedicellar vascular bundles.

The xylary strands of the upper and the middle primary branch, and those of the belonging axis or axes of subsequent order(s), normally arise from PB 4 and 5, respectively (*figs. 6* and *8*). The xylem of the lower primary branch springs partly from PB 3, partly from PB 1; that of the sidebranch in the axil of its upper bract – and that of the tertiary branch belonging to it if present – originates from PB 3. Pb 2 and 5 of the primary flower arise from PB 2. Pb 3 springs from PB 5. Pb 1 and 4 originate from PB 4 or, occasionally, from PB 1. In one case it was observed that some xylary strands of the upper primary branch arose from PB 2.

4. DISCUSSION

The inflorescence of *Mollugo nudicaulis* is dichasial, usually with a trichasial base. From the studies of HOFMANN (1973) it appears that this type of inflorescence is primitive within the Molluginaceae. The (descriptively!) umbel of *Hypertelis bowkeriana* may be thought to be derived from this type by non-initiation or abortion of the lower branch in each dichasial ramification (in some cases with the exception of that of the lower primary branch) and reduction of the number of successive ramifications, both resulting in a reduction of the number of flowers, together with the suppression of the first internode of the branches. The inflorescence of *H. salsoloides* (Burch.) Adamson (cf. HOFMANN 1973) is intermediate, apart from the presence of adventitious branches or flowers. The absence of bract traces in *H. bowkeriana* may be considered a derived character.

Whereas the inflorescential structure of both species is rather constant, the vasculature of the younger inflorescential branchings (*H. bowkeriana*), or the younger basal ramification and the branchings in the partial inflorescences (*M. nudicaulis*), shows a certain amount of plasticity. The general idea is that of a system of distribution of a limited amount of material.

The bract traces, if any, and the vascular bundles or xylary strands of the branches are provided by the facing PB in the parent stele (with or without amplification from one or both of its neighbours), or by the two PB's alternating with the branch (lower primary branch of *H. bowkeriana*). The remaining PB's and what may be left of the former ones supply the respective terminal flower. In some cases a kind of interdependency may be observed, e.g., the more PB2 in the inflorescential stalk of *M. nudicaulis* contributes to the vascular supply of the branches, the less it does to that of the primary flower; the same applies to PB 5; the larger the share of PB 2 in the vascular supply of the middle partial inflorescence, the smaller its share in that of the upper one (compare *figs. 7a/b* and *7a/c*).

In *M. nudicaulis* the lower partial inflorescence is generally slightly shifted from the median plane of tepal 3 of the primary flower towards that of tepal 1. Possibly connected with this, PB 1 in the inflorescential stalk contributes more to its vascular supply than does PB 5 (*fig. 7*). On the other hand, PB 5 is perhaps kept in reserve for the upper partial inflorescence and the primary flower. In *H. bowkeriana* the lower primary inflorescential branch and the subtending bract have a position halfway between the median planes of tepal 3 and 1 of the primary flower. PB 5 in the peduncle has no share in the xylem supply of this branch; the contribution of PB 1 is larger than it is in *M. nudicaulis* (compare *figs. 7* and *8*). Assuming the situation in *H. bowkeriana* to be derived from a condition like that in *M. nudicaulis,* this appears to be a case of vascular 'opportunism' rather than 'conservatism'.

PB 3 and 4, but only a part of PB 5 in the inflorescential stalk of *M. nudicaulis* are used up in providing the vascular supply of the bracts and partial inflorescences (*fig. 7*). This may be connected with the basitony in the inflorescential base, *i.e.* the fact that the partial inflorescence facing PB 5 is usually the weakest of the three. However, it might equally reflect that PB 1 and 2 together are not enough to supply the primary flower, and that the necessary amplification comes from PB 5 since the partial inflorescence facing the latter is the uppermost and last-initiated one. The basitony or sequence of initiation in the primary inflorescential branching of *H. bowkeriana* is more obviously reflected in the vasculature (*fig. 8*): PB 3 is always, PB 1 is usually, PB 4 is occasionally, and PB 5 is never used up in providing the xylem supply of the branches. Whereas the middle and upper primary branch are supplied by one PB each (with one observed exception), two PB's are involved in the xylem supply of the lower one, but this is also connected with its position (see above).

The slight acrotony in the dichasial partial inflorescences of *M. nudicaulis* is not clearly reflected in the vascular system (*fig. 9*). The acrotony is much stronger in the secondary and tertiary inflorescential ramifications of *H. bowkeriana*: axillary branches of the lower of the two bracts of each axis are entirely absent, in some cases with the exception of that of the lower primary branch. In the latter cases the material was too young to allow a study of the vasculature.

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