

MORPHOLOGY OF THE FLOWER IN THOTTEA SILIQUOSA AND THE EXISTENCE OF STAMINODES IN ARISTOLOCHIACEAE*

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SUMMARY

The number of stamens in the family Aristolochiaceae range between 6 and 46. This range has been speculated to be a reduction series; nevertheless, not even a single taxon within the family is so far known to possess staminodial appendages. Floral anatomical studies of the three morphotypes of the species *Thottea siliquosa* (Lamk.) Ding Hou referred by three taxonomically synonymous nomenclatural species, viz. *Apama siliquosa* Lamk., *Bragantia dalzellii* Hook. f. and *B. wallichii* W. & A., brought to light the existence of staminodes.

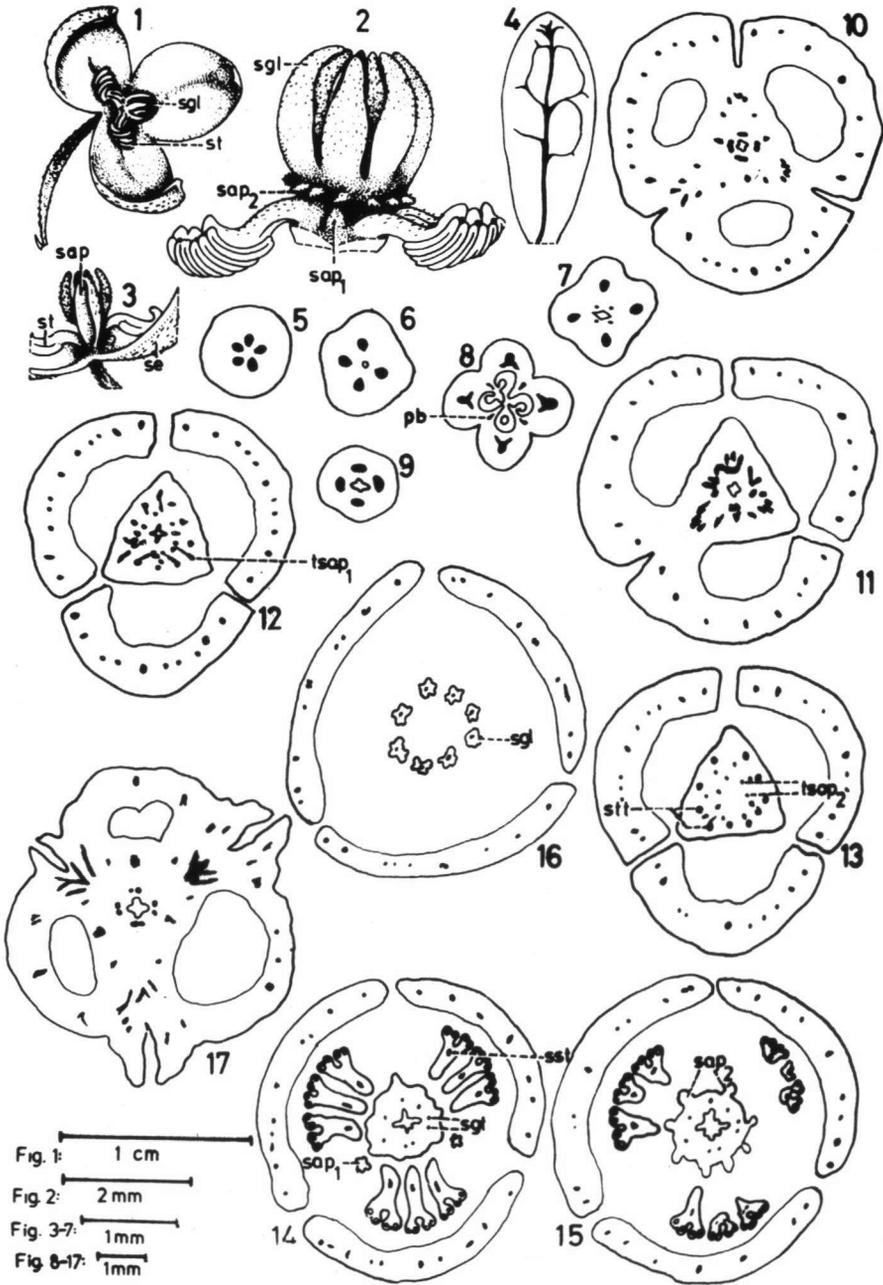
INTRODUCTION

The family Aristolochiaceae comprises nearly 7 genera and 400 species (Airy Shaw, 1973), distributed in the tropics and a few extending to the temperate (Bentham, 1880). The trimerous flowers with a predominance of zygomorphic uniseriate perianth; inferior ovary and the formation of a gynostemium by the union of the staminal filaments to the style, identify the family. Very rarely, biseriate and actinomorphic perianth and apocarpous semi-inferior pistil are also met with in some of the primitive genera (Bentham, 1880; Hutchinson, 1926).

The calycine morphology of the uniseriate perianth lobes within the family is generally agreed upon, the corolline whorl having obliterated in the course of evolution (Hutchinson, 1926; Rendle, 1925). The androecium within the family, especially the number of stamens, is known to be quite variable, ranging between 6 and 46, being arranged in 1–4 whorls (Ding Hou, 1981). However, it is interesting that within this family, with such a wide range of variability in the number of stamens, not even a single taxon is reported to have staminodes (Bentham, 1880; Ding Hou, 1981).

Among the Indian species of the regular flowered genus *Thottea*, the taxonomic circumscription of *T. siliquosa* (Lamk.) Ding Hou, as understood at present, comprises three morphotypes. These morphotypes are referable by three taxonomically

* KFRI Scientific Paper No. 59.



synonymous nomenclatural species, viz. *Apama siliquosa* Lamk., with free perianth lobes, *Bragantia wallichii* W. & A., with cupular perianth, and an imperfect species, *B. dalzellii* Hook. f. (refer Ding Hou, 1981). *Bragantia dalzellii* was found upon a singular fruiting specimen (at K) which differed from *B. wallichii* in the larger leaves and fruits. After Hooker (1886) there had been no information on this species and it remained unknown for its floral characters.

Our recent floristic explorations along the Western Ghats in Kerala helped to discover a population of plants which is referable to *Bragantia dalzellii*. The flowers in this species are similar to that in *Apama siliquosa*, but are larger and in addition are characterised by the presence of many sterile accessory floral appendages on the gynostemium. On seeing the specimens, Dr. Ding Hou at the Rijksherbarium, Leiden, expressed the need of anatomical studies in ascertaining the morphology of these accessory floral appendages and accordingly the present investigation was carried out.

MATERIALS AND METHODS

Flowers of all the three morphotypes in *Thottea siliquosa* (Lamk.) Ding Hou, characteristic of each nomenclatural species, viz. *Apama siliquosa* Lamk. (from cultivated plants), *Bragantia dalzellii* Hook. f. (Swarupanandan & Sujith 296 from Wynad) and *B. wallichii* W. & A. (Sasidharan & Swarupanandan 1996 from Sholayar) were fixed in formalin-acetic acid-alcohol. Stereoscopic examination of the flowers was done in search of accessory floral appendages. Flowers of *B. dalzellii* which have an abundance of these appendages and those of *A. siliquosa* which have an occasional association of one or two of these appendages were subjected to anatomical study. Usual methods of dehydration and embedding (Johansen, 1940) were followed. Sections were taken at 15 μm and double stained with crystal violet and erythrosin. In addition, flowers of both species were cleared in 4% KOH, simultaneously stained with basic fuchsin and the vasculature dissected out under a stereoscope. Anatomical details of the flower of *B. wallichii* are known in detail (Nair & Narayanan, 1962) and therefore anatomical studies of this species were not carried out.

Fig. 1–17. Morphology of the flower in *Thottea siliquosa* (Lamk.) Ding Hou (syn.: *Apama siliquosa* Lamk., *Bragantia dalzellii* Hook. f., *B. wallichii* W. & A.). — 1, 2 & 5–16: *Bragantia dalzellii*. 1. Flower; 2. gynostemium showing the stamens, the stigmatic lobes and the accessory floral appendages; 5–15. serial transection of a flower from below upwards. — 3, 4 & 17: *Apama siliquosa*. 3. An occasional flower with a large accessory floral appendage; 4. cleared accessory floral appendage showing the vasculature; 17. transection at the basal region of the flower. — pb: placental bundles; sap: sterile accessory floral appendages; sap₁: ibid. of the outer whorl; sap₂: ibid. of the inner whorl; se: sepal; sgl: stigmatic lobes; sgt: stigmatic traces; st: stamens; stt: staminal traces; tsap₁: vascular trace to the sterile accessory floral appendage of the outer whorl; tsap₂: ibid. of the inner whorl.

OBSERVATIONS

External morphology

In all the three species, *Apama siliquosa*, *Bragantia dalzellii* and *B. wallichii* the flowers are regular, bisexual and epigynous (fig. 1). The perianth is represented by three free but basally connate ovate lobes except in *B. wallichii*, where it is cupular and 3-lobed above. The androecium consists of 9–12 stamens arranged in a whorl, being grouped into 3 clusters of 3–4 each, and opposite to the perianth lobes. In *Apama siliquosa* and *Bragantia dalzellii* occasional variations in the number of stamens as 4 + 3 + 3 and 3 + 3 + 2 are also met with. In the former species one or two of the stamens are often with smaller anthers. The base of the stamens is adnate to the style base forming a gynostemium, characteristic of the family. In *B. dalzellii* and *B. wallichii* the base of the stamens is associated with two series of small tooth like sterile accessory floral appendages on the gynostemium (fig. 2). The outer series is composed of three solitary ascending appendages alternating with the perianth lobes (sap_1) and the inner series of 6–12 horizontally held appendages in three antistaminal clusters or forming almost a continuous whorl (sap_2). In *B. wallichii* the appendages of the inner whorl are often less in number. In *A. siliquosa* both the whorls of appendages are absent. However, out of a very large number of flowers examined, a few were found to possess one or two accessory floral appendages alternating with the perianth lobes, as an occasional case. In an extreme case, one of the flowers was found to have a more or less flat accessory floral appendage (fig. 3: sap) in a position alternating with the perianth lobes, which has the shape of a rudimentary petal. On clearing it proved that this rudimentary appendage is vascularised (fig. 4). The ovary is inferior, tetragonous and tetralocular, style short or nil and the stigma is composed of 7–9 subulate, cylindric lobes.

Floral anatomy

In both *Apama siliquosa* and *Bragantia dalzellii* the pedicel of the flower receives five vascular bundles (fig. 5). At a higher level one among these five bundles moves towards the centre (fig. 6). At the base of the ovary this bundle divides into four inversely oriented placental bundles (pb), arranged along the septal radii (fig. 7). From the outer four bundles, lateral traces are given off to these placental bundles (fig. 8). The placental bundles, after supplying the ovules, gradually fade out (fig. 9). The outer four vascular bundles traverse upwards through the floral tube. At the top of the floral tube these bundles spread and divide laterally. From the vascular bundles lying opposite to the perianth lobes the median traces for the perianth lobes are given off. These traces divide occasionally as they go upwards. Six more traces are supplied to each of the three perianth lobes which divide laterally as they go upwards. Thus, 10–11 vascular bundles are seen in each perianth lobe at higher regions (figs. 9–13).

In *Bragantia dalzellii*, after the separation of the perianth lobes, the bundles remaining in the triangular receptacle divide and give off three traces, which move to the corners (fig. 12). These traces ($tsap_1$) correspond to the three sterile accessory floral appendages of the outer whorl. But they disappear before entering the organs

concerned which separate off from the receptacle at a slightly higher level. Simultaneous with the separation of these three traces, staminal traces (stt) also are produced. A single trace supplies each of the stamens (figs. 12–15). Two rings of smaller vascular bundles are left in the centre of the receptacle (fig. 13). The outer ring consisting of 8–9 bundles soon fades out. These are the vestigial traces to the sterile accessory appendages of the inner whorl (sap_2) which develop after the separation of the stamens from the receptacle (figs. 13–16). The vascular bundles of the inner ring, the stigmatic traces (sgt), correspond in number to the number of stigmatic lobes and they traverse up to the tip in the latter (figs. 14–16).

In *Apama siliquosa*, the vascular bundles, after supplying the perianth, separates into two rings. The outer ring of nine bundles supplies the stamens and the inner ring supplies the stigmatic lobes. Here also, the number of vascular bundles in the ring varies, depending on the number of stigmatic lobes present.

DISCUSSION

Morphological details of the flowers in *Apama siliquosa* and *Bragantia dalzellii* resemble each other except for the presence of sterile accessory floral appendages and their corresponding vestigial traces in *B. dalzellii*. The floral morphology of *B. wallichii* (Nair & Narayanan, 1962) is also in general agreement with that of *A. siliquosa* and *B. dalzellii*. In this species some minor differences in the vasculature of the perianth also exist, which perhaps owe to the cupular perianth.

Of the two series of sterile accessory floral appendages found in the flowers of *Bragantia dalzellii* and *B. wallichii*, the three appendages of the outer whorl (sap_1) have a petaline morphology. These appendages alternate with the segments of the perianth lobes. The rarely met petaline appendage in *Apama siliquosa* with anastomosing vasculature (figs. 3 & 4), which is a homologue to these appendages in their position alternating with the perianth segments, evinces this conclusion. Similar conclusions have been made of the three teeth-like appendages found in the genus *Asarum* Linn. of the same family (Hutchinson, 1926; Rendle, 1925).

Further in *Bragantia dalzellii* anatomy of the flower reveals the existence of vestigial vascular traces corresponding to these appendages, but this fades out before entering the appendage. Similar vanishing traces are reported at the base of the perianth tube in *B. wallichii* by Nair & Narayanan (1962), although they did not observe the corresponding appendages. However, our present observations show the existence of these appendages in *B. wallichii* also. Nair & Narayanan (1962) interpreted these vanishing vascular traces as the probable midrib bundles of an inner whorl of perianth, i.e., of the corolla whorl, in concomitance with the interpretation by Eames & McDaniels (1947). Internal vascular morphology and the compatible external morphology therefore lead to the assumption that the accessory floral appendages of the outer whorl in *Thottea siliquosa* are vestigial and corolline. This view is also supported by the fact that in some primitive members of the family like *Saruma* Oliv., a well developed inner corolla whorl of three free petals is found. Thus, within the family

Aristolochiaceae, an evolutionary reduction series of the corolla is observable through *Saruma*, *Asarum* and *Thottea* that culminates in a uniseriate perianth of calycine morphology.

While the outer whorl of accessory floral appendages in *Bragantia dalzellii* and *B. wallichii* infer a corolline morphology, the inner whorl of sterile accessory floral appendages assumes a staminodial morphology. In *Apama siliquosa* and *Bragantia wallichii* instead of the normal 4+4+4 and 3+3+3 arrangement of the stamens, quite often a 4+3+3 and 3+2+2 arrangement and rarely one or two stamens with smaller anthers are noted. Vascular anatomy shows that aberrations such as two traces entering one and the same stamen also exist in *Apama siliquosa*. These observations confirm a reductive trend in the number of stamens within these species, thus suggesting the possibility of a staminodial homology of the inner whorl of the sterile accessory appendages. Further, the vestigial traces corresponding to these appendages originate from the very base of the staminal traces, again suggesting a staminal homology.

The number of stamens in the family Aristolochiaceae is highly variable, ranging between 6 and 46. This wide range in the number of stamens has been speculated as an evolutionary reduction series (Hutchinson, 1926). But so far not a single taxon of the family was known to possess staminodes in support of the above assumption. However, with the present finding of staminodes in *Bragantia dalzellii* and *B. wallichii* Hutchinson's (1926) assumption that the direction of evolution within the family has been towards reduction leading to fewer stamens is substantiated.

ACKNOWLEDGEMENTS

We are thankful to Dr. Ding Hou at the Rijksherbarium, Leiden for suggesting the problem. Our obligations are due to Prof. V.P.K. Nambiar, former Scientist-in-Charge, Botany Division and Dr. S. Kedharnath, Director, Kerala Forest Research Institute, for encouragement and necessary facilities.

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