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THE OCCURRENCE OF INTERCALARY AND UNINTERRUPTED MERISTEMS IN THE INTERNODES OF TROPICAL MONOCOTYLEDONS[1]

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ABSTRACT

The distribution of percent of dividing nuclei, parenchyma cell length, total cell number per internode, and total internode length were determined for successive internodes in the apex and growing vegetative internodes of 23 tropical species in 17 families of monocotyledons. Basal intercalary meristems (IM) were found in representatives of Commelinaceae, Cyperaceae, Flagellariaceae, Poaceae, Restionaceae, and Marantaceae. Uninterrupted meristems (UM) which are confined progressively to the upper region of the internode and are not isolated meristematic regions were found in the Costaceae, Dioscoreaceae, Philesiaceae, Smilacaceae, Agavaceae, Araceae, Arecaceae, Liliaceae, Pandanaceae, and Zingiberaceae. Both IM and UM were found in different species of Orchidaceae. The only morphological trait correlated with meristem type was presence of sheathing leaf bases in all species with IM. Both IM and UM are interpreted as extensions of the primary elongating meristem; the IM is disjunct, and the UM is continuous with it. The phytomer growth unit and the presence of internodal IM's cannot be applied generally to the monocotyledons.

THE PRESENCE of localized regions of meristematic activity, intercalary meristems (IM)[2], at the base of internodes is often cited by botanists as a general feature of monocotyledons. Internodal intercalary meristems are widespread in grasses, Poaceae, and occur in the Cyperaceae and Commelinaceae (see references in Discussion). However, there is a lack of published information about internode development in the other groups of monocotyledons, most of which are predominantly tropical. Tomlinson (1970) has pointed out that the common and often erroneous generalizations of the monocotyledons are based on economically important and predominantly temperate species of the Poaceae. In answer to his plea for more research on tropical representatives and in order to furnish needed data, we have undertaken the following survey of internode development in selected tropical monocotyledons. We will attempt to demonstrate the location of regions of meristematic activity in developing internodes, correlate these with morphological characters, and examine the taxonomic distribution of the types of internodal meristems.

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[2] Abbreviations used in text: IM, intercalary meristem; UM, uninterrupted meristem; In, internode.

MATERIALS AND METHODS—In order to limit the number of species used in this survey, only those with relatively long internodes in their aerial, vegetative axes were selected. Rhizomes and inflorescences were not examined. Thus, several predominantly herbaceous (e.g., Xyridaceae, Eriocaulaceae) and aquatic families were eliminated from this study. In addition, species in which internode elongation only occurs within the inflorescence (e.g., *Typha*, *Musa*) were not studied. In those species with determinate shoot growth due to terminal flowering (e.g., *Alpinia*, *Costus*, *Scleria*) or sympodial growth (e.g., *Philodendron*, *Freycinetia*, *Cordyline*) the early stages of shoot growth before inflorescence initiation were chosen for examination.

A basic assumption in our study is that sequentially developing internodes will show qualitatively the sequential ontogenetic patterns of a single internode. Although there are often quantitative changes in phyllotaxy and internode length along a shoot axis, all internodes except those at the extreme base of the shoot or in the apical inflorescence can be expected to develop similarly. In indeterminate shoots with axillary inflorescences (e.g., *Chamaedorea*, *Vanda*) all internodes are alike after the juvenile or establishment phase of the shoot.

Actively growing shoots were collected in late morning or at midday. After older leaves were removed, the apical region and successively more proximal adjacent internodes up to the youngest mature internode were fixed in FAA or CRAF (Jensen, 1962).

In long internodes (> 3–4 cm) only 1-cm seg-

ments from the upper, middle, and lower regions were fixed. The material was embedded in Paraplast, sectioned longitudinally at 10–15 μm, and stained with haematoxylin, safranin, and fast green. In order to avoid differences in mitotic activity and cell elongation that are known to occur among various tissues (Fisher, 1970; Evans, 1969), only the ground parenchyma in the center of the axis was measured, except for the more peripheral parenchyma in the hollow internodes of *Restio*. All cells were measured in the apical dome and in those young internodes lacking procambial strands. Replicate measurements were taken from the five most median longitudinal sections of the apical region. The total internode length and the number of cells in a longitudinal file for each internode (delimited from one leaf axil to the next lower axil) were measured directly with an ocular micrometer. Cell length for these internodes was calculated by dividing total internode length by total cell number.

Numbering of internodes is as follows: Internode 2 (In2) includes the node of the second leaf primordium from the apex and the internode above the third leaf. Only the upper, middle, and lower (or only upper and lower) regions were measured in internodes longer than about 5 mm. In these cases cell length was determined by the number of cells per 330 μm ocular scale. Total number of cells was also counted in internodes up to 10 mm long. Average internode length, cell number, and cell length were calculated from five replicates.

Mitotic index (= percentage of nuclei in division) of ground parenchyma was also determined. All nuclei in a field of view were counted, and the number clearly showing any stage of mitosis from prophase to telophase (including any evidence of the phragmoplast) was noted. The nuclei of many species were small or we had problems with fixation and staining which made it difficult to distinguish prophase or telophase with certainty. In such cases, only anaphase and metaphase nuclei were noted, thus greatly lowering the mitotic index. However, if this conservative procedure was followed, it was done consistently for the entire shoot, resulting in a uniformly lowered mitotic index for the species. Alternate longitudinal sections were examined to avoid duplicate counts, and approximately 1,000 nuclei were counted for each internode or region. Fewer nuclei were counted in the apical dome and in the smallest internodes. Some very short internodes were combined for these measurements and are so indicated in the graphs. No distinction was made in division counts with respect to cell plate orientation. Regions of nodal vascular plexi, if present, were not counted.

We use mitotic index as a means to qualitatively locate meristematic sites and not to detect quantitative differences in the rate of cell division. Gifford and Corson (1971) have discussed the fact that the mitotic index does not necessarily reflect the rate of cell division since the duration of mitosis and interphase can vary independently from each other.

Drawings of shoots in Fig. 3–6 were made with a Wild M20 drawing tube. Morphological illustrations in Fig. 1, 2 are the work of Priscilla Fawcett.

The species examined and their families are listed below, alphabetically by genus:

Alpinia purpurata (Vieill.) K. Schum.	[Zingiberaceae]
Chamaedorea seifrizii Burret	[Arecaceae = Palmae]
Cordyline terminalis Kunth	[Agavaceae]
Costus pulverulentus Presl. (Hybrid?)	[Costaceae]
Dendrobium superbum Reichb. f.	[Orchidaceae]
Desmoncus sp. (aff. *D. Schippii* Burret)	[Arecaceae = Palmae]
Dioscorea alata L.	[Dioscoreaceae]
Flagellaria indica L.	[Flagellariaceae]
Freycinetia cumingiana Gaud.	[Pandanaceae]
Gloriosa rothschildiana O'Brien	[Liliaceae]
Korthalsia sp.	[Arecaceae = Palmae]
Luzuriaga latifolia (R. Br.) Poir.	[Philesiaceae]
Palisota thyrsiflora Benth.	[Commelinaceae]
Philodendron oxycardium Schott	[Araceae]
Restio tetraphyllus Labill.	[Restionaceae]
Scindapsus aureus (Lind. & Andre) Engl.	[Araceae]
Scleria secans (L.) Urban	[Cyperaceae]
Smilax auriculata Walt.	[Smilacaceae]
Sobralia hybrid (*decora* × *leucoxanthe*)	[Orchidaceae]
Stromanthe sanguinea Sonder	[Marantaceae]
Thysanolaena maxima (Roxb.) Kuntze	[Poaceae = Gramineae]
Tripogandra grandiflora (Donn. Smith) Woodson	[Commelinaceae]
Vanda hybrid "Miss Joaquin" (*teres* × *hookeriana*)	[Orchidaceae]

RESULTS—*Intercalary vs. uninterrupted meristems*—In the following descriptions two contrasting types of meristematic organization are compared. An intercalary meristem (IM) is a localized region of cell division occurring between regions of non-dividing and usually mature tissues. The IM in the internodes of monocotyledons occurs at the base directly above the node, and tissue maturation is basipetal. An uninterrupted meristem (UM) is a region of cell division that, at an early stage, includes the entire inter-

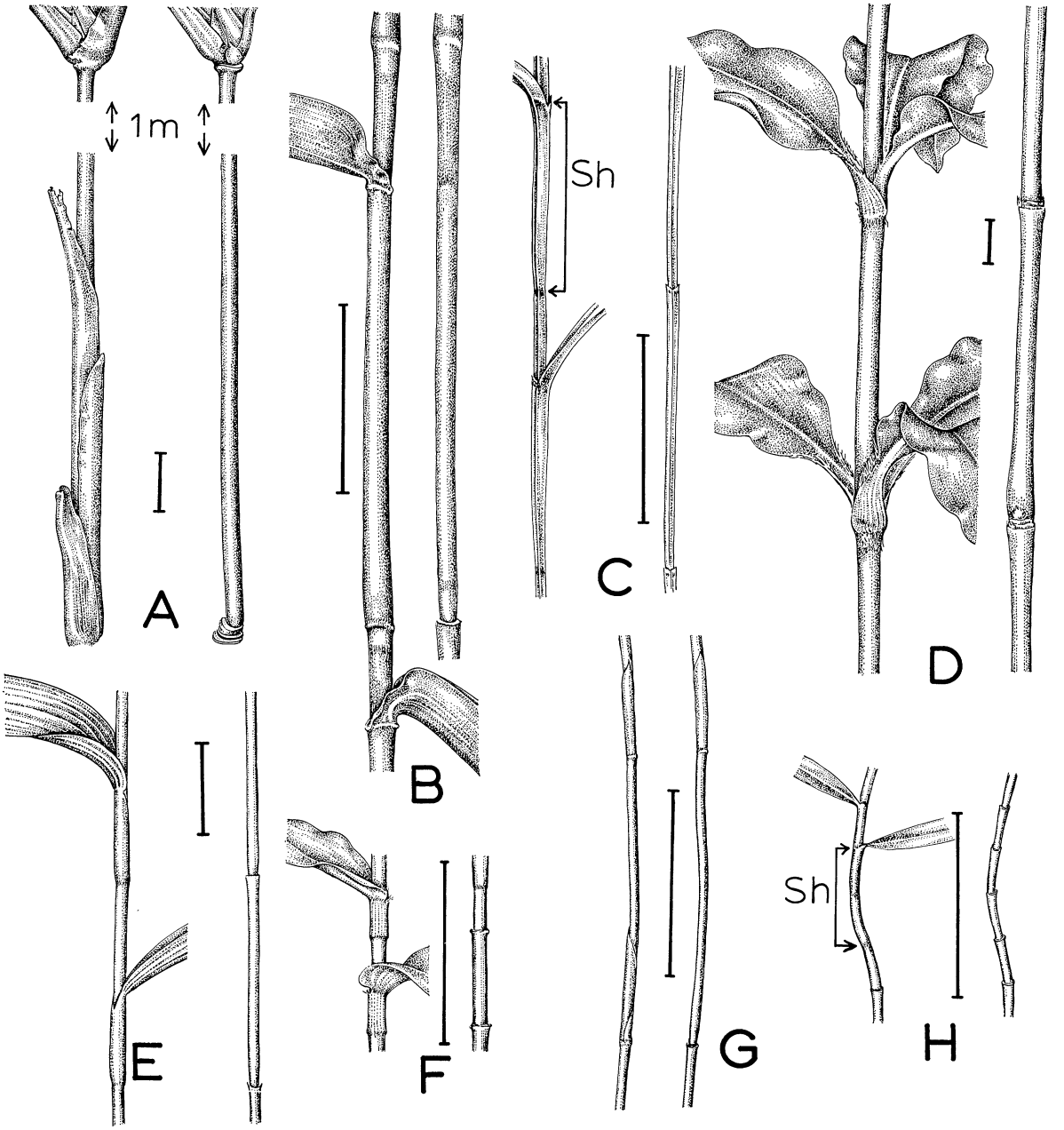

Fig. 1. Mature internodes of species with intercalary meristems. One or more leaves removed in the paired drawing to the right, showing relationship of the leaf sheath to the enclosed internode(s). Scale line represents 5 cm. A. *Stromanthe*. B. *Thysanolaena*. C. *Scleria*. D. *Palisota*. E. *Sobralia*. F. *Tripogandra*. G. *Restio*. H. *Flagellaria*. sh, sheathing leaf base.

node, but is confined progressively to the upper (distal) region of the developing internode. Unlike the IM, however, the UM is never surrounded by mature tissues. The IM of *Tripogandra* and *Thysanolaena* are described for comparison with the UM of *Korthalsia* and *Gloriosa*. A summary of the habit, morphology, and vascular structure is given first for each species, followed by a description of the anatomical data that is presented graphically in the figures.

Tripogandra (Fig. 1F, 4)—Decumbent herb with distichous leaves, branching occasional with terminal inflorescences, leaf base sheathing and

closed, node distinct with vascular plexus, vascular bundles of internode in ring with central pith.

Data for one shoot is presented in Fig. 4. The cell number in a longitudinal file and the length of successive internodes increase consistently from the second internode (In2) onward. Cell length increases slightly in In1–5. There is a striking increase in cell length in the upper and midregions of In6 and In7, with much smaller cells in the basal regions of In6 and In7. The meristematic region extends from the apex to upper In7 with a separate but distinct meristematic region in the base of In7. The mitotic index increases to a subapical maximum in the base of In5 with barely perceptible percentages of cell division in the upper and mid-regions of In6 and in the upper region of In7. A distinct peak occurs in the base of In6. There is a clear inverse relationship between cell length and mitotic index. The localized and isolated region of mitotic activity at the base of the internode (i.e., lower In7) is typical for the IM. The direction of tissue maturation within one internode is basipetal in direct relation to decreasing cell length, i.e., within In6–8 the least mature cells are found in the basal IM region, and the lignification of metaxylem first begins in the upper region of In8.

Thysanolaena (Fig. 1B, 6)—Erect reed with terminal inflorescence, leaves distichous, leaf base sheathing and closed, node distinct with vascular plexus, characteristic sclerified region approximately 1 cm long directly above node, vascular bundles of internode scattered.

The cell number and the length of successive internodes increase from In6 onward. The erratic cell numbers and lengths in In2–5 may possibly be due to the start of length variations which occur in the several internodes below the terminal inflorescence. Because of the shortness of In1, the data for it and the apex are combined. However, the apex did not show histological change indicative of flowering. Cell length increases gradually from the apex to In9. There is a decrease in cell length in the upper regions of In10 (the region of the IM) and an increase in the base of In10 (the future region of sclerenchyma noted above). In successive internodes (In11, etc.) the longest cells occupy the upper and very basal regions of the internode, and the shortest cells occur in the region just above the basal sclerenchyma. The regions of division are similarly distributed from the apex to In10 with localized peaks of mitotic activity in In11–13 isolated between regions of mature tissue, characteristic of an IM. The direction of tissue maturation within an internode is basipetal after the early maturation of the basal sclerenchyma.

Gloriosa (Fig. 2N, 3)—Climber with leaf tip tendrils, leaves alternate near base becoming subopposite to occasionally opposite or whorled distally before branching and flowering, leaf base not sheathing, node indistinct and lacking vascular plexus, vascular bundles of internode scattered.

In general the cell number in a longitudinal file and the length of successively older internodes increase. The decline in length and cell number in In2 and In3/4 is apparently due to variations in phyllotaxis since leaves 3 and 4 are subopposite. The average cell length, however, does not show this decrease as would be expected since the shorter internodes of a plant are often due to fewer, rather than shorter cells. Meristematic activity extends from the apex to the mid-region of In13. There is an obvious subapical peak in mitotic index in In9 and In10, with a relatively uniform decline in mitotic index in lower internodes. This continuous distribution of mitotic regions is typical for the UM. There is a balance between cell division and cell growth in In7–11 as shown by the relatively constant cell length during increase in cell number and internode length. Cell growth predominates in In12 and In13 which are regions of decreased percentage of cells in division. Only cell growth accounts for internode growth in the lower part of In13 in which there is no cell division. The direction of tissue maturation is acropetal in direct relation to increasing cell length, i.e., the tissues in the lower region of In13 are more mature than those in the middle and upper regions.

Korthalsia (Fig. 2F, 5)—Rattan climbing by means of spines and hooks on alternate leaves, flowering terminal (hapaxanthic), leaf base sheathing and closed, node distinct externally but lacking vascular plexus, vascular bundles of internode scattered.

The specimen examined was unknowingly collected at an early stage of inflorescence initiation in which the youngest leaf primordia subtended shortened terminal internodes. This complication accounts for the decreasing length and cell number of In1–3. There is an increase in the cell number and length of successive internodes from In4 onward. Cell length increases from In2 to In9, tends to decrease somewhat in In10 to In14, and is followed by an apparent rise in the lowermost region of In14 where tissues are almost fully mature. The region of cell division extends from the apex to below the mid-region of In14. The mitotic index is irregular, but without a repeating pattern of maxima. In general, however, the percentage of cells dividing is high until a decline takes place below the mid-region of In12. This uninterrupted region of declining meristematic activity is characteristic of a UM. The relatively uniform cell length in internodes that are elongating and meristematic (i.e., In11–14) indicates a close balance between cell division and cell growth. Data was not available for older internodes to determine whether cell elongation predominates in the final

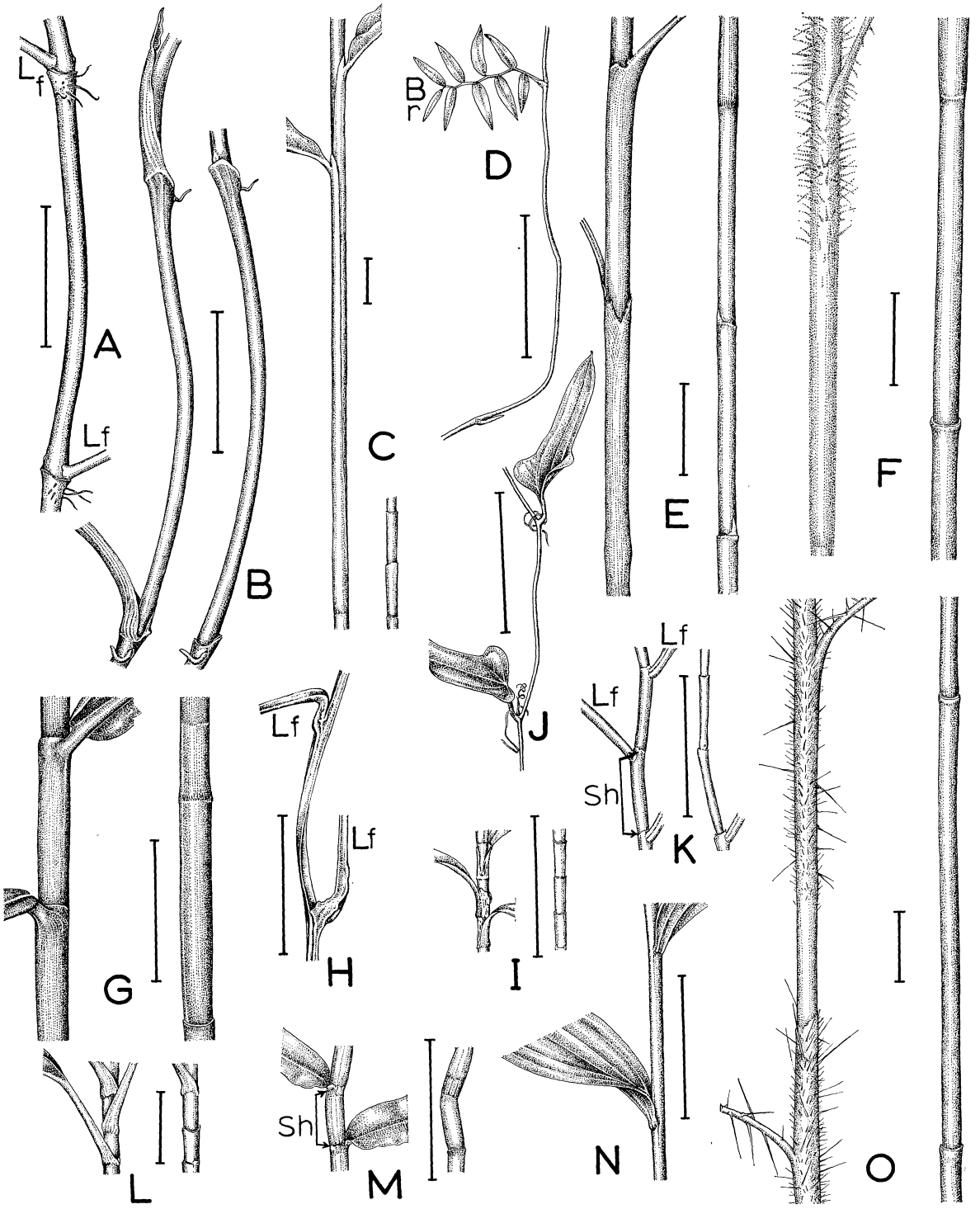

Fig. 2. Mature internodes of species with uninterrupted meristems. One or more leaves removed in the paired drawing to the right if they are sheathing, showing relationship of the leaf to the enclosed internode(s). Scale line represents 5 cm. A. *Philodendron*. B. *Scindapsus*. C. *Alpinia*. D. *Luzuriaga*. E. *Chamaedorea*. F. *Korthalsia*. G. *Costus*. H. *Dioscorea*. I. *Freycinetia*. J. *Smilax*. K. *Vanda*. L. *Cordyline*. M. *Dendrobium*. N. *Gloriosa*. O. *Desmoncus*. Lf, base of leaf; br, lateral branch; sh, sheathing leaf base.

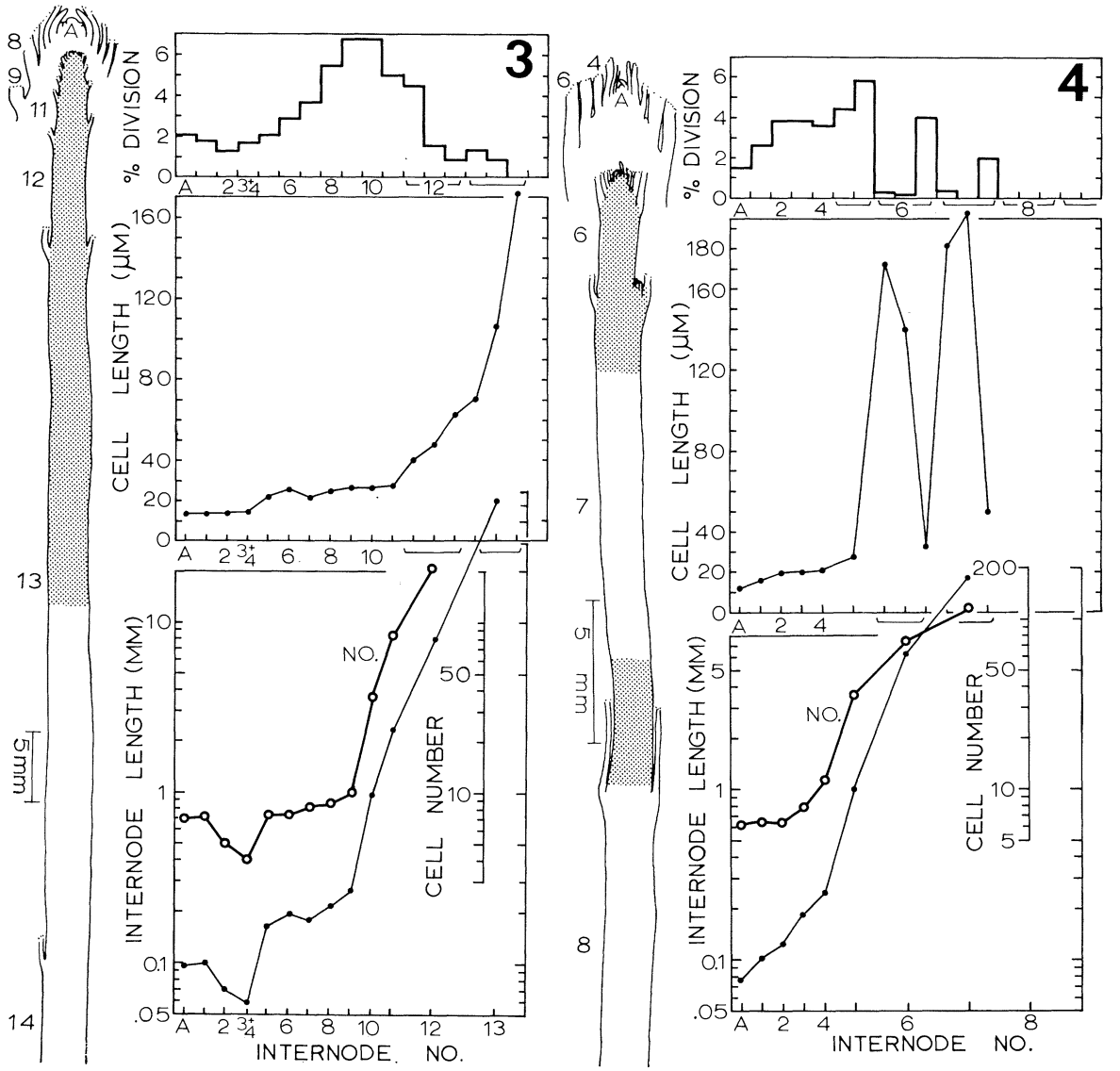

Fig. 3, 4. Comparison of mitotic index, cell length, cell number, and internode length vs. internode number in a growing vegetative shoot of two species. **3.** *Gloriosa*, with internodal uninterrupted meristems. **4.** *Tripogandra*, with internodal intercalary meristems. A, apical dome. Shaded areas, regions of cell division.

stages of internode growth as in *Gloriosa* (Fig. 3). The direction of tissue maturation is acropetal within an internode.

In summary, the basic features of the above two examples of IM are: (1) isolated meristematic regions that are disjunct from the larger subapical meristematic region; and (2) basipetal maturation in the internodes, although early histogenesis may not follow this pattern of final tissue maturation. The basic features of the above two examples of UM are: (1) an uninterrupted meristematic region from the subapex to the upper region of the oldest meristematic internode; and (2) acropetal maturation in the older internodes.

Other species with intercalary meristems—Only the mitotic index and cell length data will be presented below, although complete data on cell number and internode length were also collected and examined for each species.

Restio (Fig. 1G, 7)—Erect herb with internodes as the main photosynthetic organs, scale leaves distichous, flowering axillary and terminal,

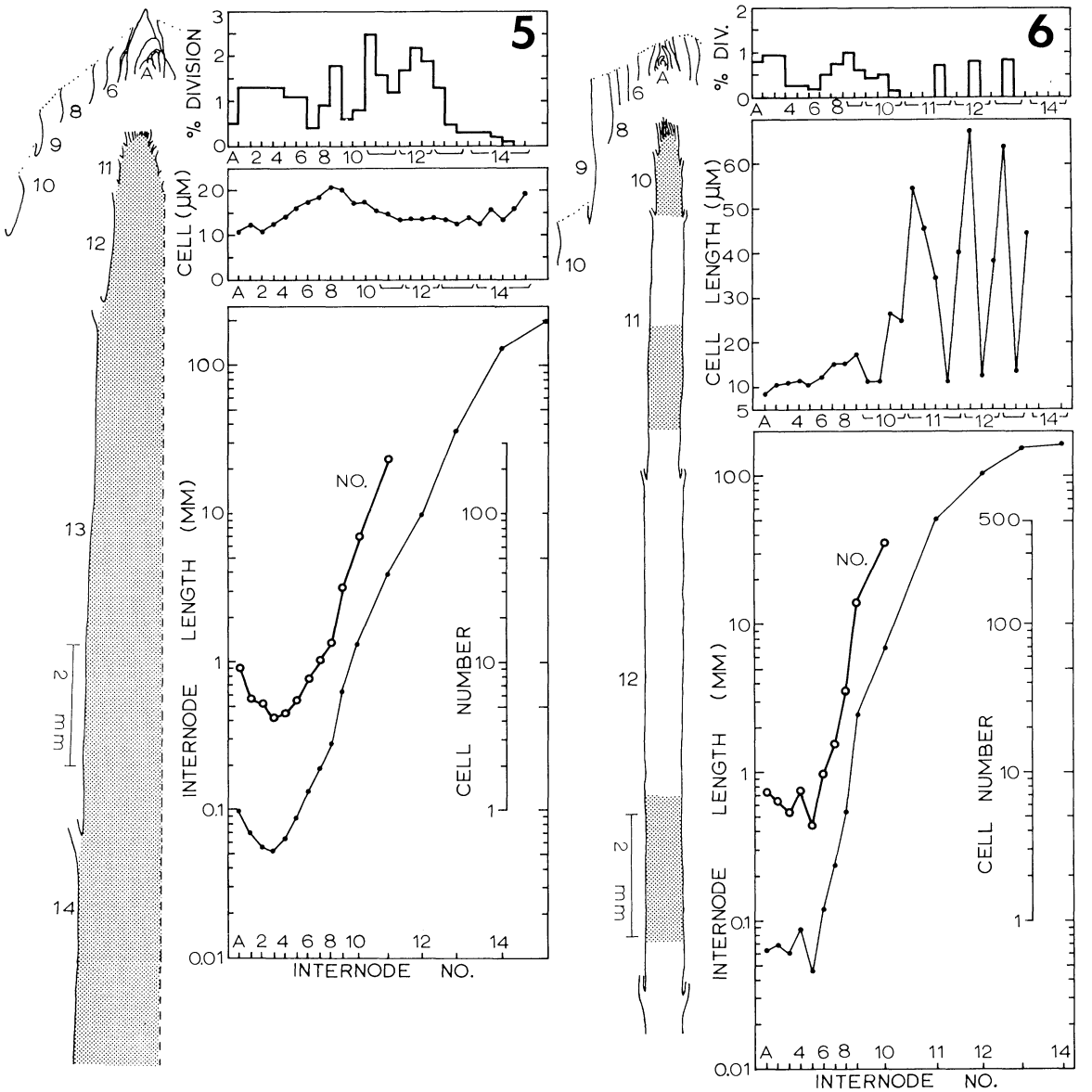

Fig. 5, 6. Comparison of mitotic index, cell length, cell number, and internode length vs. internode number in a growing vegetative shoot of two species. **5.** *Korthalsia*, with internodal uninterrupted meristems. **6.** *Thysanolaena*, with internodal intercalary meristems. A, apical dome. Shaded areas, regions of cell division.

leaf base sheathing and open, node distinct with vascular plexus, vascular bundles of internode in ring with hollow pith.

Due to their shortness, In1–2 and In3–4 are combined. Cell length remains rather uniform from In1 to In13. From In14 onward there is a repeating pattern of long cells in the upper regions (fully mature in In15) and short cells in the basal regions. The region of division extends to In14 in which the basal peak in mitotic index is related to the earliest histological localization of the IM. Active IM's are present in the bases of In15–17. A central pith was still intact in upper In17.

Sobralia (Fig. 1E, 8)—Terrestrial erect herb with terminal flowering, leaves distichous, leaf base sheathing and closed, node distinct externally but lacking vascular plexus, vascular bundles of internode scattered.

Cell length is uniform from the apex to In5. Maximum and minimum cell length occur respec-

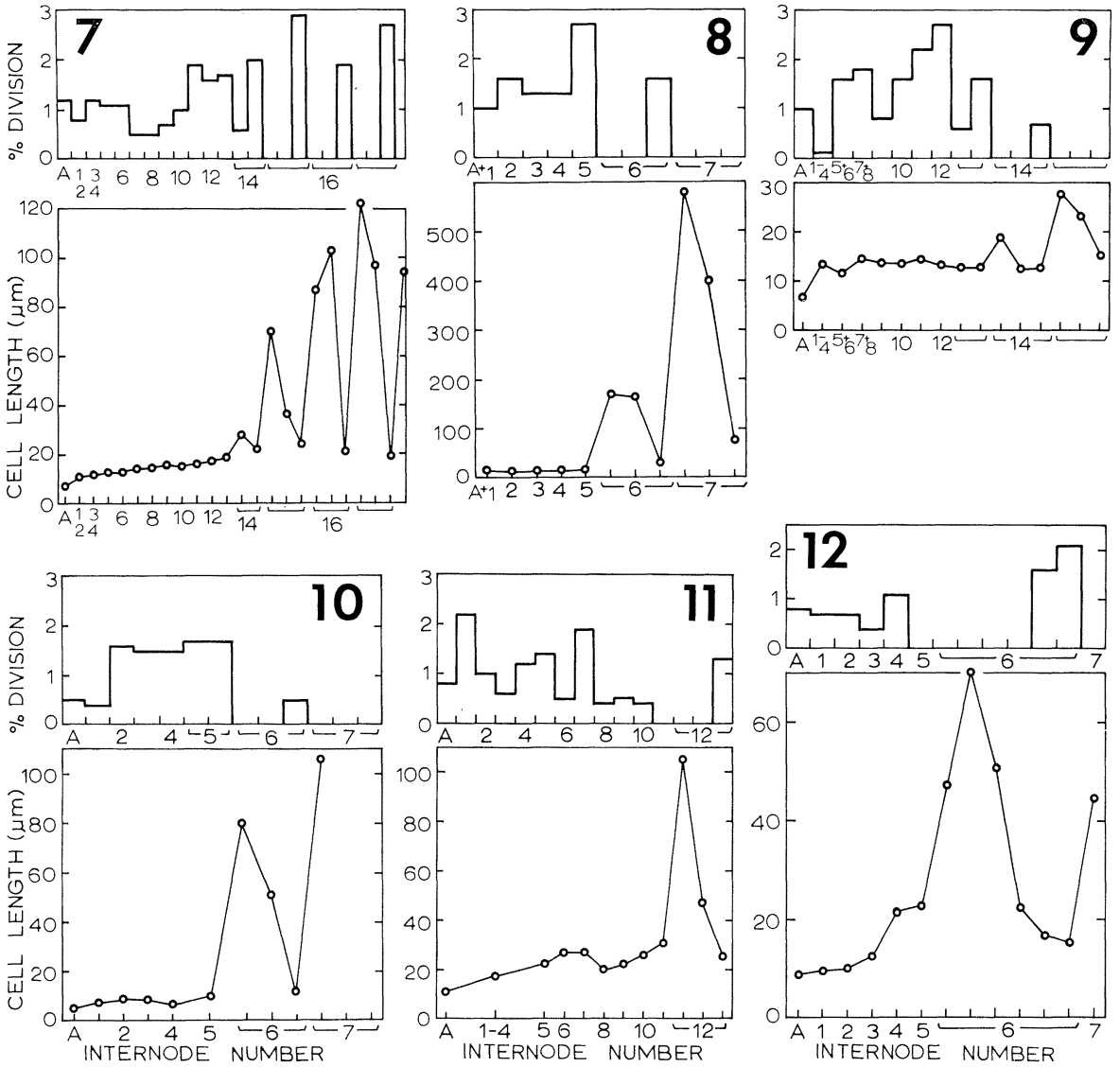

Fig. 7–12. Mitotic index and cell length vs. internode number in species with intercalary meristems. **7.** *Restio.* **8.** *Sobralia.* **9.** *Flagellaria.* **10.** *Scleria.* **11.** *Palisota.* **12.** *Stromanthe.* A, apical dome.

tively in the upper and basal regions of In6–7. The first completely mature tissue occurs in the upper and mid-regions of In7. Mitotic index increases until In5. In the first elongated internode (In6) only the base is meristematic, and it is also the only IM present in this shoot. The cells in base of In7 are immature and elongating, but are no longer meristematic.

Flagellaria (Fig. 1H, 9)—Scandent or climbing herb with leaf-tip tendrils, flowering terminal, leaves distichous, leaf base sheathing and closed, node distinct with vascular plexus, vascular bundles of internode scattered.

The youngest congested internodes are combined into three groups: In1–4, In5–6, In7–8. Cell length is constant up to In13. Elongation of cells occurs in the upper regions of In14 and In15. Cell division occurs from the apex to In13. The localized region of meristematic activity in In14 is the only active IM in this shoot. The base of In15 is immature, but not meristematic.

Scleria (Fig. 1C, 10)—Scandent climbing herb, flowering terminal, leaves alternate, leaf base sheathing and open, node distinct with vascular plexus, vascular bundles of internode scattered. Cell length is relatively uniform up to In5.

Elongated and completely mature cells occur in the upper and mid-regions of In6 and In7. The region of cell division is continuous from apex to In5. The meristematic region in the base of In6 is the only IM in this shoot.

Palisota (Fig. 1D, 11)—Erect herb, leaves spiro-distichous in groups of four with an elongated internode separating these pseudo-leaf whorls, flowering terminal, leaf base sheathing and closed, node distinct with vascular plexus, vascular bundles of internode scattered.

Cell length for In1–4 is combined. Both cell length and mitotic index data are related to the distinctive phyllotaxis of this species. Starting from the oldest region, In12 is above one leaf group, In7 is above another group, and presumably In2 is above the youngest group. An IM is at the base of In12 in which the upper and mid-regions are mature. A meristematic peak (presumably the future IM) occurs in In7 which is already noticeably elongated. Within the short internodes of a leaf group (In8–11) there is a basipetal reduction of cell division but no localized meristematic activity (e.g., no division in In11).

Stromanthe (Fig. 1A, 12)—Erect herb with 4–5 basal, distichous leaves subtending a very elongated internode topped by a crown of distichous leaves, flowering terminal, leaf base sheathing and open, node distinct externally but lacking vascular plexus, vascular bundles of internode scattered.

Cell length increases up to In5, the lowest internode of the growing leaf crown. The actively growing, elongated internode (In6) has long and fully mature cells above the lower regions of short cells. Cell division occurs from the apex to In4. There is an active IM at the base of In6.

Other species with uninterrupted meristems—Only the mitotic index and cell length data will be presented below, although complete data on cell number and internode length were also collected and examined for each species.

Luzuriaga (Fig. 2D, 13)—Twining vine with scale leaves on the primary axis studied here, lateral branches leafy, scale leaves distichous, flowering axillary, leaf base not sheathing, node indistinct and lacking vascular plexus, although developing axillary buds later develop many vascular connections at the node, vascular bundles of internode scattered.

Data for apex and the very short In1 are combined. Cell length increases slightly from apex to In12 and then rapidly increases in In13 and In14. Mitotic index peaks in the upper region of In10 and then declines. Cell division and cell elongation are almost balanced until the upper region of In13, at which level mitosis stops and cells elongate greatly.

Alpinia (Fig. 2C, 14)—Erect herb, flowering terminal, leaves distichous, leaf base sheathing and open, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Cell length increases from the apex to In4, then declines in In5 and In6, and finally increases in In7–9. Mitotic index reaches a maximum in In6 and declines irregularly to the upper region of In8. There is less of a balance between cell division and cell elongation because cell length increases in those regions with low mitotic index (e.g., peak in In4).

Dioscorea (Fig. 2H, 15)—Twining vine with alternate leaves, flowering axillary, leaf base (petiole) not sheathing, node indistinct externally but with vascular plexus, vascular bundles of internode scattered.

Cell length increases from the apex to In6 and then remains relatively constant until it increases in In12 and In13. Mitotic index fluctuates somewhat until the mid-region of In11 after which it decreases to zero in the lower region of In12.

Desmoncus (Fig. 2O, 16)—Rattan climbing by means of spines and hooks on alternate leaves, flowering axillary (pleonanthic), leaf base sheathing and closed, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Cell length is constant from apex to In6, and then increases to a broad peak at In10 with some fluctuations and perhaps a decline until there is an increase in In13. Mitotic index falls from an apical high and remains very low and constant until a subapical peak is reached in In12, and then it decreases to zero. The peak in cell division in In12 is correlated with a possible decrease in cell length in In12. There is rapid maturation after cessation of cell division since metaxylem secondary walls show pitting and early lignification in the lower region of In13, although cell division occurs in the middle of that same internode.

Dendrobium (Fig. 2M, 17)—Epiphyte climbing by roots, flowering axillary, leaves distichous, leaf bases sheathing and closed, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Cell length increases from the apex toward the base with slight decreases in In3 and lower In7. Mitotic index decreases in In1 and In2, peaks in In3, followed by a basipetal decline to zero in lower In6.

Cordyline (Fig. 2L, 18)—Erect woody shrub, flowering terminal, leaves alternate, leaf base sheathing and open, nodes distinct but lacking vascular plexus, vascular bundles of internode scattered.

The apex is sunken below the raised region of leaf insertions of the first five leaf primordia. In this region of primary thickening the leaves are

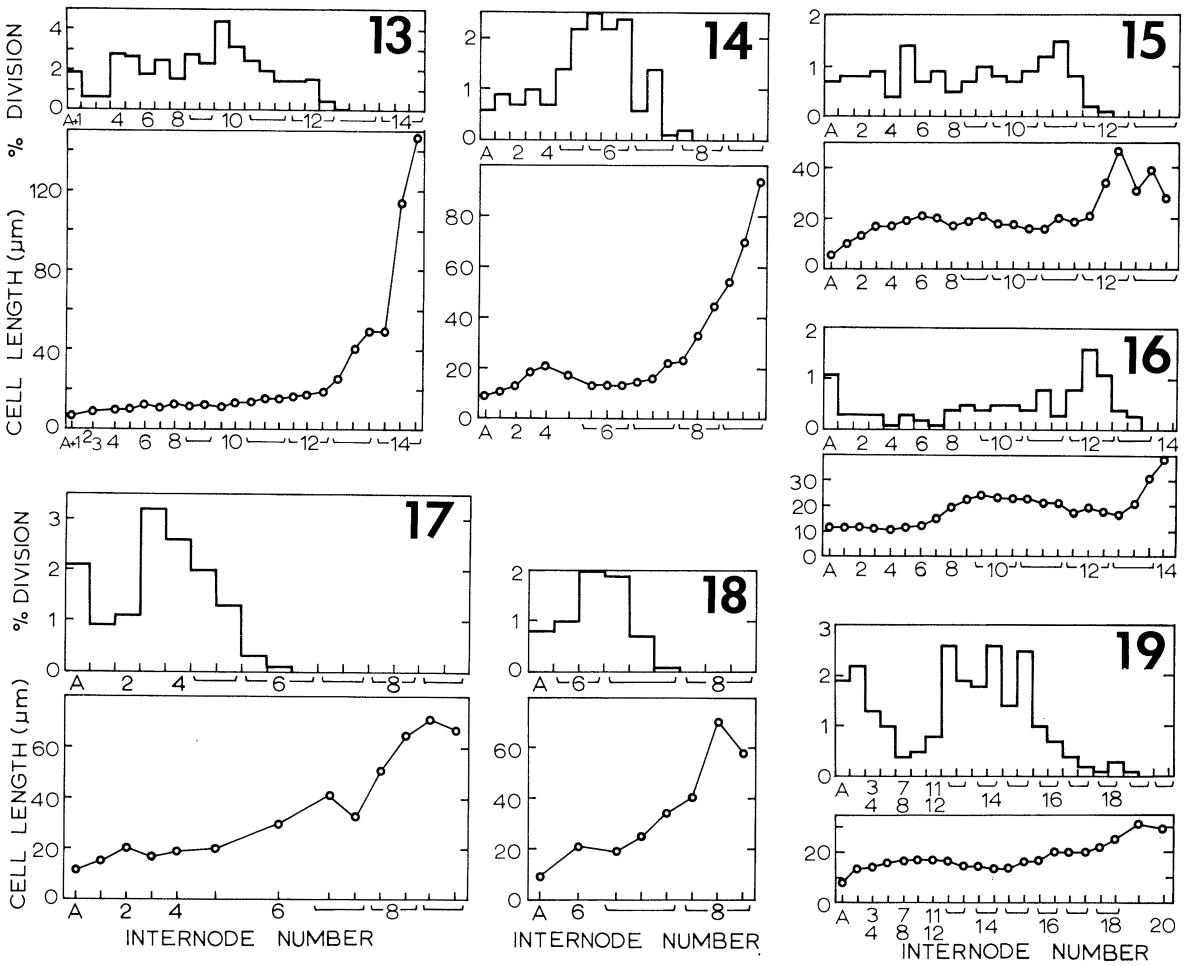

Fig. 13–19. Mitotic index and cell length vs. internode number in species with uninterrupted meristems. **13.** *Luzuriaga.* **14.** *Alpinia.* **15.** *Dioscorea.* **16.** *Desmoncus.* **17.** *Dendrobium.* **18.** *Cordyline.* **19.** *Freycinetia.* A, apical dome.

all inserted at about the same level so that there is no measurable longitudinal internode length. Therefore, the first five internodes cannot be measured. The first distinguishable internode (In6) is already 1,064 μm long. Cell length shows a relatively uniform increase. Mitotic index peaks in the lower region of In6 and the upper region of In7 and then declines.

Freycinetia (Fig. 2I, 19)—Erect woody shrub, flowering terminal, leaves alternate, leaf base sheathing and open, nodes distinct but lacking vascular plexus, vascular bundles of internode scattered.

Data for congested internodes (In1–12) are grouped in pairs. Cell length remains relatively constant with a slight decrease in In13–15, and then there is a gradual increase from In15 basipetally. Mitotic index decreases from the apex to a minimum in In7–8, then rises to a fluctuating maximum region (In13–15), followed by a basipetal decline.

Costus (Fig. 2G, 20)—Erect herb, flowering terminal, leaves alternate, leaf base sheathing and closed, nodes distinct with vascular plexus, vascular bundles of internode scattered.

In17, 18, and 20 were skipped in sampling because of the massive size of the subapical growing region of this large herb. Cell length increases to a peak in In8, then decreases to a minimum in In15, followed by a striking increase. In older internodes (In19, 21) the mid-region has shorter cells than either the upper or lower regions. The mitotic index decreases from the apex to a minimum in In9, rises to a fluctuating peak in In12–In16, and then declines with no cell division in In21. The decline in lower In15 may not be significant since it does not follow a pattern. The apparent lack of cell division in the mid-region

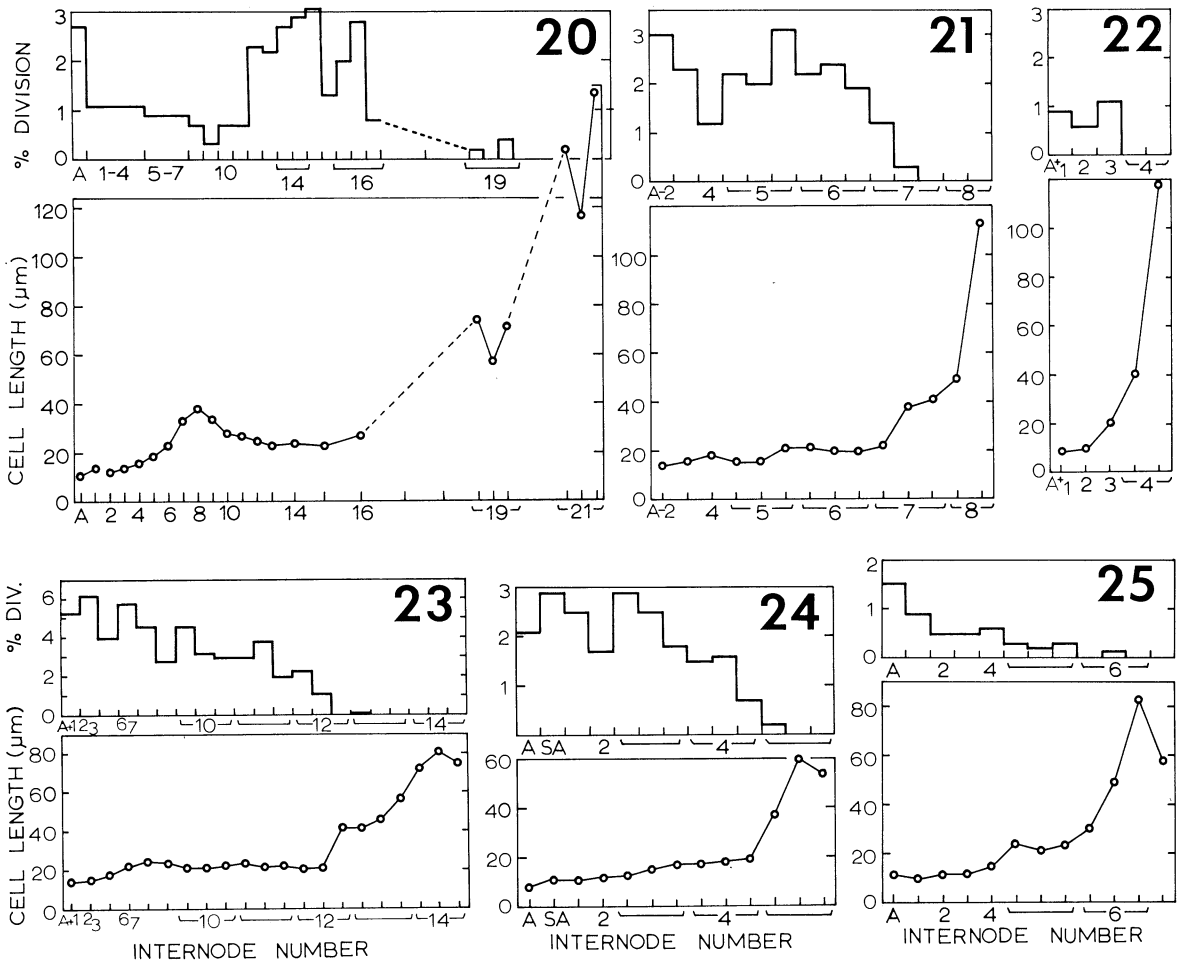

Fig. 20–25. Mitotic index and cell length vs. internode number in species with uninterrupted meristems. **20.** *Costus*. **21.** *Scindapsus*. **22.** *Vanda*. **23.** *Smilax*. **24.** *Philodendron*. **25.** *Chamaedorea*. A, apical dome; SA, subapical region above first leaf.

of In19 may be significant, although this is uncertain due to the low mitotic counts involved. The decreased cell length in the mid-region of In19 would indicate that the apparent isolated mitosis-free region of In19 is an artifact since an increase in cell length would otherwise be expected. Therefore, this species is interpreted as not possessing a defined IM, although it may represent a form of UM which is somewhat intermediate between the two types.

Scindapsus (Fig. 2B, 21)—Climber by means of roots, flowering terminal but appearing lateral, leaves alternate, leaf base sheathing and open, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Data for the apex and the first two short internodes are combined. Cell length remains relatively constant and increases in In7 and In8. Mitotic index decreases from apex to a minimum in In4, rises to a maximum in In5, and then declines.

Vanda (Fig. 2K, 22)—Erect herb or epiphyte climbing by roots, flowering axillary, leaves terete and alternate, leaf base sheathing and closed, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Data for the apex and first small internode are combined. Internode elongation is abrupt with cell length increasing after In2. Mitotic activity extends to In3 with no dividing cells in upper In4.

Smilax (Fig. 2J, 23)—Climber with stipular tendrils, leaves alternate, flowering axillary, leaf base not sheathing, node indistinct externally but with vascular plexus which is only well developed at nodes with branches, vascular bundles of internode scattered.

Data for the apex and congested internodes

(In1–7) are grouped in pairs. Cell length increases slightly from the apex to In8, then remains relatively constant until it increases below the mid-region of In12. Mitotic index in general decreases from an apical high to zero below the mid-region of In12 with a very slight amount of mitotic activity in the upper region of In13. However, the activity in In13 is so low that it is not significantly different from lower In12.

Philodendron (Fig. 2A, 24)—Climber-epiphyte by means of roots, leaves alternate, flowering, lateral, leaf base not sheathing but with a large abscising cataphyll encircling node and young leaf, node distinct above the cataphyll scar but without vascular plexus, vascular bundles of internode scattered.

There is a distinctly elongated subapical zone above the first leaf primodium (SA in Fig. 24) which may be associated with early inflorescence initiation. Cell length gradually increases from the apex to lower In4 and then rapidly increases in In5. Mitotic index increases below the apex with a possibly significant decrease in In2. There is a steady decrease in mitotic activity from upper In3 to upper In5.

Chamaedorea (Fig. 2E, 25)—Erect woody stem, leaves alternate, flowering axillary (pleonanthic), leaf base sheathing and closed, node distinct but lacking vascular plexus, vascular bundles of internode scattered.

Cell length remains constant from the apex to In3 and then increases basipetally from In4. The decrease in cell length in upper In7, which is almost fully mature, appears to be due to normal fluctuation in sampled cell lengths in mature internodes. Mitotic index decreases from an apical maximum with an isolated peak occurring in mid-In6 that is probably insignificant due to the very low count it represents.

DISCUSSION—*Differences between intercalary and uninterrupted meristems*—The results show two contrasting types of meristems in developing internodes. The IM occurs at the base of the internode, surrounded by non-meristematic regions, and cell maturation within the internode is basipetal. The UM is progressively confined to the upper region of the internode, continuous with the subapical meristematic region, and cell maturation within the internode is acropetal. Our criterion for determining meristematic sites is the presence of dividing cells. Therefore, we feel that the new data presented in the results are particularly significant since they show for the first time the exact localization of meristematic tissue by direct measurements of cell divisions, as well as histological changes (i.e., cell length and tissue maturation).

For example, in previous investigations of IM's the isolated meristematic regions have been detected by different means. Surface markings demonstrated basal regions of prolonged growth in culms of *Scirpus* (Seidel, 1955) and *Cyperus* and grasses (Buchholz, 1920). Measurement of cell length was used to locate the basal region of internode immaturity in *Triticum* (Ordina, 1952). Direct examination of tissues of sedges and grasses located basal regions of immature and dividing cells (Evans, 1965; Fisher, 1970; Kaufman, Cassell and Adams, 1965; Miltényi, 1931; Schmalfuss, 1930). However, only the first two authors (Evans, 1965; Fisher, 1970) presented complete quantitative data on the distribution of mitoses in the developing internode similar to the present study.

Well defined IM's only occur in the later stages of internodal development. In early stages the entire internode is uniformly meristematic. The size of this region remains relatively constant in the single elongated internodes of *Cyperus* and *Eleocharis* (Fisher, 1970; Evans, 1969) and initially includes the entire internode. After further internode elongation and maturation of the upper region, the meristematic region is distinguishable as an IM. In the final stages of internode development the basally isolated IM decreases in size and activity, and itself matures. Other species with a single elongated internode also show this pattern of development, e.g., *Stromanthe* (Fig. 12). The same sequence of an initially uniform internodal meristem followed by basipetal maturation with a resulting isolated IM at the base is found in species with an IM in every developing internode, e.g., *Tripogandra* (Fig. 4), *Restio* (Fig. 7), *Thysanolaena* (Fig. 6) and other grasses (Miltényi, 1931). Some species have only one internode possessing an active IM at a given time, although in the next older internode cells may still be elongating in the basal region, the former IM [e.g., *Sobralia* (Fig. 8), *Flagellaria* (Fig. 9), and *Scleria* (Fig. 10)].

Therefore, we interpret the IM as a topographically isolated extension of the sequence of internodal meristems. It is part of a developmental continuum starting at the apex, continuing to the subapical meristem which includes entire internodes, and ending with a localized basal IM as a result of the elongation and maturation of cells in the upper regions of the internode. There was no evidence of a newly initiated basal meristem in the older internodes similar to the "resumptive IM" in the gynophore of *Arachis* (Jacobs, 1947).

There were no IM's in many species. The early stages of internode development in these species have a similar distribution of meristematic activity that is identical to species which later exhibit IM's. The entire internode is initially meristematic as shown by mitotic index and cell length data (e.g., In12 in Fig. 3, In10–13 in Fig. 5, and In9–12 in Fig. 13). However, there is no isolated meriste-

matic area. Meristematic activity declines in the basal region of the internode with concomitant acropetal maturation. The remaining upper meristematic region is not an IM because the lower region of the next younger internode is still meristematic, e.g., In6 and In5 in Fig. 17. In some species with nodal vascular plexi, cell division may stop in the nodal tissue before division stops in the upper region of the internode below, e.g., *Dioscorea* (Fig. 15). However, in such cases there are never fully mature nodal tissues between regions of meristematic internodal tissues. For convenience, the pattern of an initially uniform meristematic internode followed by acropetal decline in mitotic activity and acropetal maturation is referred to as an uninterrupted meristem (UM).

In dicotyledons it would seem that the UM is the common pattern of internode development, based on the few published studies of meristematic organization of internodes. The developing internodes of *Syringa* and *Helianthus* (Wetmore and Garrison, 1961; Garrison, 1973) have a meristematic region progressively confined to the upper region. Presumably, the younger internodes were completely meristematic. The data showing increase in cell number during the gradual acropetal maturation of tissues in internodes of *Phaseolus* and other species (Enright and Cumbie, 1973; Grisebach, 1843) also indicate that these species have UM's. Unfortunately, many studies on localization of internode extension by using surface markings are not useful in determining location of internodal meristems.

The data from such studies on internode extension have shown some variation in growth patterns including indications of intercalary growth in species of Apiaceae, Polygonaceae, Caryophyllaceae, and Chenopodiaceae (Grisebach, 1843; Fahn, 1974). However, there are no published studies on the distribution of mitotic activity in these few examples that would demonstrate the presence of internodal IM's.

Taxonomic distribution of internodal IM—The families that have an internodal IM as demonstrated in our survey (shown by asterisks) are listed below. Citations of previous studies in which cell length, division, or elongation data clearly show the presence of an IM are also noted. The classification scheme is the Liliatae (= Monocotyledonae) of Cronquist (1968).

Commelinidae
- Commelinales
  - Commelinaceae* (Buchholz, 1920; Scott and Priestley, 1925)
- Restionales
  - Flagellariaceae*
  - Restionaceae*
- Juncales
  - Juncaceae (from unreported observations)
- Cyperales
  - Cyperaceae* (Buchholz, 1920; Schmalfuss, 1930; Seidel, 1955; Evans, 1965; Fisher, 1970)
  - Poaceae* (Buchholz, 1920; Schmalfuss, 1930; Miltényi, 1931; Sharman, 1942; Ordina, 1952; Kaufman, et al., 1965)
- Zingiberales
  - Cannaceae (Buchholz, 1920)
  - Marantaceae*

Liliidae
- Orchidales
  - Orchidaceae (*Sobralia*)*

We must stress that the above list is only valid for IM's of the shoot internode and does not include the flower or inflorescence axis. Of the three species of Orchidaceae examined only *Sobralia* has an IM. The UM of *Vanda* and *Dendrobium* may be more typical for the family. It appears that there is an IM at the base of the peduncle or inflorescence in many families, e.g., Xyridaceae, Eriocaulaceae, Typhaceae, Amaryllidaceae, and related families. However, only developmental data on the localization of cell division can unequivocally demonstrate the presence of an IM. The presence of distinct nodes and sheathing leaves cannot be used alone for determining the meristem type (as seen in Table 1).

Only the Commelinidae and Liliidae of Cronquist's (1968) four subclasses of the monocotyledons have representatives with IM's. Although the Arecidae definitely lack IM's, the Alismatidae have not been examined carefully enough to be certain. In general it is obvious that, other than the numerous grasses and sedges, the majority of monocotyledonous families which have representatives with elongated internodes lack IM's. The larger tropical groups such as the epiphytic orchids, aroids, and palms have UM's, as do most other tropical groups we have surveyed. Because grasses and sedges are temperate and economically important, they have been studied in greater detail than the more numerous tropical monocotyledons. This emphasis has lead to erroneous grass-oriented generalizations about monocotyledons as a whole.

It may be tempting for some workers to use the distribution of IM's in monocotyledons in discussions of monocotyledon phylogeny since IM's seem to occur in the specialized families of the Commelinidae and Liliidae. However, we feel that such a use of this information is premature. Our survey only gives an indication of the range and possibly the distribution of meristem types in species with elongated vegetative internodes. The occurrence of both the IM and UM in one natural family, the Orchidaceae, hints at the presence of parallel evolution in the origin of elongated internodes. The presence of IM's in the Poaceae and some Orchidaceae would also suggest similar but phylogenetically unrelated developmental patterns. A detailed survey of the internodal meristem types

TABLE 1. *Distribution of families with respect to meristem type and morphological characters of the leaf and node of species examined*

	Leaf base			Nodal vascular plexus	
	Sheathing		Not sheathing		
	Open sheath	Closed sheath		Present	Absent
INTERCALARY MERISTEM	Cyperaceae Marantaceae Restionaceae	Commelinaceae Flagellariaceae Orchidaceae[a] Poaceae	None	Commelinaceae Cyperaceae[b] Flagellariaceae Poaceae Restionaceae	Cyperaceae[c] Orchidaceae[a] Marantaceae
UNINTERRUPTED MERISTEM	Agavaceae Araceae[d] Pandanaceae Zingiberaceae	Arecaceae Costaceae Orchidaceae[e]	Araceae[f] Dioscoreaceae Liliaceae Philesiaceae Smilacaceae	Costaceae Dioscoreaceae Philesiaceae Smilacaceae[g]	Agavaceae Araceae Arecaceae Liliaceae Orchidaceae[e] Pandanaceae Zingiberaceae

[a] *Sobralia* only.
[b] *Scleria* only.
[c] *Cyperus* only (Fisher, 1970).
[d] *Scindapsus* only.
[e] *Dendrobium* and *Vanda* only.
[f] *Philodendron* only, cataphyll sheathing.
[g] Vascular plexus weakly developed.

in the Orchidaceae might well clarify this question.

Significance of the primary elongating meristem—In his review of stem elongation Sachs (1965) has re-emphasized the fundamental importance of the subapical meristematic region in shoot apices which give rise to most of the cells of the stem. He introduced the term "primary elongating meristem" to stress that extensive subapical meristematic regions are responsible for rapid and prolonged stem elongation found in grass inflorescences and bolting dicotyledonous species. However, he was unable to present much quantitative evidence for such a large subapical meristem because of the few published studies which examined directly the regions of mitotic activity throughout a shoot. Our study presents quantitative data that fully support his views. All of the species examined in our study show such a primary elongating meristem, although it is present in varying degrees. Climbers such as *Gloriosa*, *Korthalisia*, *Luzuriaga*, and *Dioscorea* (Fig. 3, 5, 13, 15) have the largest primary elongating meristems in which the meristematic region extends 37.6, 180.6, 18.8, and 45.8 mm, respectively, from the apical dome.

There is a definite subapical peak in mitotic index greater than that for the apical dome in many species (Fig. 3–5, 8–10, 13–20). In other species there is a general decline in mitotic index from its initial high in, or adjacent to, the dome (Fig. 23, 24, 25). Thus, if we use mitotic index as a measure of meristematic activity, we find that in most species the primary elongating meristem is most active some distance away from the apical dome, often with intervening regions that are meristematically less active. However, since the mitotic index does not necessarily represent the true rate of cell division (Gifford and Corson, 1971), more reliable methods will be needed to substantiate this apparent subapical rise in mitotic activity.

During the development of the IM, the primary elongating meristem in effect is subdivided and extended down the axis by its own isolated segments, the IM's. Therefore, stem elongation may result from two different arrangements of the primary elongating meristem. It may be enlarged and include many internodes, but it remains a continuous meristematic zone in which there are UM's. On the other hand, it may extend for a great distance from the apical dome over many internodes, mainly because of its subdivision into IM's.

Both the UM and IM are regions of dividing cells that are often highly vacuolated, a characteristic that is often neglected in generalizations about "the meristematic cell" (Priestley, 1929). The highly vacuolated cells with thin parietal cytoplasm which occur in the IM are similar to vacuolated meristematic cells in active cambium (Lesham, 1973).

Morphological correlations with meristem type—The distribution of families with respect to morphological features and meristem type is presented in Table 1. Both IM's and UM's occur in species with sheathing leaf bases that are either closed (forming an unbroken tube), or open (overlapping but unfused margins). There is no correlation between type of leaf sheath and meristem type. However, the IM is absent in species lack-

ing a sheathing leaf base. Although this is not unexpected since the basal IM is presumably physically supported and protected (as noted by Haberlandt, 1914), there may well be other physiological functions of the sheath upon the IM, e.g., constraint or light filtration. There is no correlation between presence or absence of a nodal vascular plexus and meristem type. This is especially evident in the Cyperaceae in which some species with an IM have a nodal plexus (*Scleria*), and some lack it (*Cyperus*).

Certain features of the leaf were also compared with meristem type. Presence or absence of a ligule was not correlated with meristem type since both the ligulate Poaceae and the non-ligulate Cyperaceae and Commelinaceae have IM's. In the Arecaceae there are ligulate and non-ligulate species, but all have UM's. Both Costaceae and Zingiberaceae are ligulate with UM's.

Leaf size or shape has no correlation with meristem type. Large and often petiolate leaves occur in the Poaceae, Commelinaceae, and Marantaceae, all with IM. Although most species with IM's have strap-shaped (graminaceous) leaves, *Restio* has small scale leaves with the stem axis being the primary photosynthetic organ. Scale leaves are also associated with the IM in *Equisetum* (Golub and Wetmore, 1948) and *Ephedra* (Dayes-Dujeu, 1957). On the other hand, scale leaves also occur on the primary axis of *Luzuriaga* which has the UM. *Asparagus* (Liliaceae) with scale leaves also seems to have the UM (unpublished observations).

Recently Madison (1970) has reaffirmed the usefulness of analyzing monocotyledon morphology and growth in terms of repeating growth units, phytomers. The concept of the phytomer is based on the jointed stems of grasses, e.g., *Poa*, and it consists of the leaf, the internode below, and the upper region of the node with bud and adventitious roots. In monocotyledons with an IM and nodal vascular plexus (Poaceae, some Cyperaceae, Commelinaceae, Flagellariaceae, and Restionaceae) such a phytomer concept may be useful, as in the analysis of shoot growth in annual grasses (Stubbendieck and Burzlaff, 1971; Hyder, 1972) or in the developmental interpretation of the internode being derived from the lower region of the leaf insertion (Sharman, 1942). However, the relationship between the growth of a leaf and the internode below it is not always constant and may change during the ontogeny of the shoot (Heimsch and Stafford, 1952). The phytomer concept is not applicable in monocotyledons without an IM or nodal vascular plexus since defined repeating units of growth are not present. In species with a UM and lacking a nodal plexus, there is little or no distinction between node and internode except for the actual leaf insertion. Kaufman (1959) rejected use of a phytomer (= phyton) concept in the grass *Oryza* because of the difficulty in defining distinct morphological units and the absence of a basal IM. In *Alstroemeria* (Alstroemeriaceae), which presumably has a UM, Priestley, Scott, and Gillet (1935) concluded from their analysis of vascular bundle development that the shoot was composed of growth units extending through 16 internodes. Such an interpretation of an internode composed of many overlapping units seems highly artificial, particularly in light of the continuous primarily elongating meristem and the UM. In conclusion, the phytomer concept may be applicable to certain species of grasses and a few other groups, but it cannot be applied generally to monocotyledons.

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