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THE PATTERN OF VASCULAR BUNDLES IN THE STAMENS OF NYMPHAEA LOTUS L. AND ITS BEARING ON STAMEN MORPHOLOGY

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In 1969 I published, together with P. G. Heinsbroek, a paper on the anatomy of the stamens of *Victoria amazonica*. The flowers used in that study came from plants which were cultivated in the green-house of the Leiden Botanic Garden. Because the possibility could not be excluded that the structures then observed were partly the effect of green-house conditions, I subsequently took the opportunity to study flowers of well developed plants, which were cultivated in the open air under the tropical conditions of the Botanic Garden at Bogor*). The results were exactly the same. Apart from the set of central vascular bundles, normal in laminar structures, there proved to be a peripheral sheath of bundles consisting of abaxial bundles, terminating half way up the stamen, as well as adaxial bundles. All bundles run parallel and the central ones branch upwards into the fertile region of the stamen. The adaxial bundles anastomose at the lower end of the pollen sacs and one of the resulting anastomoses pursues its course in the middle between the thecae. In literature the last mentioned vascular bundle had been named the 'auxiliary vein' (Moseley, 1958). Its position is opposed to the normal median vein, and its xylem pole is inverted.

This vein played a role in diverse morphological opinions on the flat stamens. American authors (Eames, 1961), who advocated the primitiveness of laminar stamen structure, disposed of the auxiliary vein by considering it as an insignificant vein. Schneider (1976) thinks the peripheral bundle system is explicable in functional terms. On the other hand, the discovery of the opposed median auxiliary vein was welcomed by authors like Leinfellner (1956), who thought, mainly on the ground of teratology, that the stamens are diplophyllous structures, that is consist of a dorsal and a ventral blade fused medianly. By this view the existence of apparently homogeneous laminar stamens in *Ranales* had been difficult to explain. However, now the auxiliary vein could be considered as the median vascular bundle of the fused ventral blade, as requested by the theory. Meeuse (1972) took up the suggestion brought forward in our paper of 1969, namely that the stamen vasculature consisted of a bract component (the abaxial bundles) and a flattened axis component (the central and adaxial bundles), in analogy with the Coniferous female cone scale. According to Meeuse this is proof of his thesis that the structure of the stamen in the *Ranales* is a bract amalgamated with an axial system. However, careful comparison with the results of Cécile Lemoine-Sebastian (a.o. 1972) show that the vascular patterns are different from a situation as described above.

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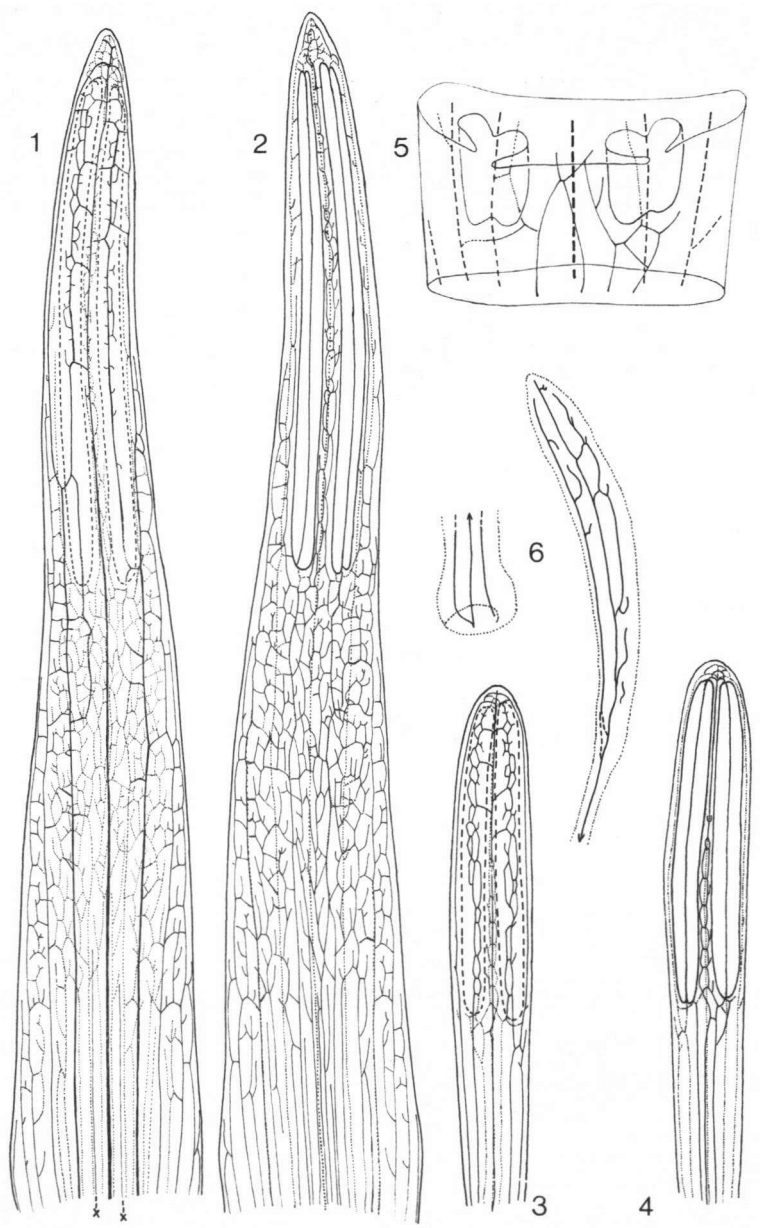

Nymphaea lotus — Fig. 1. Outer stamen, cleared. Abaxial view. Interrupted lines: pollen sacs in the background; dotted lines: vascular bundles in the background; crosses: two abaxial system bundles. 7 x. — Fig. 2. Ibidem, adaxial view. 7 x. — Fig. 3. Inner stamen, abaxial view. 7 x. — Fig. 4. Inner stamen, adaxial view. 7 x. — Fig. 5. Detail of inner stamen at lower end of pollen sacs. Interrupted lines: vascular bundles in the background. 30 x.

Nymphaea gigantea — Fig. 6. Stamen, cleared. Anther turned 90 degrees. Pollen sacs removed. 7 x.

Our study of 1969 showed that, next to a normal set, a peripheral set of bundles occurs in all the floral appendages intermediate between innermost stamens and outermost petals. It is only at the location of the pollen sacs that the formation of the adaxial bundles is blocked. In the outer stamens, in which the thecae are separated by a wider stretch of sterile tissue, there is a slightly anastomosing adaxial bundle system instead of a straight auxiliary vein. After comparing all the intermediate androecial members, the auxiliary vein in *Victoria* appears to be nothing more than a special member of an adaxial, distally anastomosing, part of a peripheral bundle system. Schneider (1976) agrees with these observations.

The Bogor material permitted the study of the sequence of lignification of the vascular bundles. The central bundles are ahead of the peripheral ones. In general there is an upward and outward sequence. The lignification of the anastomoses of the adaxial system at the lower end of the pollen sacs and of the auxiliary vein take place at the same time.

In the same pond of the Bogor Botanic Garden *Nymphaea lotus* is cultivated. A study of its stamens gave similar results (figs. 1—5) with some variations. The abaxial system is restricted to two simple basal short bundles (indicated by crosses in fig. 1), or is absent. In the outer stamens the adaxial bundles form a large anastomosing network in the whole of the stamen except at the site of the thecae, that is they are also present in the median region between the thecae. There are often connections between the central and adaxial system. Also in the inner stamens there is a slightly anastomosing adaxial system instead of a straight 'auxiliary vein'. Therefore it follows with stronger reason that the 'auxiliary vein' is part of the adaxial peripheral anastomosing system. It cannot be adduced as proof neither for the diplophyllous nor for the amalgamation theory of the stamen.

In the study of 1969, Heinsbroek and the present author suggested that the stamens investigated were flattened three-dimensional structures of unknown homology. In the following I will try to amend this. Firstly, the Australian *Nymphaea gigantea**), which forms a separate subgenus according to Conard (1905), does not have laminar stamens at all. All stamens have terete filaments with a single vascular bundle, and an anther quadrangular in transverse section. Only the filaments of the outermost stamens may have a broadened base with two small short lateral vascular bundles. However, in the anther the thecae are separated by a median stretch of tissue, well vascularised (fig. 6). In it the median bundle gives off anastomosing radial branches (the abaxial system), and two basal lateral branches which anastomose forming an 'auxiliary vein' that may show some ramifications. The conclusion is that also in a quadrangular anther peripheral bundles may occur, if only sterile tissue with a certain radial extension occurs. Secondly, it appears that none of the lateral members of the main central system of vascular bundles in flat stamens of *Victoria* and in *Nymphaea* bear a constant relation to the location of the pollen sacs, the median bundle excepted; lateral bundles may occur if only sterile tissue with a certain tangential extension occurs. There is a consistent correlation between the occurrence of vascular bundles and the width or thickness of the stamens in all cases studied.

As a conclusion I think that, on the ground of the vasculature, the stamens in these taxa must be considered as structures which have become large and flat by an increase of sterile tissue, which is a specialization for these groups. The starting condition may have been stamens with the form of terete microsporangiophores. Therefore, the theory adopted by Moseley and Eames, stating that these stamens are primitive, and the terete

*) Material from natural localities near Townsville (Queensland, Australia), and from the Missouri Botanic Garden.

stamens of the other Dicotyledons derived, must be discarded. Also, in *Nymphaea lotus* as in *Victoria*, the anatomy does not fit in with the amalgamation theory of Meeuse, and the diplophyllous theory of Leinfellner.

It has been suggested by several authors that the increase in size, and therefore the increase in the number of vascular bundles, is related with pollination by crude beetles (Carlquist 1969, Gottsberger 1974, and Stebbins 1974). The pollination by beetles in these plants is a well known feature, especially for *Victoria* (Knoch, 1899). Recently it was again reported for two nocturnally flowering species of *Nymphaea*, by Cramer, Meeuse & Teunissen (1975). The *Nymphaea lotus* plants used for the present study flowered also during the night at Bogor. The pollination method of *Nymphaea gigantea* — with slender stamens — is undescribed ; these plants flowered in day-time.

My conclusion on anatomical grounds that the increase in size of the stamens is a specialisation in these plants, is in accordance with the view of Prance & Arias (1975) that the cantharophily in *Victoria amazonica* is secondary, not primitive, given that the correspondence between increase in size and cantharophily is real.

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