

STUDIES ON THE VENATION PATTERN IN FERNS I. ANASTOMOSES AND
OTHER FEATURES IN *ADIANTUM INCISUM* FORSK. (*A. CAUDATUM*
SENSU BEDD., NON LINN. PRO PARTE)

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ABSTRACT

Anastomoses, though infrequent, occur in the dichotomous venation of *Adiantum incisum* Forsk. Generally more than one anastomosis does not occur in a single leaflet, but in three leaflets there were two anastomoses each. The anastomoses are classified into seven types. In Type I two branches of a single vein-dichotomy unite and the branches separate immediately after fusion. Type II anastomosis is similar to Type I but the branches do not separate after confluence. In Type III adjacent branches of two vein-dichotomies unite and separate after a short area of confluence. In Type IV two closely adjacent branches of two vein-dichotomies are interconnected by a very short transverse commissural vein. Type V is similar to Type IV but the commissural vein is obliquely oriented. Type VI is characterized by the formation of an areole by the union of an unbranched arcuate vein and one of the branches of its sister vein lying above it. The region of confluence is very short and the branches again separate. Type VII is similar to Type VI but the branches do not divide after fusion. Vein approximations have been observed in addition to blind vein-endings, sinus vein-dichotomy, detached vein and marginal blind vein-dichotomy. It has been considered that the separation of *Hewardia* to a distinct genus is unjustified. Certain phylogenetic aspects of vein-approximations and anastomoses are discussed.

INTRODUCTION

Open dichotomous venation characterized by the repeated forking and marginal ending of several diverging veinlets is found in the foliage leaf of several fossil and living ferns. This type of venation is considered primitive (on the basis of fossil records) and excepting for a dissenting note by Wagner (1952) there has been a consensus of opinion that reticulate venation which became common during the mesozoic era has evolved by the progressive union of veins from the ancient forms of dichotomous venation (Potonie, 1912; Bower, 1923; Teixeira, 1955; Zimmermann, 1959). The regular occurrence of open dichotomous venation in primitive families of ferns and the existence of transition between dichotomous and reticulate venation in the juvenile and adult leaves of certain taxa are regarded as further evidence of the derived nature of reticulate vasculature (see Bower, 1935; Foster, 1961). Nevertheless, details regarding the pat-

terns of anastomoses and other peculiarities of venation found simultaneously along with open dichotomous venation in ferns have not received adequate attention. In the present paper some interesting aspects of the venation system of *Adiantum incisum* Forsk. (*A. caudatum* sensu Bedd., non Linn. pro parte) are dealt with.

MATERIALS AND METHODS

Leaves were obtained from plants growing in Belgharia, 24-Parganas, W. Bengal, through the courtesy of Mr. Ranjit K. Ghosh of the Botanical Survey of India, Calcutta. Voucher specimen R. K. Ghosh 956 collected on 20.3.1972 is deposited in the herbarium of the Cryptogamic unit of the Botanical Survey of India, Calcutta. Additional material was obtained from Indian Botanic Garden, Sibpur, through the kindness of Mr. D. N. Guhabakshi. They were cleared in 5 per cent sodium hydroxide solution for 24 hours and later in concentrated chloral hydrate. Staining was done in a few cases

with 1 per cent safranin. Otherwise, the observations are based on unstained but cleared leaflets mounted in glycerine. Diagrams were drawn with the help of camera lucida. The following data are presented after examining 900 leaves.

OBSERVATIONS

The pinnae are nearly sessile, almost parallelogram-shaped or cuniate dimidiate, with the basiscopic side straight and horizontal and the acroscopic side more or less cut, often, into 4 lobes. One of the lobes is sometimes bilobed. Very rarely sinuses may be deeper than half the width of the pinna. The apex of the lobes are often slightly crenate. Although the nature, dissection and lobing of the segments vary from pinna to pinna, the general ground-plan of organization is very similar. In some cases the major lobes may be shallowly lobed again.

The delicate pattern of open dichotomous venation of very prominent veins is a characteristic feature of the pinna. The ground-plan of pinna venation comprises of well-marked system of dichotomizing veinlets. Dichotomous systems of veinlets are symmetrical and clearly defined in the lower region of the pinna. The petiole has a single vascular strand and it divides into two while entering the pinna. At the base of the pinna the two veins again divide into two each. These four main veins repeatedly divide and each main system enters a main lobe of the pinna (Fig. 1). Thus there is a correlation between the main vein-systems and the number of main lobes in the pinna *i.e.* each lobe is vascularized by independent veinlet-systems (Figs. 1, 2). Subsequent dichotomies of the main veins show marked fluctuations as a result of which the number of marginal vein-endings vary in each lobe; there may be 3-7 vein-endings in each lobe of the pinna. Variation in the general pattern of venation has been observed in several cases. While majority of the marginal vein-endings terminate beneath crenatures in the acroscopic

margin, others were unrelated to these crenatures. In several cases crenatures were not well-marked. Even then, their positions can be easily determined. The veins which are not related to crenatures can be called as blind vein-endings. Foster (1959) and Foster and Arnott (1960) used the term blind vein-ending in a slightly different sense. In *Kingdonia* a vein usually entered a marginal tooth, but those veins which were unrelated to the tooth were called by them as blind vein-endings. Usually the blind vein-endings are marginal on the lateral sides of the pinna (Fig. 2). Sometimes they occur just below the sinus which separates either the secondary lobes or the primary lobes. Sometimes it is seen just below the shallow incision which separates two crenatures (Fig. 3). The blindly ending veinlets may be long or short, branched or unbranched (Fig. 3). Marginal blind vein-dichotomies have been observed (Figs. 2, 4, 11) in four leaves. Branched veins below the sinus are called sinus-vein-dichotomy by Foster and Arnott (1960). In *A. incisum* only two sinus vein-dichotomies have been observed (Fig. 1). The veinlets derived from sinus-vein-dichotomy diverge into the marginal region of adjacent lobes or lobules and end blindly (Fig. 1). As a result of sinus-vein-dichotomy the veinlets vascularise two separate but adjacent divisions of the pinna. This is in contrast to the typical condition where all the vein-endings in a lobe or lobule originate from the same vein-system. Similar sinus-vein-dichotomies are also known in *Circaea* (Foster, 1970).

Another deviation was the presence of unconnected veins extending from the margin for a little or long distance and without any basal connection. Only three leaves of this kind have been observed. The unconnected vein may be central or marginal (Figs. 5, 7, 8) in position. Similar unconnected veins have been reported in *Ginkgo* by Arnott (1959), *Kingdonia* (Foster and Arnott,

1960) and *Circaeaster* (Foster, 1970). As suggested by Foster and Arnott (1960) these unconnected veins may represent arrested stages in the differentiation of xylem of vein-endings. It also raises certain interesting questions which can only be resolved by detailed study of vein differentiation.

Six cases of vein-approximations (Foster, 1966) *i.e.* transition between open dichotomous venation and true anastomoses, were observed in the present study. These vein-approximations do not have any definite position in the pinna (Figs. 3-6, 9, 11). In open dichotomous venation the adjacent branches of successive vein-dichotomies extend more or less parallel and equidistant from each other (Foster, 1963). On the other hand, an anastomosis represents the confluence of the xylem of two juxtaposed veins and the formation of an elongated closed areole (Foster, 1966). In vein-approximation the tracheary elements of the adjacent branches of a pair of very closely placed veins are separated by parenchyma and hence the areole will be opened at the distal end. Approximation may be in the lateral, central, basal or distal region of the pinna.

Anastomoses were present. Out of the 900 leaves examined 28 leaves (3.1 per cent) showed one kind of anastomosis or the other. For convenience the following seven types of anastomoses (Fig. 20) have been recognised in the present study.

TYPE I. Here the areole is created by the union of two branches of a single vein-dichotomy (Figs. 9, 20) and the branches separate immediately after union. Such areoles were always near the acroscopic margin. This type of anastomosis was observed only in 4 leaves (14.3 per cent of the total number of leaves showing anastomosis).

TYPE II. Here the areole is formed by the union of two veins produced by a single dichotomy as in Type I, but the vein formed by the union do not divide (Figs. 10, 11, 13). Arnott (1959) designated this as A Type

of anastomosis. This type is generally confined to the leaf-margin as has been reported in *Ginkgo* by Arnott (1959). Generally more than one anastomosis of this kind could not be observed in a single leaflet. But in three leaflets two anastomoses each were seen. Seven leaflets (25 per cent of the total number of leaflets with anastomosis) had Type II anastomosis.

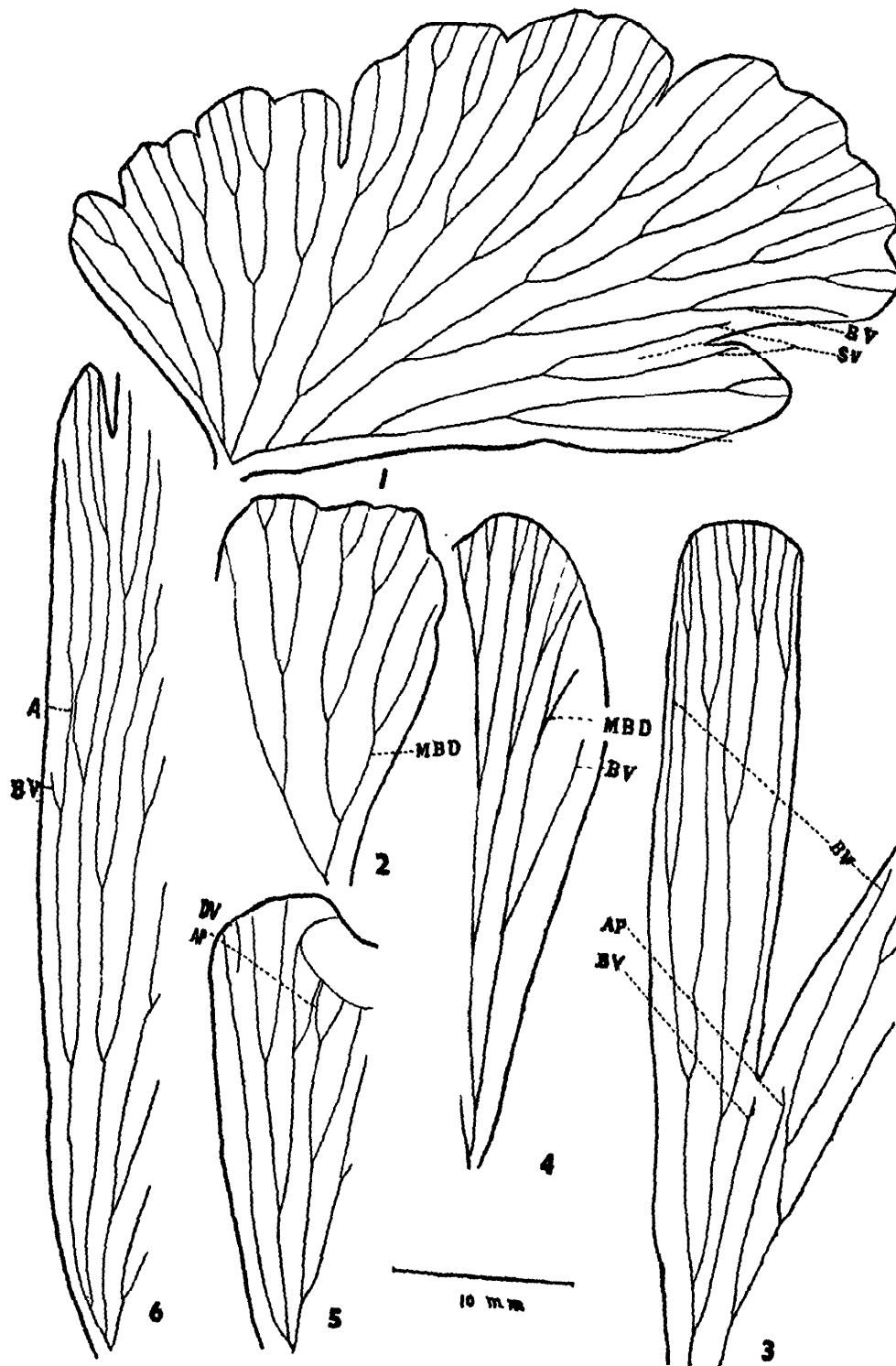
TYPE III. In this type of anastomosis adjacent branches of two vein-dichotomies unite and separate after a short area of confluence (Fig. 12, 20). After their separation, above the area of fusion, the two veins diverge towards the leaflet margin. This type of anastomosis was observed only in two leaflets (7.15 per cent of the total leaflets with anastomosis). In one of them it was at the base of the leaf while in the other it was towards the apex. Type III anastomosis in *A. incisum* is essentially similar to Type D anastomosis of *Ginkgo* (Arnott, 1959) and Type I anastomosis in *Circaeaster* (Foster, 1966). This type of anastomosis is also known in petals of *Ranunculus* (Banerji and Mukerji, 1970).

TYPE IV. The salient feature of this type of anastomosis is that two adjacent branches of two vein-dichotomies are interconnected by a very short transverse commissural vein. This type of anastomosis was observed in two leaves (7.15 per cent of the total number of leaves with anastomosis).

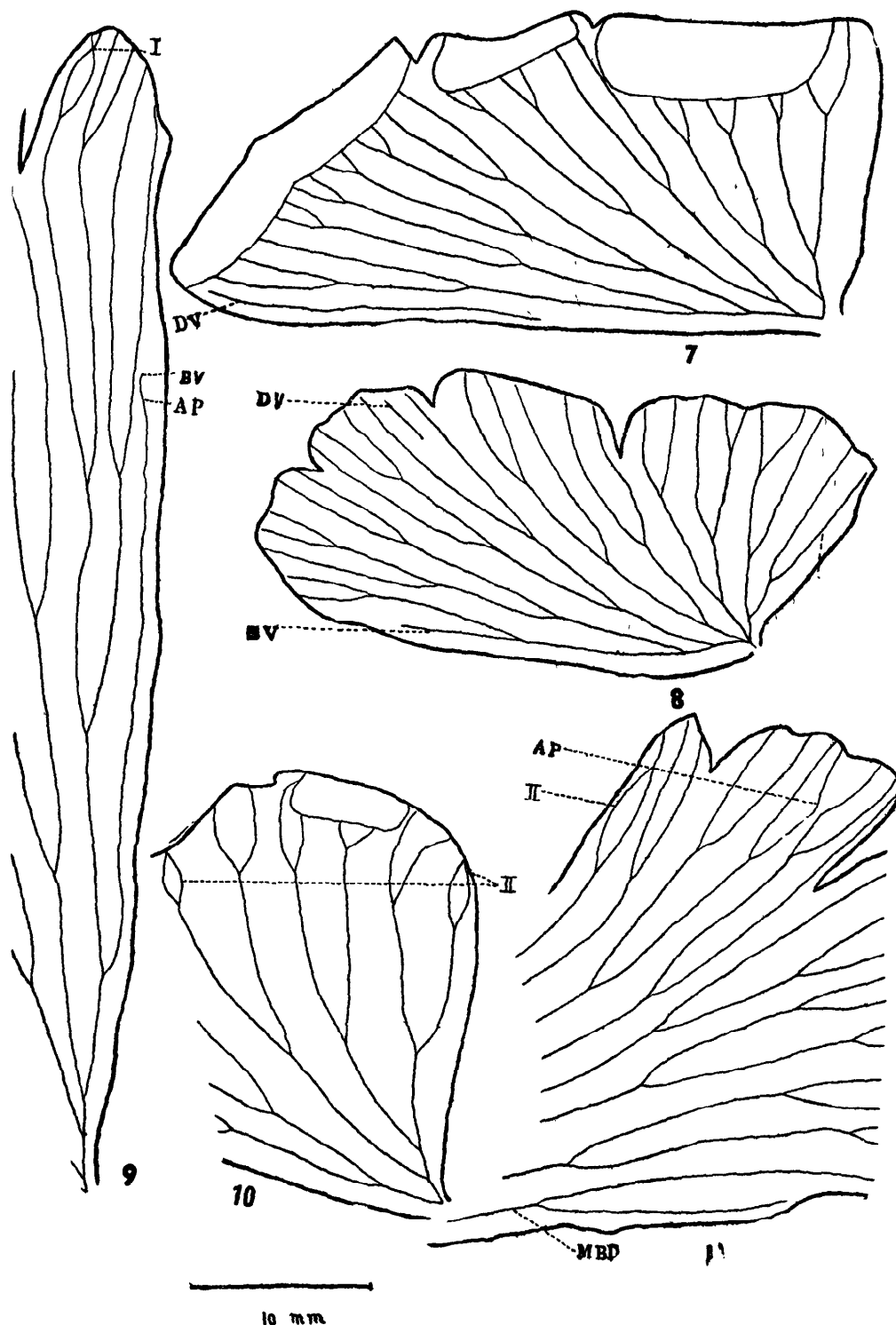
Type IV anastomosis is similar to Type C vein-anastomosis in *Ranunculus* (Arnott and Tucker, 1963).

TYPE V. Type V anastomosis is similar to Type IV described above but the commissural vein is obliquely oriented (Fig. 14). This anastomosis is essentially similar to Type III anastomosis described by Foster (1966) in *Circaeaster*. Type V anastomosis was observed only in one leaflet (3.57 per cent of the total number of leaves with anastomosis).

TYPE VI. The characteristic feature of

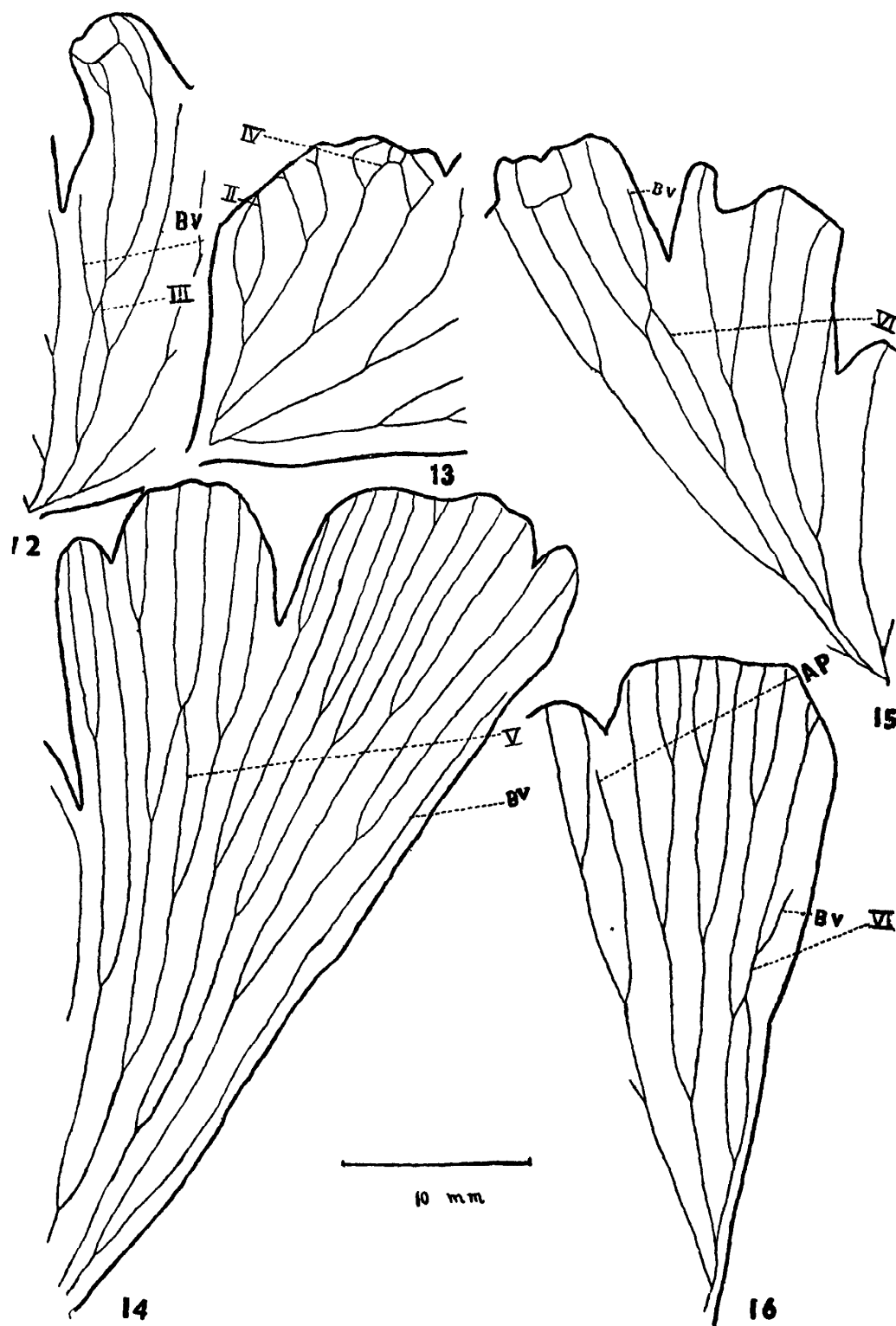
Figs. 1-6: Venation pattern in *Adiantum incisum* Forsk.

1. Leaflet showing sinus-vein dichotomy and blind vein-endings. 2. Part of leaflet showing marginal blind dichotomy. 3, 6. Parts of leaflets showing blind vein-endings and vein approximations. 4. Part of leaflet showing marginal blind dichotomy and blind vein-ending. 5. Part of leaflet showing detached vein and vein approximation. A, AP, vein approximation; BV, blind vein-ending; DV, detached vein; MBD, marginal blind dichotomy; SV, sinus vein-dichotomy.



Figs. 7-11: Venation pattern in *Adiantum incisum* Forsk.

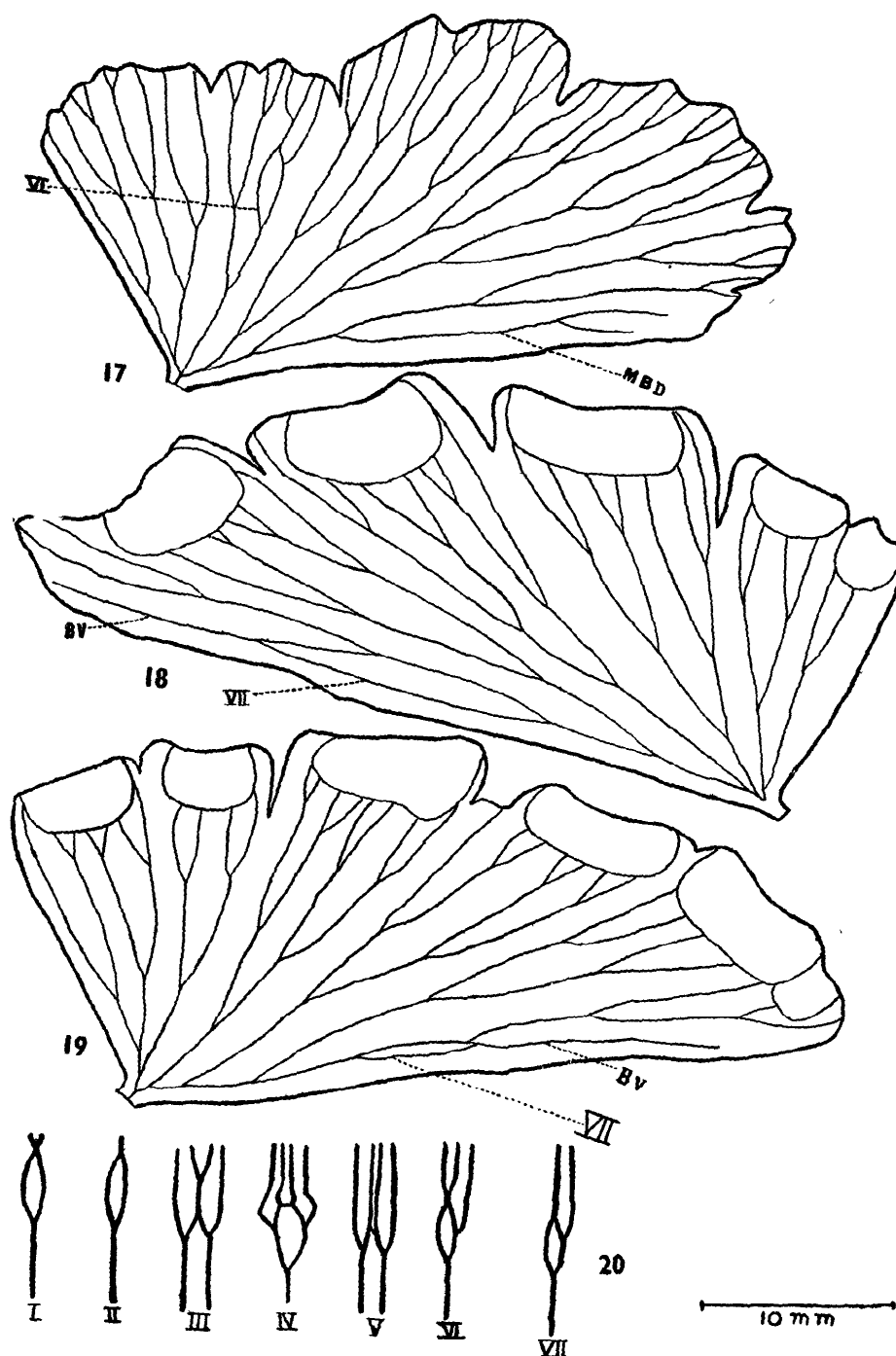
7. Leaflet showing detached vein. 8. Leaflet showing detached vein and blind vein-ending. 9. Part of leaflet showing Type I anastomosis, vein approximation and blind vein-ending. 10. Part of leaflet showing two Type II anastomoses. 11. Part of leaflet showing marginal blind dichotomy, vein approximation and Type II anastomosis. AP, vein approximation; BV, blind vein-ending; DV, detached vein; MBD, marginal blind dichotomy. I—II, Types of anastomoses.



Figs. 12-16: Venation pattern in *Adiantum incisum* Forsk.

12. Part of leaflets showing blind vein-ending and Type III anastomosis. 13. Part of leaflet showing Type II and Type IV anastomoses. 14. Part of leaflet showing blind vein-ending and Type V anastomosis. 15. Part of leaflet showing blind vein-ending and Type VI anastomosis. 16. Part of leaflet showing blind vein-ending, vein approximation and Type VI anastomosis.

AP, vein approximation, BV, blind vein-ending. II-VI Types of anastomoses.



Figs. 17-20: Venation pattern in *Adiantum incisum* Forsk.

17. Leaflet showing marginal blind dichotomy and Type VI anastomosis. 18. Leaflet showing blind vein-ending and Type VII anastomosis. 19. Leaflet showing blind vein-ending and Type VII anastomosis. 20. Diagrammatic representation of various types (Types I to VII) of anastomoses in *Adiantum incisum* Forsk.

BV, blind vein-ending; MBD, marginal blind dichotomy; I—VII various types of anastomoses.

this type of anastomosis is that an areole is formed by the union of an unbranched arcuate vein and one of the branches of its sister vein lying above it (Figs. 15-17, 20). The region of confluence is short and after the separation of the two strands, the upper portion of the arcuate vein (if the anastomosis is on the lateral side of the pinna) either terminates blindly or ends at the acroscopic margin or (if the anastomosis is on the central portion of the pinna) the separated veins terminate at the acroscopic margin.

This pattern is distinct from Types III, IV and V dealt with above in which union occurs between two of the branches of a pair of adjacent vein-dichotomies. This type has been observed in nine leaves (31 per cent of the total number of leaves with anastomosis). Frequently the areole is in the central portion of the pinna.

Type VI anastomoses are similar to Type IV anastomosis in *Circaeaster* (Foster, 1968).

TYPE VII. This type of anastomosis is similar to Type VI described above but with one difference. The tip of an arcuate vein converges toward and become completely fused with the branch of a vein-dichotomy present above it (Figs. 18, 19, 20). This type was observed in three leaves (10.71 per cent of the total number of leaves with anastomosis). This type of anastomosis was always on the lateral margin of the pinna and the confluent vein ended blindly.

DISCUSSION

Hooker and Baker (1868) divided the genus *Adiantum* into two subgenera, *Euadiantum* with veins not anastomosing and *Hewardia* with veins anastomosing. The plant on which the present observations are based fall under *Euadiantum*. Sprecher (1907) remarked that foliar venation in *Adiantum* (sensu *Euadiantum*) is devoid of anastomosis. Holttum (1954) states that the veins in the leaflet of the genus are always strictly dichotomous. The results of the present

study show that several distinct types of anastomoses exist in *A. incisum*.

Subgenus *Hewardia* is sometimes treated as a distinct genus (Smith, 1841) on the basis of anastomosing veins. Copeland (1947) states that "anastomosis is sometimes casual rather than well-fixed." The data presented above show that subgenus *Hewardia* is not the only *Adiantum* showing anastomosis. In addition to *Adiantum incisum*, other species also show anastomosis (authors' unpublished observations). On these grounds, as observed by Hooker (1859) and Copeland (1947), it is not worthwhile to maintain *Hewardia* as a distinct genus on the basis of anastomosing veins alone.

No anastomosis was observed in any of the thirty leaves of *A. indicum* Ghatak examined by the present authors. This shows that in the genus, *A. indicum* represents one extreme and *Hewardia* represents another extreme. *A. incisum* seems to represent an intermediate condition in the evolution between a purely open dichotomous venation and a fully anastomosed condition. Similar instances are known in the genus *Anemia*. According to Mickel (1962), subgenus *Coptophyllum* are open dichotomously veined and devoid of anastomosis while the subgenus *Anemia* has pinnae which are either weakly anastomosed (*A. herzogii*) or conspicuously areolate veined (*A. phyllitidis*).

The frequency of blind vein-endings in *Kingdonia* according to Foster (1971) may be correlated to some extent with the large size of the leaf and relatively profuse venation. He thinks that frequency of blind vein-endings probably represents normal deviation which occurs in the dichotomous venation patterns of a wide variety of plants. The present authors do not think that in *Adiantum incisum* the size of the leaflet and the number of veins in it have any correlation with blind vein-endings.

The question arises whether unbranched blind vein-endings represent the persistence

of the vascular supply of suppressed lobes. This is possible only if the vascular strands are conservative. What is the significance of the presence of blind vein-endings in some and its absence in majority of leaflets? A plausible explanation cannot be given at present for this phenomenon.

Wagner (1952) and Chrtek (1962, 1963) consider that dichotomous venation is not primitive but derived. Foster and Arnott (1960), Arnott and Tucker (1963) and Banerji and Mukerji (1970) on the other hand think that open dichotomous venation is primitive. Following the same line of argument put forward by Foster and Arnott (1960) it could be considered that open dichotomous venation and the types of anastomoses found in *A. incisum* are unspecialized ancient types. Potonie (1912) while dealing with the phylogenetic origin of anastomoses, states that "... at least the palaeozoic reticulations originated by the lateral joining of originally separate veins and not by *de novo* formations of anastomoses. One can see, that the anastomoses extend obliquely upwards and will be easily convinced that they are the lowermost portions of the branches of two dichotomies whose upper portions have united to a single vein. At other points one sees these branches of a dichotomy, after a preliminary union, again separating from each other." Types C and D observed by Arnott (1959) in *Ginkgo* and Types I and II observed by Foster (1968) in *Circaeaster* correspond to Potonie's description. Their observations fit in with Type III anastomosis in *A. incisum*. This type of anastomosis can be considered as one of the most ancient types as has been suggested by Foster (1968). He (1968) has raised the question, how should one interpret phylogenetically the apparently simple type of anastomosis in which an areole is created by the union of two branches of a single dichotomy? Such areoles are not recorded among fossil plants. Type II anastomosis described in the pre-

sent study (Type A of Arnott, 1959) which is the most common in *Ginkgo* has also been reported in Cycads, a few ferns such as *Stenochlaena palustris* (Burm.) Bedd., *Anemia herzogii* Rosenstock (Foster, 1968) and *Regnellidium* (Pray, 1962), petals of *Ranunculus* (Arnott and Tucker, 1963) and in the leaves of *Circaeaster* (Foster, 1968) and *Utricularia* (Subramanyam, 1969). Foster (1968, p. 64) states that the phylogenetic status of this type of anastomosis "in the living ferns and seed plants must for the present remain an entirely open question." The present authors consider that this is also one of the most ancient types of anastomoses. The fact that this type of anastomosis has not been observed in fossil plants may be due to inadequate observation. A critical examination should be made of the venation of fossil ferns.

Foster observed a very rare type of vein-approximation in *Circaeaster* in which the branches of a bifurcated vein came very close to each other. This he regarded as the transition between Type A anastomosis of Arnott (1959) and a normally bifurcated vein. Type I anastomosis of the present study where the two branches of a single vein-dichotomy reunite and separate immediately after union can be considered as the next step above the type of approximation observed by Foster and the one below Type II in which the reunited vein continues as a single vein. Fig. 6 depicts an approximation which is intermediate between Types III and IV and open dichotomy. The vein approximation in Fig. 16 represents an intermediate stage between open dichotomy and Type V of Foster (1968).

It is of interest that similar types of anastomoses are met with in phylogenetically widely separated taxa showing dichotomous venation in their parts such as leaves of *Circaeaster*, Cycads (Foster, 1961, 1966), *Ginkgo* (Arnott, 1959), *Utricularia* (Taylor, 1964; Subramanyam, 1969), *Adiantum* (present

study) and other ferns (Pray, 1962; Foster, 1968) and petals of some flowering plants (Gumppenberg, 1925; Kausmann, 1941; Hammen, 1948; Arnott and Tucker, 1963; Banerji and Mukerji, 1970; Banerji, 1971; Subramanyam and Nair, 1973). This supports the contention of Foster (1968) that a parallel evolution of similar types of anastomoses has very probably occurred in morphologically divergent and taxonomically unrelated plants. The different types of anastomoses reported probably show the various trends through which reticulate venation has evolved.

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