

Diversity of Nodal Structure in *Mallotus nudiflorus* (L.) Kulju & Welzen (Euphorbiaceae) – insight into the evolution of “Howard’s Split-Lateral”

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ABSTRACT

In 1970, Howard proposed a fifth type of nodal anatomy pattern, where a single vascular trace from the stele is associated with more than one leaf and termed it as “split-lateral”. Several workers observed this type of nodal vascular trace in different angiosperm families, but with rather conflicting interpretations. The present study added another family – Euphorbiaceae – in the list of such nodal type and, based on the observation of different nodal configurations of the species *Mallotus nudiflorus* (L.) Kulju & Welzen (basionym *Trewia nudiflora* L.), the evolutionary consequences of “split-lateral” were discussed.

KEY WORDS

Nodal anatomy,
“split-lateral”,
evolution,
Euphorbiaceae.

RÉSUMÉ

Diversité de la structure nodale chez Mallotus nudiflorus (L.) Kulju & Welzen (Euphorbiaceae) – un aperçu sur l’évolution du « modèle latéralement divisé de Howard ».

En 1970, Howard a proposé un cinquième modèle d’anatomie nodale, dans lequel une trace vasculaire unique issue de la stèle est rattachée à plus d’une feuille, et l’a désigné comme « latéralement divisé ». Plusieurs chercheurs ont détecté ce modèle dans différentes familles d’angiospermes, mais avec des interprétations assez contradictoires. La présente étude signale sa présence dans une autre famille – les Euphorbiaceae – et, fondées sur les différentes configurations nodales observées dans *Mallotus nudiflorus* (L.) Kulju & Welzen (basionyme *Trewia nudiflora* L.), les conséquences évolutives de ce modèle « latéralement divisé » sont discutées.

MOTS CLÉS

Anatomie nodale,
“latéralement divisé”,
évolution,
Euphorbiaceae.

INTRODUCTION

Sinnott (1914) established a classification of nodal anatomical structure and proposed three nodal types, unilacunar, trilacunar and multilacunar and advocated trilacunar as basic nodal structure of angiosperms from which unilacunar type has been evolved either through approximation of two lateral traces or simply by abolition of them, whereas, multilacunar type has been originated by amplification of gaps and traces from the basic trilacunar type. Marsden & Bailey (1950) proposed a fourth type of nodal anatomy in *Clerodendrum trichotomum* Thunb. (Verbenaceae) where two traces departed from the stele and entered the leaf together but were independent in origin from separate parts of eustele and remained separate to varying degrees in the petiolar length and the blade. Subsequent to Sinnott's publication many individual workers have drawn the attention to the variation of nodal anatomical configuration.

The association of a single bundle from the stele of mature stem with more than one leaf had come into lime light only after Howard who termed such type of specialized structure as "split-lateral", best designated here as "Howard's Split-lateral" – the fifth type of nodal structure. Howard had tried much to solve the conflicting interpretation of such a situation and offered the term "split-lateral" for such specialized nodal configuration.

The earliest example of this nodal type is noticed in the illustration published by Nägeli (1858) in *Sambucus nigra* L. (Sambucaceae; previously treated under Caprifoliaceae/or Caprifoliaceae *s.l.*). In this illustration one nodal trace divides into two, each going to respectively opposite leaves. After that several workers have reported such situation in different families, however, it was Swamy & Bailey (1950) and Swamy (1953) who tried to explain the ontogeny or to some extent phylogeny of such specialized structure while studying the vesselless genus *Sarcandra* Gardner and latter on *Chloranthus* Sw. of the family Chloranthaceae. They referred to this type of nodal structure as a modified unilacunar type, for the marginal strands of opposite leaves originated from two "common gaps". They explained the situation and expressed their opinion

that this is not a dichotomy of a single strand but the approximation or fusion of two strands that enter the stele through the same gap from opposite leaves. In Chloranthaceae Swamy (1953) stated that "the four marginal veins (two for each of the oppositely arranged leaves) arise from two 'common gaps' in contrast to the typically trilacunar nodal situation where the four marginal strands of two leaves confront a corresponding number of independent gaps" and considered the nodal pattern as modification of the unilacunar type. The same structure had been designated as "Compound bundle" by Esau (1945) or "Composite trace" by Mitra & Majumdar (1952) in *Sambucus glauca* Nutt. (Sambucaceae) and *Ixora parviflora* Vahl (Rubiaceae) respectively.

Such specialized situation whether should designate a "Compound bundle", "Composite trace" or an approximation of two traces entering a "Common gap" or a single trace which divides becoming a "split-lateral" is a matter of controversy.

This nodal structure drawn much attention and Howard along with other previous workers had also presented its occurrence in many members of unrelated families of flowering plants, viz. Caprifoliaceae *s.l.* or Sambucaceae (Nägeli 1858; Esau 1945; Howard 1970), Chloranthaceae (Rousseau 1927; Swamy & Bailey 1950; Swamy 1953), Compositae (Carlquist 1957), Gentianaceae (Howard 1970), Gesneriaceae (Howard 1968, 1970), Rhizophoraceae (Howard 1970), Rubiaceae (Varossieau 1940; Mitra & Majumdar 1952; Howard 1970), Zygophyllaceae (Cunnigham 1927; Howard 1970).

Later Puff (1978) added a monotypic family Myrothamnaceae in the list of this nodal type while studying the representative member *Myrothamnus flabellifolius* Baillon. In *Myrothamnus flabellifolius*, like in other plants known to have split-lateral traces for their opposite gamophyllous leaves, the lateral traces fork however within the leaf and not, as usual, in the stem. He stated that "as 'stem' and 'leaf', however, must developmentally and morphologically be considered a continuous system (see Howard 1974), this peculiarity of *M. flabellifolius* appears to be of little significance". Lastly, Dickison (1980) and Neubauer (1984) reported "split-lateral" traces in few members of the family Cunoniaceae and Melastomataceae respectively.

During the elaborate investigation over large number of specimens Howard (1968, 1970) tried to solve this controversy and discarded the opinions of Esau (1945), Swamy & Bailey (1950), Mitra & Majumdar (1952), Swamy (1953) and stated that “if one accepts the acropetalous development of xylem within the procambial strand from the stem into the leaf, this condition can be called a split-lateral trace” and based on this opinion he termed such specialized nodal structure as “split-lateral”. No doubt this opinion superseded over Swamy & Bailey’s or Swamy’s “common gap” or Mitra & Majumdar’s “composite trace” or Esau’s “compound bundle”.

During anatomical study of Euphorbiaceae I came across one interesting species *Mallotus nudiflorus* (L.) Kulju & Welzen (= *Trewia nudiflora* L.), a very common tree to the tropical climate in India, popularly known as “Pituli” to the common people. Diverse nodal anatomy of this species well provides the support towards the understanding of evolutionary consequences of “split-lateral”.

MATERIAL AND METHODS

Most of the samples of the species *Mallotus nudiflorus* were collected by the author from different parts of West Bengal and its surrounding states, India. Twigs of the specimens were preserved in FAA (Formaldehyde solution [40%] 5 ml: Glacial Acetic Acid 5 ml: Ethanol [70%] 90 ml) for detailed anatomical study. A series of free hand transverse sections were made of each individual twigs. Sections were stained with 1% Safranin and mounted in 10% Glycerin. In some cases, conventional method of wax embedding and microtome sectioning (Johansen 1940) was done. Permanent slides were prepared and these are kept in Calcutta University Herbarium (CUH). The diagrammatic presentations of the nodes as in the transverse sections were drawn under mirror type Camera Lucida. Sometimes sections were photographed using Olympus Microscope, model no. CH20i. The camera lucida drawings are here provided with explanation of series of development.

OBSERVATIONS

The typical trilacunar three traced condition is the representative nodal structure in this species as in most of the members of the family Euphorbiaceae (Fig. 1C, D). Here six lacunae are present for two oppositely arranged leaves (three for the members with alternate or spiral phyllotaxy). The first two opposite cotyledonary leaves in the seedlings retained the primitive triple-traced condition and are supplied by six traces, three to each, one median and two laterals (Fig. 1A). The green leaves of the seedlings and young plants are alternately arranged and also supplied by three traces, one median and two laterals, without showing any deviation (Fig. 1B).

In a second situation at one side of the node there are two well separated gaps with their own traces, entering the respective opposite leaves. However, the other side shows a single gap with a single “split-lateral trace” which, after splitting above, gives two halves of the trace girdling the node in opposite directions and supplying the respective leaves (Fig. 1E-G). Interestingly almost same situations have been observed in few other nodes, however, gaps between the lateral traces are significantly less numerous and very close to each other.

In a third situation (Fig. 1H-J) at one lateral (here right) side the two gaps approximated to very close in such a way that it may be a mistake as a single gap with two traces. However, a tiny part of the parent vascular cylinder may occur in between these two traces (Fig. 1H, I, at right, pc). During the outward movement of the traces they push the parent stelar part towards cortex, however, soon the stelar part returns to its original position and ultimately joined with the parent cylinder. The respective traces move towards each of their opposite leaf bases (Fig. 1J[It]).

However, the most significant event operated on the other lateral (here right) side of the same node, where a true “unilacunar two traced” situation has been observed. Two very distinct independent traces originated within a single gap. After departure, each of the traces again girdles half way the stem as in other cases and enters the respective opposite leaves (Fig. 1H-J).

The “single gap two traced” situation has also been observed in some other nodes, however, the opposite lateral gap with a “split-lateral” trace instead of two closely approximated lateral gaps with their respective traces as seen in the previous cases (Fig. 1K-M).

In many cases typical “split-laterals” have been observed for both the leaves. Here four gaps have been seen at node. The median traces originate independently for both the opposite leaves. The four lateral traces, however, evolve due to splitting of two traces at both lateral sides. After splitting, one of the halves moves towards opposite direction and enter to the respective leaf. Each leaf, therefore, was supplied with a median trace, and one half of each of two lateral traces ($1/2+1+1/2$) (Fig. 1N-P).

After sequential arrangement of the events, it is observed that the two lateral bundles gradually approach to each other very closely and often are separated only by very small segment of the parent cylinder or even by a single row of xylem elements (Fig. 2D-F). At the next stage they reach within a single gap, i.e. single gap with two traces (Fig. 1H-M). In the final step ultimately a single trace is observed within a gap as “split-lateral” which is probably produced due to the fusion of these two lateral traces.

Thus Euphorbiaceae appears to be the twelfth angiosperm family with split-lateral traces.

Another unusual situation has also been observed. In this case one true “split-lateral” is seen, which after splitting moves towards opposite directions as usual and enters respective leaf. But at other side the trace never divides, moreover, moves desperately towards the base of one of the opposite leaves. Therefore, one leaf was observed with three traces, one median, one half of the “split-lateral” trace and one entire lateral trace ($1/2+1+1$). However, other leaf has only two traces, one median and other is with the rest half of the “split-lateral” ($1/2+1+0$) (Fig. 2A-C, below and above respectively).

Howard (1970) had also reported all these above mentioned situations along with many other unusual conditions while studying the nodal anatomy in *Alloplectus ambiguus* Urb. of the family Gesneriaceae. However, he noticed the close proximity of two lateral gaps as well as traces on either sides

of the median in case of *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) (Howard 1970: fig. 5A). But he had never seen two traces within a single gap, which is most important to understand the evolutionary consequences of “split-lateral”.

DISCUSSION

Swamy & Bailey (1950) referred to the node as a “modified unilacunar type”, for the marginal strands of opposite leaves originated from the two common gaps. They stated that in the genera *Chloranthus* and *Sarcandra* (Chloranthaceae) the lateral traces of the pairs of leaves traverse the node in the cortex before entering the stele through the same gap. They emphasized that this is not a dichotomy of a single strand but the approximation and fusion of two strands and they support that at lower levels in the stem the bundles appear to separate and join different parts of the eustele. Swamy (1953) stated that “it appears reasonable to consider the nodal structure of *Chloranthus*, *Sarcandra* and the like as being a modification of the unilacunar type on account of their sporadic occurrence, always among representatives that possess predominantly unilacunar nodal anatomy.” However, they did not consider the possibility of recognizing this specialized situation in the families having both unilacunar and trilacunar members as also stated by Howard (1970) and significantly in the present study on a member of the family Euphorbiaceae. The same structure had been designated as “compound bundle” by Esau (1945) during the study of the vascularization of vegetative shoot of *Sambucus glauca* Nutt. (Sambucaceae) and as “composite trace” by Mitra & Majumdar (1952) while studying the development of the leaf primordium at the shoot apex of *Ixora parviflora* Vahl (Rubiaceae).

Whether it is a “compound bundle” (Esau 1945), or a product of union of two traces, i.e. “modified unilacunar type” (Swamy & Bailey 1950; Swamy 1953) or a “composite trace” (Mitra & Majumdar 1952) or a “split-lateral” (Howard 1970; Puff 1978; Dickison 1980; Neubauer 1984) the evolutionary consequences is not discussed by the authors. It is also true that the acropetalous development of xylem

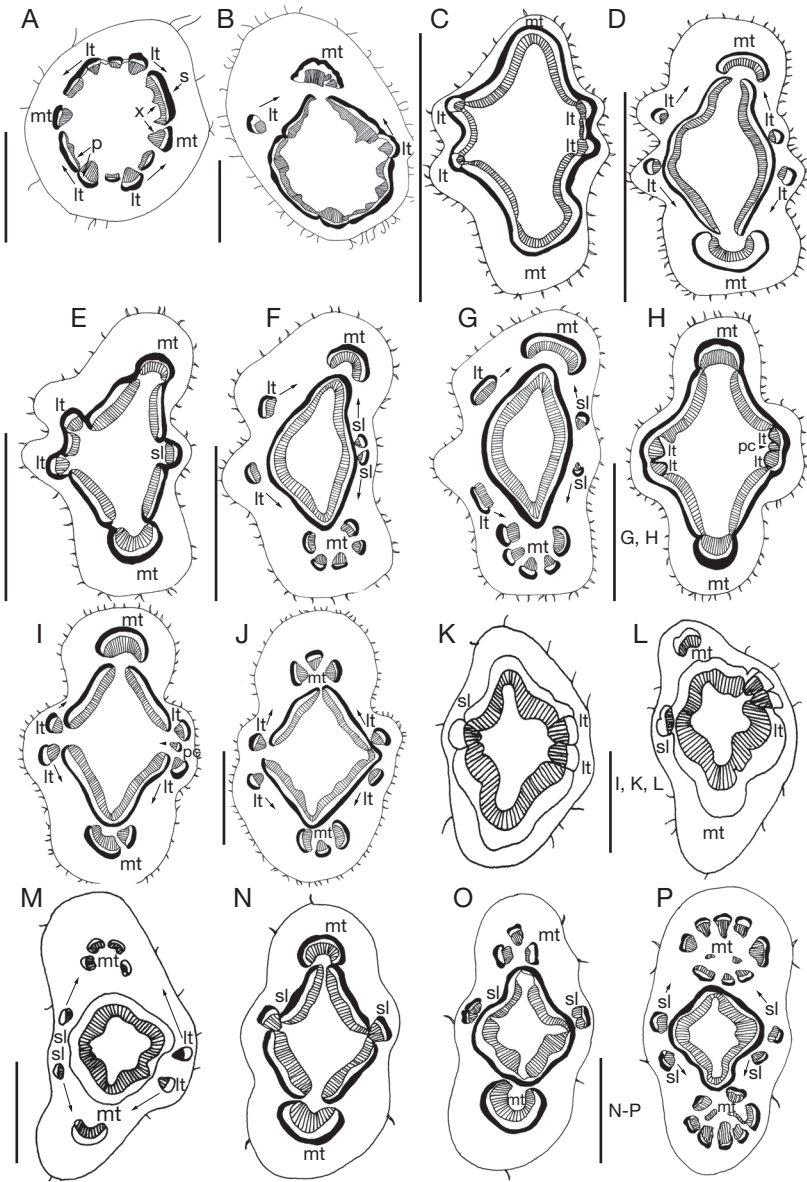


FIG. 1. — Nodal configurations of *Mallotus nudiflorus* (L.) Kulju & Welzen: **A**, trilocular three traces for both cotyledonary leaves; **B**, trilocular three traces for first alternate green leaves in seedling; **C**, **D**, typical trilocular three traces situation for both the opposite leaves; **E-G**, left side with two separate lateral traces and right side with a “split-lateral”; **H-J**, left side with two separate traces within a single gap and right side with very closely approximated two traces with separate gaps, note the tiny part of parent vascular cylinder in between the traces (**I**); **K-M**, left side with two separate traces within a single gap and right side with a “split-lateral” (note sclerenchymatous layer absent); **N-P**; typical “split-lateral” situation for both the opposite leaves, note initiation of division of “split-laterals” (**O**). Abbreviations: **lt**, lateral trace; **mt**, median trace; **pc**, parent vascular cylinder; **sl**, split lateral; **p**, phloem; **s**, sclerenchyma; **x**, xylem. Scale bars: **A**, **B**, 1 mm; **C**, **D**, 5 mm; **E-P**, 4 mm.

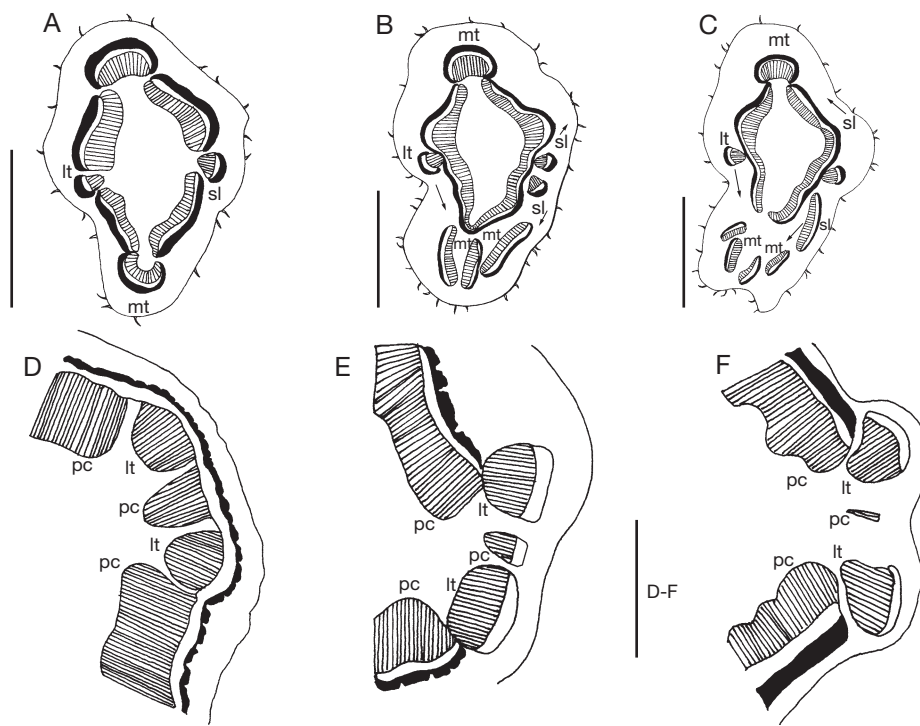


FIG. 2. — Nodal configurations of *Mallotus nudiflorus* (L.) Kulju & Welzen (continued): **A-C**, left side with a single trace and right side with a “split-lateral”, note the independent origin of median trace in each case; **D-F**, right side of one of the three different nodes with two lateral traces, note gradual reduction of parent stellar part between the traces and approximation of traces; single row of xylem of parent stele in F. Abbreviations: see Fig.1. Scale bars: A-C, 3 mm; D-F, 0.5 mm.

within the procambial strand from the stem to the leaf is a universally accepted fact as also considered by Howard (1970). Therefore, it is no doubt a “splitting condition”. However, the present observation supports that the “split-lateral traces” are evolved through the fusion of two strands.

Sinnott (1914) and Metcalfe & Chalk (1950) had mentioned that trilacunar three traces condition is the typical nodal anatomy to the family Euphorbiaceae. Though unilacunar single trace is present in *Antidesma*, in some species of *Phyllanthus* (sometimes treated under distinct family Phyllanthaceae) and in few species of *Euphorbia* and other related genera, bilacunar two traces in few species of *Euphorbia* and multilacunar multitrace condition is reported in *Ricinus communis* L. (Sinnott 1914; Reynolds 1942; Metcalfe & Chalk 1950; Sehgal & Paliwal 1974; Thakur & Patil 2002, 2006; Tadavi & Bhadane 2013).

This specialized structure was though reported from eleven other families, however, the present study deals with such type of nodal anatomy, better referred here as “Howard’s Split-Lateral” in the family Euphorbiaceae. The adult plant of *Mallotus nudiflorus* has opposite leaves and exhibits several nodal anatomical situations that have been presently observed, the most significant one is the presence of lateral lacuna with two traces (single gap with two traces or unilacunar two trace condition).

The third situation (Fig. 1H-J) of present study is very important and significant to understand the origin as well as the evolution of the “split-laterals” and may reflect its status whether it is a single trace that splitted into two parts and after a journey halfway the stem entered to the opposite leaves or two merged traces as stated by Swamy & Bailey (1950), Swamy (1953) or a “composite trace” that has originated from a single gap then dividing into two girdling traces ultimately

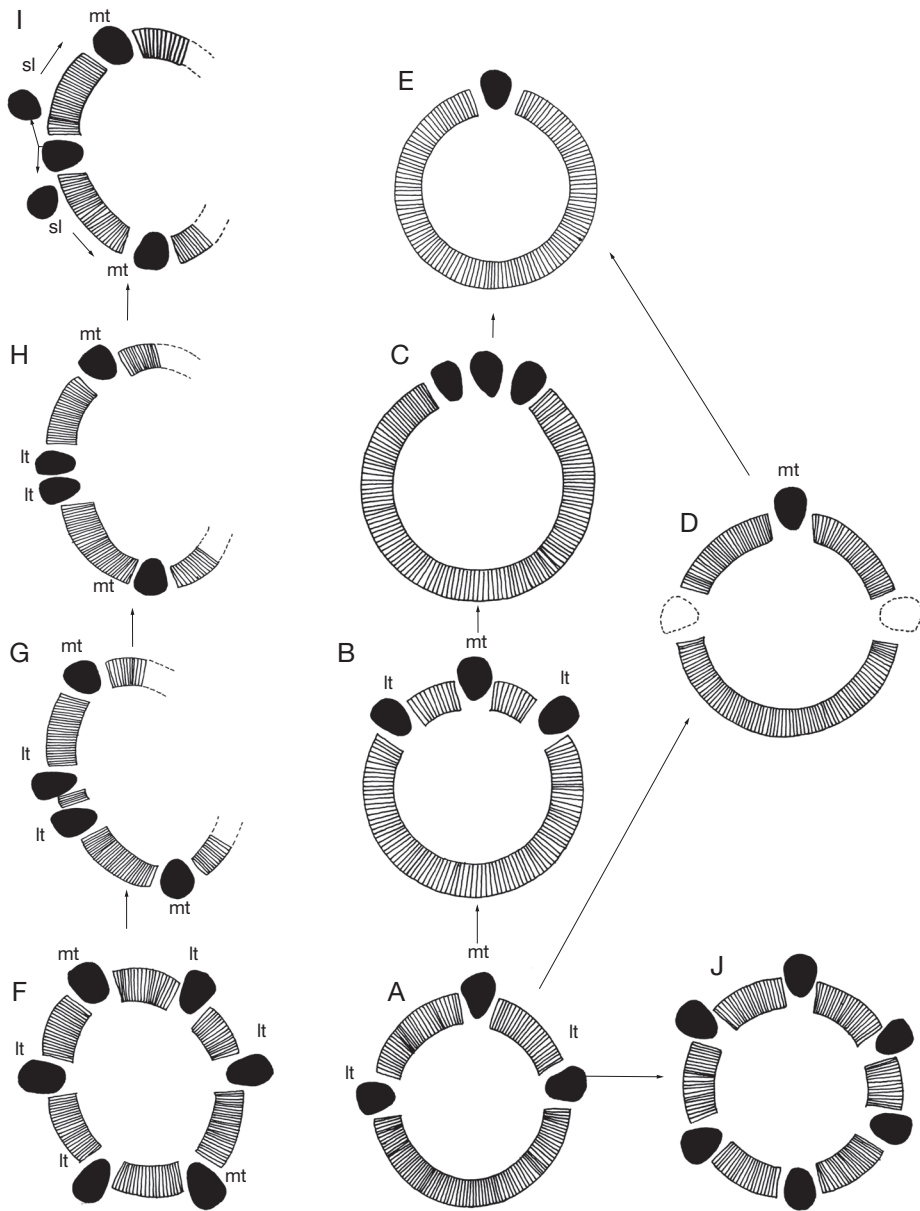


FIG. 3. — Transections as diagrammatic illustrations of nodal vasculature pattern and probable steps of evolutionary developmental stages based on Sinnott (1914): **A-C, E**, development of unilacunar node from trilacunar through approximation of lateral gaps and traces; **A, D, E**, development of unilacunar node from trilacunar through abolition of lateral gaps and traces; **A, J**, development of multilacunar node from trilacunar through amplification of gaps and traces; **F-I**, Development of “split-laterals” from basic trilacunar in opposite leaves; **F**, typical trilacunar three trace situation for both the opposite leaves; **G**, approximation of lateral gaps and traces, note tiny part of parent vascular cylinder between the traces; **H**, two lateral traces within a single gap; **I**, Typical “split-lateral” situation, note the movement of “split-lateral” after division; **A-E, J**, after Sinnott (1914); **F-I**, present study. Abbreviations: see Figure 1.

participating in the vascular supply of opposite leaves as advocated by Mitra & Majumdar (1952) for *Ixora parviflora* Lam. (Rubiaceae), or a “compound bundle” as referred by Esau (1945). As evident from the Fig. 1H-J and Fig. 2D-F, in course of evolution due to more proximity of the two lateral strands they come closer and closer, even present independently within a single gap and at more advanced state due to fusion of the two, a single trace has been developed and a single trace is seen within a single gap (“split-lateral trace”), which ultimately splitted into two, each girdles halfway the stem at opposite direction towards the base of opposite leaves and enters to the respective ones (Figs 1; 2). The approximation of two lateral traces is a continuous phenomenon as evident from the present study. The two traces gradually approximated in such a way that the parent cylinder between them reduced successively and often only a single row of xylem elements gets opportunity to develop in between them (Fig. 2D-F).

Such type of approximation theory had been first advocated by Sinnott (1914) during the investigation on the phylogeny of the Angiosperms and expressed his opinion regarding the evolution of nodal structure. Sinnott (1914) had considered trilacunar three traced condition as more primitive than unilacunar and multilacunar nodes. The multilacunar type has been derived by an amplification of the three original bundles and gaps, while the unilacunar node has evidently been derived by a reduction of the trilacunar, either through the approximation of the three gaps and their coalescence into one (Sinnott 1914: for Chenopodiaceae, figs 7, 8, for Brassicaceae, figs 13, 14, or for Aquifoliaceae, figs 19, 20), or through the disappearance of the two lateral bundles and gaps (Sinnott 1914: for Rosaceae, figs. 15&16).

Most of the recent authors believe either the unilacunar two trace node [in this concept trilacunar situated in between uni- and multilacunar nodes] (Canright 1955; Carlquist 1957), or trilacunar node having median gap with two traces [in this concept trilacunar had placed earlier than uni- and multilacunar situations] (Taktajan 1969), is the primitive condition. Significantly, between both these cases there is always a close relationship and therefore, every possibility occurs to develop all three nodal structures from any one of them.

Even if the opinion of Sinnott (1914) regarding the evolution of nodal anatomy is slightly different as discussed before, the approximation theory he adopted and advocated is proved again by the various nodal patterns exhibited by *Mallotus nudiflorus*.

Howard (1970) also observed such type of approximation of bundles in case of *Faramaea occidentalis* (L.) A. Rich. (Rubiaceae) collected from Panama. However, he did not report the “unilacunar two trace” condition in any of his studied materials. If the approximation theory of Sinnott is considered (which was proved by him with several examples) to form a single trace then it is very clear that the “split-laterals” of *Mallotus nudiflorus* (= *Trewia nudiflora*) is indeed a product of fusion of two neighboring lateral traces. In the successive stages of progression these two traces approximated to very close and ultimately fused to form a single trace. After that in case of true “split-lateral” situation it divides into two traces, moves each one at opposite direction and enters to the respective leaf.

The intermediate situation was represented by the “unilacunar two trace” situation, where two lateral traces ultimately reach to a single gap though the traces have originated independently. At the final stage of progression they fused to form a single trace. This single trace shared by two opposite leaves, becomes a “split-lateral”. As acropetal development is the universally accepted hypothesis, therefore, the lateral trace, at final stage from the parent stelar cylinder, after departure from a single gap splitted into two parts and ultimately girdle at opposite directions in cortex and enter to their respective leaves.

The critical observation on the Howard’s study also reveals the close relationship of trilacunar node and “split-lateral” in case of *Alloplectus ambiguus* Urb. of the family Gesneriaceae. The plants show typical “split-lateral” nodal structure in wild, however, when they grow in greenhouse, the nodal structure varies greatly (Howard 1970, fig. 3). Significantly, among the variable nodal configurations true “split-lateral” as well as true trilacunar three traced situation has been noticed (Howard 1970, fig. 3A,C). This fact as well as present study on *Mallotus nudiflorus* of Euphorbiaceae clearly indicates the evolutionary linkage between these two types of nodal configurations.

Both the families Gesneriaceae and Euphorbiaceae are characterized by trilacunar nodes in most of their members, though few of them have “split-lateral” nodes as discussed earlier. However, significantly the members having “split-lateral” also shows trilacunar condition in many nodes even in the same plant. Interestingly the cotyledonary nodes along with nodes of young plant (alternate phyllotaxy) of *Mallotus nudiflorus* possess trilacunar nodal configuration. The cotyledonary nodal structure has long been considered as more conservative than the nodes of mature plants. Trilacunar nodal structure can be thus considered as the basic nodal configuration and “split-lateral” is a derived one.

This fusion of traces again was advocated partly by Swamy & Bailey (1950) and Swamy (1953). So, both the opinions are considered here for explaining the evolutionary consequences of “split-lateral traces”. Based on the approximation theory of Sinnott (1914) it can be concluded that “split-lateral” is an evolved state (Fig. 3I) deriving from the basal most Sinnott’s trilacunar node (Fig. 3F).

The “split-lateral” traces, though sporadically reported from different families, however, become a family characteristic in Myrothamnaceae. The two members of this family i.e. *Myrothamnus flabellifolius* Baillon and *M. moschatus* Baillon both possess split-lateral traces (Puff 1978), such a nodal configuration is then of great taxonomic value and worthy of recognition. Till date 12 families of angiosperms are reported having such specialized nodal anatomical structure.

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