DNA Content of Leaf and Callus Nuclei

Fig. 5 shows DNA values expressed in arbitrary units, as measured in vascular parenchyma, leaf parenchyma, like-bundle sheath and callus cells at different days of culture.

In the control the pattern of distribution of DNA content is slightly different in the three tissues compared: vascular nuclei fell into class 2 to 4C, the parenchyma nuclei into 2 to 8C and the bundle sheath nuclei into 4 to 8C. DNA content seems to increase in the two last tissues as the culture progresses. By the fourth day values higher than 32C can be found in the like-bundle sheath cell nuclei.

After 12 days in culture the original leaf tissues are practically dirupted by the callus. By this reason results presented in Fig. 5 are only referred to callus tissue. DNA in this young callus is distributed into three classes: 2C, 4C and 8C. With 2 months of culture the endopolyploidy of the whole callus seems to increase as cell differentiation is taking place.

DNA Synthesis

The cytophotometric data are confirmed by the results of ^{3}H-Thymidine pulse treatments into leaf material during the first hours in culture. DNA synthesis was detected in vascular, parenchyma and like-bundle sheath cells and the results are summarized in Fig. 6.

The number of nuclei showing thymidine incorporation increases rapidly between 12 and 24 h of culture; this rate is less marked in following hours up to 60 h of culture. This trend is specially evident in the nuclei of vascular bundles and probably denots DNA synthesis prior to the beggining of cell proliferation through mitosis. First divisions were detected at 48 h. In like-bundle sheath cells, labell at 12 h, seems to be the highest in all cells analysed. The pattern of incorporation after 24 h of culture in these two types of nuclei is similar. These results can probably be explained assuming that thymidine uptake is related to endoreduplication and mitotic cycles necessary for endopolyploidization
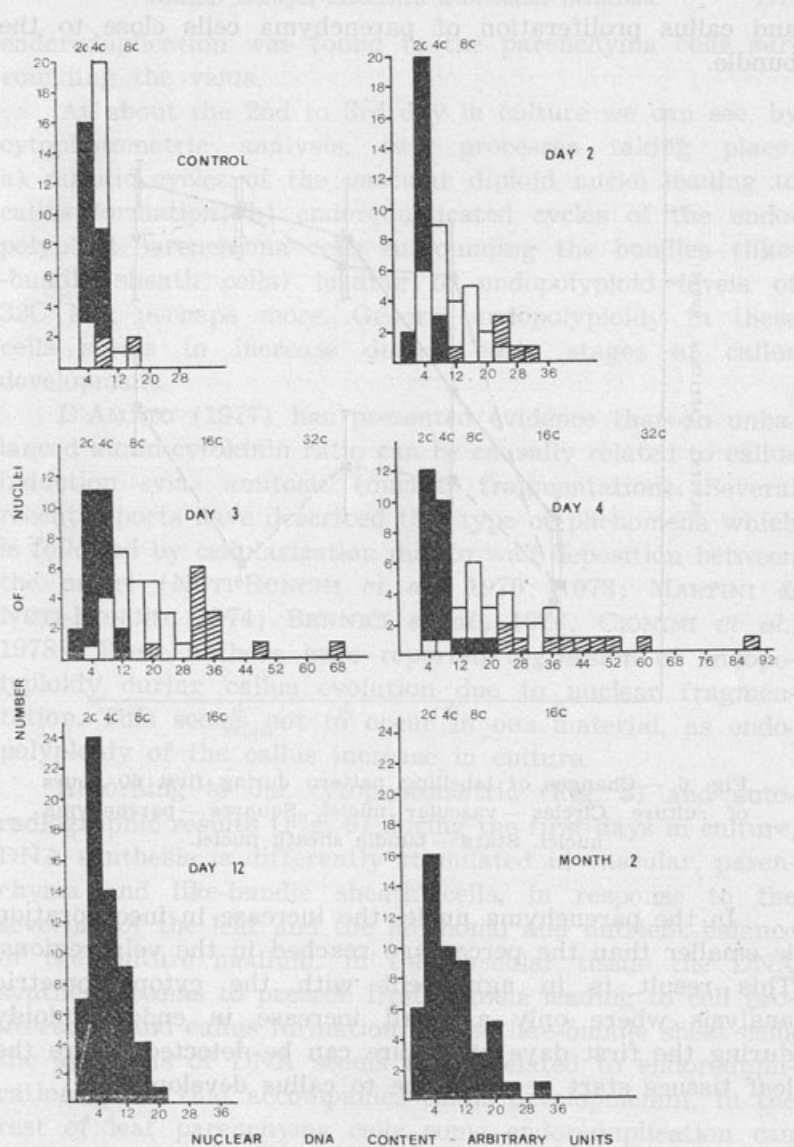
CONTROL

DAY 2

DAY 3

DAY 4

DAY 12

MONTH 2

NUMBER OF NUCLEI

NUCLEAR DNA CONTENT - ARBITRARY UNITS

Fig. 5. — Changes of DNA content during callus induction. Black bars — vascular bundles and callus. Open bars — leaf parenchyma. Hatched bars — like-bundle sheath.

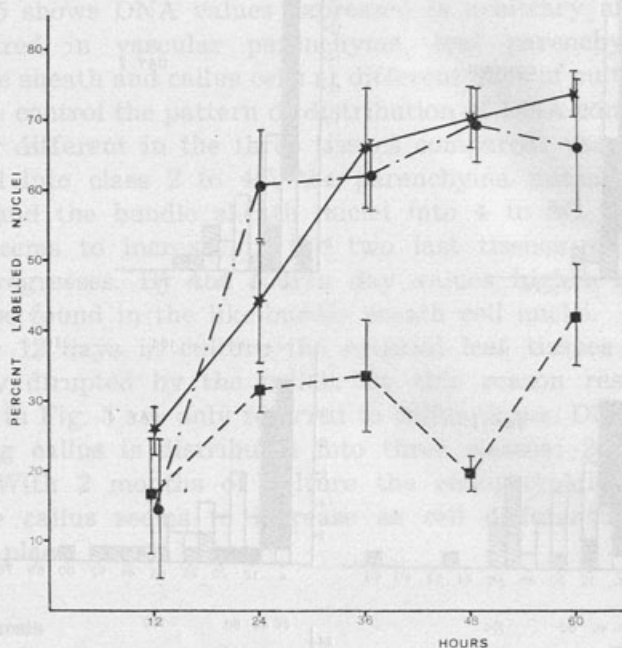and callus proliferation of parenchyma cells close to the bundle.

Fig. 6. — Changes of labelling pattern during first 60 hours of culture. Circles — vascular nuclei. Squares — parenchyma nuclei. Stars — bundle sheath nuclei.

In the parenchyma nuclei the increase in incorporation is smaller than the percentage reached in the vein regions. This result is in agreement with the cytophotometric analysis where only a small increase in endopolyploidy during the first days in culture can be detected before the leaf tissues start necrosis due to callus development.

DISCUSSION

The results of the present work have shown that, during the first days in culture of *L. maritima* leaf tissues, callus initiation is only restricted to the vascular meristematic cells of diploid constitution. As a concomitant phenomena,

endoreduplication was found in the parenchyma cells surrounding the veins.

At about the 2nd to 3rd day in culture we can see, by cytophotometric analysis, two processes taking place: a) mitotic cycles of the vascular diploid nuclei leading to callus formation; b) endoreduplicated cycles of the endopolyploid parenchyma cells surrounding the bundles (like--bundle sheath cells) leading to endopolyploid levels of 32C and perhaps more. General endopolyploidy in these cells seems to increase during early stages of callus development.

D'AMATO (1977) has presented evidence that an unbalanced auxin-cytokinin ratio can be causally related to callus induction «via» amitosis (nuclear fragmentation). Several recent reports have described this type of phenomena which is followed by cellularization due to wall deposition between the nuclei (NUTI-RONCHI *et al.*, 1970; 1973; MARTINI & NUTI-RONCHI, 1974; BENNICI *et al.*, 1976; CIONINI *et al.*, 1978). These authors have reported regression of endopolyploidy during callus evolution due to nuclear fragmentation. This seems not to occur in our material, as endopolyploidy of the callus increase in culture.

According to our cytophotometric (Fig. 5) and autoradiographic results (Fig. 6) during the first days in culture, DNA synthesis is differently stimulated in vascular, parenchyma and like-bundle sheath cells, in response to the severing of the leaf and the hormonal and nutrient balance of the culture medium. In the vascular tissue the DNA synthesis seems to precede first mitosis leading to cell proliferation and callus formation. In the like-bundle sheat cells the synthesis of DNA seems to be related to endoreduplication cycles that accompanies callus developmemnt. In the rest of leaf parenchyma cells some endoreduplication can also occur.

On the other hand, during callus growth we found some evidence that endopolyploidy increases (Fig. 5), a result that seems to contradict the hypothesis of nuclear fragmentation. In fact, at least during the first 60 hours of culture our autoradiographic results do not give any

support to the idea of nuclear fragmentation as have been reported in other materials (NUTI-RONCHI *et al.,* 1973).

The present results show that endopolyploidy of the developed callus of *L. maritima* leaves arises «de novo», as only cambial diploid cells seem to undergo citokynesis from where callus nodules are originated. The increase of endopolyploidy in cells surrounding the nodules may be related to the production of more master copies in order to meet the heavy demands for RNA production involved in callus induction and formation (ROBERTS, 1976). As we can see in Fig. 6 the ^{3}H-Thymidine incorporation in like-bundle sheath cells at 12 hours of culture seems to be higher than in other tissues. Since no cell division was found in those cells, this probably suggests that the endoreduplication have already started at this time, representing perhaps the first indication for callus formation. We think that these results support the hypothesis that DNA synthesis in these cells may play some role in the control of the development of vascular nodules from which callus are formed.

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TYPE NUMBERS
OF THE *H. J. SCHLIEBEN* COLLECTION
KNOWN TO EXIST AT LISC, 1980

E. J. MENDES & J. BALSAS

Centro de Botânica, Junta de Invesstigações Científicas do Ultramar

PTERIDOPHYTA:

Actiniopteris dimorpha Pichi-Serm. — 1938.
Trichomanes digitatum Sw.
    var. *ulugurense* Reim. — 3028.

ANNONACEAE:

Artabotrys rupestris Diels — 1688.
Lettowianthus stellatus Diels — 5579.
Ophrypetalum odoratum Diels — 5670.
Popowia buchananii (Engl.) Engl. & Diels
    var. *tricantha* Diels — 5890.
Popowia dictyoneura Diels — 1686.
Uvaria decidua Diels — 5812.
Xylopia collina Diels — 5470.

MENISPERMACEAE:

Desmonema schliebenii Diels — 5838.

CAPPARIDACEAE:

Maerua schliebenii Ch. Gilg — 5266.

FLACOURTIACEAE:

Caloncoba cauliflora Sleumer — 1346 & 4254.
Holmalium elegantulum Sleumer — 6111.

Kiggelaria flavo-velutina Sleumer — 3528.
Rawsonia ulugurensis Sleumer — 2795 & 2965.
Scolopia minutiflora Sleumer — 5756.

GUTTIFERAE:

Allanblackia ulugurensis Engl. — 2958.

THEACEAE:

Adinandra schliebenii Melch. — 3175.

STERCULIACEAE:

Cola discoglypremnophylla Brenan & Jones — 5433.
Dombeya trichoclada Mildbr. — 1051A.
Sterculia schliebenii Mildbr. — 5243.

TILIACEAE:

Grewia filipes Burret — 6033.
Grewia meizophylla Burret — 5876.
Grewia schliebenii Burret — 3224.

HUGONIACEAE:

Hugonia arborescens Mildbr. — 5188.

MALPIGHIACEAE:

Triaspis schliebenii Alfons Ernst — 6093.

GERANIACEAE:

Geranium schliebenii R. Knuth — 3486.

BALSAMINACEAE:

Impatiens magnifica G. M. Schulze — 4091.
Impatiens thamnoidea G. M. Schulze — 2951.
Impatiens tricaudata G. M. Schulze — 3554.

RUTACEAE:

Vepris schliebenii Mildbr. — 5759.

OCHNACEAE:

> *Ochna schliebenii* Sleumer — 5777.
> *Ouratea lutambensis* Sleumer — 6110.

DICHAPETALACEAE:

> *Dichapetalum schliebenii* Mildbr. — 5344.

OLACACEAE:

> *Olax pentandra* Sleumer — 5205.

AQUIFOLIACEAE:

> *Ilex mitis* (L.) Radlk.
>   var. *schliebenii* Loes. — 3529.

VITACEAE:

> *Ampelocissus schliebenii* Werderm. — 6040.
> *Cissus egestosa* Werderm. — 6136.
> *Cissus macrantha* Werderm. — 6216.
> *Cissus viniferoides* Mildbr. — 1840.

MELIANTHACEAE:

> *Bersama gracilipes* Mildbr. — 1354.

CONNARACEAE:

> *Vismianthus punctatus* Mildbr. — 5757.

LEGUMINOSAE (Caesalpinioideae):

> *Copaifera schliebenii* Harms — 6123.
> *Erythrophloeum africanum* (Welw.) Harms
>   var. *stenocarpum* Harms — 6536.
> *Hoffmanseggia insolita* Harms — 5682.

LEGUMINOSAE (Mimosoideae):

> *Acacia joachimii* Harms — 5636.
> *Acacia schliebenii* Harms — 5565.
> *Xylia schliebenii* Harms — 5752.

LEGUMINOSAE (Papilionoideae):

Afrormosia schliebenii Harms — 5588.
Craibia schliebenii Harms — 3192.
Crotalaria pterocalyx Harms — 5781.
Crotalaria schliebenii Polhill — 2371.
Dalbergia acariaeantha Harms — 5508.
Erythrina schliebenii Harms — 5237.
Indigofera latibracteata Harms — 2458.
Ormocarpum schliebenii Harms — 6038.
Platysepalum inopinatum Harms — 5392.
Rhynchosia calobotrya Harms — 6183.
Rhynchosia ischnoclada Harms — 5614.
Vigna ulugurensis Harms — 3235.

COMBRETACEAE:

Combretum schliebenii Exell & Mildbr. — 6480.
Combretum stenanthoides Mildbr. — 5212.

MYRTACEAE:

Syzygium parvulum Mildbr. — 3922.

MELASTOMATACEAE:

Dissotis schliebenii Markgraf — 6068.
Gravesia riparia A. & R. Fernandes — 3424.
Memecylon lutambense Markgraf — 5688.

PASSIFLORACEAE:

Adenia dolichosiphon Harms — 6001.
Adenia lindiensis Harms — 6066.
Adenia schliebeni Harms — 5975.
Paropsia schliebeniana Sleumer — 5442.

CUCURBITACEAE:

Coccinia ulugurensis Harms — 3643.
Momordica pycnantha Harms — 5932.
Momordica schliebenii Harms — 3660.

BEGONIACEAE:

Begonia stolzii Irmsch. — 135.

RUBIACEAE:

Pavetta schiebenii Mildbr. ex Bremek. — 5845.
Pavetta tendagurensis Bremek.
   var. glabrescens Bridson — 5821.
Psychotria castaneifolia Petit — 3342.
Psychotria cyathicalyx Petit — 4649.
Psychotria megistantha Petit — 3414.
Psychotria pseudoplatyphylla Petit — 4362.
Psychotria schiebenii Petit — 1733.
Rutidea orientalis Bridson — 1554.
Tapinopentas ulugurica Verdc. — 2730.

CAMPANULACEAE:

Lobelia dealbata E. Wimm. — 2798.
Lobelia giberroa Hemsl.
   var. iringensis E. Wimm. — 1400.
Lobelia saliensis E. Wimm. — 2033.
Lobelia usambarensis Engl.
   var. hispidella E. Wimm. — 2921.
Lobelia unamata E. Wimm. — 2934.

PRIMULACEAE:

Anagallis schliebenii R. Knuth & Mildbr. — 1420.

MYRSINACEAE:

Rapanea gracilior Mildbr. — 3921.
Rapanea schliebenii Mildbr. — 3591.

SAPOTACEAE:

Mimusops acutifolia Mildbr. — 6102.
Mimusops aedificatoria Mildbr. — 3896.
Mimusops schliebenii Mildbr. & Schulze — 2520.

OLEACEAE:

> *Jasminum ellipticum* Knobl. — 5991.
> *Jasminum stolzeanum* Knobl. — 5955.
> *Jasminum tomentosum* Knobl.
>   var. *lutambense* Knobl. — 5558.
> *Olea kilimandscharica* Knobl. — 5065.
> *Olea schliebenii* Knobl. — 3553.

ASCLEPIADACEAE:

> *Tylophora gracillima* Markgraf — 3067.

STRYCHNACEAE:

> *Strychnos angolensis* Gilg
>   var. *tanganykae* Duvign. — 1932.

GENTIANACEAE:

> *Urogentias ulugurensis* E. & Ch. Gilg — 2786.

CONVOLVULACEAE:

> *Ipomoea heterocalyx* Schulze-Menz — 3250.
> *Ipomoea lutambensis* Schulze-Menz — 6181.
> *Ipomoea microcalyx* Schulze-Menz — 1947.
> *Ipomoea trinervia* Schulze-Menz — 6285.

SOLANACEAE:

> *Solanum inaequiradians* Werderm. — 2707.
> *Solanum lignosum* Werderm. — 3150.
> *Solanum schliebenii* Werderm. — 3415.

BUDDLEJACEAE:

> *Adenoplusia ulugurensis* Melch. — 2756.

SCHROPHULARIACEAE:

> *Graderia iringensis* Melch. — 1414.

GESNERIACEAE:

Didymocarpus stolzii Engl.
        var. *minor* Mansf. — 3421.
Linnaeopsis subscandens B. L. Burtt — 2936.
Saintpaulia inconspicua B. L. Burtt — 3068.
Streptocarpus bambuseti B. L. Burtt — 4094.
Streptocarpus glandulosissimus Engl.
        var. *longiflorus* Mansf. — 4094.
Streptocarpus bullatus Mansf. — 3586.
Streptocarpus minutiflorus Mansf. — 3585.

ACANTHACEAE:

Chlamydostachya spectabilis Mildbr. — 3755.
Crabbea longipes Mildbr. — 6004.
Dicliptera insignis Mildbr. — 5240.
Dicliptera olitoria Mildbr. — 2295 [1].
Dischistocalyx pubescens Lindau
        var. *longipilosus* Mildbr. — 3568.
Isoglossa oreacanthoides Mildbr. — 2983.
Isoglossa schliebenii Mildbr. — 4102.
Justicia dolichopoda Mildbr. — 5847.
Justicia psammophila Mildbr. — 3309.
Pseuderanthemum campylosiphon Mildbr. — 2810.
Pseudoblepharis insignis Mildbr. — 5871.
Schliebenia secunda Mildbr. — 5394.

VERBENACEAE:

Clerodendrum formicarum Gürcke
        var. *sulcatum* Thomas — 3217.
Clerodendrum johnstonii Oliv.
        var. *sulcatum* Thomas — 4130.

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[1] In its protologue, *Notizbl. Bot. Gart. Mus. Berl.* **11**: 1085 (1935), only one unnumbered and undated gathering is quoted: «Bez. Mahenge: Ngombe, ca. 400 m.ü.M., Parklandschaft. Kraut, meist kriechend. Blüten lila. Auf Kipogoro: l u m b u t s c h u l u. Blätter werden als Gemüse gegessen». The LISC specimen is labelled as follows: «Mahenge-Bezirk c. 500 m.ü.M. Ngombe, Parklandschaft, Kraut c. 40-60 cm, haufig, Bl. lila. 9.6.1932. H. J. Schlieben 2295».

AMARANTHACEAE:

Cyatula divulsa Suesseng. — 2245.

HYDROSTACHYACEAE:

Hydrostachys insignis Mildbr. & Reim. — 1110A.

THYMELAEACEAE:

Peddiea subcordata Domke — 3092.

EUPHORBIACEAE:

Omphalea mansfeldiana Mildbr. — 5289 & 6206.
Ricinodendron gracilior Mildbr. — 5669.
Ricinodendron viticoides Mildbr. — 5590.

BUXACEAE:

Notobuxus obtusifolius Mildbr. — 5818.

ORCHIDACEAE:

Aërangis schliebenii Mansf. ex Schlieben — 6419.
Liparis latialata Mansf. — 3091.
Microstylis schliebenii Mansf. — 1848.
Polystachya convallarioidea Mildbr. — 2743.

ZINGIBERACEAE:

Aframomum laxiflorum Loesener ex Lock — 3094.

IRIDACEAE:

Gladiolus trichophyllus Diels — 1136A.

LILIACEAE:

Anthericum collinum v. Poellnitz — 3183.

COMMELINACEAE:

Coleotrype brueckeriana Mildbr. — 1910.

CYPERACEAE:

Cladium flexuosum (Boeck.) C. B. Clarke
var. *polyanthemum* Kükenth. — 6139.

GRAMINEAE:

Andropogon lindiensis Pilger — 6290.
var. *hirsutissima* Pilger — 6447.
Andropogon chirensis Hochst. — 6075.
Andropogon spanianthus Pilger — 1015.
Aristida cumingiana Trin. & Rupr.
var. *reducta* Pilger — 2468.
Aristida schliebenii Henr. — 2317.
Beckera scabra Pilger — 999.
Brachiaria coronifera Pilger — 439; 768 & 1031.
Digitaria comifera Pilger — 6151.
Digitaria gymnostachys Pilger — 6267.
Digitaria ulugurensis Pilger — 3640.
Eragrostis adenocoleos Pilger — 6381.
Eragrostis blastocaulos Pilger — 1029.
Eragrostis lukwangulensis Pilger — 3545.
Eragrostis muerensis Pilger — 6289.
Eragrostis setulifera Pilger — 2318.
Hyparrhenia iringensis Pilger — 828.
Melinis inamoena Pilger — 736.
Panicum adenophyllum Pilger — 6064.
Panicum issongense Pilger — 2130.
Panicum lindiense Pilger — 6243.
Panicum lukwangulense Pilger — 3520.
Panicum maximum Jacq.
var. *pubiglume* K. Schum. — 3737.
Panicum microlemma Pilger — 6231.
Perotis leptopus Pilger — 2316.
Schizachyrium inspersum Pilger — 1025.
Stenotaphrum diplotaphrum Pilger — 6545.

THE STRANGE
HISTORY OF *HERMAS PILLANSII*

B. L. BURTT

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ABSTRACT

It is argued that *Scabiosa lanata* Hill (1763) is based wholly on the illustration published by J. BURMAN (1739) as *Scabiosa hirsuta, foliis nervosis rubrotundis, floribus proliferis*. It is further argued that the plant originally illustrated was *Hermas pillansii* Norman (Umbelliferae). The validity of HILL's name is questioned.

THERE are three components to this story. The first is an illustration made at the Cape of Good Hope about 1685 and reproduced by BURMAN in 1739: the second is HILL's description and plate of *Scabiosa lanata* (1763): the third is *Hermas pillansii* C. Norman (1928). I shall argue that these three components all refer to a single species. The eclipse of this species between 1763 and 1928 supplies one of the strange elements in the story: the relation between HILL's account and that of BURMAN supplies the other.

The illustration was one of those drawn by HENDRIK CLAUDIUS for NICHOLAAS WITSEN of Amsterdam and it came to form part of the collection known as the *Codex Witsenii.* I have not seen the original; the information I use here comes from BURMAN's reproduction *(Rar. Afr. Pl. dec.* 8, tab. 72, fig. 3; 1739) and his comments, some of them quotations from the original notes in *Codex Witsenii.*

In the *Codex* this illustration (cf. fig. 1) was labelled *Angelica africana, Montana, odorata, floribus viridibus.* That is, it had been recognized as a member of Umbelliferae, was aromatic, and had green flowers: a perfectly possible plant.
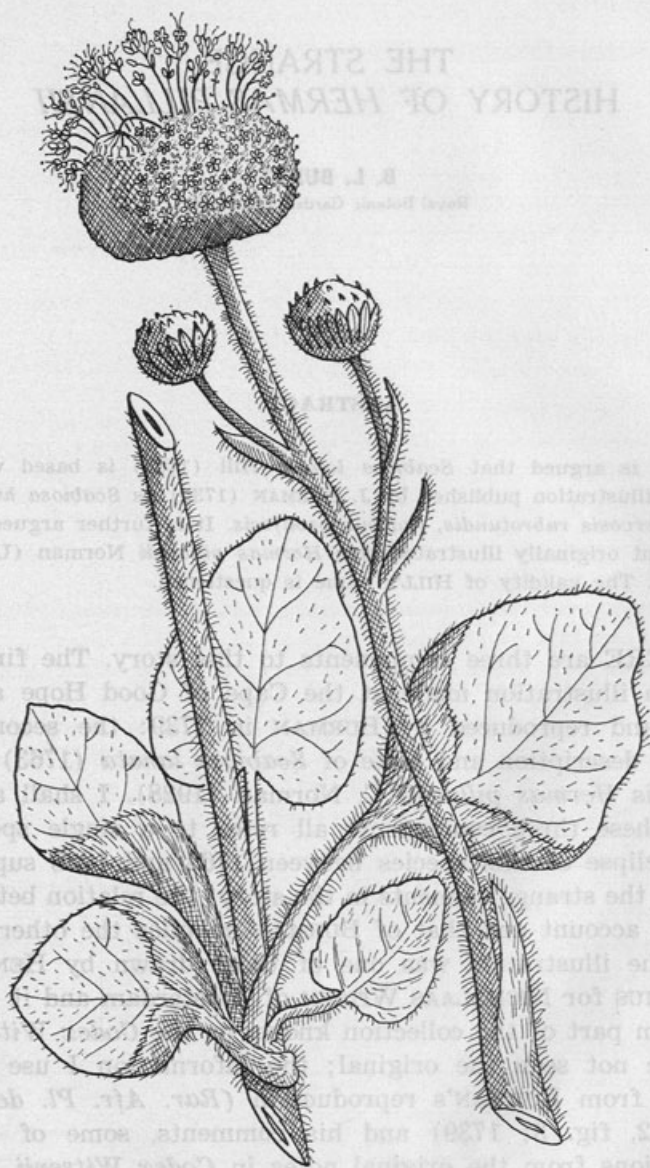
Fig. 1. — *Scabiosa hirsuta, foliis nervosis subrotundis floribus proliferis;* copied from Burman, Rar. Afr. Pl. dec. 8, tab. 72, f. 3 (1739).

Admittedly the woolly cordate entire leaves may have seemed odd for Umbelliferae, though, except for the indumentum, both the leaves and the tight inflorescence might have evoked some faint memory of *Eryngium alpinum,* with a touch of *Astrantia* about the head. Be that as it may, BURMAN decided that the plant could not belong to Umbelliferae. He consulted GARCIN and between them they decided it must be a scabious: *Scabiosa hirsuta, foliis nervosis subrotundis, floribus proliferis* was the name BURMAN gave it. It may be mentioned that a search in all likely places in the BURMAN herbarium at Geneva failed to produce any specimen of the plant; but this was not unexpected as, at the time of writing, BURMAN clearly had none and was working entirely from the plate and accompanying notes.

In 1763 JOHN HILL published volume five of his *Vegetable System,* and this volume includes scabiouses. Here we find (tab. 33) *Scabiosa lanata,* a name not previously published. HILL gave an account of this plant, and said that BURMAN alone of earlier botanists had known it. He does not give a precise reference, but the plant we have just been discussing was the only *Scabiosa* described by BURMAN, so there is no doubt about this. If there had been, a comparison of the plates would soon dispel it, for there are some remarkable likenesses (cf. fig. 2 with fig. 1). The resemblances in the leaves are so striking that HILL's look very much as though they were copied from BURMAN. The heads on HILL's plate are flatter and look more like those of a scabious; however it is remarkable that where the plates diverge HILL's follows not BURMAN's plate but BURMAN's text comments. BURMAN said the plant was a scabious, and HILL's illustration looks in general like one: BURMAN said the flowers were green and HILL's plate shows green flowers. It is difficult to believe that HILL's plate is not a copy based on BURMAN's but modified to fit BURMAN's text. Thus one must ask, did HILL ever have a specimen of this plant? His description admittedly includes much circumstantial detail, such as reference to the springiness of the indumentum on the stem, but when it has been carefully studied one can only conclude that it really adds nothing to the information given

B. L. Burtt

Fig. 2. — *Scabiosa lanata* Hill; based on the plate in HILL, Vegetable System (folio ed.) 5: t. 33 (1763), × c. ½.

by BURMAN. HILL said that his plant, unlike BURMAN's, was not proliferous. Nevertheless he shows a detached head, scabious-like as are the others, but proliferous. I therefore consider that HILL's illustration and description of *Scabiosa lanata* was based solely on BURMAN's plate and description, not on a plant or specimen in his own possession.

This suggestion is not so outrageous as it may seem. Writing of another work by HILL, *Eden or a compleat body of gardening,* HENREY (1975, 2: 97-98) notes that «a number of the figures have been copied from the Hortus Floridus of Crispian van de Paase the Younger». For *Eden,* as for the *Vegetable System,* the drawings were advertised as being «all made from nature by Dr. HILL». That this one plate in the *Vegetable System* should have been based on a previously published illustration, rather than on a specimen, is therefore not unthinkable.

Further evidence that HILL had no specimen of *Scabiosa lanata* is that the plate lacks a drawing of a single flower removed from the head: this is present on almost all the other plates of *Scabiosa.* It is clear, from the introductory discussion of volume five, and from plate 1 (showing the details of the flower head), that HILL understood the structure of a scabious quite well. Had he seen a specimen of this plant he would have quickly realized that it was wrongly placed in *Scabiosa.*

The real test of this argument clearly lies in finding the plant that these plates are intended to portray. There is no known *Scabiosa* that is strongly aromatic, or has thick woolly entire cordate basal leaves or has green flowers, either in South Africa or anywhere else. However, as recently as 1928 the late CECIL NORMAN described a 'new' species of the umbelliferous genus *Hermas, H. pillansii,* from the Cape Peninsula. It bears a very fair resemblance to CLAUDIUS' illustration as reproduced by BURMAN. This plate shows several leaves with the margins infolded towards the base, but there is one at the back of the figure which is flat and cordate: this is the typical leaf-base of *Hermas pillansii.* The flower head in *H. pillansii* is not so dense as in BURMAN's plate, but that may be because it is not proliferous.

Hermas pillansii grows on mountain cliffs and has roots smelling strongly of carrots. BURMAN, quoting from the notes in *Codex Witsenii,* gives the habitat as «scarcely approachable rocks» and says the smell is so strong that it will last in a room for a week after the plant has been removed. *Hermas pillansii* has yellowish green flowers; BURMAN writes 'floribus viridibus' in his phrase name, but quotes 'ex luteo virentes' in the text.

H. pillansii is distinguished from the other species by the umbels being round-topped (ADAMSON & SALTER, 1950, p. 615). CLAUDIUS' illustration shows a round-topped head. I believe there can be no doubt that the plant drawn by CLAUDIUS about 1685 is *Hermas pillansii,* described by NORMAN in 1928. *Scabiosa lanata* Hill is the same species: the differences in his plate, that make the plant look more like a scabious, were not taken from a specimen but from his own imaginative interpretation of BURMAN's comments and name.

It must be mentioned that BURMAN's illustration is cited by SONDER (in HARVEY & SONDER, 1862, 567) under *Hermas ciliata,* without comment. However, it cannot be that species, which differs, amongst other things, in having glabrous stems. The only other possibility, apart from *Hermas pillansii,* is *H. gigantea* L. f.; however this species has a much longer, oblong leaf-blade which is white-woolly on both sides; BURMAN clearly says his plant has leaves green above white-woolly below. *Hermas pillansii* has leaves sparsely villous above (and thus appearing green) and white-woolly below. This seems to be the only possible identification for the plant.

These conclusions lead to a very awkward nomenclatural situation. Must HILL's epithet *lanata* now be adopted in *Hermas* to replace *H. pillansii?* First, what is the type of HILL's name? On the evidence given above it can only be CLAUDIUS' illustration. Neither BURMAN nor HILL added anything more to that illustration than we could add looking at it today. It is an illustration without dissections: of itself it could not validate a name. Why then should *S. lanata* Hill be valid because HILL wrote down what he saw by looking

at the plate? My only hesitation about rejecting HILL's name as invalid, is the uncertainty whether the principle could be unduly extended and cause chaos. Certainly a description that only records vegetative features has to be accepted in principle: in practice it may well have to be rejected if no type specimen is extant and especially if it has been placed under the wrong genus. However it would then be *nomen dubium* not *nomen invalidum.*

Nevertheless my hesitation about outright rejection does not permit me to go to the other extreme and accept HILL's name as valid. At the moment I throw it into the arena tagged *'nomen invalidum?':* let us see what the nomenclatural lions make of it.

Thus we have the following situation:

Hermas pillansii C. Norman in Journ. of Bot. **66**: 195 (1928); Adamson & Salter, Fl. Cape Penins. **616** (1950).

Syn.: [*Angelica africana, montana, odorata, floribus viridibus* Codex Witsenii (n. v.)].

[*Scabiosa hirsuta, foliis nervosis, subrotundis, floribus proliferis* Burman, Rar. Afr. Pl. dec. 8, 199, tab. 72, fig. 3 (1739)].

[*Scabiosa lanata* Hill, Syst. Veg. (folio) 5: 46, tab. 33 (1763), (ed. 2) 5: 46, tab. 33 (1772); (quarto) 5: 62, tab. 33 (1763); (octavo) 5: 86, tab. 33 (1763) — nomen invalidum?].

It will be noted that I have quoted HILL's Vegetable System in folio, quarto and octavo editions. The folio and octavo are described both in HENREY (1975, 3: 56-59) and in STAFLEU & COWAN (1979: 202-203, 1979). The quarto is not recorded in either of these works, but there is a copy in the library of the Royal Botanic Garben, Edinburgh, and another in that of the University of Edinburgh. Mr. M. V. MATHEW (librarian at the Royal Botanic Garden, Edinburgh) will publish a bibliographical account of this edition shortly.

I am indebted to Miss R. M. SMITH for the preparation of the figures.

1240   *B. L. Burtt*

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CHROMOSOME STUDIES
ON *TRILLIUM KAMTSCHATICUM* PALL.

XXXI. ON THE LIPID AS ONE OF THE CHROMOSOME
CONSTITUENTS

by

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DURING the last decade much attention has been paid by a number of cytologists to the problems surrounding DNA which is the main element of chromosome constitution. On the other hand, however, it has generally been suggested that lipids may play an important role as a constituent of protoplast, through so many works on the so-called «liposomes». On this basis, I attempted to demonstrate first the existence of lipids within DNA or chromosomes and secondly to invoke a role for them as binding substances. Up to the present, I am not aware of such an experiment as shown in the present paper, though a few workers demonstrated histochemically the presence of lipids in chromosomes, and WILKINS and his associates (cf. BUSH, 65, p. 105) suggested that sphingomyelin or other lipids are present in deoxyribonucleoprotein preparations from their X-ray diffraction studies.

MATERIAL AND METHODS

Some scores of corms of *Trillium kamtschaticum* grown in our experimental garden were collected on late November

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1965 for materials of the present work. The PMCs at this date proved to be at leptotene to zygotene of the first meiotic division. When whole anthers are put on water-wet blotting paper in petri-dishes, meiosis in their PMCs proceeds in normal fashion and attain to tetrad stage about one week later.

With the object of pulling lipid out of chromosomes, these dishes were put in a vacuum dessicator whose strength of diminution in air pressure is 14 mm Hg. by the exertion for 4 minutes. Then they are reverted to usual atmosphere condition for about half an hour, and further they are again subject to the same procedure. In the present work, this repeating was carried out in four classes, 3, 5, 8 and 12 times. For PMCs of each class, were made acetocarmine preparations pretreated with water (MATSUURA '38) and observations were done under a phase-contrast microscope. Besides PMCs, the tapetum cells and plasmodium were also supplementally observed.

OBSERVATIONS

Myelin formes

The preparation made immediately after the diminished pressure procedure are always characterized by the occurrence of myelin forms which lie in the medium surrounding PMCs or tapetum plasmodium (Text-figs. 1-3). As already described by many workers (cf. YASUI '38), their forms are various, thin thready, headed thready, spherical, bladder-like, rodshaped, spirally coiled, etc. They are instantly changing their forms, being swollen, adsorbing water and about two days lather they fuse together making a very thin film on the surface of the medium (Text-fig. 2).

The myelin makes a strong contrast to the lipid in chromosomes in that the former is easily pulled out of the cells, whereas in the latter stronger exertion of the procedure is required for pulling it out of chromosomes, thus suggesting that the former exists as free drops, while the latter is strongly combined with chromosome structure. In

the present work, it was shown that at least 12 times exertion of the procedure is necessary for this purpose.

The decomposition of nuclear envelope, nucleolus and cell-wall

One of the most striking features of the malignancy is the absence of nuclear envelope, nucleolus and cell-wall as well (Plate I and others). These malignant features
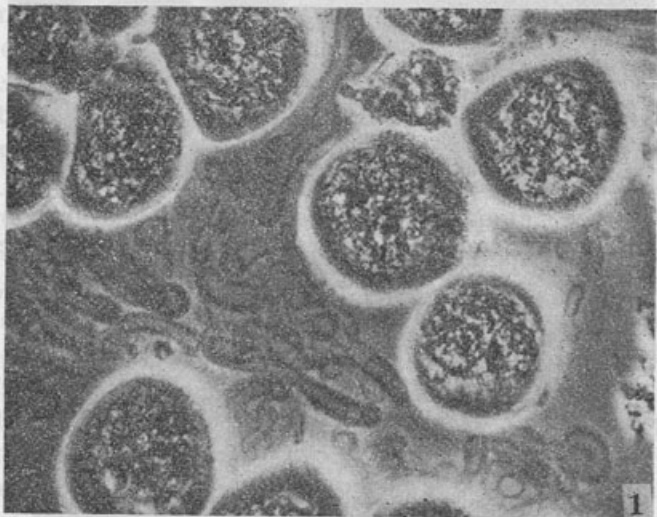

Fig. 1. — Myelin forms in acetocarmine medium surrounding PMCs at meiotic prophase. The same scale as figs. 2 and 3.

continue during the whole cycle of meiosis and the following mitosis, so indicating that these structures or cell organs are to be considered as those holding identity, as do the chromosomes and the other organelles. Also it is conceivably suggested that these malignancies are so related one another in function by the absence of their existence and hence their function. Furthermore they may have common effects on the other cellular activities. Thus the appearance of myelin forms as mentioned above may owe to lipid drops streamed out of these structures. It is also interesting to note, in
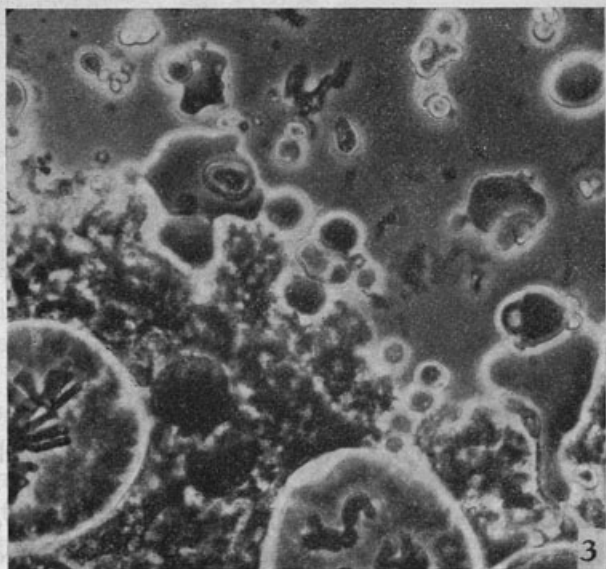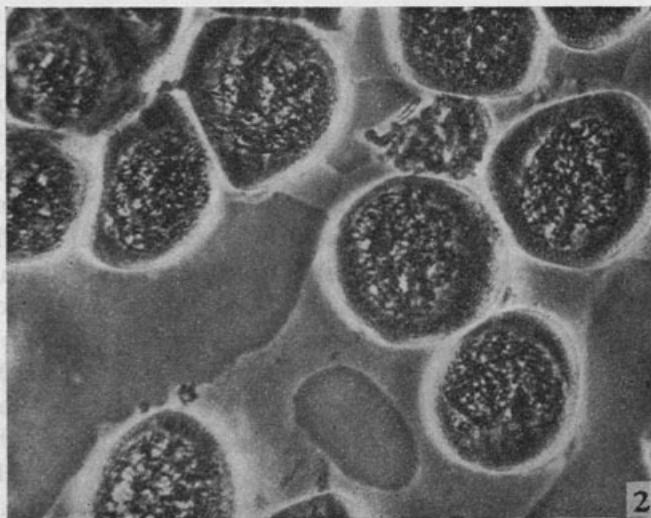
Figs. 2 & 3. — 2, the same region as 1, 50 hrs later.
3, represents myelin forms originated from tapetum
plasmodium. Calibration bar equals 50 μm.
All to same scale.

such naked nuclei as well naked cells how are deformed the mode of cell division and of chromosome structure and its behavior.

«Lipidated» chromosomes

The «lipidation» of meiotic chromosomes is recognizable as the eruptions all over the chromosomes. They appear either as blight whitish patches or coats covering the chromosome surface or as larger globular clusters at arm ends, both distal and proximal (viz. the kinetochore region). Such a specified localization of lipid gatherings seems to give direct evidence for that these are intrinsic ones of chromosomes, not the additives of external ones; that is, these lipid substances which are most probably lipoproteins are regarded as one of chromosome constituents.

Such «lipidated» chromosomes act like hitherto known sticky ones of a mutationally arisen individual, being similar in that they give rise to sticky adhesions between two or more chromosomes and to the formation of «sticky bridges» and fragments at anaphase when the chromosomes or chromatids associated in such adhesions move to opposite spindle poles. Here, however, the degree of stickiness is much greater than that in naturally found cases. Very frequently several chromosomes adhere together in complex fashion, so making impossible to analyze the chromosome identity.

In the preesnt case, the adhesions usually occur between an arm end and another end, between an end and an interstitial part and between an end and a kinetokore region, as diagrammatically represented in Text-fig. 4.

These types of adhesions give rise to corresponding types of fragments which are categorized as free fragments (*abbr.* f), a fragment attached to chromosome end (fe), a fragment attached to interstitial chromosome part (fi), and fragment attached to kinetochore (fk). Besides these, there are more complicated adhesions, such as multiple fusion involving more than three arms at one point, fusion along entire arms, adhesives covering an entire bivatent, etc. Moreover the fragmentation may occasionally involve entire

arms, breakage of the chromosome occurring at a locus close to the kinetochre (F). Thus F fragmentations may distinguish correspondingly to the f ones as F, Fe, Fi and Fk.
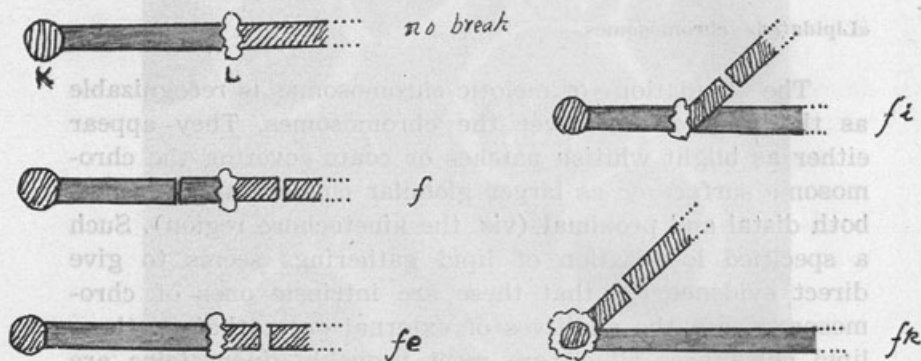

Fig. 4. — Diagrammatic representation of the origin of f, fe, fi and fk types in «lipidated» chromosomes. K stands for kinetochore and L for lipid cluster.

The frequency of these fragments was recorded in the total 50 cells in which each member of the complement was analyzable (Table I).

By the way, the frequency of primary chiasmata (cf. MATSUURA, '41) in those 50 cells was only 18, that is 3.8 % per cell indicating much lower frequency of chiasma formation as compared with that in the control material.

TABLE I

Frequency of various types of fragments at MI

Total cell no.	f	fe	fi	fk	F	Fe	Fi	Fk	Total
50	2	4	1	1	3	1	—	2	14 (28 %)

Next, concerning the deficiencies in nucleokinesis at Meta-and Anaphase I, the following facts are noteworthy. (i) Variable modes of chromosome spiralization (Plate I, 2-11). In most cells the spiralization is distinctly much larger in dimension as compared with that of the control. In some

cells, however, they are much thiner and more elongated. Such variable effects on the chromosome structure seem to be due to depend on somewhat decrease in viscosity of chromosome matrix owing to the defficiency of lipid materials resulting in larger chromonema spirals as well as somewhat decrease in chromosome matrix formation itself yielding smaller spirals. (ii) Scattering location of the chromosomes over the equational plate (Plate I, 9, 10). This is regarded to be due to the absence of the nuclear envelope and also to the discrepancy in structure and function of atractoplasm. (iii) Non-disjunction of bivalents, seemingly depending upon the same above mentioned reasons (Plate I, 12, 13). (iv) Asynchronization of nucleokinesis between different cells as in different chromosomes within the same cell (Plate I, 8). This lack of unification in nucleo- or chromosome-kinesis is regarded as also due to the lack of nuclear envelope. Lastly (v) Apparently rare occurrence of bridges and fragments at anaphase I (Text-fig. 5). As described above, the breakage of chromosome at the adhesion regions is of rather meagre occurrence in spite of numerous adhesions and too the frequency of fragments at anaphase is very much smaller than that expected. Being different from the usual breaks followed by exchanges between homologuous chromosomes, here the break points are masked by lipid clumps at metaphase, being not easily distinguishable as breaks, and at anaphase such fragments may go to the pole together with the attached chromosomes, instead remaining on the equatorial plate as usual (Plate III). This is the reason why in sticky chromosomes breaks and fragments are scored as less frequent ones.

«Pollen plasmodium» and crystallization of chromatin

At anaphase I, some half-bivalents tend to aggultinate together as shown in Plate I, 8. Such a tendency is more clealy distinguished at further stages, where the chromosomes enter individually into interphase, making several chromatin masses of different sizes (Plate I, 14, 15). These deformed nuclei have no nuclear envelope and no nucleolus
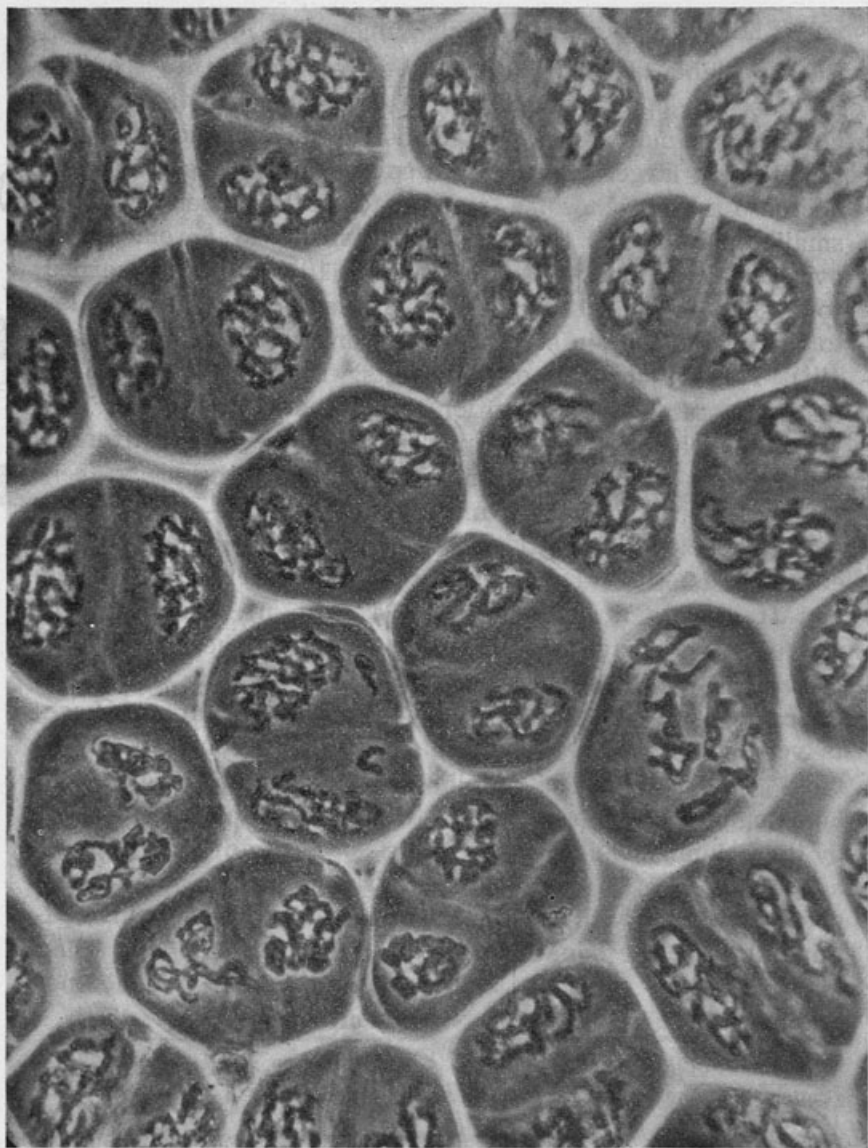
Fig. 5. — A group of PMCs at anaphase I in this material, indicating how bridge and fragment formation is of rather rare occurrence in spite of sticky configurations occurring at metaphase I. Calibration bar equals 50 μm.

as well. Furthermore at these stages the formation of cell wall and callose is severely deficient, so inducing the plasmodium instead of the tetrads. Such «pollen plasmodium» becomes bigger by fusing together with neighboring pollen plasmodium. The chromatin aggultination proceeds further and gives rise to definite conical bodies, each of which contains much compressed chromatin mass at its center and is enveloped by thick lipid rim (Plate IV, 3). Later on, these bodies are subject to strong elongation and the inside chromatin comes to change into a number of microfibrils which are arrayed in the bundle (Plate IV, 6). Since chromatin deprived of lipid is considered to be nucleoprotein, these phenomena are assumed to be its crystallization and growth. In fact, many true crystals of various sizes are observable within the pollen plasmodium. These crystals are always covered by thin lipid film (Plate IV, 6-8). The bundle of these microfibrils are broken down transversally at nearly equal intervals (Plate IV, 5). Such breakage seems to proceed further and lastly severe pulverization takes place untill pulverized particles become so small as they can not be caught by a light microscope (Plate IV, 9).

In comparison of these series of events in the pollen plsmodium were studied with those in the tapetum plasmodium. The results indicated that the both were entirely identical with each other (Plate V).

COMMENTS AND SUMMARY

By means of putting the anther of *Trillium kamtschaticum* under strongly diminished air pressure, many malignant symptoms were found to occur in cellular activities in general, nucleokinesis and chromosome structure and its behavior. The symptoms are related to the lack or defficiency of lipid substances. They are listed as follows:

i) The appearance of myelin forms.
ii) The decomposition of nuclear envelope, nucleolus and cell-wall.

[161]

   iii) The occurrence of nuclear extrusion [1].

   iv) The formation of «lipidated» chromosomes.

    v) The formation of «pollen» plasmodium.

   vi) The crystallization of chromatin substances and their severe pulverization.

Based on a chain of these events, it was concluded that the lipid is an important element of chromosome constituents, and play an important role for the maintenance of chromosome organization.

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[1] This topic was not be dealt with in the present paper. The concerning data will be published in another paper of this series.

PLATES

Plate I

PLATE I

Demonstrating how PMCs deprived of lipids are maligrant in structure, function and movement of the chromosomes in metosis I. 1, A cell at diakinesis I. Note the non-formation of nuclear envelope, this situation being the same in all other figures. 2-4, 6, 7 and 11, Cells at metaphase I, showing variant chromonema spirallization. 5, Showing asynchrony in division, left cell being at anaphase, while right one at metaphase. 8-10, 12 and 13, Cells at anaphase. Asynchrony in chromosome kinesis (8), bridge formation (9), rampant orientation of each half-bivalents over the cell (10), chromosomes clumping together due to severe «lipidation» (12), abnormal formation of cell plate independent of chromosome movement (12, 13). 14, 15, Cells at further stage. Formation of interphase nuclei of various sizes (14). Pseudo-tetrad formation (15).

Plate I

Plate II

Plate III

PLATE II

PMCs at metaphase I (1-5 appended with respective explanatory sketches, 1a-5a), showing «lipidation» and adhesions of the chromosomes. The same designation of the chromosomes of a complement as in the other papers of this series by me has been adopted in the present paper; capital letters, A-E, designate the five chromosome (bivalent) types of a complements, small letters, a-e, stand for univalents, or half-bivalents and letters suffixed by f indicate fragment chromosomes. Configurations in right cell in 4 are too complicated to be analyzed.
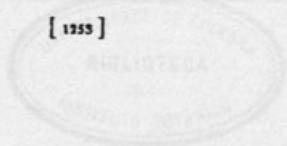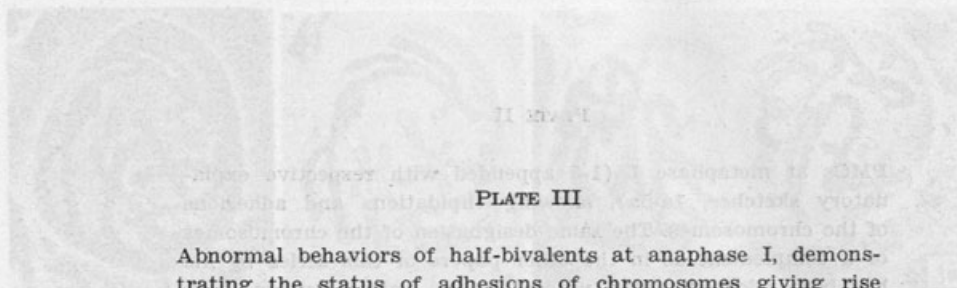
Plate II

PLATE III

Abnormal behaviors of half-bivalents at anaphase I, demonstrating the status of adhesions of chromosomes giving rise to the formation of bridges and fragments (1-5) and non--disjuction of paired half-bivalents (6, 7).

Plate III
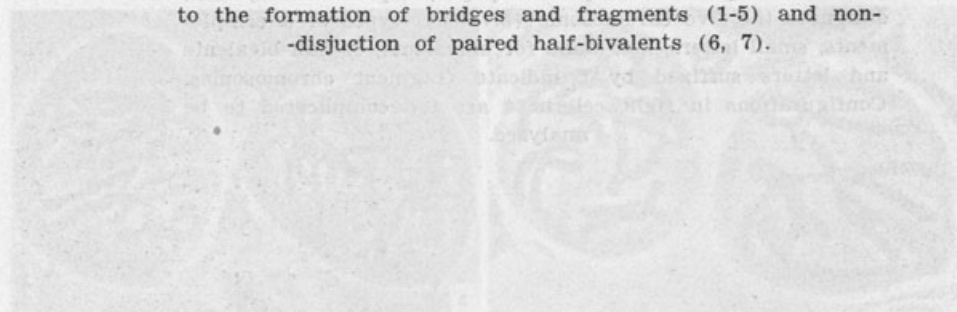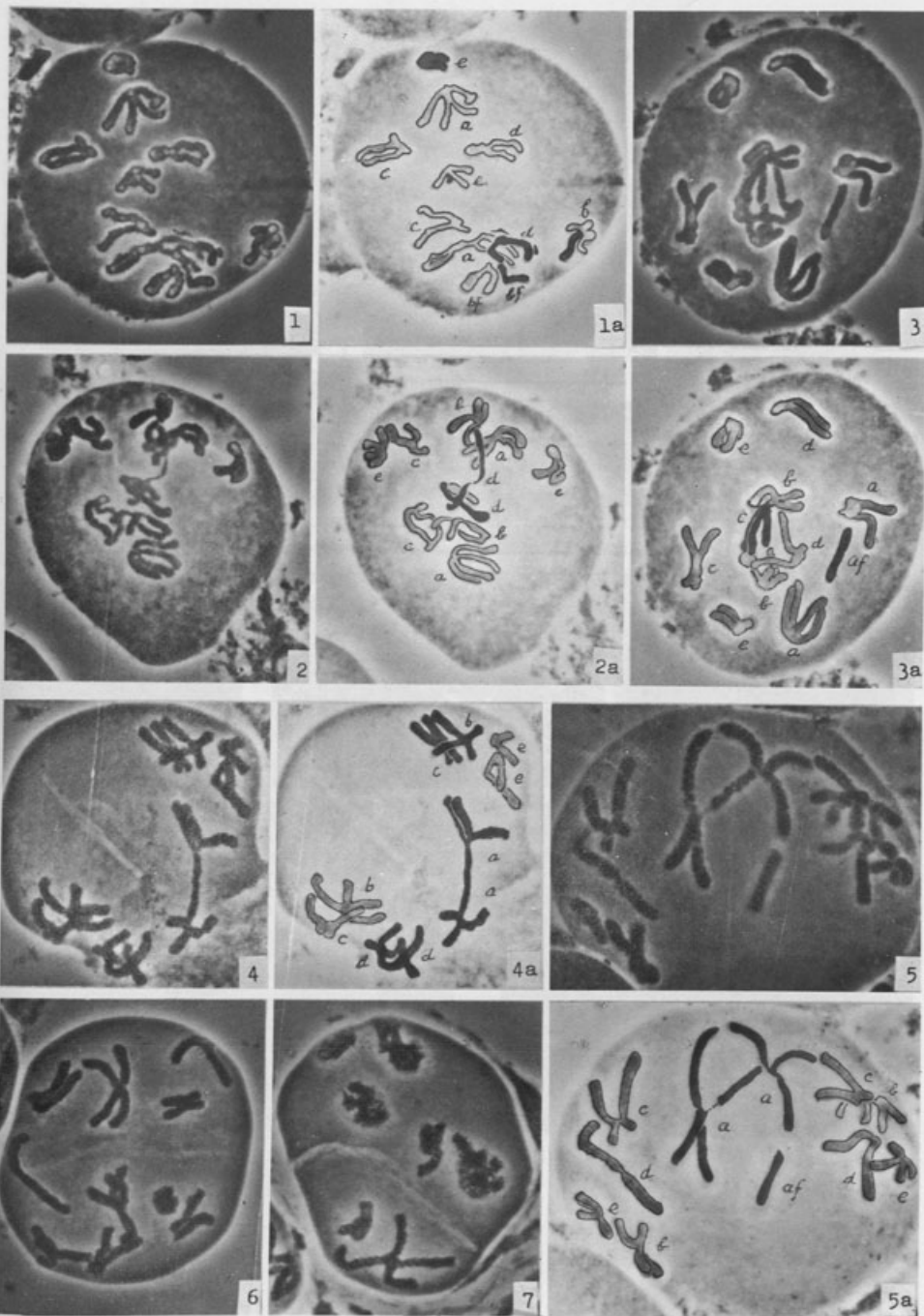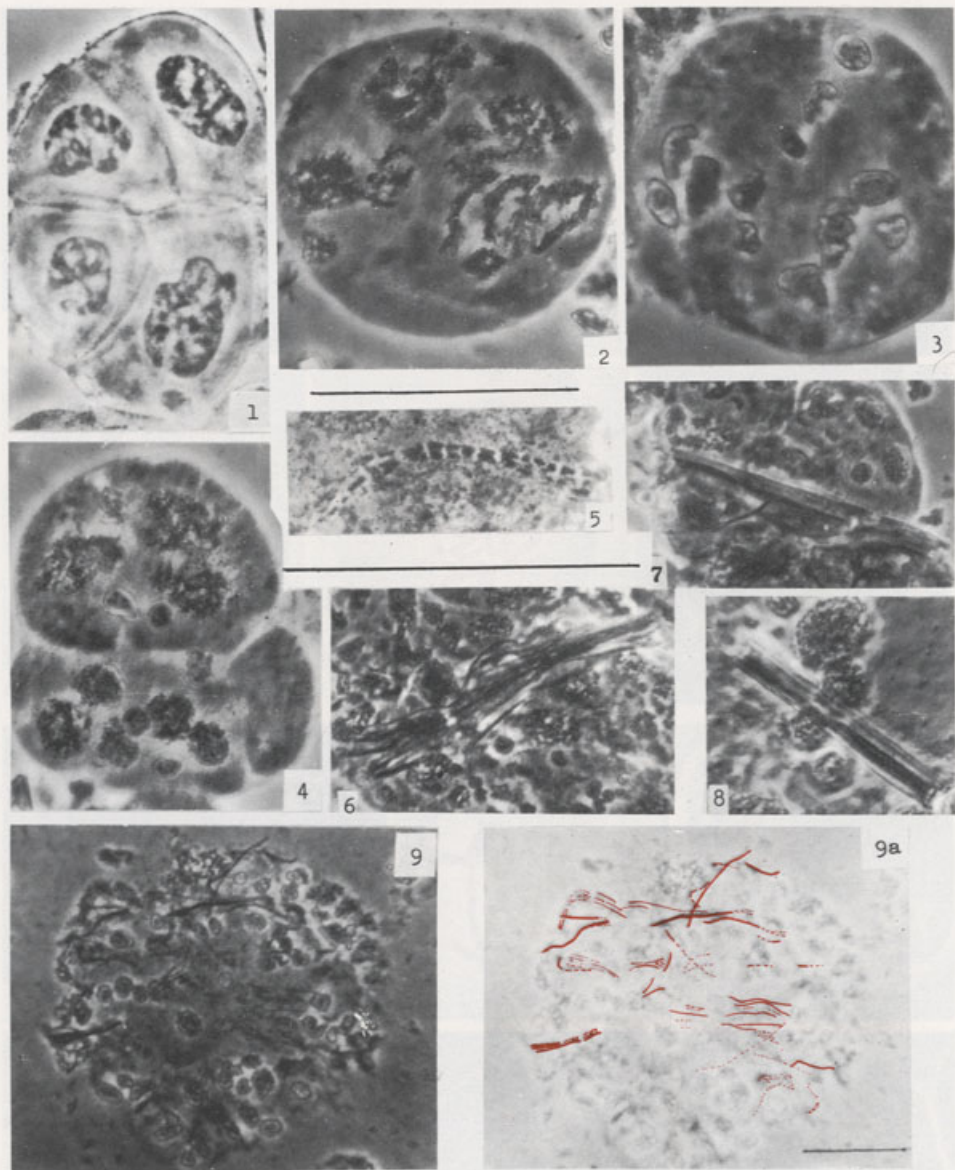
Plate IV

Plate V

PLATE IV

Demonstrating the severe destruction of chromosome organization at the end stages of meiosis. Refer to text, p. 1249. 1. only one case of apparently normal tetrad formation. 2-4, the formation of «pollen» plasmodium. 6, initiation of pulverization of elongated microfibrils bundle. 6, a bundle of microfibrils coated by lipid layer. 7, 8, crystals of ribonuclear proteins also coated by lipid layer. 9 and its explanatory figure, 9a, showing extreme pulverization of chromatin microfibrils.

Plate IV
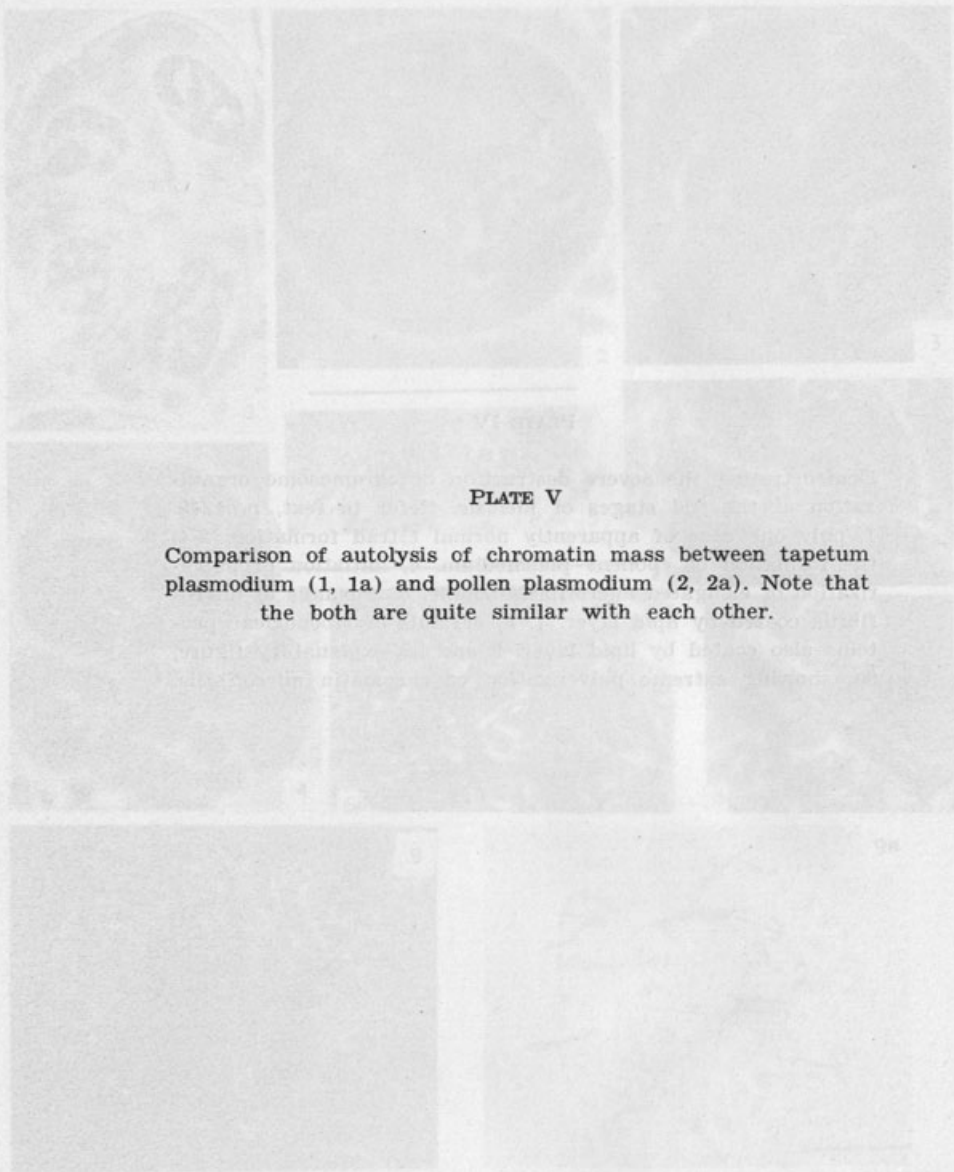
PLATE V

Comparison of autolysis of chromatin mass between tapetum plasmodium (1, 1a) and pollen plasmodium (2, 2a). Note that the both are quite similar with each other.

Plate V
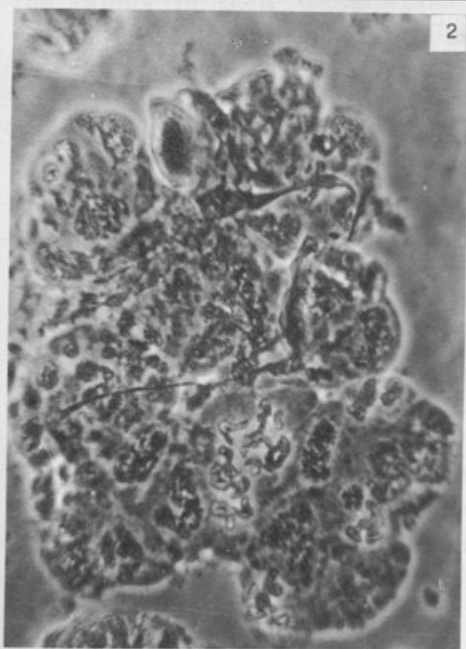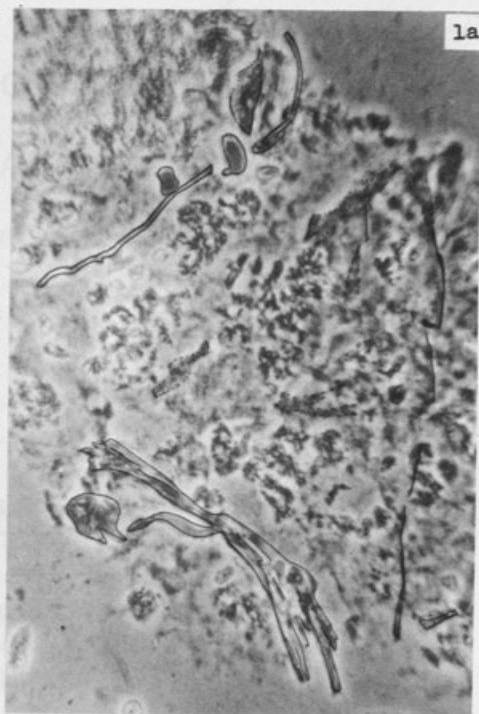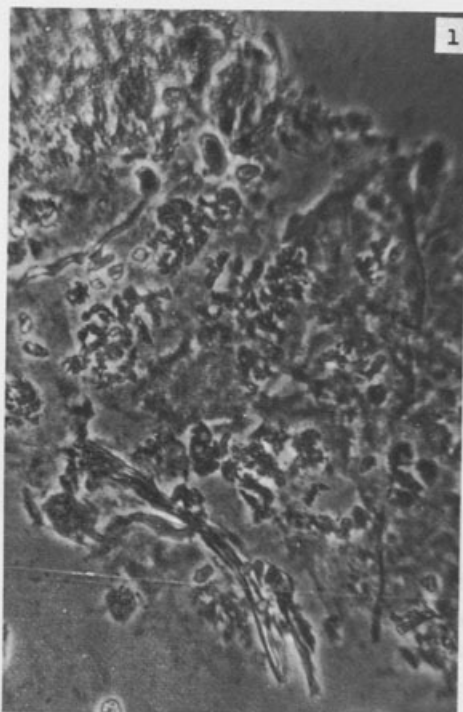
CORRELATION OF CYTOLOGY
AND PHYTOCHEMICAL CONSTITUENTS
IN LABIATAE

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INTRODUCTION

THE group Labiatae is a dicotyledonous family of angiosperms. The position and relationship of some of the taxa within the family have formed subjects of considerable debate. BENTHAM & HOOKER (1873) included the family in their Gamopetalae, which was incorporated in between Polypetalae and Monochlamydeae. In ENGLER & PRANTL's (1897) system, it was superseded by four other groups as far as the advanced status was concerned. HUTCHINSON (1969) placed the family at the top of his Herbaceae, a group of fundamentally herbaceous plants. However, in the present review, BRIQUET's system of classification as published in ENGLER & PRANTL's Die Natürlichen Pflanzenfamilien (1877) has been followed. This system, besides being a phylogenetic one, deals with the delimitations of several genera which are subdivided into different subgenera and/or sections. These detailed delimitations have enabled the present authors to ascertain their status and affinity, while dealing with cytological and phytochemical findings. The principal objective has been to determine correlations, if any, between the chromosomal complements on the one hand and the phytochemical constituents on the other. A brief account of the BRIQUET's system (1897) is given here:

The entire family is divided into eight subfamilies, namely Ajugoideae, Prostantheroideae, Prasioideae, Scutellarioideae, Lavanduloideae, Stachydoideae, Ocimoideae and Catopherioideae. Of these, Ajugoideae, Stachydoideae and Ocimoideae have beem further split into different tribes (ending with *-eae*) and subtribes (ending with *-nae*). Ajugoideae has been divided into two tribes Ajugeae and Rosmarineae and Stachydoideae into twelve tribes and subtribes (such as, Marrubiae, Perilomieae, Nepetae, Brunellinae, Melittinae, Lamiinae, Glechoneae, Salvieae, Meriandreae, Monardeae, Hormineae, Lepechinieae, Melissinae, Hyssopinae, Thyminae, Menthinae, Perillinae and Pogostemoneae) and Ocimoideae into subtribes Hyptidinae, Plectranthinae and Moschosminae. All the genera included in this review, except *Rosmarinus, Glechoma, Anisomeles* and *Origanum,* have been further subdivided into different subgenera and/or sections, each comprising of species related to each other.

In the present review, in addition to considering the correlation of cytology and phytochemistry of the Labiatae, the status and affinity of these plants in BRIQUET's system have also been taken into account. Such a correlated approach to the principal genera of the mint family through evidences from cytology, phytochemistry and taxonomy was deemed desirable to solve the problems of taxonomic dispute in this family. While dealing with the chromosome number, only recent records have been mentioned.

Cytology and phytochemistry of the species — a correlated analysis

In the subfamily Ajugoideae, three genera — *Ajuga* and *Teucrium* of tribe Ajugeae and *Rosmarinus* of Rosmarineae — have been included in this review. *Ajuga reptans* L. having n = 16 chromosomes (MAJOVSKY *et al.,* 1974) contains harpazide and harpazide acetate (KOMISSARENKO *et al.,* 1976), which are not found in any member of the subfamily Ajugoideae. In *Teucrium,* the compound is different — teucrin P (POPA *et al.,* 1977) and a diterpenoid picropoline (BRIESKORN & THOMAS, 1966). Their chromosome numbers,

being n = 13 (MARKOVA & THU, 1974) and 26 (UECH, 1974a, b), are *also different.*

The position of *Rosmarinus* has been a debated one. It has been kept under Ajugoideae by BRIQUET (1897) and separated and elevated to a subfamily level (Rosmarinoideae) by MELCHIOR (1964). The chromosome number of *R. officinalis* L., the only species both cytologically and phytochemically studied, is 2n = 24 (NATARAJAN, 1978), whereas in *Ajuga* it is 32 and in *Teucrium* 26 and 52. Though the chromosome number itself can not be considered as the determining character between the two genera of the subfamily, the difference in chromosome number is manifested clearly. But, the chemical components noted in *R. officinalis* are α-and β-pinenes, satinene, camphene, μ-phellandrene, ρ-cymene, eucalyptol, camphor, terpineol, borneol, linalool, borneol acetate, geraniol (KARAWYA *et al.*, 1970), royleanone and cryptotanshinone (BRIESKORN & BUCHBERGER, 1973), none of which is found in other genera of Ajugoideae. This may, to some extent, support the separation of the genus from Ajugoideae and elevation to a subfamily Rosmarinoideae, as done by MELCHIOR (1964). However, more confirmatory evidences are needed from other species of Ajugeae and Rosmarineae to substantiate their separation and elevation.

In *Scutellaria,* belonging to a separate subfamily Scutellarioideae, varying compounds, including sterols, flavones and alkaloids are found. None of the intermediates of the flavone biosynthetic pathway has yet been reported in this genus. However, the final flavone products of their derivatives invariably occur. Scutellarin (scutellarein-5-glucuronide), which is a glucoside derivative of scutellarein (5:6:7:4' — tetrahydroxyflavone) is found only in *S. columnae* All. (MARSH, 1955) having polyploid forms with 2n=32, 34 chromosomes (BAKSAY, 1958; MARKOVA & THU, 1974). The parent compound scutellarein is found in the diploids — *S. orientalis* L. (BEKIROV *et al.*, 1974) with 2n = 16 chromosomes (QUÉZEL, 1957) as well as in several other species, such as, *S. polybdon* (BANDYUKOVA & BOIKOVA, 1969), *S. prze-*

walskei (DENIKEEVA *et al.*, 1970) etc., whose chromosome numbers are not reported.

It is remarkable that carthamidin and isocarthamidin are found only in *S. baicalensis* Georgi (TAKIDO *et al.*, 1976). This species has a chromosome number $2n = 18$ (SUZUKA, 1953), a number unknown for the genus. Even though baicalin is also found in other species, it appears that the alteration in the haploid chromosome number ($n = 9$) may be associated with the change in the phytochemical component. Such alterations might have occurred following gene mutation, resulting in the evolution of new compounds.

Baicalin (baicalein-6-glucuronide), a glucoside of flavone baicalein, is present in several species, such as, in *S. altissima* L. (BESHKO *et al.*, 1975), *S. baicalensis* (KHNYKENA, 1962), *S. orientalis* (BEKIROV *et al.*, 1974), etc. having both $n = 8$ (MORTON, 1973) and 9 chromosomes (MARKOVA & IVANOVA, 1974) as haploid numbers. But the parent compound baicalein is found only in species having haploid chromosome numbers either as 8 or its derivatives as in *S. altissima* (BESHKO *et al.*, 1975) with $2n = 28$ and 34, *S. orientalis* (BEKIROV *et al.*, 1974) with $2n = 16$ chromosomes, etc.

In general, the species of *Scutellaria* are homogeneous in their contents of different compounds, such as, baicalein, baicalin, scutellarein, scutellarin, etc. Cytologically also, different species of this genus show homogeneity in having $n=8$, 10, 11, 16, 17, 18 and its derivatives. The chromosome numbers of three species of *Scutellaria* have been reported for the first time by the authors — *S. adenostegia* with $2n=20$ (SINGH, 1979), *S. intermedia* having $2n=22$ (SINGH, 1979) and *S. haematochlora* with $2n = 20$ chromosomes (personal communication, in press). None of these species have been studied from the phytochemical aspect. Both aneuploid and polyploid series are seen and the base number appears to be 8, as believed by DARLINGTON & WYLIE (1955) also. This basic number may have given rise to other numbers through duplication and polyploidy. As a few species, such as *S. galericulata* L. contain cytotypes, it will be worthwhile to find out the correlation of such cytotypes with chemical contents.

Of the four sections of the genus *Lavandula* under the subfamily Lavanduloideae, only some of the members of the section Stoechas have been studied both cytologically and phytochemically. In Stoechas, the chromosome numbers reported are n = 15 each. *L. stoechas* L. contains 2n = 30 chromosomes (VON BOTHMER, 1970), *L. pedunculata* Cáv. 2n = 30 (GARCIA, 1942) and *L. dentata* L. 2n = 45 chromosomes (NESTERENKO, 1939). Cineole and camphor are the two compounds common to all the three (DE PASCAUL TERESA *et al.*, 1976), whereas feuchone is seen only in the diploid species, *L. stoechas* (GRANGER *et al.*, 1973) and *L. pedunculate* (DE PASCAUL TERESA *et al.*, 1976). The uniformity in chemical content, correlated with homogeneity in chromosome number, related to a slight variation due to genotypic differences is quite remarkable. In *L. officinalis* Ch., the chromosome numbers reported are 2n = 36 (LAWS, 1930) 42 and 48 (BUYUKLI, 1970), 50 (MAKINO, 1951) and 54 chromosomes (DELAY, 1947) and this species has not been listed under any section of the genus. A variety of compounds has been found in this species, including cineole, borneol and camphor (TOORE & CARMEN, 1974). With the range of cytotypes so far reported, it would be worthwhile to correlate their genetic constitution with the chemical constitution. In general, *Lavandula,* as a genus, is quite remarkable in having camphor as its component in all the species worked out so far. In view of the similarity in chemical contents of the three species as well as that of *L. officinalis,* which also resembles other species in chemical constitution, it is likely that the genus has a common basic number from which the other forms have arisen through polyploidy, aneuploidy and hybridization. The homogeneity of the genus as a whole appears unquestionable.

The subfamily Stachydoideae is wide in scope and has a number of taxa within its orbit (namely, Marrubiaeae, Pevilomiiae, Nepetae, Brunellinae, Mellillinae, Lamiinae, Glechoneae, Salvieae, Meriandreae, Monardeae, Hormineae, Lepechinieae, Melissinae, Hyssopinae, Thyminae, Menthinae, Perillinae and Pogostemoneae). Though 8 or 9 chromosomes are the deep-seated numbers, yet aneuploidy is not very

uncommon. In the genus *Marrubium* of Marrubiaeae, the chromosome numbers reported so far are 32, 34 and 54, the chemical constituents being peregrinine and its derivatives, marrubiin and stachydrine. Though species differ with regard to the content of some specific derivatives, yet a general uniformity in the chemical constituents is noted — *Marrubium catariifolium* containing peregrinol (POPA & SALEI, 1973), *M. leonuroides* having dihydroperegrinin (POPA & SALEI, 1973), *M. peregrinum* L. containing peregrinol (SALEI *et al.*, 1966; POPA & SALEI, 1973), peregrinin (POPA & SALEI, 1973) and peregrinine (SALEI *et al.*, 1966) and *M. praecox* with peregrinol (POPA & SALEI, 1973). The occurrence of 2n = 34 (STRID, 1971) and 54 (PODLECH & BADER, 1974) chromosomes in *M. alternidens* Rech. f. and 32 (MARKOVA & IVANOVA, 1971) and 34 (MAJOVSKY *et al.*, 1970*a, b*) in *M. peregrinum* L. indicates intraspecific variations. The number 2n = 34 may be a derivative of 32 or 36 in *M. vulgare* L. (HEISER & WHITAKER, 1948) through duplication of one or more chromosomes or an aneuploid cross between x = 8 and x = 9 chromosomes.

In the allied genus *Sideritis,* under the same tribe, though chemical constituents have been analysed in 9 species (namely, *S. angustifolia* Lag., *S. canariensis, S. candicans, S. catillaris, S. grandiflora, S. lagascana, S. montana* L., *S. pusilla* (Lge.) Pan and *S. valverdii*), cytological observations have been made on only three, namely *S. angustifolia* with 2n = 24 (FERNANDEZ-PERÁLTA *et al.*, 1978), *S. montana* having 2n = 32 (FERNANDEZ-PERÁLTA *et al.*, 1978) and *S. pusilla* showing 2n = 22 chromosomes (FERNANDEZ--PERÁLTA *et al.*, 1978). The chemical compositions of the different species of the genus show qualitative differences. The above three species, so far cytologically studied, show differences in chromosome number as well as in the chemical constituents. Pusillatriol and its derivatives are the principal components in *S. pusilla* (GARCIA DE QUESADA *et al.*, 1974), jativatriol in *S. angustifolia* (VON CARSTENN-LICHTERFELDE *et al.*, 1974), several alkaloids, tannins and saponins in *S. montana* (DZHUMAZHANOVA, 1968) and kaurene and beyerene in *S. lagascana* and *S. valverdii* (DE QUESADA *et al.*,

1974). In absence of any further data on chemical consti-
tuents in the genus *Sideritis,* it is difficult to comment on
the homogeneity of the genus. In this genus, however,
$x = 8$ chromosomes may represent the basic set from which
others have been derived.

In Nepetae, two genera (*Glechoma* and *Nepeta)* have
so far been studied, both from cytological and chemical
standpoints. Extensive investigations have been carried out
in the latter. In the genus *Glechoma* having only one species
(*G. hirsuta* Waldst. *et* Kit.) with $2n = 36$ chromosomes
(MARKOVA & THU, 1974), the principal chemical constituents
are phytol, β-sitosterol and betulin (POPA & PASECHNIK,
1974). In absence of further data on cytology and phyto-
chemistry, it would not be proper to comment on the genus.
However, the presence of some of the triterpenoids (betulin
and aleanolic acid) and β-sitosterol in *Glechoma hirsuta*
and some of the species of *Nepeta* [betulin in *N. aragonensis*
(VON CARSTENN-LICHTERFELDE *et al.,* 1973), oleanolic acid
in *N. teydea* (BRETÓN *et al.,* 1970) and β-sitosterol in
N. industana Hains (SESHADRI & SHARMA, 1973) and *N. teydea*
(BRETÓN *et al.,* 1970)], together with the basic set of $x = 9$
chromosomes in both the genera, evidently bring them
together to be closetted under a single tribe Nepetae. In the
genus *Nepeta,* a large number of terpenoids has been recorded
in different species, namely, in *N. cataria* L. (REGNIER *et al.,*
1967), *N. citriodora* (REGNIER *et al.,* 1967), *N. leucophylla*
Benth. (GUPTA, 1973) and *N. mussini* (REGNIER *et al.,* 1967).
In addition to these, nepetalactone and epinepetalactone in
N. cataria L., *N. citriodora* and *N. mussini* (REGNIER *et al.,*
1967) and nepetrin and nepetin in *N. hindustana* Hains
(SESHADRI & SHARMA, 1973) and their derivatives are also
common in all the species. Sterols (β-sitosterol) too, are
found in a few. Even in the absence of certain derivatives
of a parent compound, a general uniformity in the phyto-
chemistry is noticeable. The chromosome number too, is
mostly $n = 9$ [as in *N. cataria* L. (LEE, 1969; PODLECH &
DIETERLE, 1969), *N. hindustana* (VIJ & KASHYAP, 1976),
N. leucophylla (GILL, 1969), *N. mussini* (VAKAR & LESHU-
KOVA, 1970)] with occasional polyploids and aneuploids,

such as, in *N. cataria* with 2n = 30 (MAJOVSKY *et al.*, 1970*a, b*), 32 (BUSHNELL, 1936), 34 (MARKOVA & THU, 1974) and 36 chromosomes (LEE, 1969; PODLECH & DIETERLE, 1969). The genus is marked by uniform chromosome number with common chemical constituents.

The tribe Lamiinae presents certain interesting features from the phytochemical standpoint. Though flavones, flavanols, sterols and alkaloids have been found in different genera of the group, one can establish a pattern of their presence correlated with their genotypic constitution. In the genus *Lamium,* the common constituents of all the species are quercitrin or its derivative quercimeritrin, caffeic acid and to some extent kaempferol (DUCHNOWSKA & BORKOWSKI, 1964; KRITIKOS & HARVALA, 1970). The chromosome numbers reported for the species of the genus are 2n = 18 in *L. amplexicaule* L. (MARKOVA & THU, 1974) and *L. purpureum* L. (MARKOVA & THU, 1974); 2n = 16 (MARCHAL, 1920), 18 (BHATTACHARYA, 1976) and n = 9 (MHATTACHARYA, 1976) and n = 9 + 1B chromosomes (GILL, 1970) in *L. album* L., 2n = 18 (MAJOVSKY *et al.,* 1974) and n = 9 chromosomes (KLIPHUIS & WIEFFERING, 1972) in *L. maculatum* L.

The species *L. album* can serve as a good material for the analysis of the effect of B-chromosomes on the phytochemical constituents. In *Lagochilus,* three species (*L. inebrians* Bunge, *L. pubescens* Vved. and *L. setulosus*) have so far been analysed for the chemical contents and the alkaloid stachydrine has been found to be common to all (PULATOVA, 1969). Of these, *L. inebrians* and *L. pubescens* have been cytologically studied, both showing 2n = 34 chromosomes (ZAKHARYEVA & ASTANOVA, 1968). The chromosome number is quite different from those of *Lamium* spp. and possibly derived from a cross between species having n = 8 and 9 chromosomes, followed by doubling of the complement. The presence of certain similar constituents in all the three species, along with identical and high chromosome numbers in at least both the species, is significant.

In *Galeopsis,* two species, namely, *G. ladanum* L. and *G. speciosa* Mill., have been phytochemically and cytolo-

gically analysed, indicating the presence of flavonoids, alkaloids and saponins (HRYTSENKO & ZINCHENKO, 1967). The chromosome number, being n = 8 (LÖVE & LÖVE, 1956), is also identical in both, unlike *Lagochilus* and *Lamium*. Added to the prevalent deep-seated chromosome number of n = 8 or 9 in the Lamiinae, two more numbers have been found to occur, namely n = 10 in *Anisomeles ovata* R. Br. (BIR & SIDHU, 1974) and n = 11 in *Ballota nigra* L. (VAN LOON & DE JONG, 1978), the chemical constituents being ovatodiolide in the former (HODAC *et al.*, 1963) and ballonigrin in the latter (SAVONA *et al.*, 1976).

In Lamiinae, therefore, each genus so far studied from both cytological and phytochemical standpoints, has distinct phytochemical characteristics associated with distinct chromosome numbers. However, the chromosome numbers x=8, 9, 10, 11 and 17 are quite likely derivatives from a basic set of 8 or 9, as evidenced especially by intraspecific variation in some of the species, for example, *Lamium album*, having 2n = 16 and 18 chromosomes.

In *Salvia* (tribe Salvieae) there are series of chromosome numbers in different species, such as, n = 6, 7, 8, 9, 11, 12, 15, 16, etc. Intraspecific polyploids [such as, in *S. carduacea* Benth. having 2n = 24 (STEWART, 1939) and 32 chromosomes (EPLING *et al.*, 1962), *S. virgata* Ait. with 2n = 16 (AFZAL-RAFII, 1971) and 32 chromosomes (BENOIST, 1937)] and aneuploids [such as, *S. nemorosa* L. with 2n = 12 (MAJOVSKY *et al.*, 1970a, b) and 14 chromosomes (MARKOVA & IVANOVA, 1974); *S. officinalis* L. with 2n = 14 (ILL, 1971a) and 16 chromosomes (SCHEEL, 1931) and *S. verbenaca* L. with 2n = 42 (KRAMER *et al.*, 1972), 54 (BHATTACHARYA *et al.*, 1971), 60 (DAHLGREN, 1971) and 64 chromosomes (VAN LOON *et al.*, 1971) are also common in the genus. However, of all the numbers, n = 8 chromosomes appear to be more prevalent as compared to those of the rest of species of *Salvia*.

Phytochemical studies have been carried out in nearly twenty species. Majority of them are characterized by having terpenoids like α- and μ-pinenes (MULLER & MULLER, 1964; PETRI VERZAR & MARIA, 1974; IVANIC & SAVIN, 1976);

cineole (MULLER & MULLER, 1964; MULLER, 1965; IVANIC
& SAVIN, 1976), borneol (PETRI VERZAR & MARIA, 1974;
IVANIC & SAVIN, 1976); linalool (SHEVCHENKO & TIKHOMI-
ROVA, 1973; IVANIC & SAVIN, 1976); geraniol (SHEVCHENKO
& TIKHOMIROVA, 1973), camphor (MULLER & MULLER, 1964;
MULLE, 1965; PETRI VERZAR & MARIA, 1974) etc., sapogenin,
like aleonolic acid (BRIESKORN *et al.*, 1961; PETTIT *et al.*,
1966; GONZALEZ *et al.*, 1975) and sterols, such as β-sitosterol
and others (BRIESKORN *et al.*, 1961; GUSAKOVA *et al.*, 1968;
GONZALEZ *et al.*, 1975). Flavonoids (like apigenin, luteolin,
kaempferol, kaempferide, gengkwanin, chrysoeriol, ayanin,
etc.) and their derivatives are also very common in the
species of *Salvia* (GELLA & PROKOSHERA, 1970; WOLLEN-
WEBER, 1974). Though, several of the compounds and their
derivatives are also common among the species, a clear
correlation as in Lamiinae could not be established between
species with distinct chromosome numbers and their phyto-
chemical constituents. Moreover, inspite of the wide diversity
in chromosome number, intraspecific variation clearly indi-
cates that they are all indirect or direct derivatives of a
common basic set (SINGH & SHARMA, unpublished 1980).
The gametic number being 8 or its multiple, it is quite
likely that this number is the basic number for this
genus also.

In the genus *Hyssopus* of subtribe Hyssopinae (Sta-
chydoideae), phytochemical investigation has been carried
out on three species only, namely, *H. ferganensis, H. offici-
nalis* L. and *H. seravschanicus* (Dul.) Pazij. Of these, the
report of chromosome number is available for the last two
only — both having $2n = 12$ chromosomes (REESE, 1952b;
MATVEEVA *et al.*, 1968b; MARKOVA & THU, 1974). Cytos-
terine, betulin, oleanic and ursolic acids are the important
constituents in *H. ferganensis* and *H. seravschanicus* (ZOTOV
& KHARANOVICH, 1975) and α- and β- pinenes, α-terpinine,,
pinocampheol, cadalene (SHARMA *et al.*, 1963; JOULAIN,
1976), pinic, pinonic and myrtenic acids (JOULAIN & RAGAULT,
1976) in *H. officinalis*. The genus is quite homogeneous
from both cytological and phytochemical standpoints.

However, the chromosome number is rather unusual, in having 6 as the haploid number.

Of the subtribe Thyminae (Stachydoideae), only two genera (*Origanum* and *Thymus*) have been studied from phytochemical and cytological points of view. The chromosome numbers are remarkably uniform, being n = 15 and 14, the former a deep-seated number both in *Origanum* and *Thymus*. The interspecific variations noted in several species of *Thymus*, including *T. vulgaris* L. with 2n = 30 (NATARAJAN, 1978) and 56 chromosomes (BONNET, 1966) suggest that the two chromosome numbers (n = 15 and 14) may be derived one from the other. Only in *T. serpyllum* L., 2n = 20 (ROHWEDER, 1937) and 24 chromosomes (JALAS & POHJO, 1965a, b) are recorded, though the phytochemical constituents are mostly common to other species of *Thymus*. The way through which it has been derived is yet to be investigated. Out of the 24 species, phytochemically analysed, 15 — *T. caucasicus* Willd., *T. collins* Bieb. with 2n = 30 chromosomes, *T. dagestanicus* with 2n = 28 chromosomes (GOGINA & SVETOZATOVA, 1972), *T. desyatoviae* Ronn., *T. forminii* Klock et Shost., *T. karamarianicus* Klock *et* Shost., *T. marschallianus* Willd., having 2n = 28 chromosomes (TRELA-SAWICKA, 1970, 1972), *T. soshowskyi* Grossh. with 2n = 60 chromosomes (GOGINA & SVETOZATOVA, 1972), *T. tuflisiensis* Klok. *et* Schost. showing 2n = 56 chromosomes (MATVEEVA & TIKHONOVA, 1968a, b), *T. trautvetteri* Klok. *et* Short. and *T. ziaratinus* Klok. *et* Shost., *T. pastoralis* Hjin., *T. pseudonummularis* with 2n = 30 chromosomes (JALAS & KALEVA, 1967) and *T. rariflorus* C. Koch. — contain caffeic acid, 1-caffeylglucose, 6-caffeylglucose, rosemarinic acid and garashangin (SIMONYAN *et al.*, 1972). This remarkable uniformity indicates that *Thymus* is a very natural assemblage. Therefore, both cytological and phytochemical studies confirm the homogeneity of the genus. At the same time, the presence of the same basic chromosome number (x = 15) and the common occurrence of some of the terpenoids (such as carvacrol and thymol) and a sapogenin in both *Origanum* and *Thymus* species strongly

suggest the inclusion of both the genera under the same subtribe Thyminae.

The genus *Mentha,* belonging to subtribe Menthinae (Stachydoideae), is one of the most important taxa in Labiatae, both from commercial and medicinal standpoint. It is widely cultivated for the content of menthol, its derivatives and other important chemical principles. The species, which have been studied both from cytological and phytochemical standpoints, belong to different sections, namely, Eupulegia containing *Mentha pulegium* L., Audiberliae having *M. arvensis* L., Capitatae including *M. aquatica* L. and Spicatae with *M. viridis* L., *M. longifolia* (L.) Huds. and *M. spicata* L. The chromosome number in *M. pulegium* ranges from 10 to 46 (NAGAO, 1941; PÓLYA, 1950; MORTON, 1956; SOBTI, 1965; VON BOTHMER, 1970; MAJOWSKY *et al.,* 1970; NATARAJAN, 1978). Majority of them are multiples of 5. Such low chromosome numbers have not been found in any other sections of *Mentha,* so far cytologically studied (except, a few scattered reports in some of the species).

Phytochemical studies have shown that pulegone is the principal constituent in *M. pulegium* (MURRAY *et al.,* 1971) in addition to methone (CHOPRA *et al.,* 1964; ZWAVING & SMITH, 1971; FRAZÃO *et al.,* 1974; ALPMEN, 1975), cadenene, piperitenol, isopulegone and pulegone (CHOPRA *et al.,* -964), menthol (FRAZÃO *et al.,* 1974; ALPMEN, 1975), and limonene (ZWAVING & SMITH, 1971). Pulegone is the immediate precursor of menthofuran (FUJITA, 1960), which occurs widely in all other species of *Mentha*. The precursor of both pulegone and menthofuran, that is, linalool, also occurs profusely in all other species. Except in *M. pulegium,* the chromosome numbers in all other species of *Mentha* are multiples of either 8 or 9. It appears, therefore, that *M. pulegium* with its principal constituent pulegone and chromosome number of multiples of mostly 5 or 10 is rightly placed in a separate subgenus Eupulegia under the genus *Mentha*. The chromosome number noted for the species during the investigation carried out by the authors is $2n = 20$ (SINGH & SHARMA, unpublished 1980). A large number of cytotypes of *M. pulegium* is also on record. It is

of interest that reproduction of the species is practically vegetative which has also been selected for commercial propagation. Such large scale vegetative propagation has undoubtedly helped in the survival of the cytotypes in nature.

The species *Mentha aquatica,* on the other hand, studied in this laboratory (SINGH & SHARMA, unpublished, 1980), has 96 chromosomes in its somatic cells indicating a high polyploid constitution. Phytochemical studies have revealed a wide range of compounds — menthofuran being the principal constituent (MURRAY *et al.,* 1971). The others worth mentioning are apigenin, acacetin, luteolin and their glycosides (BURZANSKA-HERMANN *et al.,* 1977), caryophyllene, limonene, germacrene D, bicyclogermacrine, viridiflerol, menthone, menthol (MULINGRE & MAARSE, 1974), α- and β-pinenes, sabinene, myrcene, cineole, cis- and trans-ocimenes, γ-terpinene, linalool, sesquiterpene — KW, humulene (HEFENDEHL, 1967), ε-cadinene and isopino-camphone (SHIMIZU *et al.,* 1966).

A wide range of cytotypes, like *M. pulegium,* has been recorded in *M. arvensis* also, their chromosome numbers ranging from $2n = 24$ (OUWENEEL, 1968) to 132 (MORTON, 1956) with polyploids (NAGAO, 1941; OLSSON, 1967; OUWENEEL, 1968; TAYLOR & MULLIGAN, 1968; BELYAEVA & KOVINEVA, 1972) and aneuploids (WOLF, 1929; NAGAO, 1941; TAYLOR & MULLIGAN, 1968). *M. longifolia* as well has many cytotypes with chromosome number between $2n = 18$ (HEIMANS, 1938) to 84 (NAGAO, 1941). As compared to *M. pulegium,* in all other species studied by the authors (SINGH & SHARMA, unpublished, 1980), the chromosome numbers are, in general higher than those of the former. The lowest chromosome number in *M. pulegium* with pulegone as its principal constituent and comparatively higher chromosome number in other species having menthofuran (an oxidation product of pulegone) as the dominating phytochemical constituent indicates a correlation between cytological features and phytochemistry. Though it is premature to state precisely the chromosomes involved in causing this difference, without a correct estimation of the phytochemistry of each cytotype, the remarkable distinction of the

subgenus Pulegium from the rest (both in cytology and phytochemistry) is evident.

In the subfamily Ocimoideae, two genera — *Coleus* and *Ocimum* of subtribes Plectranthinae and Moschosminae respectively — have been subjected to phytochemical and cytological analysis. In *Coleus*, β-sitosterol-β-D-glucoside (MISRA *et al.*, 1976) is the principal constituent. The chromosome numbers, so far reported in two species of *Coleus* — *C. aromaticus* Benth. with 2n = 32 chromosomes (MORTON, 1962) and *C. blumei* Benth. having 2n = 24 (MORTON, 1962), 48 and 72 chromosomes (MORTON, 1962) — show mostly a multiple of 8 with numerous cytotypes in *C. blumei*. In view of a large number of chemical constituents in the species as well as the occurrence of several cytotypes, it would be necessary to have a correlated approach of the chromosome complements on one hand, and the phytochemical constituents on the other, of the individual cytotypes.

The genus *Ocimum* is one of the most important taxa in the family Labiatae from a phytochemical standpoint. The entire genus is extremely uniform and homogeneous with characteristic eugenol content (DUTT, 1939; RAKSHIT, 1939; PING-HSIEN YEH, 1960; MANITTO *et al.*, 1974; ROVESTI, 1975). Camphor is also one of the constituents in several species of the genus, such as, *O. basilicum* L. (SOBTI *et al.*, 1976); *O. canum* Sims. (PUSHPANGADAN *et al.*, 1975) and *O. kilimandscharicum* Guerke (CHOWDHRI & HAKSAR, 1964; MOOKHERJEA, 1973). Cinnamic acid (ALI & SHAMSUZZAMAN, 1968*a, b*; NIGAM & RAO, 1968), a precursor of eugenol (MANNITTO *et al.*, 1973; 1974) as well as camphene (NIGAM *et al.*, 1965; POGANY *et al.*, 1968), geraniol (NIGAM *et al.*, 1970; GUPTA *et al.*, 1971), ocimene (PING-HSIEN YEH, 1960; NIGAM & RAO, 1968; GUPTA *et al.*, 1971), eucalyptol (GUPTA *et al.*, 1971), thymol (TALALAJ, 1964; SOFOWARA, 1970; SOBTI *et al.*, 1977) and several other constituents of essential oil characterize this genus.

In all the species, wherever extensive investigations have been carried out, several cytotypes have been revealed, the predominant chromosome number being x = 8. For instance, the diploid chromosome number range in *O. basilicum* is 16

(Sz.-Borsos, 1970) to 48 (Mehra & Gill, 1972), in *O. canum* 24 (Pushpangadan *et al.*, 1975; Singh & Sharma, 1978) to 26 (Bhattacharya, 1978; Singh & Sharma, 1978), in *O. gratissimum* L. 40 (Singh & Sharma, 1981) to 64 (Golubinski, 1936), in *O. suave* Willd. 32 (de Wet, 1958; Morton, 1962), in *O. viride* Willd. 38 (Singh, 1978) to 64 (Sobti, personal contact), in *O. sanctum* L. 32 (Mehra & Gill, 1972; Singh & Sharma, 1978) to 64 (Golubinski, 1936), in *O. americanum* L. 72 (Singh & Sharma, 1981; Pushpangadan *et al.*, 1975) to 84 (Singh & Sharma, 1981) and in *O. kilimandcharicum,* it is 76 (Kumar *et al.*, 1957; Singh, 1978). In the investigation carried out by the authors, several populations of *Ocimum* species have been studied, showing the chromosome numbers as 2n = 24 and 26 in *O. canum* (Singh & Sharma, 1981), 2n = 72 (Singh & Sharma, 1981) and 84 in *O. americanum* (Singh & Sharma, 1981), 2n=40 in *O. gratissima*, 2n = 38 in *O. viride* (Singh, 1978), 2n = 32, 34 and 36 (Singh & Sharma, 1981) in *O. sactum,* 2n = 48 in *O. carnosum* Link et Otto. (Singh, 1978) and 2n = 76 in *O. kilimandscharicum.*

The species *O. americanum,* with 2n = 72 chromosomes, has been assumed by Pushpangadan *et al.* (1975) to be derived from two different parents — *O. canum* (2n = 24 chromosomes) and *O. basilicum* (2n = 48 chromosomes) containing citral (Dwivedi *et al.*, 1963) and methyl chavicol (Nigam *et al.*, 1970; Manitto *et al.*, 1974; Nigam and Rao, 1968), respectively. Pushpangadan *et al.* (1975) reported the presence of both the components in *O. americanum.*

The nature of nucleolar chromosomes in two chemotypes of *O. americanum* (chemotypes 'methyl chavicol' having 6 or two types and 'citral' with 8 such chromosomes of three types) is different (Singh & Sharma, 1981). It is likely that such structural changes in the nature of these chromosomes might have involved the genes for methyl chavicol and citral.

Pushpangadan *et al.* (1975) recorded that in *O. canum,* camphor is found in 2n = 26-chromosomed type, whereas in 2n = 24-chromosomed type, the principal constituent is linalool. During the present work, a sample of seeds with

reported content of linalool (PUSHPANGADAN *et al.,* 1975) has also showed 26 chromosomes in somatic cells. It is likely that both the components (linalool and camphor) are present in the type with 2n = 26 chromosomes. This fact is supported by SOBTI *et al.* (1978). It indicates that the additional chromosomes in this chemotype (2n = 26) are responsible for bringing about certain desirable phytochemical qualities. *O. americanum,* on the basis of phytochemical constituents and chromosome numbers, has been treated as species distinct from *O. canum* (SINGH & SHARMA, 1981). The two species are sympatric in distribution.

The species *O. gratissimum* and *O. viride* of the subgenus Gratissima, show certain interesting features during the authors' investigation. The former species (where two populations have been studied, both showing 2n = 40 chromosomes) contains β-sitosterol (ALI & SHAMSUZZAMAN, 1868*a b*), while the latter (having 2n = 38 chromosomes only) is not reported to contain this chemical constituent at all. The presence of the parent intermediate compounds, such as, geraniol, geranyl acetate (SOBTI *et al.,* 1978), farnesene (NIGAM *et al.,* 1970), squalene (NICHOLAS, 1962), and β-sitosterol, of sterol-biosynthesis in several species of *Ocimum* suggests that sterol-biosynthesis does exist in the genus, which probably *O. viride* lacks. This deficiency of a particular compound indicates its correlated connection with the lack of a pair of small chromosomes in the latter species (SINGH & SHARMA, 1981), *O. viride,* studied here, is deficient in containing a pair of chromosomes with very short arms. The other terpenoids, such as, thymol, are common in both the species (TALALAJ, 1964; SOFOWORA, 1970). However, it is to be recorded that SOBTI (personal communication) has found 2n = 40 chromosomes in *O. viride.* It would be worthwhile to find out the chemical constituent in that population, which may provide a definite evidence of the correlation as suggested.

The species *O. kilimandscharicum,* having considerable commercial importance due to its camphor content, has not been included in any of the sections of the genus in BRIQUET'S (1897) system. This species has an unusual number of

$2n = 76$ chromosomes (SINGH & SHARMA, 1981). The phytochemical constituents found in the species are camphene, mycene, β-phellandrene, terpinene, ρ-cymene, borneol, selinene (NIGAM *et al.*, 1955), β-sitosterol, oleanolic acid and ursolic acid (MOOKHERJEA, 1973) with very high camphor content (MOOKHERJEA, 1973). The meiotic analysis also shows the evidence of duplication of chromosomes with high multivalent formation (SINGH & SHARMA, 1981). However, the segregation is quite regular as seed formation is profuse and no other aneuploids have been found in this species. In any case, populations from Calcutta (altitude 7 metres), of temperate as well as from Gureghar (altitude 1392 metres) of subtemperate areas, show the same chromosome number (SINGH & SHARMA, 1981). The extent to which this unusual chromosome number, noted in this species, is correlated with its high camphor content, indicates the need for a through analysis of other populations as well. It is remarkable here that only the 26-chromosomed *O. canum* and this species (both having additional chromosomes in their genetic complements — 2 in the former and 4 in the latter) have camphor as their constituent.

The basic number for the genus has been suggested as $x = 8$ chromosomes (VAARAMA, 1947; DARLINGTON & WYLIE, 1955). However, for the Basilicum group (including sections Ocimodon and Gymnocimum of BRIQUET) of the genus, $x = 12$ has been considered as the base number by MORTON (1962) and others. In BRIQUET's (1897) system of classification, *O. gratissima, O. suave* and *O. viride* (all belonging to the same group Gratissima) have been isolated from *O. sanctum* to be included with *O. basilicum* and *O. canum* under the section Ocimodon.

In the first three species, the basic chromosome number appears to be eight. Added to this, the characteristic chemical constituent eugenol is same in all these four species. Hence, the separation of these three species from the *Ocimodon* and their incorporation in *Hierocimum* parallel to *O. sanctum* is suggested. The status of *O. selloi* and *O. nudicaule,* whose chromosome number is not known and phytochemical study also is insufficient, can not be ques-

tioned. The base number for the rest of species *(O. americanum, O. basilicum, O. canum, O. kilimandicharicum)*. may be suggested as 12, which might have arisen from $x = 8$ chromosomes. The occurrence of $2n = 84$ chromosomes in one population of *O. americanum* is an added evidence in favour of 12 as the base number in this species. In view of the presence of the extensive number of cytotypes present in most of the species, it is difficult to indicate precisely a particular chromosome number to be the basic one. However, on the basis of secondary association of bivalents during meiosis, an initial base number of $x = 4$ chromosomes has been suggested by the present authors in *O. sanctum* (SINGH & SHARMA, 1981) and BHATTACHARYA (1978) in *O. canum* with $2n = 26$ chromosomes (a material identified as *O. americanum*).

CONCLUSIONS

The following conclusions may be arrived at on the basis of the analysis of available data on cytology and phytochemistry:

The separation of the genus *Rosmarinus* from Ajugoideae and elevating it to a separate family Rosmarinoideae, as done by MELCHIOR, is supported.

The species of *Scutellaria* of the subfamily Scutellarioideae are homogeneous in their contents of different compounds, such as baicalin, scutellarin and derivatives. Their homogeneity is also reflected in their cytology, though a clear cut correlation between the two is yet to be worked out. In *Lavandula,* the uniformity in chemical content may be associated with homogeneity in chromosome number. All the species are characterized by their camphor content. A common basic chromosome number for the genus has been suggested.

The genus *Marrubium* of Stachydoideae is uniform in its chemical constituents, whereas in *Sideritis* the species differ markedly. The differences in their chromosome numbers are also quite marked. In the tribe *Nepetae,* the genera *Nepeta* and *Glechoma* are allied in both the phyto-

chemistry and chromosome number. In Laminae, each genus has distinct phytochemical characteristics, associated with distinct chromosome numbers. In *Salvia* (tribe Salvieae), intraspecific variations are quite common. The species are characterized by having terpenoids, flavonoids and their derivatives. A clear correlation between phytochemistry and cytology could not be established and $x = 8$ appears to be the basic chromosome number for the genus. The genus *Hyssopus* is quite uniform in its cytology and phytochemistry, with $x = 6$ chromosomes representing the basic number. The presence of the same basic chromosome number, that is, $x = 15$ and the common occurrence of some terpenoids and a sapogenin in both *Origanum* and *Thymus,* strongly suggest their homogeneity and justify their inclusion under the same subtribe Thyminae.

In the genus *Mentha* (Stachydoideae), a clear correlation has been shown between the two different basic chromosome numbers, that is, $x = 5$ and 6 and their chemical contents. The species, with $x = 5$ as the base number, have a different dominating chemical content (pulegone), in contrast to species showing $x = 6$ chromosomes and having mentho furan as the principal constituent. The position of different species of *Mentha* under different subgenera of the genus in BRIQUET's system is supported on the basis of their cytology and phytochemistry.

Ocimum, of the subfamily Ocimoideae, besides having a correlation between different cytotypes and phytochemistry, shows a relationship between the number and structure of nucleolar chromosomes. The chemical contents of the cytotypes show a general homogeneity as well.

It has been suggested that changes in the number and structure of nucleolar chromosomes may simultaneously involve genes for different chemical constituents, as in *O. americanum.* The two chemotypes of this species contain methyl chavicol and citral separately. Its origin from a cross between *O. basilicum* and *O. canum* has been endorsed on the basis of their phytochemistry and cytology.

On the same grounds, *O. canum* has been considered as a species distinct from *O. americanum.* The separation

of *O. gratissimum, O. suave* and *O. viride* from the section
Ocimodon and their incorporation in Heirocimum of the
genus *Ocimum* parallel to *O. sanctum* has been suggested.

Though, x= 8 and 12 have be considered as the basic
chromosome numbers, on the basis of secondary association
of the bivalents met with in some of the species, a lower
base number of 4 has been suggested for the genus as
a whole.

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REGULATION
OF CELL DIVISION IN MERISTEMS
I. MITOSIS

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SUMMARY

The dependence relationship between macromolecular synthesis before and during mitosis and some of the mitotic morphogenetic processes have been analyzed in *Allium cepa* L. meristems.

Initiation of mitosis depends on protein(s) synthesized in early G_2 while is independent of any G_2-synthesized RNA.

This G_2 protein diffuses from advanced nuclei throughout cytoplasm and anticipates mitotic entrance in lagging nuclei sharing a common cytoplasm. Apparently this protein has to do with the mitotic synchronization observed by metaphase in plurinucleate cells.

Progression of the chromosome condensation cycle in prophase depends on protein synthesized in early prophase, while the breaking down of nuclear envelope (which marks the end of the prophase) depends on RNA synthesized in mid-prophase.

In anaphase, centromere migration, but not division, depends on a simultaneous high energy supply. Finally, chromosome decondensation in telophase accelerates when simultaneous protein synthesis is interrupted. Simultaneously with this acceleration, there is advancement of nucleologenesis, a morphogenetic process which takes place in telophase and whose completion depends on a short period of RNA synthesis at the very start of nuclear transcription in telophase. This newly synthesized RNA acts as a trigger of the nucleologenesis assembly process.

Lastly, the reinitiation of a new cell cycle seems to depend on proteins synthesized during telophase, stressing the close integration between cellular functioning in interphase and mitosis.

V IRCHOW's aforism «omnis cellula e cellula» was but a scientific prediction in 1855, since cell division was still unknown. BALBIANI (1876) described how nuclei became transformed in a number of «bâtonnets étroits» which first coalesced and afterwards divided in two groups. Improvement of fixing and staining conditions as well as the development of immersion objectives increased the accuracy of the cellular observations.

In 1879, FLEMMING, SCHLEICHER & STRASBURGER, independently, described the process of nuclear division after their observation on living material. The two former scientists observed embryonic cells of salamander, STRASBURGER those of *Tradescantia* staminal hairs. The described nuclear division was called mitosis by FLEMMING and karyocinesis by SCHLEICHER.

The similarity in the process for both plant and animal cells proved to extend to its biological basis as well as to the compartmentation in phases, to their sequence and, probably, to the regulatory mechanisms which control cellular proliferation as well.

The present work will cover the regulatory points operating on nuclear division control, i. e. the mechanisms implicated in the precise distribution of the hereditary material. It is mainly intended to be a revision of a portion of the experiments carried out in root meristems by our group in Madrid.

1. Premitotic requirements

The nucleus is that portion of the cell which possesses the hereditary information of the organism. Hence, the importance of its unaltered permanence and its duplication. The doubling of the nucleus is the cellular way of preparing its equivalent partition into the two descendant nuclei. Doubling and division are the two main stages of the cell division cycle (Fig. 1), this cell cycle being the basic process which provides the whole organism with all its structural and physiological units. Doubling of cellular material takes place in interphase, the duplication of genome being confined

to S period, while both nuclear and cytoplasm division occurs later on.

The cell cycle is a gene programmed event in the cellular life, as gene analysis in lower eukaryotes have brightly shown (HARTWELL, 1971; HOWELL, 1974; FRANKEL & DE BAULT, 1976). Hence, gene information is sequentially expressed throughout the cell cycle allowing its progression. For this, we may consider that cells in a proliferative tissue are indeed differentiated to proliferate.

There may be controls operating in the initiation of replication, in the initiation of division, in its termination probably. The study of the sequential triggers operating in cycle progression is a main stream in the area of cell proliferation since its knowledge is the perequisite for handling it.

In relation to the initiation of nuclear division it could be thought that the mere termination of replication might be the trigger. However endoreduplication (D'AMATO, 1964; NUTI-RONCHI, AVANZI & D'AMATO, 1965; TSCHERMAK-WOESS, 1971 & NAGL, 1974) and polytenia (AVANZI, BRUNORI & D'AMATO, 1969; BRADY & CLUTTER, 1974) are two processes which positively prove that this is not the case. The existence of 4C cells in temporarily quiescent meristems (SANS & DE LA TORRE, 1979) as well as the fact that when deprived from aminoacids they stop in G_2 (VAN't HOF, HOPPIN & YAGI, 1973) reinforce these facts.

In 1974 GONZALEZ-FERNANDEZ, GIMENEZ-MARTIN, FER-NANDEZ-GOMEZ & DE LA TORRE studied the protein requirements in the premitotic period, G_2. For this, they used a synchronous cell population labelled as binucleate in the meristem. Fig. 2 shows how binucleate cells are formed by a short treatment with caffeine, which labels those spontaneously synchronous cells traversing telophase. The binucleate cells formed by the caffeine treatment immediately initiates their interphase. This binucleate cell population is easily distinguished from the mononucleate cells which form the meristem. They can be followed throughout their cycle and the duration of the different cell compartments directly measured. The timing of the different cycle com-

partments under control conditions were previously known (LOPEZ-SAEZ, GIMENEZ-MARTIN & GONZALEZ-FERNANDEZ, 1966; GONZALEZ-FERNANDEZ, GIMENEZ-MARTIN & DE LA TORRE, 1971a). In order to test whether any protein synthesized in G_2 was involved in the entrance onto mitosis the experimental scheme used is shown in Fig. 3. Sequential treatments with a protein synthesis inhibitor (anisomycin) proved to affect entrance into mitosis in a differential way. Only those treatments covering the 19-20th. interval of the interphase prevented cells from entering into prophase. Accordingly, the last protein required for nuclear division to take place was synthesized in the early G_2.

This regulatory step located in G_2 was further analyzed by using a different cell system: homokaryotic plurinucleate cells formed by caffeine inhibition of two sequential cytokineses (Fig. 4).

Fig. 5 shows such a 2n-2n-2n-2n-2n plurinucleate cell, whose two central nuclei often fuse in a tetraploid nucleus (Fig. 6), so that a 2n-4n-2n cell is formed. Less frequently fusion takes places between terminal nuclei and its corresponding adjacent nucleus so that a 4n-4n binucleate cell is formed. Though plurinucleate cells initiates prophase asynchronously, there is a strict synchrony in metaphase (Fig. 7) and anaphase (Fig. 8).

The development of the cell cycle in the nuclei of these cells was followed so that nucleus-cytoplasm relationships were made evident (Fig. 9). There was a clear asynchrony in the development of replication in the different nuclei which shared the common cytoplasm. This asynchrony,

Fig. 1. — Diagrammatic representation of cell cycle. It starts when cell in interphase is ready to divide. Leftwards, prophase, metaphase, ana- and telophase follow, with the result of formation of two cells which qualitatively are identical to the premitotic cell, while quantitatively have half its content.
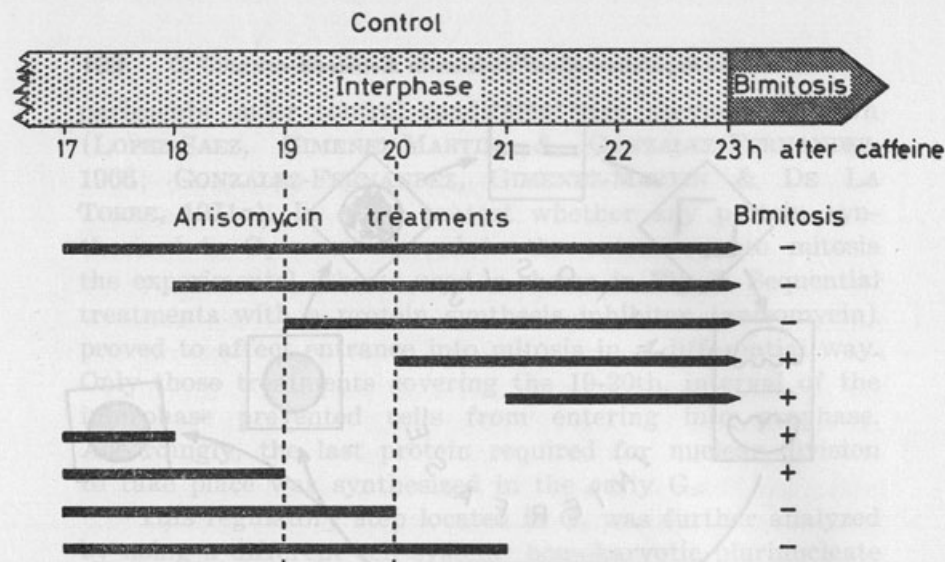
Fig. 2. — When cells progressing through their telophase are treated with caffeine, they are unable to form the cytokinetic plate, so that a binucleate cells is formed. This binucleate cell starts its new cycle immediately after its formation.
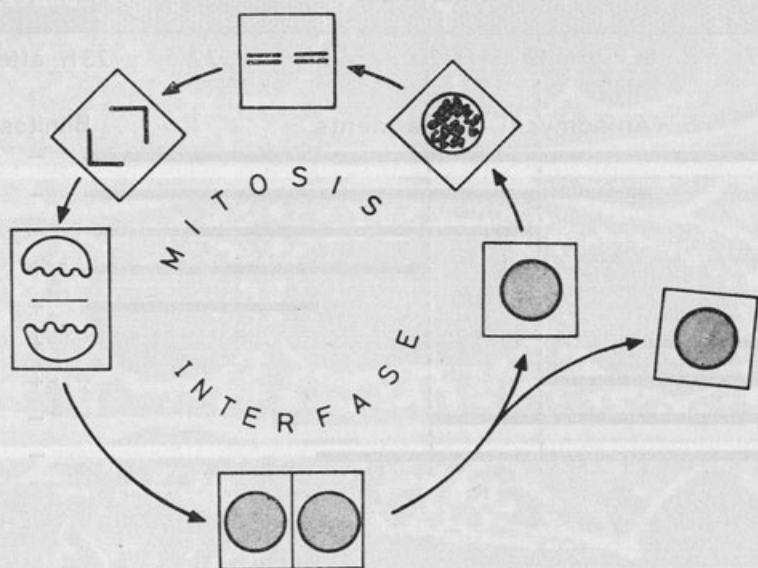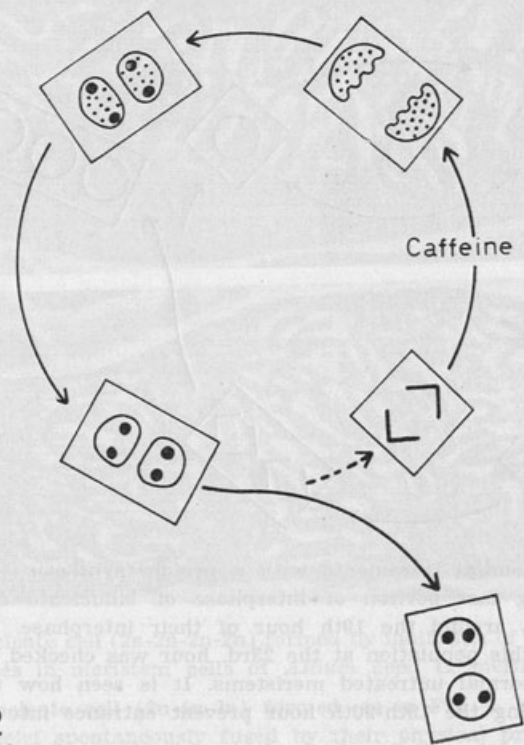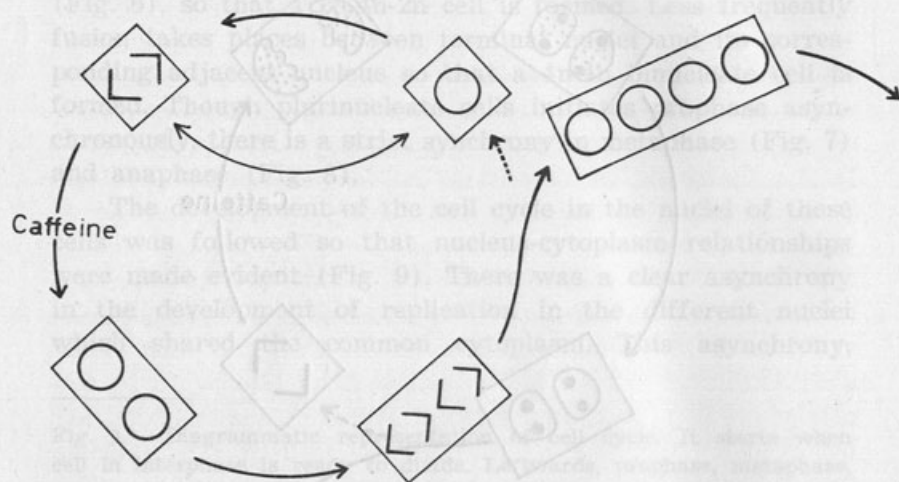
Caffeine

1

2

Fig. 3. — Sequential treatments with a protein synthesis inhibitor (aniso-mycin) during last portion of interphase of binucleate cells. These cells start their G₂ around the 19th hour of their interphase. The presence of prophases in this population at the 23rd. hour was checked, when they were observed in normal untreated meristems. It is seen how those treatments covering the 19th-20th hour prevent entrance into mitosis.

Fig. 4. — Formation of 8n plurinucleate cells by a double treatment with caffeine, so that during the first one telophases give rise to binucleate cells. These binucleate cells when in their next telophase (bitelophase) if treated again by a second caffeine-treatment produce the tetranucleate cells which immediately start their next interphase.
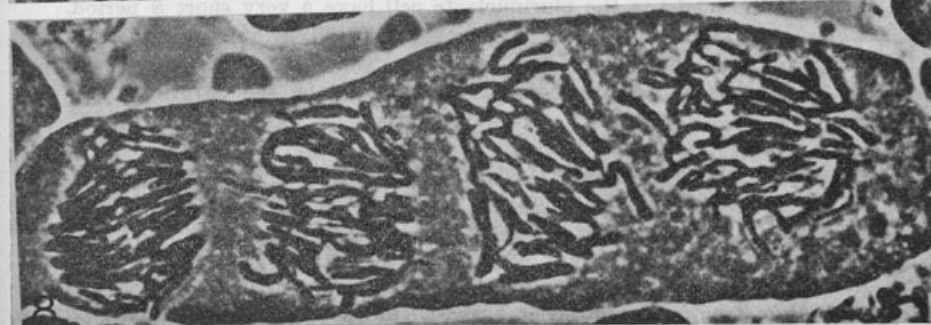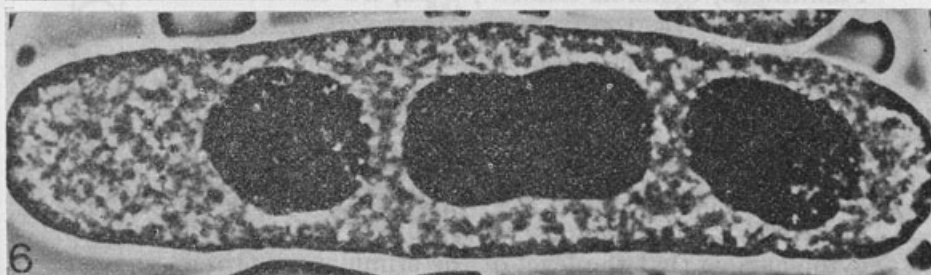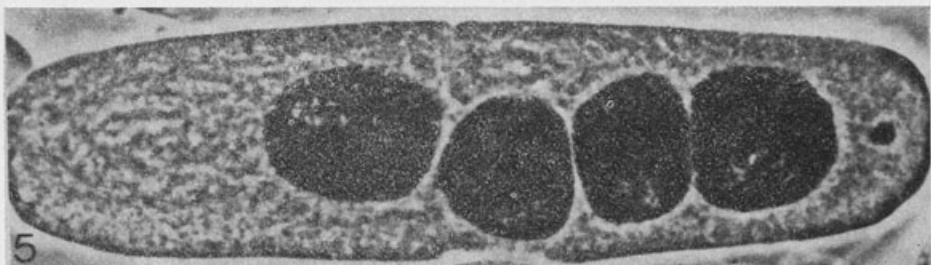
Fig. 5.—Plurinucleate cell (2n-2n-2n-2n) formed by inhibition of two sequential telophases in meristem cells of *Allium cepa* L. meristems.

Fig. 6. — Plurinucleate cell (2n-4n-2n) formed, as in Fig. 5, but whose two central nuclei spontaneously fused by their physical proximity.

Fig. 7. — Plurinucleate cell whose 4 nuclei are synchronously traversing metaphase. Synchrony from metaphase onwards is the rule in these plurinucleate cells, though they enter prophase asynchronously.

Fig. 8. — Synchronous plurinucleate cell in anaphase.

measured as different length of the replication period (S period) was partially compensated by the shortening and lengthening of the respective G_2 and prophase, so that all nuclei were again synchronous by metaphase (GONZALEZ-FERNANDEZ, GIMENEZ-MARTIN, DIEZ, DE LA TORRE & LOPEZ-SAEZ, 1971*b*; DE LA TORRE & GIMENEZ-MARTIN, 1977).

It was theoretically suggested a role of that protein synthesized in G_2 in the synchronization of homokaryotic nuclei sharing a common cytoplasm. Nuclei having first ended the S period reached first the G_2 control point and, accordingly, they started the synthesis of that regulatory protein(s). The protein synthesized diffused throughout cytoplasm so that the level of the stimulatory protein enough to trigger mitosis in the advanced nucleus was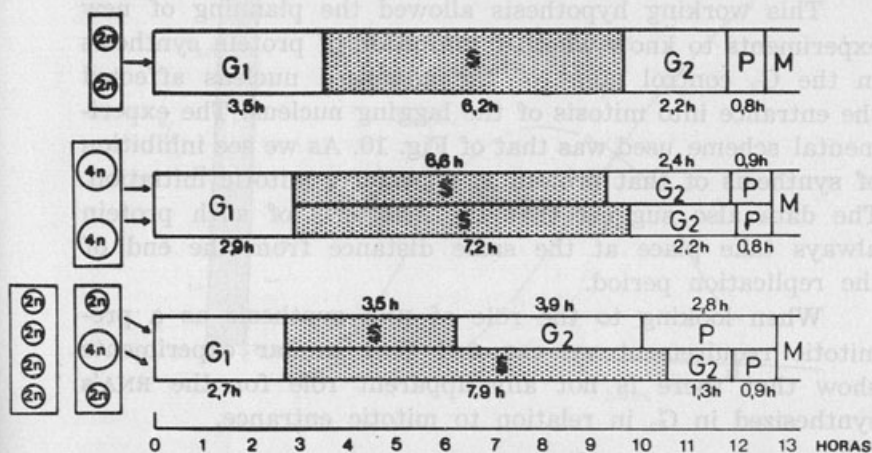 reached later than in a mononucleate cell. On the other hand, the lagging nucleus got a similar cytoplasm level of the mitotic stimulus, even early than its entering into G_2. For this reason, the lagging nucleus will have a shorter G_2.

Fig. 9. — Relative duration of the different cycle comportments in 2n-2n and 4n-4n binucleate cells (upper and mid bars respectively) as well as in 8n plurinucleate cells (lower bar). We can see how the nuclei of the plurinucleate cells replicate their DNA in times which essentially differs from those of the 2n-2n binucleate cells. Some of the nuclei in the plurinucleate cell have a very short S period, while other show longer S. However all nuclei in the plurinucleate cell reach metaphase in a total synchrony. The synchronization process involves a compensation of the S period by the duration of G_2 + prophase.

Fig. 10. — Analysis of the effect of protein synthesis inhibition on G_2 of plurinucleate cells. Anisomycin was used as a protein synthesis inhibitor in *Allium cepa* L. meristems. All the sequential treatment covering from the 6th. hour up to the 12th. hour of interphase were accomplished. For the sake of simplicity, we have only represented those two treatments covering early G_2 in fastly replicated nuclei as well as in their late G_2. Only when these plurinucleate cells are treated on early G_2 of fast nucleus there is a lengthening of G_2 both in «fast» and «slow» nuclei. Moreover, both nuclei start prophase synchronously. This advancement in reaching cellular synchronization points out the possible involvement of the G_2-protein in this process.

Figure showing cell cycle phases with boxes labeled 2n and 4n:

Top row (2n): G₁ (3,5h), S (6,2h), G₂ (2,2h), P, M (0,8h)

Middle rows (4n): S (6,6h), G₂ (2,4h), P, M (0,9h); G₁ (2,9h), S (7,2h), G₂ (2,2h), P, M (0,8h)

Bottom rows (2n/4n): G₁, S (3,5h), G₂ (3,9h), P (2,8h), M; G₁ (2,7h), S (7,9h), G₂ (1,3h), P (0,9h), M

Time axis: 0 1 2 3 4 5 6 7 8 9 10 11 12 13 HORAS

9

2. Requirements in prophase

Nuclei that are ready and stimulated in G₂ start their prophase. Morphologically, prophase is easily recognizable by the increase in chromatin condensation which leads to a gradual discrimination of individual chromosomes as well as the nucleolar desorganization. Prophase ends when nuclear envelope breaks down.

sincronia

Figure with rows labeled:

Plur. control: G₁, S, G₂, P, M (with S and G₂, P below)

Anisomic.: G₁, S (black block), P, M

Time axis: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 Horas

10

This working hypothesis allowed the planning of new experiments to know whether inhibition of protein synthesis in the G_2 control point of the advanced nucleus affected the entrance into mitosis of the lagging nucleus. The experimental scheme used was that of Fig. 10. As we see inhibition of synthesis of that protein in G_2 affects mitotic initiation. The data also suggest that the synthesis of such protein always take place at the same distance from the end of the replication period.
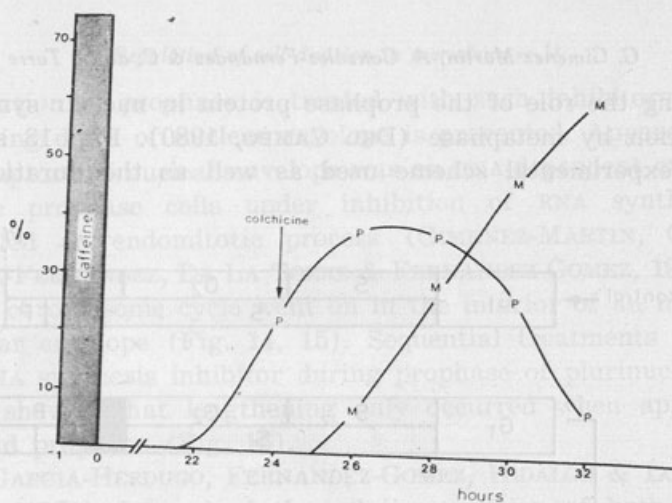
When looking to the role of RNA synthesis as a premitotic requirement we can tell that similar experiments show that there is not any apparent role for the RNA's synthesized in G_2 in relation to mitotic entrance.
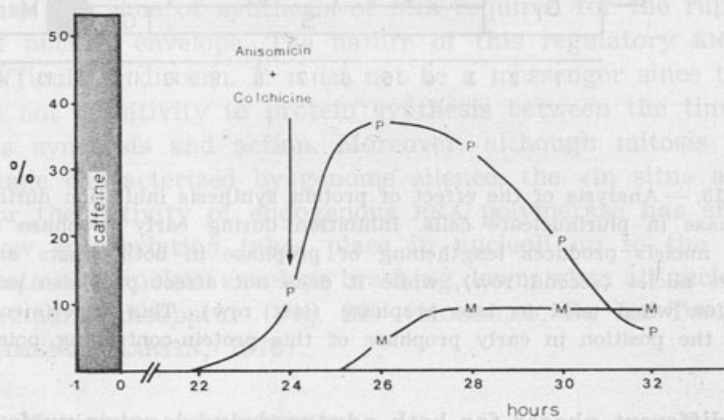
2. Requirements in prophase

Nuclei that are ready and stimulated in G_2 start their prophase. Morphologically, prophase is easily recognizable by the increase in chromatin condensation which leads to a gradual discrimination of individual chromosomes as well as for the nucleolar desorganization. Prophase ends when nuclear envelope breaks down.

It was systematically accepted that a cell which had started prophase was inevitably commited to complete it. However, this is not the case. In 1974 GARCIA-HERDUGO, FERNANDEZ-GOMEZ, HIDALGO & LOPEZ-SAEZ (1974) wanted to know whether there were some controls regulating the development of prophase. For this, they took the synchronous cell population labelled as binucleate and they studied the kinetics of its mitotic development (bimitosis) (Fig. 11). When protein synthesis was inhibited in such population around mitotic entrance, the kinetics of entering into prophase was unaltered (Fig. 12). However, metaphases hardly appeared. This was interpreted as a revision of the prophase back to interphase. The experiments showed that some protein(s) synthesized in prophase regulates the normal progression of prophase itself towards metaphase.

In 1979 and 1980, similar experiments are being carried out in homokaryotic plurinucleate cells as a way of deter-

70

50

%

30

10

caffeine

colchicine

-1   0   22   24   26   28   30   32

hours

11

50

% 40

30

20

10

caffeine

Anisomicin
+
Colchicine

-1   0   22   24   26   28   30   32

hours

12

Fig. 11. — Analysis of mitotic entrance into mitosis in binucleate cells.
Colchicine is given from the 24th. hour onwards. A vawe of prophases
is recorded, followed by an accumulation line for metaphases
(colchicine effect).

Fig. 12. — Analysis of mitotic entrance into mitosis in the binucleate
cells when protein synthesis is inhibited by anisomycin from the 24th.
hour onwards, when colchicine is also used. The wave of prophases
is similar to that in control conditions (Fig. 11). However metaphases
do not accumulate, suggesting reversion of prophase under the protein
synthesis inhibition in prophase.

mining the role of the prophase protein in nuclear synchro-
nization by metaphase (DEL CAMPO, 1980). Fig. 13 shows
the experimental scheme used as well as the duration of
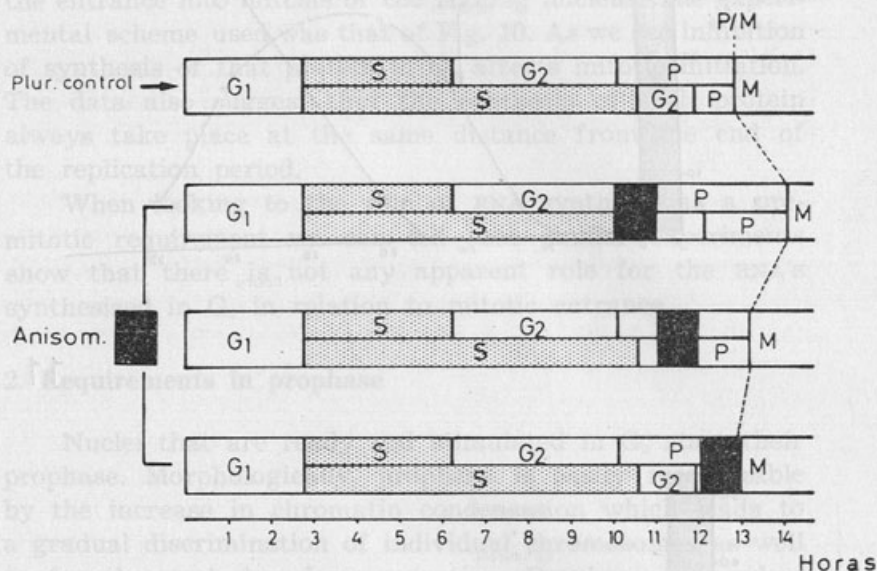
13

Fig. 13. — Analysis of the effect of protein synthesis inhibition during
prophase in plurinucleate cells. Inhibition during early prophase of
«fast nuclei» produces lengthening of prophase in both «fast» and
«slow» nuclei (second row), while it does not affect prophase pro-
gression when used in late prophase (last row). This experiments
show the position in early prophase of this protein-controlling point.

the different phases for both advanced and lagging nucleus
in these cells.

The results show that inhibition of protein synthesis
in the start of the prophase in the advanced nuclei lengthens
prophase both in advanced and lagging nuclei, while if
applied farther into prophase does not alter both kinetics.

In relation to the role of RNA synthesis in prophase,
GONZALEZ-FERNANDEZ, FERNANDEZ-GOMEZ, STOCKERT & LOPEZ-
SAEZ, 1970a; GONZALEZ-FERNANDEZ, GIMENEZ-MARTIN &
LOPEZ-SAEZ, 1970b had already shown that when a cell

population in prophase is treated with such inhibitors the breaking down of nuclear envelope is prevented. Apparently the rupture of nuclear envelope was an RNA-dependent event. Those prophase cells under inhibition of RNA synthesis initiated an endomitotic process (GIMENEZ-MARTIN, GON-ZALEZ-FERNANDEZ, DE LA TORRE & FERNANDEZ-GOMEZ, 1971), since chromosome cycle went on in the interior of an intact nuclear envelope (Fig. 14, 15). Sequential treatments with an RNA synthesis inhibitor during prophase of plurinucleate cells showed that lengthening only occurred when applied in mid prophase (Fig. 16).

GARCIA-HERDUGO, FERNANDEZ-GOMEZ, HIDALGO & LOPEZ-SAEZ (1974) determined the relative position of both RNA and protein synthesis into prophase, by modifying the time of initiation of the inhibitory treatment. The results (Figs. 17, 18) showed that the prophase zone where synthesis of regulatory proteins took place was located earlier than the zone of synthesis of RNA required for the rupture of nuclear envelope. The nature of this regulatory RNA is difficult to discern. It must not be a messenger since there is not sensitivity to protein synthesis between the time of its synthesis and action. Moreover, although mitosis is a stage characterized by genome silence, the «in situ» assay for the activity of endogenous RNA polymerase has shown how transcription takes place in nucleoli up to the very instant of nuclear envelope breaking down, when all nucleolar remnants disappear (Fig. 21) (MORCILLO, DE LA TORRE & GIMENEZ-MARTIN, 1976).

3. Metaphase requirements

After nuclear envelope breaks down metaphase starts. Chromosomes migrate towards the cell equator; very longitudinal half chromosome ends its dehelicoidization while remaining united by the centromere.

The breaking down of nuclear envelope allows the direct contact between nuclear and cytoplasmic components and, as a result, there is an almost instantaneous connexion between centromeres and centrioles, or the atraction poles
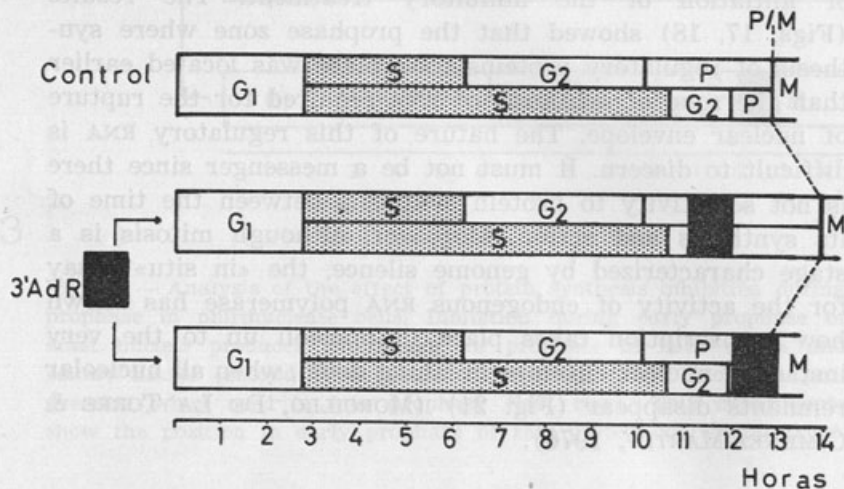
14

Endomitosis

Duplicacion

15

16
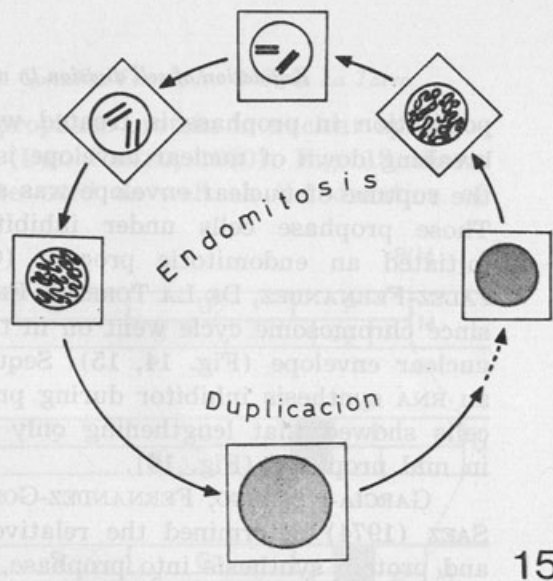
Fig. 14. — Binucleate cell which has been treated with an RNA-synthesis inhibitor (3'-deoxyadenosine) during prophase. Breaking down of nuclear envelope does not take place (as confirmed by electron microscopy). On the other hand, chromosome condensation goes on, so that highly condensed chromosomes are seen in the interior of the nuclei. The process resembles initiation of endomitosis.

Fig. 15. — Schematic representation of endomitosis, process which spontaneously occurs in some plant tissues. A cell ready to divide reaches prophase. Nuclear envelope rupture does not occur and divided chromatids stay and decondense. This nucleus which possesses 4n chromosomes (tetraploid) initiates a new cycle.

Fig. 16. — Effect of an RNA synthesis inhibitor (3'-deoxyadenosine) when applied in the prophase of 8n plurinucleate cells. Inhibition at mid prophase but not on other times lengthens prophase in both «fast» and «slow» nuclei.
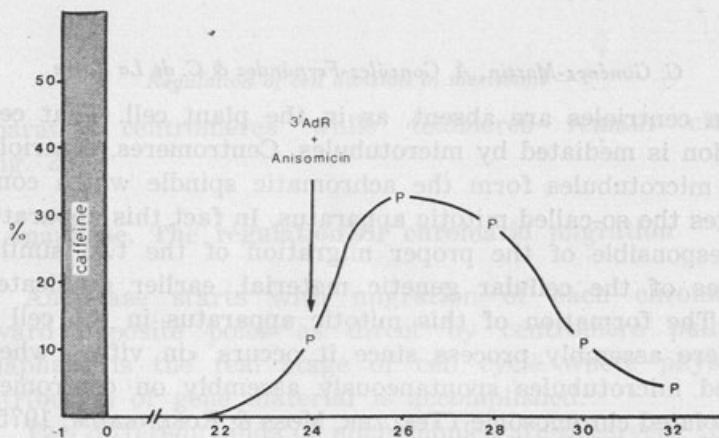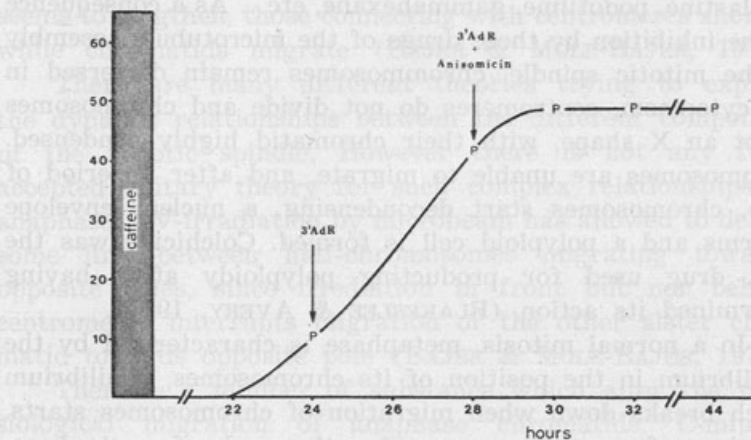
Fig. 17. — Analysis of prophase wave in the binucleate cell population, when both RNA and protein synthesis are simultaneously blocked from the 24th. hour of interphase onwards. The wave resembles that obtained when inhibiting protein synthesis alone (Fig. 12). This suggests that the prophase protein synthesis step is located earlier in prophase than the RNA-synthesis step.

Fig. 18. — Analysis of the prophase wave in the binucleate cell population. The experimental scheme involves the inhibition of RNA synthesis (by 3'AdR) from the 24th. hour onwards, and simultaneous inhibition of RNA and protein syntheses from the 28th. hour of interphase. The curve shows how the cells are permanently blocked in prophase, confirming the sequence of protein and RNA synthesis control points in prophase.

when centrioles are absent, as in the plant cell. That cennection is mediated by microtubules. Centromeres, centrioles and microtubules form the achromatic spindle which constitutes the so-called mitotic apparatus. In fact this apparatus is responsible of the proper migration of the two similar halves of the cellular genetic material, earlier duplicated.

The formation of this mitotic apparatus in the cell is a mere assembly process since it occurs «in vitro» where added microtubules spontaneously assembly on centromere of isolated chromosome (TEELZER, MOSS & ROSENBAUM, 1975).

Drugs which block polymerization of the microtubule monomeres stop «in vivo» the formation of the mitotic apparatus. They are called c-mitotic drugs and mitotic poisons. The most well-known of these drugs are colchicine, vinblastine, podofiline, gammahexane, etc... As a consequence of the inhibition by these drugs of the microtubule assembly in the mitotic spindle, chrommosomes remain dispersed in the cytoplasm, centromeres do not divide and chromosomes adopt an X shape, with their chromatid highly condensed. Chromosomes are unable to migrate, and after a period of time, chromosomes start decondensing, a nuclear envelope reforms and a polyploid cell is formed. Colchicine was the first drug used for producting polyploidy after having determined its action (BLAKESLEE & AVERY, 1937).

In a normal mitosis, metaphase is characterized by the equilibrium in the position of its chromosomes, equilibrium which breaks down when migration of chromosomes starts. Division of centromeres marks the end of metaphase. However between the division of centromeres and the migration of chromatids it is possible to distinguish another conditioning factor, the simultaneous availability of energy. Hence, under deprived cellular O_2-concentration (8-oxiquinoline-treatment, TJIO & LEVAN, 1951; hypoxia, GIMENEZ-MARTIN & LOPEZ-SAEZ, 1962) this chromosomal migration towards cellular poles either does not take place, or takes place very slowly (Fig. 19, 20). The situation was reversed at once when O_2 was supplied (GIMENEZ-MARTIN & LOPEZ-SAEZ, 1962). Metaphase chromosomes under hypoxia show

separated centromeres while telomeres remain closed (Fig. 20).

4. **Anaphase. The regulation of chromatid migration**

Anaphase starts with migration of each chromatid toward opposite poles as direct by centromere pulling. Anaphase is the real stage of cell cycle where physical distribution of gene material is accomplished.

Two different kinds of microtubules are observed: those continuous microtubules (MTs) i. e., giving from pole to pole, and on the other hand, those microtubules which go from each centromere to its opponent pole. They follow different kinetics in anaphase for as those continuous MTs seems to lengthen, those connecting with centromeres shorten while chromatids migrate (BAJER & MOLE-BAJER, 1972).

There are many different theories trying to explain the dynamic relationships between the different component of the mitotic spindle. However there is not any fully accepted unitary theory for such complex relationships in anaphase. UV-irradiation by microbeam has allowed to detect some link between half-chromosomes migrating towards opposite poles, since irrediation in front but nor behind centromeres interrupts migration of the other sister chromatid towards opposite pole (BAJER & MOLE-BAJER, 1979).

There is a number of substance which alter the physiological migration of anaphase chromatids. C-mitotic substances modify the number of atraction poles. MAZIA, HARRIS & BIBRING, 1960; GIMENEZ-MARTIN & LOPEZ-SAEZ, 1960; HERVAS, FERNANDEZ-GOMEZ & GIMENEZ-MARTIN, 1974) was able to induce the formation of 3 or 4 chromosomes poles and, as a consequence of observing qualitative and quantitative unbalanced gene distribution.

5. **Telophase**

The arrival to poles of both groups of quali- and quantitative similar chromatids originates two nuclei qualitatively identical to that which initiated mitosis, but quantitatively

with only half its content. This process allows the physiological activity of nucleus to be resumed, both in relation to its structural and functional reorganization. However, when multipolar cells are formed by unequal distribution of chromosomal material, nuclei are unbalanced in the sense that they are genetically different to the initial, this difference producing changes in their activity.

The first sympton of telophase is the nucleus/cytoplasm compartmentation, for a nuclear envelope is reformed around of each chromosomal group. This reformation occurs idependently of the chromosome content and of the functions which those chromosomes are able to assume. Under the electron microscope it is seen how telomeres present remnants of old nuclear envelope, which probably act as the assembly nucleus of endoplasmic reticulum to constitute the new nuclear envelope.

In telophase, chromosomes start decondensing. This process of chromosome decondensation is accelerated by simultaneous inhibition of protein synthesis (MORCILLO & DE LA TORRE, 1979a). This suggests that chromosome condensation actively depends on protein synthesized during mitosis itself, both in prophase (as earlier commented) and in telophase.

Simultaneously to the chromosome decondensation nucleolar reformation takes place. This nucleologenesis is always linked to the intranuclear presence of a NOR, as it has been shown in aneuploid nuclei produced by unbalanced

Fig. 19. — *Allium cepa* L. chromosomes from meristems treated by 8-oxiquinoline. The diploid chromosome number $2n = 16$ is confirmed: The pair of satellized chromosomes is easily distinguished the degree of extension of their secondary constriction being different for each chromosome of the pair. Chromosomes are fully condensed. Most chromatids have lost their relational coils. Centromeres remain undivided and no anaphases are observed during treatment.

Fig. 20. — *Allium cepa* L. chromosomes from meristems under hypoxia conditions. Chromatids remain parallel while some centromeres are already divided. Migration of chromatids is not observed under hypoxia, so that chromosomes remain dispersed throughout cytoplasm.
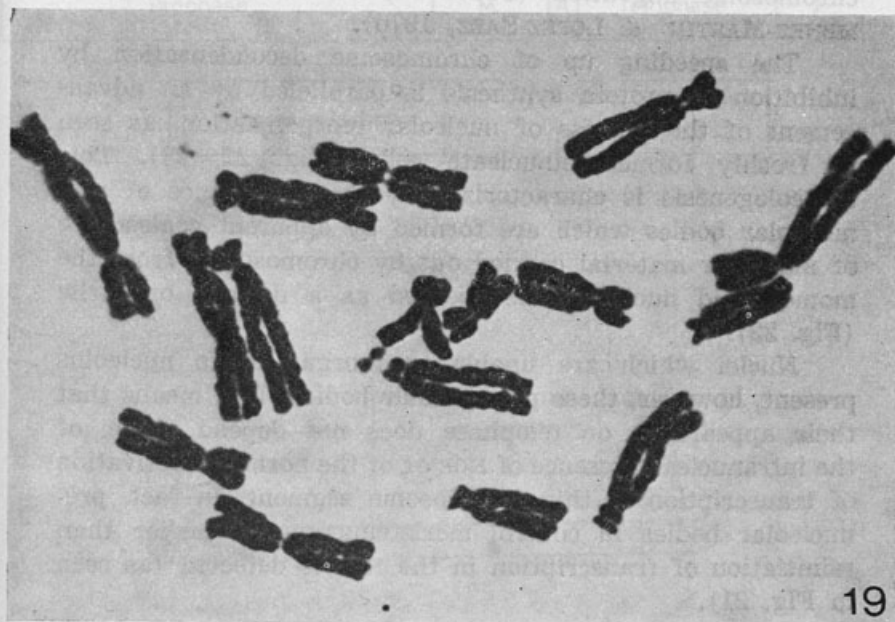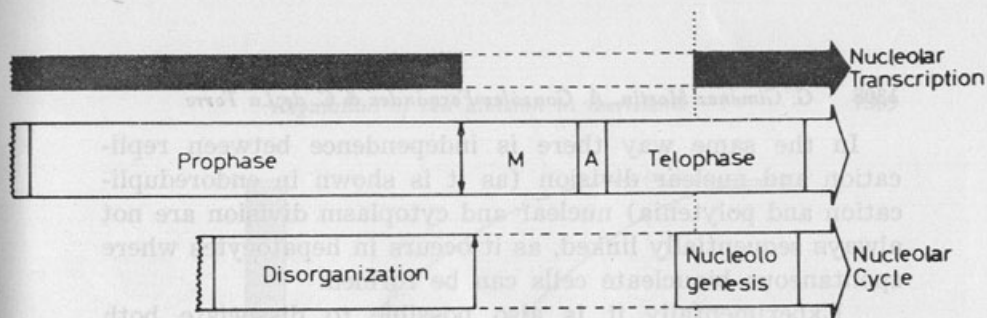
chromosome migration (STOCKERT, FERNANDEZ-GOMEZ, GI-
MENEZ-MARTIN & LOPEZ-SAEZ, 1970).

The speeding up of chromosome decondensation by
inhibition of protein synthesis is paralleled by an advan-
cement of the process of nucleolar reorganization, as seen
in freshly formed binucleate cells (Fig. 22, 23). This
nucleologenesis is characterized by the appearance of pre-
nucleolar bodies which are formed by apparent coalescence
of nucleolar material carried out by chromosomes from the
moment old nucleolus disappeared as a defined organelle
(Fig. 22).

Nuclei which are unable to reorganize its nucleolus
present, however, these prenucleolar bodies. This means that
their appearance on telophase does not depend either of
the intranuclear presence of NOR or of the normal reactivation
of transcription in this chromosome segment. In fact, pre-
nucleolar bodies in control meristems appear earlier than
reinitiation of transcription in the NOR is detected (as seen
in Fig. 21).

Nucleologenesis appears regulated by chromosome con-
densation in the time while it depends on the existence of
a NOR, whose reactivation produces as a first effect the
coalescence of prenucleolar bodies on it. Hence, inhibitor
of protein synthesis advanced nucleologenesis, while tetra-
ploid nuclei induced by c-mitotic drugs which produced an
increased chromosome condensation show a lengthened
nucleologenesis time.

Inhibitors of RNA synthesis given at the time of nucleo-
logenesis prevents NOR activity to reinitiate. Simultaneously
we can observe how prenucleolar bodies remain and new
nucleolus is not formed. Experiments with sequential
inhibition of RNA-synthesis throughout telophase (Fig. 24)
have shown that the reinitiation of RNA synthesis which is
enough to allow nucleologenesis to complete covers, in fact,
a very limited zone of telophase. This new RNA synthesized
in telophase behaves as an initiator or trigger of nucleolo-
genesis process which from this time onwards seem to be
a mere assembly of the dispersed nucleolar material (MOR-
CILLO & DE LA TORRE, 1979b).

Nucleolar Transcription

Prophase | M | A | Telophase

Disorganization | Nucleolo genesis | Nucleolar Cycle

21

Caf

80 —
60 —
40 —
20 —
%

1 2 3 4 5
Time after caffeine, h
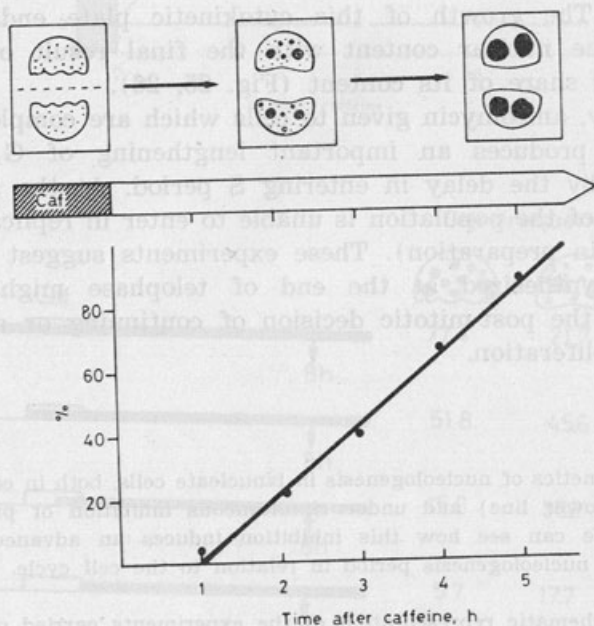
22

Fig. 21. — Matching of nuclear transcription with mitotic phases and with phases of the nuclear cycle, as measured in the total meristem population of *Allium cepa* L. meristems. The diagram shows how nucleolar transcription stops at the very end of prophase as it restarts by midtelophase, after the presence of prenucleolar bodies which characterizes nucleologenesis is detected.

Fig. 22. — The use of binucleate cells for studying nucleologenesis rate. A freshly formed binucleate cell, formed by caffeine-inhibition of cytokinesis, is characterized by the presence of prenucleolar bodies (middle figure in upper row). Binucleate cell with fully organized nucleoli is depicted at the right. The graph shows how the recording of the frequency of binucleate cells with fully organized nucleoli at different times after the binucleate cells production gives us a way of estimating the minimum and the medium and maximum nucleologenesis time in these cells.

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In the same way there is independence between replication and nuclear division (as it is shown in endoreduplication and polytenia) nuclear and cytoplasm division are not always sequentially linked, as it occurs in hepatocytes where spontaneous binucleate cells can be formed.
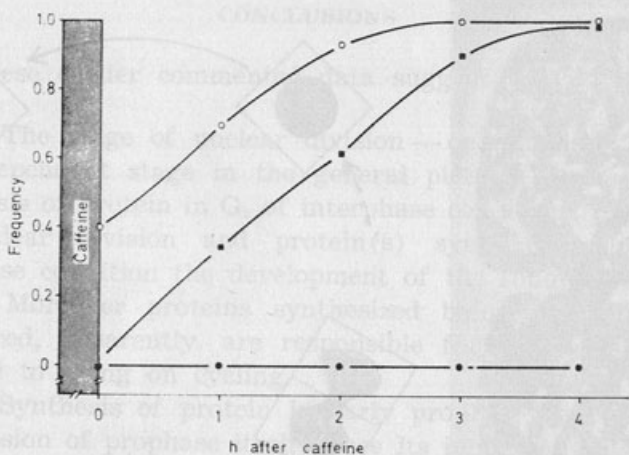
Experimentally it is also possible to dissociate both nuclear and cytoplasmic division, allowing either only mitosis to take place (caffeine-mediated effect) or only cytoplasmic division to occur (ethidium bromide effect). In this last example the development of the cytokinetic plate occurs at the expected time when the nucleus still remains in prophase. The growth of this cytokinetic plate ends by dividing the nuclear content with the final result of an unbalanced share of its content (Fig. 25, 26).

Finally, anisomycin given to cells which are completing telophase, produces an important lengthening of G_1, as measured by the delay in entering S period. At the same time 50 % of the population is unable to enter in replication (SELMAN, in preparation). These experiments suggest that proteins synthesized at the end of telophase might be related to the post-mitotic decision of continuing or abandoning proliferation.

Fig. 23. — Kinetics of nucleologenesis in binucleate cells, both in control conditions (lower line) and under simultaneous inhibition of protein synthesis. We can see how this inhibition induces an advancement of the nucleologenesis period in relation to the cell cycle.

Fig. 24. — Schematic representation of the experiments carried out to detect the role of reinitiation of RNA synthesis in the nucleologenesis process. Binucleate cells were used in all cases. The treatment With an RNA synthesis inhibitor (3'deoxyadenosine or ethidium bromide) was progressively displaced in relation to the caffeine treatment. 8h after the end of this treatment, the frequency of nuclei with fully organized nucleoli (last column) was recorded. We can see how inhibition of RNA synthesis from 1 hour after caffeine onwards does not affect nucleologenesis, though as we saw in Fig. 22 at this time only very few cells showed fully organized nucleoli. The experiments suggest nucleologenesis depends on RNA synthesized during telophase and the first hour of interphase, but not on later synthesis.

23

Cell frequency, %

Caf.	77.4	21.7	0.9
A	77.4	21.7	0.9
	↓ 8h		
B	51.8	45.6	2.6
	↓ 8h		
C	15.6	36.2	48.2
	↓ 8h		
D	5.7	17.7	76.6
	↓ 8h		
E	1.4	5.8	92.8
	↓ 8h		
F	–	2.2	97.8
	↓ 8h		
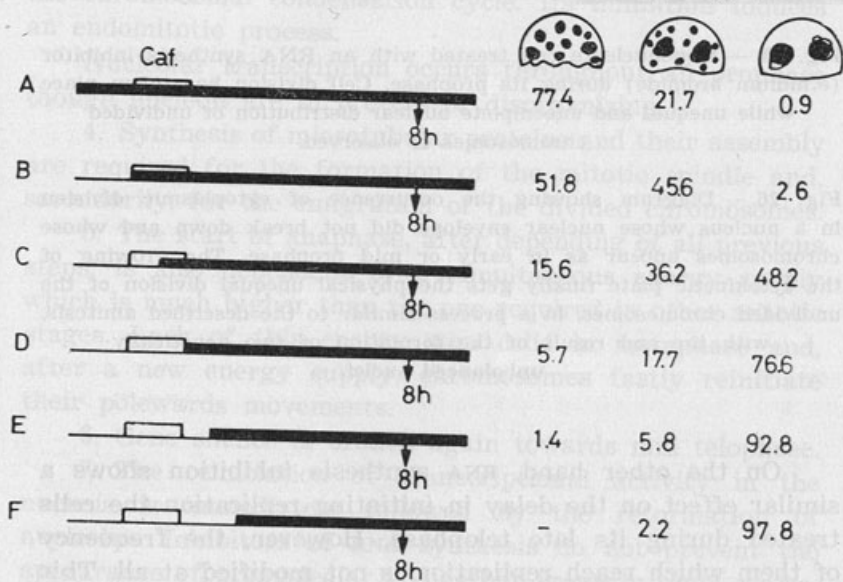
24
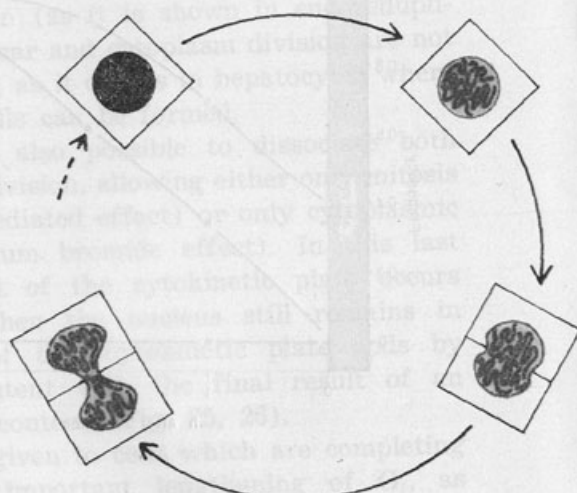
Fig. 25. — Mononucleate cell treated with an RNA synthesis inhibitor (ethidium bromide) during its prophase. Cell division has taken place while unequal and uncomplete nuclear distribution of undivided chromosomes is observed.

Fig. 26. — Diagram showing the occurrence of cytoplasmic division in a nucleus whose nuclear envelope did not break down and whose chromosomes appear as in early or mid prophase. The growing of the cytokinetic plate finally gets the physical unequal division of the undivided chromosomes, in a process similar to the described amitosis, with the end result of the formation of two genetically unbalanced nuclei.

On the other hand, RNA synthesis inhibition shows a similar effect on the delay in initiating replication the cells treated during its late telophase. However, the frequency of them which reach replication is not modified at all. This RNA synthesis in mitosis might well be related to the protein synthesized much later in the cycle, in the initiation of G_2, protein which controls the entering into mitosis of the cells.

CONCLUSIONS

These earlier commented data suggest that:

1. The stage of nuclear division — or mitosis — is not an independent stage in the general picture of the cycle. Synthesis of protein in G_2 of interphase conditions the start of nuclear division and protein(s) synthesized in late telophase condition the development of the following interphase. Moreover proteins synthesized before telophase is completed, apparently, are responsible for the decision of the cell to going on cycling.

2. Synthesis of protein in early prophase controls the progression of prophase itself, since its inhibition make the cell to reverse towards interphase.

3. RNA synthesized towards midprophase acts on the breaking down of nuclear envelope while does not affect the chromosomal condensation cycle. Its inhibition induces an endomitotic process.

Nucleolar transcription occurs throughout all prophase though nucleoli are in process of disorganizing.

4. Synthesis of microtubular proteins and their assembly are required for the formation of the mitotic spindle and, secondarily, for the emigration of the divided chromosomes.

5. The start of anaphase, after depending of all previous steps, is also dependent of a simultaneous energy supply which is much higher than the one required in other mitotic stages. Lack of this energy stop cells in metaphase and, after a new energy supply, chromosomes fastly reinitiate their polewards movements.

6. Gene silence is broken again towards mid telophase.

7. The reinitiation of transcriptional activity in the nucleus is immediately followed by the reformation of nucleolus. Inhibitors of RNA synthesis do not prevent the appearance of prenucleolar bodies but prevents their coalescence in the new nucleolus.

8. Inhibitors of protein synthesis facilitate the decondensing of chromosomal material and, simultaneousiy, advance of nucleolar reorganization.

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REGULATION
OF CELL DIVISION IN MERISTEMS

II. CYTOKINESIS

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ABSTRACT

Cytokinesis occurs generally by cell plate formation in meristem cells. The cell plate arises in the mid region of the cell and is «spun out» toward the edges. The new plasma membrane cannot simply be an extension of the preexisting plasmalemma as it could be in cytokinesis by cleavage. The position of the cell plate is determined by the preprophase microtubule band and the cytoplasm division has only a «chance» to divide in each cell cycle, since the inhibition of one cytokinesis gives rise to a permanent binucleate cell.

Plant cytokinesis can be considered as a topographycally organized secretion process, where the cell plate is formed by the coalescence in the equational plane of small vesicles produced by Golgi bodies. The membranes of these vesicles make up the new plasma membrane and the contents of the vesicles gives rise to the amorphous matrix of the new wall. Therefore, origin, translocation and fusion of the small Golgi vesicles are the physiological processes involved in plant cytokinesis. Meanwhile, the production, accumulation, arrangement and fusion of Golgi vesicles are the morphological phases of cell plate formation.

Experimental analysis with selective inhibitors has demonstrated the essential role of Golgi apparatus in the small vesicle production, of the microtubules in vesicle translocation, and of the membrane fusion reaction for vesicle arrangement and coalescence. Lastly, calcium and magnesium appear to be cytokinesis requirements by afecting membrane fusion.

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FOLLOWING *karyokinesis* or *mitosis,* which separates sister chromatids from one another to each pole, *cytokinesis* eventually takes place, and this cytoplasmic division may be considered as the last event of one cell cycle.

Cytokinesis (from greek: cytoplasmic movement) occurs generally by furrowing in animal and by cell plate formation in plant cells. But this statement is, of course, an oversimplification, for not only in animal cells cytokinesis takes place by furrowing, but also in algae, fungi and most meiotic divisions in vascular plants, while centrifugal formation of the cell plate is ubiquitous in vascular plants. Generally, cytokinesis overlaps the last third of mitosis and represents a small fraction of the whole cycle time (2-4 %), taking place only in a few minutes in most species. This formation of a new cell wall takes place by the so-called *phragmoplast* (from greek, phragma = separation), which appears as a plasma body in the equatorial region of the mitotic apparatus during anaphase and telophase. Inside the phragmoplast small droplets form a plane which is perpendicular to the spindle axis and equidistant from the two anaphase poles. This plate arises in the mid region of the cell and is «spun out» toward the edges. The new plasma membrane cannot simply be an extension of the preexisting plasmalemma as it could be in cytokinesis by cleavage. Apparently, the position of the future cell plate is simultaneously determined with the location of the mitotic apparatus during prophase and it has been demonstrated that the *preprophase microtubule band* determines metaphase plane and cell plate position in normal mitosis and cytokinesis as well as in highly asymetrical ones (PICKETT-HEAPS, 1969).

STRASBURGER's studies (1875) of cell division *in vivo* in stamen hair cells of *Tradescantia* already described the phragmoplast as a filamentous texture and the cell plate formation as the fusion of granules («Köperchen»). Later BELAR (1929) & BECKER (1938) studied the earlier stages of cell plate development, showing in a series of elegant experiments that this structure is double with a soft consistency in its interior.

At anaphase, the first indication of cell plate formation was the appearance of stainable nodules in the equatorial plane and these nodules were originally believed as thickened spindle fibres but BECKER (1935) showed that the small droplets were able be vitally stained with vacuome dyes, such as neutral red or cresyl blue. In fixed preparations, the small granules apparently agglutinated with the spindle fibers of the phragmoplast, whilst on observation in living and unflattened state in *Tradescantia* stamen hairs, they are identified as a semi-liquid region.

Eventually, the small droplets coalesce to form the cell plate across the mother cell. This plate, which starts near the center of the equatorial plane, grows outward to the lateral walls, in a similar way to the openning of an iris diaphragm. This plate can be stained vitally with basic dyes, such as ruthenium red or methylene blue, suggesting the presence of acidic compounds like pectin precursors and other uronides.

Now, it is well known that the phragmoplast initiates from remnants of the achromatid spindle, but later the cytoplasm bordering the spindle region also contributes. «Phragmoplast filaments» are composed of microtubules bundles, and the particles which appear in the phragmoplast are Golgi bodies.

The fibrillar component of the phragmoplast has a transport function. The dimensions of particles entering the phragmoplast suggest that they correspond to Golgi bodies. BAJER (1965) & BAJER & ALLEN (1966) have clearly demonstrated with interference microscopy that the transport of a considerable amount of organic matter toward the cell plate is an important process involved in plant cytokinesis, and they have proposed that some kind of co-operation between particles and «phragmoplast filaments» is responsible for this mass transport.

PHASES OF CYTOKINESIS

As many others biological processes, cytokinesis appears to be a continuous one in which it is difficult to separate the various mechanisms that operate as one harmonious whole or equally difficult to dissect the process into phases.

However, electron microscopy has revealed the ultrastructural stages of plant cytokinesis. Former studies, with permanganate fixation, were able to find the membrane behaviour during cell plate formation (PORTER & MACHADO, 1960; PORTER & CAUFIELD, 1960; WHALEY & MOLLENHAUER, 1963; FREY-WYSSLING, LOFEZ-SAEZ & MUHLETHALER, 1964; RISUEÑO, GIMENEZ-MARTIN & LOPEZ-SAEZ, 1968; MOLLEN-HAUER & MOLLENHAUER, 1978) and latter approaches, with glutaraldehyde fixation, have confirmed the basic findings and suggested an important role for microtubules in the process (ESAU & GILL, 1965; PICKETT-HEAPS & NORTHCOTE, 1966; HEPLER & NEWCOMB, 1967).

The ultrastructural study of normal cytokinesis allows to distinguish several phases, which overlap each other like tiles on a roof (Fig. 1).

Fig. 1. — Schematic diagram of plant cytokinesis showg the different phases.

I — Production of Golgi vesicles. During anaphase and telophase many dyctiosomes are accumulated on the outer surface of the interzonal spindle and the small vesicles appear uniformly distributed throughout the cytoplasm.

II — Accumulation of Golgi vesicles. During early telophase Golgi vesicles accumulate in the middle of the equatorial region forming as a cloud between the two telophasic nuclei.

III — Arrangement of Golgi vesicles. During telophase, the small vesiclés become arranged in the equatorial plane. This phase, as the vesicle accumulation, begins in the central region and proceeds centrifugally.

IV — Fusion of Golgi vesicles. The coalescence of the vesicles begins in the inner part of the forming cell plate during middle telophase. When the growing cell plate reaches the longitudinal walls of the mother cell cytokinesis is complete and two daughter cells have become independent.
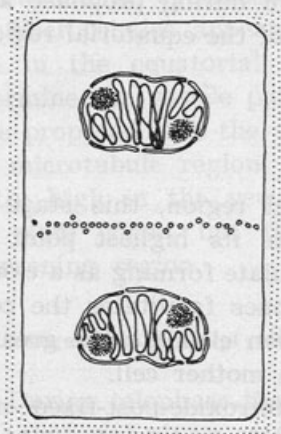
Plant cytokinesis
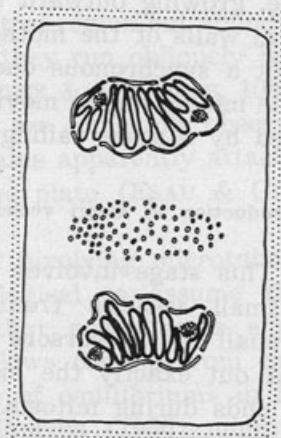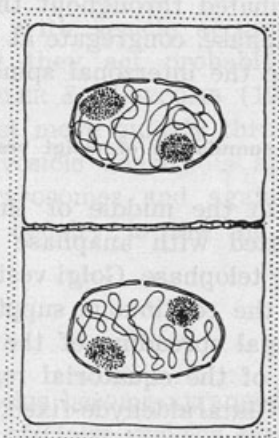

I. Production   II. Accumulation

III. Arrangement   IV. Fusion

Fig. 1.

In order to understand in an easy way the characteristic features of cytokinesis it should be born in mind that cell plate formation begins in the central area of the equatorial plane, growing outward throughout this plane toward peripheral walls of the mother cell. That is to say, the process is not a synchronous one in the whole plane but it begins in the middle region moving centrifugally as a circular wave arised by a stone falling into water.

1) Production of Golgi vesicles

This stage involves the formation, in large quantities, of small vesicles from Golgi bodies. The dyctiosomes marshall the precursors of the cell plate. It is difficult to point out exactly the moment at which this phase begins and ends during mitosis. However, likely the period of the highest production rate lasts from metaphase. During anaphase and telophase many dyctiosomes are accumulated on the border of the phragmoplast, on the outer surface of the interzonal spindle. The small vesicles, uniformly distributed throughout the cytoplasm during prophase and metaphase, congregate at the center of the equatorial region, inside the interzonal spindle.

2) Accumulation of Golgi vesicles

In the middle of the equatorial region, this stage is initiated with anaphase and reaches its highest point at early telophase. Golgi vesicles accumulate forming as a cloud, and the continuous supply of new ones facilitates the centrifugal spreading of the accumulation cloud to the greater part of the equatorial region of the mother cell.

Glutaraldehyde-fixed, osmium tetroxide-post-fixed material has revealed the involvement of the microtubular system in this stage of cell plate formation (ESAU & GILL, 1965; PICKETT-HEAPS & NORTHCOTE, 1966; HEPLER & NEWCOMB, 1967).

During accumulation of Golgi vesicles, a great density of microtubules occurs through the central part of the

mitotic cell, where microtubules run parallel to one another and perpendicular to the prospective plane of the plate. As the accumulation cloud expandes and the small vesicles are superseded by continuous portions of cell plate, the microtubules are absent from the central region but abundant at the cell plate edges, from which they run obliquely back toward the two anaphase poles (HEPLER & NEWCOMB, 1967).

In longitudinal sections, vesicles are commonly observed between the microtubules in long chains apparently attached to one another and flowing into the plate (ESAU & GILL, 1965; HEPLER & JACKSON, 1968).

The great evidence accumulated involving microtubules in cytoplasmic streamings makes logical to assume that interzonal spindle is the system that accumulates small vesicles by producing cytoplasmic flows coming from each daughter nucleus to rest in a «zone of equilibrium» in the equatorial region. As proposed by PORTER (1966) microtubules may determine the channels along vesicles move, and this idea is consistent with observations by ESAU & GILL (1965) and HEPLER & NEWCOMB (1967) on microtubular system during cytokinesis.

Microtubules appear concerned with vesicle accumulation in the equatorial region and they act probably to determine the vesicle pathway. HEPLER & NEWCOMB (1967) have proposed that the vesicles must move quickly through the microtubule region, since the vesicle density is apparently high in the vecinity of dictyosomes and again in the plate edges, but this vesicle density is low in the intervening region.

3) Arrangement of Golgi vesicles

During telophase the small vesicles become arranged in the equatorial plane, so that a row of Golgi vesicles can be observed along this plane in longitudinal sections. As the vesicle accumulation, this phase begins in the central region and proceeds centrifugally.

The expanding plate is always rimmed by clusters of Golgi apparatus producing small vesicles, and large numbers

of Golgi vesicles continue to be added to the cell plate during
late telophase.

In relatively advanced stages of plate formation vesicles
of two different sizes, both the smaller vesicles and the
larger ones can be identified (LOPEZ-SAEZ, RISUEÑO &
GIMENEZ-MARTIN, 1966; WHALEY, DAUWALDER & KEPHART,
1966). The smaller ones, measuring about 50-100 nm in
diameter, appear to be the direct product from the Golgi
bodies, while larger vesicles, which are observed only in or
near the zone of the cell plate, appear to arise from fusion
of the smaller vesicles (HEPLER & NEWCOMB, 1967).

4) Coalescence of Golgi vesicles

The fusion of Golgi vesicles starts in the inner part of
the equatorial plane. At the beginning, during middle
telophase coalescence, arrangement and congregation can
be observed respectively in the inner, intermediate, and
marginal parts of the forming cell plate. This kind of
observation clearly makes evident the course of the over-
lapping phases which make up cytokinesis.

The study of transverse sections from telophase cells
has confirmed the centrifugal growth of the cell plate and
revealed that microtubules almost entirely disappeared from
the region of vesicle fusion, being observed in large numbers
near the plate edge, where an earlier stage of development
is observed (HEPLER & NEWCOMB, 1967).

While this stage of coalescence proceeds many vesicles
fuse between the clusters of microtubules in the established
plane of the growing plate. The origin of plasmodesmata
from entrapped elements of the endoplasmic reticulum is
generally accepted to take place during this phase, when
the continued growth of the cell plate constrics cytoplasmic
strands and eventually catchs some tubules of endoplasmic
reticulum (FREY-WYSSLING, LOPEZ-SAEZ & MUHLETHALER,
1964). Finally, the growing cell plate reaches the longitudinal
walls of the mother cell. Cytokinesis is complete and two
daugher cells have become independent.

Later development transforms the cell plate into the middle lamella of the mature cell wall.

EXPERIMENTAL ANALYSIS OF PLANT CYTOKINESIS

The induction of binucleate cells in a proliferative population by any treatment constitutes a very good test for screening of cytokinesis inhibitors. Thus, RISUEÑO, GIMENEZ-MARTIN & LOPEZ-SAEZ (1968) selected thermal shock, colchicine and lindane, caffeine and high hydrostatic pressure as cytokinesis inhibitors. In the screening, a lot of difefrent chemical drugs and physical agents were tested, bearing in mind that the more different the nature of a binucleating agent the more probability of a particular mechanism of action.

In relation to the cytokinesis phase preferentially blocked we know nowadays three groups of treatments: 1) Inhibitors of Golgi vesicle production, 2) inhibitors of vesicle accumulation and 3) inhibitors of arrangement and fusion of Golgi vesicles.

1) Vesicle production blockage

When meristem cells are submitted to a sublethal thermal shock for one hour at 40-42° C, during recovery in culture conditions many binucleate cells can be detected in the meristem population. Light microscopy shows the absence of phragmoplast in telophases inmediately after shock, but no apparent distortion of the interzonal spindle. Under the electron microscope, any cell structure but Golgi bodies appears morphologically well preserved. However, dyctiosomes characterized in these cells as piles of flatened sacs are not more apparent. Likely, some thermolabil factor is essential to preserve the Golgi body structure and after this treatment small and flat sacules can be observed stattered throughout the ground cytoplasm. These structures do not accumulate wall precursors or segregate small vesicles in their edges. As a consequence, telophases show a very low number of Golgi vesicles and the accumulation and

following phases for cell plate formation are missed. Logically, blockage of the first stage in a chain of events disturbs the whole process inhibiting cell plate formation.

Recently, MEYER & HERTH (1978) has described 2,6-dichlorobenzonitrile as an effective inhibitor of cell plate formation, without affecting nuclear division. This herbicide was introduced as a cellulose-synthesis inhibitor in higher plants (HOGETSU, SHIBAOKA & SHIMOKORIYAMA, 1974) and it seems to be a chemical candidate for blocking Golgi vesicle production, although there is no direct evidence supporting this hypothesis for the moment.

2) Vesicle accumulation blockage

The c-mitotic substances, colchicine and lindane, are characterized essentially by their effects on the microtubule depolimerization. Any interference in this system affects cytokinesis by completely or partially inhibiting the formation of the cell plate.

The characteristic effect of colchicine is to produce polyploid cells. We observe that after more than 3 h treatment the chromosomes of the dividing cells are dispersed throughout the cytoplasm, the Golgi apparatuses are producing vesicles in apparently normal quantities, and the number of these vesicles in the cytoplasm is increasing. When the chromosomes are enclosed within the nuclear envelope, a polyploid nucleus is formed, while the small vesicles remain dispersed about the cytoplasm. In this case, both the distribution of the nuclear material and the division are observed to have been inhibited.

Fig. 2. — Schematic diagram of cytokinesis inhibition by caffeine or high hydrostatic pressure.

In both cases the I (production of Golgi vesicles) and the II (accumulation) phases of cytokinesis were observed to prōceed normally.

III — The cloud of vesicles spreads on the equatorial region without arrangement.

IV — Finally the vesicles disperse throughout the cytoplasm without form the cell plate. The result is a binucelate cell.

Cytokinesis inhibition by caffeine
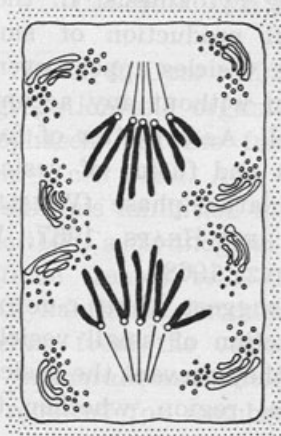
I. Production   II. Accumulation

III. Prolonged
accumulation   IV. Dispersion

Fig. 2.

When the incubation with colchicine affects anaphase cells, where chromosome distribution took place but cell plate formation is at the very beginning, the treatment induces binucleate cells by inhibiting cytokinesis. In these cells, there is apparently a normal production of smal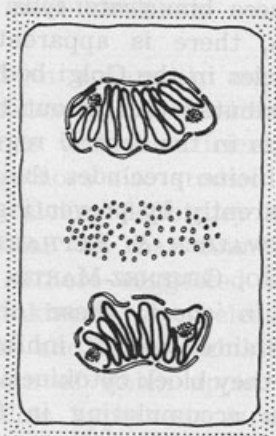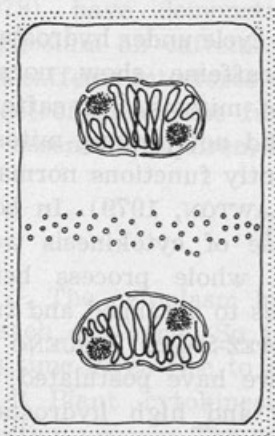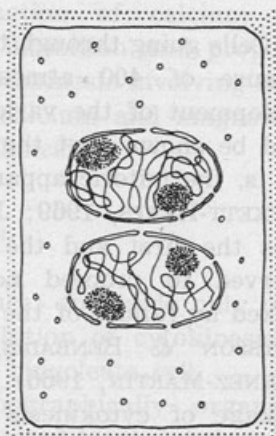l vesicles in the Golgi bodies and these vesicles appear evenly distributed throughout the cytoplasm without any accumulation in the central region of the cell. As a matter of fact, colchicine precludes the arrangement and fusion of vesicles apparently by preventing the accumulation phase (WHALEY, DAUWALDER & KEPHART, 1966; PICKETT-HEAPS, 1967; RISUEÑO, GIMENEZ-MARTIN & LOPEZ-SAEZ, 1968).

In short, these observations suggest that c-mitotic substances do not inhibit the production of small vesicles, but they block cytokinesis insofar as they prevent the vesicles from accumulating in the equatorial region, whether the nuclear material is distributed or not.

3) Vesicle arrangement and fusion blockage

Cells going through their division cycle under hydrostatic pressure of 400 atmospheres or caffeine show normal development of the various phases of mitosis. For caffeine could be shown that the treatment did not prolong mitosis, this is, the mitotic apparatus apparently functions normally (PICKETT-HEAPS, 1969; JUNIPER & LAWTON, 1979). In both cases the first and the second phase of cytokinesis were observed to proceed normally, the whole process being blocked by failure of the small vesicles to arranged and fuse (DEYSSON & BENBADIS, 1966; LOPEZ-SAEZ, RISUEÑO & GIMENEZ-MARTIN, 1966). Therefore, we have postulated the blockage of cytokinesis by caffeine and high hydrostatic pressure at level of the arrangement of vesicles in the equatorial plane (Fig. 2).

Certainly, none of the treatments which have been used to inhibit cytokinesis has proved capable of blocking only the fusion of the small vesicles with a certain degree of selectively: that is, once the arrangement took place the

process led, through coalescence, to the formation of the new wall.

CALCIUM AND MAGNESIUM REQUIREMENTS

PAUL & GOFF (1973) described an apparently normal aggregation and organization of vesicles in caffeine-treated telophases, but the fusion of vesicles was insufficient to form a cell plate. And when these authors also studied the cytokinesis inhibition in the case of calcium deficiency they described a cytological picture similar to that found in caffeine treated cells. Thus, these authors suggested that methyxanthines interfere with cytokinesis by releasing calcium from the vesicle membranes and/or by inhibiting the membrane-associated ATPase, both of which appear to be required for membrane fusion. This hypothesis is consistent with POSTE and ALLISON's suggestion about the requirement of ATP and Ca^{++}, Mg^{++} activated ATPase for membrane fusion (POSTE & ALLISON, 1971).

Recently, BECERRA (1977) and BECERRA & LOPEZ-SAEZ (1978) have demonstrated the action of calcium and magnesium on caffeine cytokinesis inhibition and proposed that caffeine interferes with plant cytokinesis involving some aspect of membrane fusion, where calcium and magnesium are essential requirements for cytokinesis.

CONCLUSIONS

1. The cytoplasm has the «chance» to divide only once in each cell cycle. So that the inhibition of cytokinesis at this time gives rise to a permanent binucleate cell.

2. Plant cytokinesis is a topographically organized secretion process. The cell plate is formed by the coalescence in the equatorial plane of small vesicles produced by Golgi bodies. The membranes of these vesicles make up the plasma membrane of the new cell surfaces; and the contents of these vesicles gives rise to the amorphous matrix of the new wall. Therefore, origin, translocation and fusion of these

vesicles are the physiological processes involved in plant cytokinesis.

3. The production, accumulation, arrangement and fusion of Golgi vesicles may be considered the morphological phases of cell plate formation.

4. C-mitotic drugs inhibit the accumulation phase of cytokinesis by destroying the fibrillar component of the phragmoplast, hence the microtubular system appears to be essential for vesicle translocation.

5. Caffeine and high hydrostatic pressure are efficient inhibitors of the vesicle arrangement and coalescence. Apparently, arrangement and coalescence of Golgi vesicles are dependent of membrane fusion and likely a certain degree of fusion of small vesicles is required for a narmal arrangement.

6. Calcium and magnesium are essential requirements for cytokinesis by affecting likely the membrane fusion reaction.

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NOTAS
SOBRE BORAGINACEAS ESPAÑOLAS

I. *LITHODORA PROSTRATA* (LOISEL.) GRISEB.
Y *L. DIFFUSA* (LAG.) I. M. JOHNSTON.

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RESUMEN

Tras un estudio de material español de *Lithodora* y del tipo de *Lithospermum diffusum* Lag., se ha llegado a la conclusión de que *Lithodora prostrata* (Loisel.) Griseb. y *L. diffusa* (Lag.) I. M. Johnston deben separarse a nivel específico. Se propone la nueva conbinación: *L. prostrata* subsp. *lusitanica* (Samp.) Valdés, comb. nov.

SUMMARY

As a result of the study of spanish material of *Lithodora* and the type of *Lithospermum diffusum* Lag., the separation of *Lithodora prostrata* (Loisel.) Griseb. and *L. diffusa* (Lag.) I. M. Johnston is made. The following new combination is proposed: *Lithodora prostrata* subsp. *lusitanica* (Samp.) Valdés.

LAGASCA (1805: 39), describió una nueva especie de *Lithospermum* con el nombre de *L. diffusum*. Un año más tarde, LOISELEUR-DESLONGCHAMPS (1806: 105), describió *Lithospermum prostratum,* basándose en material procedente de Bayona (Bajos Pirineos, Francia). Al separar GRISEBACH (1844: 85) el género *Lithodora,* incluyó en él *Lithospermum prostratum* Loisel., estableciendo por tanto la combinación *Lithodora prostrata* (Loisel.) Griseb.

DE CANDOLLE (1846: 81) consideró que *Lithospermum diffusum* Lag. y *Lithospermum prostratum* Loisel. consti-

tuían una sola especie, para la que adoptó el nombre de LOISELEUR-DESLONGCHAMPS, ya que creyó que *L. diffusum* había sido descrito por LAGASCA en 1816.

COSSON (1849: 42) separó como *Lithospermum prostratum* var. *erectum* unas plantas del S de España (Alcalá de los Gazules, Cádiz). Dicha variedad se encuentra también en Portugal y fue elevada a categoría de especie por SAMPAIO (1913: 123) con el nombre de *Lithospermum lusitanicum*.

Al aceptar la separación de *Lithodora* del antiguo género *Lithospermum,* JOHNSTON (1924: 56) establece la nueva combinación *Lithodora diffusa* (Lag.) I. M. Johnston, incluyendo como sinónimos *Lithospermum diffusum* Lag., *Lithospermum prostratum* Loisel. y *Lithodora prostrata* Griseb. Adoptó por tanto el criterio de DE CANDOLLE, seguido hasta ahora por la mayoría de los autores, de reconocer una sola especie, aunque indicó más tarde (JOHNSTON, 1953: 267) que se trataba de una especie muy variable que necesitaba un estudio detallado. Siguiendo esta indicación, PINTO DA SILVA & ROZEIRA (1964: 170) consideraron que las plantas del centro y sur de Portugal, SW de España y N de Marruecos, constituían una subespecie independiente: *Lithodora diffusa* subsp. *lusitanica* (Samp.) P. Silva & Rozeira (= *Lithospermum prostratum* var. *diffusum* Cosson).

La mayoria de los autores están de acuerdo en aceptar la existencia de una sola especie, que ocupa las regiones atlánticas y subatlánticas comprendidas entre Finisterre (Francia) y el NW de Marruecos, penetrando por el sur de España hasta la provincia de Málaga. Para esta especie se han utilizado más frecuentemente los nombres *Lithospermum diffusum* Lag., *Lithospermum prostratum* Loisel. y *Lithodora diffusa* (Lag.) I. M. Johnston. A partir de PINTO DA SILVA & ROZEIRA (l. c.), se reconoce la existencia de dos subespecies: la típica, que ocupa toda la parte norte del área de distribución de la especie (desde Finisterre hasta la cuenca del Tajo), y la subsp. *lusitanica* (Samp.) P. Silva & Rozeira, que ocupa la parte sur, desde la cuenca del Tajo, hasta el NW de Marruecos, con algunas localidades aisladas en el N de Portugal.

Dentro del género *Lithodora,* lo que se ha venido llamando hasta ahora *L. diffusa* presenta una disposición del androceo muy notable. En todas las especies conocidad de este gènero, los cinco estambres se insertan a la misma altura en el tubo de la corola o en la garganta. Sin embargo, en esta especie los estambres se insertan a distintas alturas, lo que confiere a este taxón una situación tan peculiar dentro del género, que JOHNSTON (1953: 267) formó con dicha especie la sección *Lasioglottis.* Esta situación es semejante a la que dentro del género *Macrotomia* DC. persenta *M. echioides* (L.) Boiss. que es igualmente la única especie de este género con estambres insertos a distintas alturas (HUYNH, 1971).

Con motivo de unos estudios sobre Boragináceas españolas, el autor de esta nota ha podido comprobar que dentro de lo que se ha venido llamando *Lithodora diffusa, Lithospermum prostratum* o *L. diffusum,* se encuentran dos grupos de plantas muy differentes, sobre todo en cuanto a la posición del androceo se refiere.

Un grupo está formado por plantas que presentan estambres insertos a distintas alturas obre el tubo de la corola, con anteras de 0,6 a 1,3 (-1,8) mm. Tienen además inflorescencias con (3-) 6-14 flores, y núculas densa y diminutamente tuberculadas. Las plantas que presentam estos caracteres se extienden desde Finisterre (Francia) hasta Marruecos.

Otro grupo está formado por plantas que presentan estambres insertos aproximadamente a la misma altura, ya sea hacia la parte media del tubo de la corola o en la garganta, con anteras de 1,2 a 1,5 mm. Tienen además inflorescencias con menos flores: 2 a 6 (-10), y núculas lisas. Las plantas que presentan estos caracteres se encuentran restringidas a diversas localidades de los montes de Léon y Cordillera Cantábrica, descendiendo en Santander hasta algunas localidades costeras, como San Vicente de la Barquera, Suances y Santoña.

Por los datos cariológicos de que se dispone hasta el momento, ambos grupos presentan distinto número cromosómico. FERNANDES & LEITÃO (1972: 390) indicaron 2n = 32 para material de S. Paulo de Frades, Coimbra, perteneciente

al primer grupo, mientras que KÜPFER (1974: 34) indicó
2n = 16 para material de Peña Olvidada (Picos de Europa,
Santander), recuento que hay que referir al segundo grupo,
como se ha podido comprobar estudiando el material utili-
zado por este autor (NEU 00009).

Dada la importancia que la morfología floral tiene en
la taxonomía de Boragináceas, no se duda en separar ambos
grupos con categoría específica.

Se identifica el primer grupo, con estambres insertos a
distintas alturas, con *Lithospermum prostratum* Loisel. y
dentro del género *Lithodora* debe por tanto denominarse
Lithodora prostrata (Loisel.) Griseb.

En cuanto al segundo grupo, con estambres insertos a
la misma altura, se identifica con *Lithospermum diffusum*
Lag., por las razones que se indican más adelante, y ha de
denominarse por lo tanto *Lithodora diffusa* (Lag.) I. M.
Johnston.

Se indican a continuación los nombres correctos, sinó-
nimos, caracteres diferenciales y distribución de ambas
especies, así como de las categorias infraespecíficas
reconocidas.

Lithodora prostrata (Loisel.) Griseb., *Spicil. Fl. Rom.* 2: 85
(1844).

   Lithospermum prostratum Loisel., *Fl. Gall.* 1: 105
(1806).

Subarbusto de ramas decumbentes, ascendentes o erectas,
con hojas seríceas, o estrigosas e hirsutas. Inflorescencias
con (3-) 6-14 flores, alargándose en la maduración hasta
40 (-70) mm. Corola con garganta y tubo ± densamente pelo-
sos interiormente. Estambres insertos a distintos niveles por
encima de la mitad del tubo o hacia la garganta, con ante-
ras de 0,6-1,3 (1,8) mm. Núculas 1-3 maduras por flor, de
2-3,5 × 1,3-2 mm., densa y diminutamente tuberculadas.

Numero cromosómico. 2n = 32 [FERNANDES & LEITÃO,
1972: 390, sub *L. diffusa* (Lag.) I. M. Johnston].

Distribución. Región atlántica de Europa y Africa, desde Finisterre (Francia) hasta el NW de Marruecos. En el S de España, este taxon penetra hasta la provincia de Málaga.

JOHNSTON (1953: 267) describió esta especie como monomórfica, aunque indicó haber encontrado diferencias en la longitud de los estilos y tamaño de las anteras. El estudio de abundante material de sus dos subespecies, permite asegurar que en ambas se presenta una clara distilia, situación que se encuentra en todas las especies de *Lithodora* de la Peninsula Ibérica. *L. fruticosa* (L.) Griseb. presenta, sin embargo, distilia imperfecta, ya que los estambres se encuentran siempre insertos en la parte superior del tubo de la corola, variando solamente la longitud del estilo, que es largo en las plantas longistilas, de manera que sobrepasa las anteras, y corto, alcanzando aproximadamente la mitad de la longitud del tubo de la corola, en las plantas brevistilas.

Subsp. **prostrata**

Decumbente. Hojas planas o de margen ligeramente recurvo, patentes, seríceas, con pelos de las hojas viejas de base pustulada. Corola con tubo de (8-) 10-12 mm. y limbo (9-) 10-13 mm., con garganta densa y largamente pelosa. Anteras 1-1,3 mm. Núculas 2-2,5 (-3,5) $\times$ 1,3-2 mm., ovoideas.

Distribución. Región Atlántica europea, desde Finisterre (Francia) hasta la cuenca del Tajo (España y Portugal).

Presenta distilia, con dos formas bien distintivas. Las plantas longistilas presentan los estambre insertos en 3 niveles por encima de la mitad del tubo o hacia la garganta, y estilo largo, de maneira que el estigma queda por encima del anillo de pelos de la garganta, aproximadamente hacia la mitad del limbo de la corola. Las plantas brevistilas presentan los estambres insertos en la garganta a tres niveles en un espacio corto, con filamentos de 0,5 a 1,5 mm., y estilo corto, que no llega a la mitad del tubo, quedando aproximadamente a la altura que ocupa el estambre mas inferior de las flores longistilas.

Subsp. **lusitanica** (Samp.) Valdés, comb. nov.

> *Lithospermum lusitanicum* Samp., *Lista Herb. Port.*: 123 (1913).
>
> *Lithodora diffusa* subsp. *lusitanica* (Samp.) P. Silva & Rozeira, *Agron. Lusit.* 24: 170 (1964).

> *Lithospermum fruticosum* Brot., *Fl. Lusit.* 1: 292 (1804), non L. (1753).
>
> *Lithospermum prostratum* var. *erectum* Cosson, *Not. Pl. Midi Esp.* 1: 42 (1849).

> *Lithospermum diffusum* var. *erectum* (Cosson) Rouy, *Fl. Fr.* 10: 314 (1908).

> *Lithospermum fruticosum* subsp. *diffusum* Maire, in Jahand. & Maire, *Cat. Pl. Maroc* 3: 602 (1934).

Ascendente o erecta. Hojas fuertemente recurvas, adpresas o patentes, con indumento doble: strigoso de pelos largos de base pustulada, sobre todo en el haz, e híspido, de pelos cortos, más abundantes en el envés. Corola con tubo de 8-9,5 mm. y limbo de 8-9 mm., con garganta y parte superior del tubo escasamente pelosa, con 5 bandas longitudinales de pelos largos, a casi glabra. Anteras 0,6-1,3 (-1,8) mm. Núculas 3-3,5 × 1,8-2 mm., oblongas.

Distribución. Desde la cuenca del Tajo hasta el NW de Marruecos, con algunas localidades aisladas en el N de Portugal (Pinto da Silva & Rozeira, 1964: 171), penetrando en el S de España hasta la provincia de Málaga.

Presenta distilia. Las formas longistilas tienen 5 bandas de pelos en la garganta y estambres insertos a tres alturas por encima de la mitad del tubo, o cerca de la garganta, con filamentos de 0,5 a 1,2 mm. De ellos, generalmente 2 están algo mas altos, y otros dos, alternando con los anteriores, algo mas bajos; el quinto estambre se inserta un poco por debajo de los demás. El estilo es largo, situándose el estigma hacia la garganta o por encima de la misma. Las plantas brevistilas presentan garganta casi glabra y estambres a distintas alturas. Generalmente, tres de ellos se

insertan hacia la garganta y tienen filamentos de 1 a 1,3
(-1,8) mm., y los otros dos, con filamentos de 0,4 a 0,6 mm,
están insertos por encima de la mitad del tubo. El estilo
es corto, alcanzando aproximadamente la mitad del tubo de
la corola.

Lithodora diffusa (Lag.) I. M. Johnston, *Contr. Gray Herb.
Harvard Univ., new ser.* 73: 56 (1924), excl. syn. *Lithos-
permum prostratum* Loisel. et *Lithodora prostrata*
Griseb.

Lithospermum diffusum Lag., *Var. Ci.* 4 (19): 39
(1805).

Subarbusto con ramas decumbentes, despues ascendentes,
con hojas seríceas ó hirsutas. Inflorescencias con 2-6 (-10)
flores, alargándose en la maduración hasta 30 (-50) mm.
Corola con garganta y tubo provistos interiormente de abun-
dantes pelos largos. Estambres insertos a la misma altura
hacia la parte media del tubo o en la garganta, con anteras
de 1,2-1,5 mm. 1-2 (-4) núculas maduras por flor, de 2,5-3 $\times$
$\times$ 2 mm., lisas.

Numero cromosómico. 2n = 16 (KÜPFER, 1974: 34).

Tipo. Asturias (Arvas, VII-VIII, *Lagasca* (MA 96526,
lectotipo).

Distribución. Montes de León, Cordillera Cantábrica y
zonas bajas de la provincia de Santander.

LAGASCA (1805: 39) no indicó ninguna localidad al des-
cribir *Lithospermum diffusum*. Sin embargo, años más tarde
(LAGASCA, 1816: 10) repitió literalmente la descripción
original de esta especie, sin hacer referencia al trabajo de
1805, añadiendo como localidades para la misma: «in dumetis
prope Arvas, Pajares et in perquampluribus aliis Principatus
Asturicensis plagis».

El autor de esta nota está de acuerdo con COLMEIRO
(1858: 192) en que el trabajo de 1805 fue un anticipo del

de 1816, ya que el mismo LAGASCA escribió «doy unicamente el extracto de mis observaciones... reservando para una obra posterior, que espero publicar muy pronto, hablar con la extensión debida» (LAGASCA, 1805: 34). La obra a que se refería era sin duda su *Genera et Species Plantarum* (1816), que es la más extensa de este autor, ya que su proyectada Flora Española no llegó a publicarse (véase LAGASCA, 1924: 2).

Por ello, aunque en 1805 no indicó material alguno, puede asegurarse que utilizó para describir *Lithospermum diffusum* el indicado en 1816.

En el herbario del Jardín Botánico de Madrid (MA), se conservan dos pliegos de *Lithospermum diffusum* recolectados por LAGASCA; uno (MA 154902) en León y otro (MA 96526) en Arvas (= Colegiata de Arbas, Puerto de Pajares, León, que a principios de siglo XIX se escribía con «v», como indica LAÍNZ, 1975: 66). Este último corresponde a la primera de las localidades específicamente citadas por LAGASCA (1816: 10). Se puede afirmar por las noticias históricas que se tienen, que LAGASCA recolectó en León y Asturias, y muy concretamente en Arbas (= Arvas) en 1803 (LAGASCA, 1805: 38; COLMEIRO, 1858: 192; PEREZ DE CASTRO, 1971: 5; CASASECA, 1976: 194), por lo que no hay duda de que este es parte del material a que LAGASCA (1816: 10) hizo referencia, por lo que se toma el ejemplar contenido en el pliego procedente de Arbas (=Arvas, MA 96526) como tipo de *Lithospermum diffusum* Lag.

Estudiado con detalle este ejemplar, se ha comprobado que se trata de una planta brevistila que presenta los estambres insertos en la parte superior del tubo, con anteras largas situadas todas a la misma altura.

La morfología floral corresponde por lo tanto a la que presenta este taxón, por lo que no hay duda de que el primer nombre aplicado al mismo es *Lithospermum diffusum* Lag. y por tanto, el nombre de este taxón en el género *Lithodora* es *Lithodora diffusa* (Lag.) I. M. Johnston, a pesar de que JOHNSTON aplicó este nombre a las plantas con estambres

insertos a distintas alturas, o sea, a *Lithodora prostrata* (Loisel.) Griseb.

Lithodora diffusa (Lag.) I. M. Johnston es una especie distila. Las plantas longistilas presentan estambres insertos por encima de la mitad del tubo, con filamentos de apenas 0,5 mm., y estilo largo, que casi alcanza la base de los lóbulos de la corola. Las plantas brevistilas presentan los estambres insertos en la base de la garganta, con filamentos de c. 2 mm., de manera de que las anteras alcanzan la base de los lóbulos de la corola, y el estilo corto, quedando el estigma un poco por encima de la mitad del tubo de la corola.

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LA PRAIRIE MONTAGNARDE
DES MONTS LOMA (SIERRA LEONE)

par

PAUL JAEGER et JACQUES-GEORGES ADAM †

SOMMAIRE

RÉSUMÉ

Enclave herbacée dans l'étage montagnard forestier, la prairie d'altitude du Loma doit son origine et sa pérennité, non pas au climat, mais au feu. Elle s'est substituée à une forêt basse — maquis à *Dissotis leonensis* — trouée de clairières édaphiques où, depuis des âges reculés, se sont perpétués des orophytes non forestiers. En refoulant cette forêt vers les hauts sommets rocheux, le feu a favorisé l'extension de la prairie et, partant, la savanisation de l'étage culminal.

I — LA DORSALE LOMA-MAN

Aspects physiques et biogéographiques

A quelques 250 km de la côte du golfe de Guinée, et parallèlement à elle, une ligne de hauts reliefs s'étire d'une façon subcontinue en direction NW-SE, depuis les contreforts orientaux du Fouta-Djalon jusqu'aux hauteurs de Man en Côte d'Ivoire, soit une distance de 350 à 400 km. Il s'agit de la dorsale Loma-Man ou chaîne guinéenne (44). Elle est formée d'une succession de plateaux et de massifs sans direction orographique prédominante où «au premier
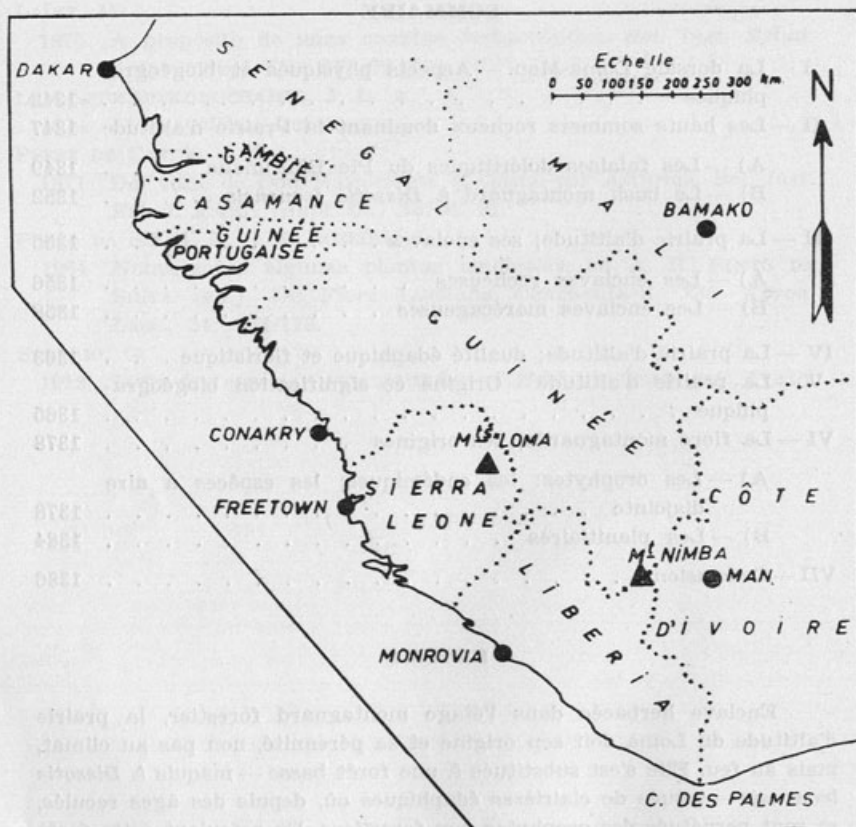

Fig. 1. — Les monts Loma dans le cadre géographique ouest africain.

abord l'observateur ressent une impression de confusion et de désordre» (83).

Cette chaîne s'inscrit à l'intérieur du bouclier libérien d'âge précambrien; elle constitue une unité orographique qui par A. AUBRÉVILLE fut définie comme le sous-domaine afro-montagnard occidental (12). Caractérisés, sur le plan floristique par un important fond commun, chacun des massifs de cette chaîne — Loma, Fon, Simandou, Ziama, Nimba, Dans — se distingue néanmoins, sur le plan physique et biogéographique, par une «personnalité» qui lui est propre.

En raison de l'inclinaison NW-SE de l'axe de la dorsale, ses deux extrémités se trouvent décalées quant à leur latitude: alors que le Loma et le Nimba s'étirent respectivement entre 9°00 à 9°17′ et 7°25′ à 7°45 LN, la localité de Man se situe par 7°24′ LN. Il en résulte de l'Est à l'Ouest un amenuisement progressif de la pluviosité et, partant, un appauvrissement de la flore en espèces ombrophiles. La dorsale Loma-Man culmine en Sierra Leone au Pic Bintumane (monts Loma) à 1924 m[1] qui, de ce fait, est le sommet le plus élevé de l'Afrique occidentale à l'ouest de la chaîne camerounaise. Le Nimba, à cheval sur la Guinée, la Côte d'Ivoire et le Libéria, plafonne au mont Richard-Molard à 1752 m; grâce aux travaux de R. SCHNELL et de J. G. ADAM (119; 2), il est actuellement le massif ouest africain le mieux connu quant à sa flore et sa végétation. Le Fon-Simandou atteint 1656 m et le Ziama culmine à 1350 m au mont Ghali. Près de Man, en Côte d'Ivoire, le massif des Dans est constitué par tout un ensemble de dômes rocheux étudiés successivement par A. CHEVALIER et par A. AUBRÉVILLE: le mont Dou (1370 m), le Tonkoui (1190 m), le mont Momy (1180 m). Le Nimba, affecté par des plissements antécambriens est formé, essentiellement, de schistes et de quartzites redressés, le tout fortement ferruginisé. D'un bout à l'autre ce massif est dominé par une crête étroite taillée en «lame de

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[1] Valeur obtenue à la suite de 9 lectures du point d'ébullition de l'eau bidistillée effectuées à plusieurs jours d'intervalle, en oct.-nov. 1944, au sommet du Pic Bintumane.

couteau ébréchée» limitée, de part et d'autre, par d'abrupts versants herbeux (119; 78).

Orienté parallèlement par rapport au Nimba mais situé, contrairement à celui-ci, à latitude moins basse et au nord
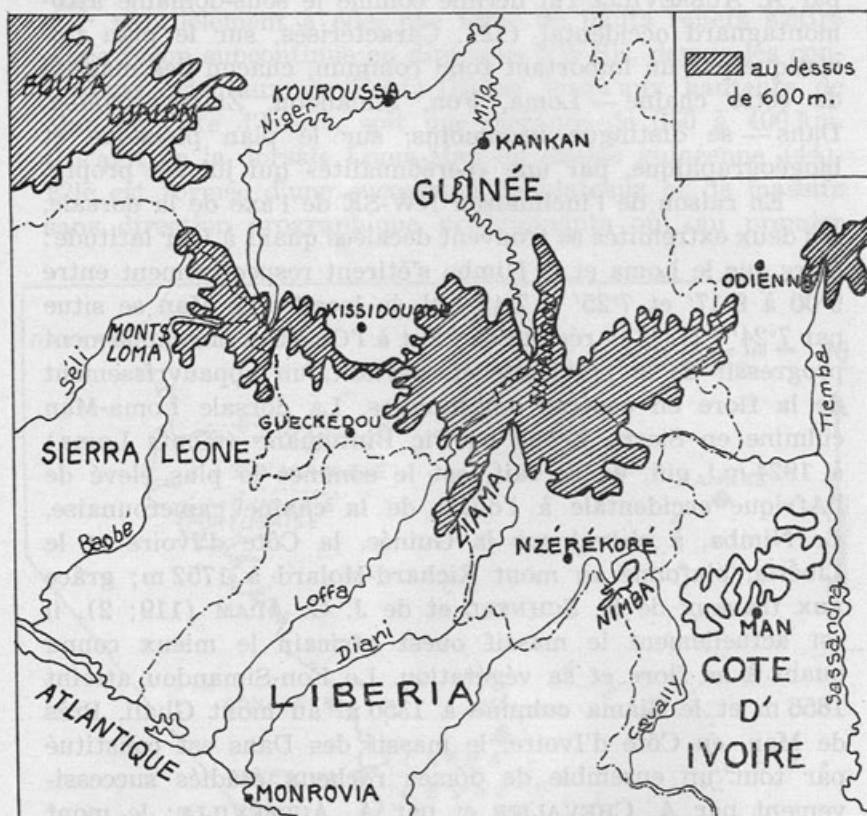
Fig. 2. — La dorsale Loma-Man et la partie orientale du Fouta-Djalon
(d'après P. JAEGER, M. LAMOTTE et R. ROY).

de la limite actuelle de la forêt dense, le massif du Loma, quelques venues doléritiques mises à part, est d'une ossature essentiellement granitique. Il est constitué par la juxtaposition de quatre blocs montagneux alignés du nord au sud, séparés les uns des autres par des cassures, souvent vives, drainées par des cours d'eau torrentiels (v. fig. 3).

Le bloc septentrional, le plus élevé, correspond à la puissante pyramide du Pic Bintumane; elle est couronnée par un minuscule plateau sommital limité au Sud, à l'Ouest et au Nord par d'abruptes coulées doléritiques.

Au Sud d'une cassure drainée en sens inverse par les eaux du Kongbundu et du Neji, s'étale une vaste étendue d'allure quadrangulaire (4 à 5 × 5 à 6 km), le Plateau. Il est limité à l'Est et à l'Ouest par des pentes raides et drainé, dans le sens nord-sud, par toute une série de ruisselets à cours grossièrement parallèles, le Miramira étant le plus proche du rebord oriental (v. fig. 5).

Au Plateau qui est par excellence le domaine de la prairie d'altitude fait suite, vers le Sud, la région la plus accidentée du massif où se dressent les dômes granitiques du Serelen-Konko (1480 m) et du Sarabaldou (1330 m), ainsi que les crêtes rocheuses en dents de scie du Da-Oulen (1470 m) et du Fuen-Koli (1400 m) (v. fig. 5).

Enfin, le massif s'achève au Sud, au-delà de la vallée du Wuliko, par un haut plateau orienté SW-NE qui, vers son extrémité orientale, est dominé par la coupole granitique du Peran-Konko (860 m).

A. AUBRÉVILLE (6; 12) et R. SCHNELL (119) ont fait remarquer que dans les massifs montagneux de la dorsale Loma-Man la végétation climacique «tant sur les crêtes que dans les régions basses» est de nature forestière. L'individualisation au-dessus de 1000 m-1200 m de forêts montagnardes à *Parinari excelsa* permet à ces auteurs de définir, dans ces montagnes, deux étages de végétation: un étage guinéo-équatorial inférieur occupé par le forêt dense humide de basse altitude et un étage guinéo-équatorial supérieur ou étage à *Parinari excelsa,* parfois désigné sous le nom d'étage culminal, occupé à la fois par la forêt montagnarde (71) et par la prairie montagnarde elle même dominée, au Loma, par quelques hauts sommets rocheux.

Vers sa limite supérieure la forêt montagnarde s'effiloche en une série généralement divergente de trainées arborées, les galeries forestières d'altitude; le plus souvent disposées en éventail, elles jalonnent le thalweg humide des vallées et des ravins, escaladent les pentes herbeuses les plus
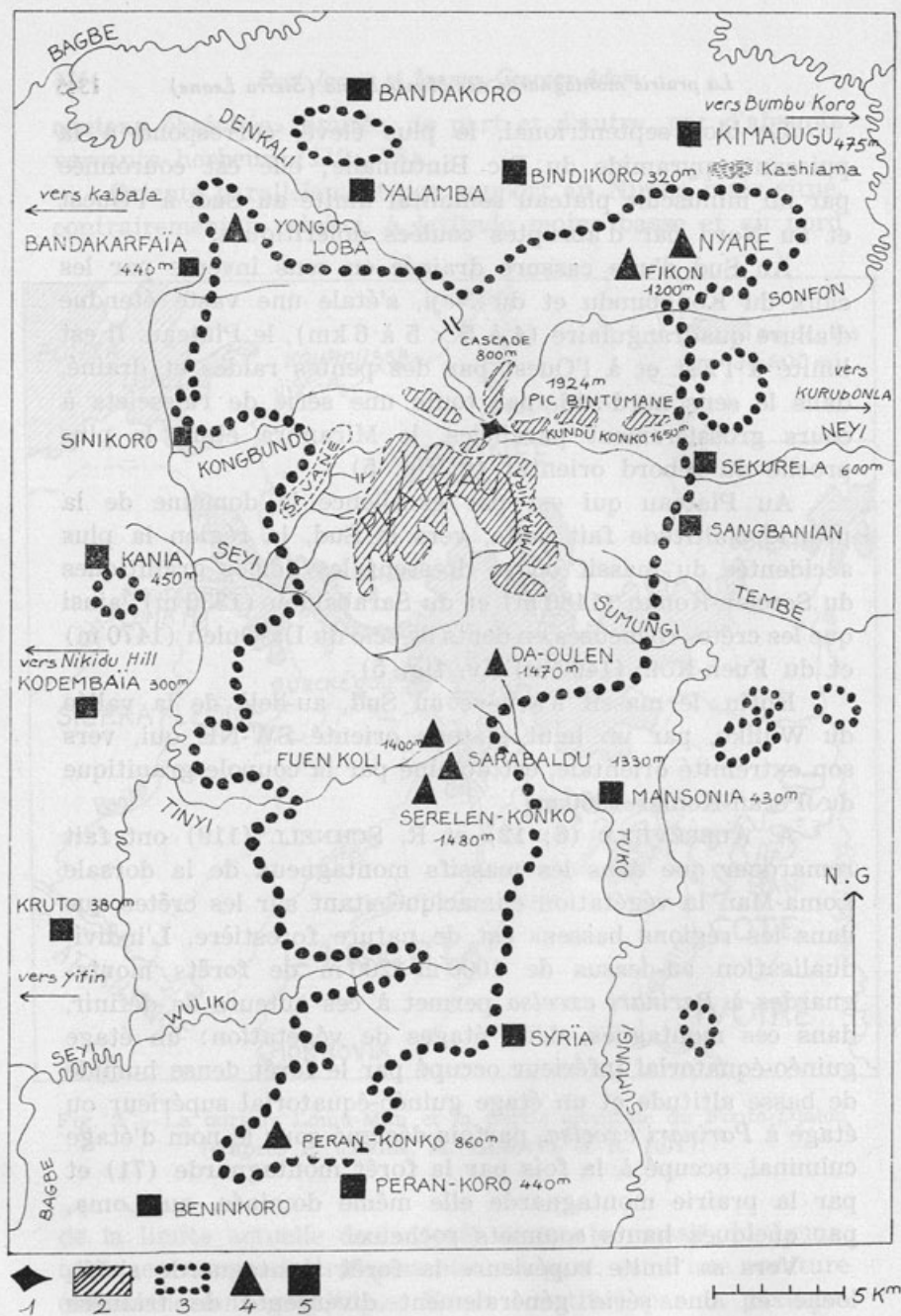
Fig. 3. — Le Massif des Monts Loma (carte semi-schématique d'après
S. DAVEAU; modifié).

1 — Pic Bintumane; 2 — Eperons du Pic Bintumane et Plateau;
3 — Limites du Massif; 4 — Sommets; 5 — Villages.

raides pour, finalement, se dissoudre dans la prairie montagnarde bien avant d'avoir atteint les sommets (v. fig. 4).

En raison de son orientation subméridienne et, partant, de son exposition aux vents dominants, mousson et harmattan, on n'est nullement suppris de constater qu'au Loma la forêt couvre d'un seul tenant non seulement l'ensemble des versants ouest et sud-ouest, mais aussi une grande partie du massif au Sud du Plateau, à l'exception toutefois des hauteurs qui ceinturent le Serelen-Konko, secteur soumis au vent d'Est.

Il en va différemment du versant oriental qui reçoit l'harmattan de plein fouet; là le manteau forestier a été morcelé en lambeaux d'étendue variable, séparés les uns des autres par des couloirs herbeux, tantôt larges, tantôt étroits, occupés jusque vers 1000 m par la savane guinéenne banale à *Lophira lanceolata, Parkia biglobosa, Pterocarpus erinaceus, Cussonia barteri...* et, au-delà, par la savane submontagnarde à *Kotschya lutea* avant de déboucher sur la prairie d'altitude; ce sont là autant de voies qu'empruntent les feux pour accéder à l'étage culminal et même jusqu'au sommet du Pic Bintoumane (v. fig. 6).

La présente note est consacrée à l'étude de l'étage supérieur du Loma et, plus spécialement, à celle de la prairie montagnarde et des sommets rocheux qui l'encadrent, la forêt ayant fait l'objet d'un travail antérieur (71). De plus, en cours d'étude une certaine importance est accordée aux orophytes, à ces végétaux qui trouvent en altitude les conditions optimales à leur survie; on tâchera de répondre aux problèmes que posent leur répartition, leur origine, leur signification biogéographique.

II — LES HAUTS SOMMETS ROCHEUX DOMINANT LA PRAIRIE D'ALTITUDE

Une des originalités du Loma réside en la présence autour de la Prairie d'altitude de quelques hauts sommets rocheux ayant donné asile à des orophytes, espèces résiduelles ou endémiques. Comme au cours des époques révolues des échanges ont dû se faire entre ces sommets et la prairie située en contre-bas, la signification biogéographique de

Vallée du Dankali

*Pic Bintumane
(Monts Loma)
Versant Nord-ouest
d'après J.G. Adam*

Fig. 4. — Versant NW du Pic Bintumane (au fond); bassin de réception du Denkali avec cascade vers 800 m (J. G. ADAM dess. oct. 1944).

celle-ci n'apparaitra en pleine lumière que grâce aux données fournies par les hauts somemts qui l'encadrent.

Parmi ceux-ci nous distinguerons d'une part les abruptes dolériritiques qui ceinturent le Plateau sommital du Pic Bintumane et, d'autre part, les dômes granitiques du Serelen-Konko, du Sarabaldou et les crêtes déchiquetées, également de nature granitique, du Da-Oulen et du Fuen Koli.

A)   Les à-pics dolériritiques du Bintumane

Dans tout le massif du Loma il n'y a pas d'affleurement dolériritique aussi spectaculaire que celui des falaises qui limitent le plateau sommital du Pic Bintumane; particulièrement développés face à l'Ouest, au Sud et au Sud-ouest, ces abrupts sont soumis à un mode d'usure qui se traduit à la fois par le débit dans le sens vertical et dans le sens transversal des colonnes basaltiques. Il en résulte, principalement vers le sommet de ces colonnes, une superposition de blocs rocheux dont certains semblent en équilibre instable (70) (v. photo 9).

Ainsi se créent, tant dans le sens vertical que dans les sens horizontal, toute une série de fentes, de crevasses, d'anfractuosités; certaines, en s'élargissant, forment des cavités ombragées dont les parois suintantes témoignent d'un microclimat frais et humide; elles se garnissent d'un placage d'Hépatiques *(Plagiochasma* sp.) et de coussinets de Mousses *(Polytrichum* sp.); ce milieu s'avère éminemment favorable aux Fougères: *Dryopteris manniana, D. pentheri, D. athamantica;* on y remarque aussi des herbacées comme: *Arthraxon lancifolius, Utricularia* sp... des orophytes à aire disjointe comme *Cyperus mannii, Streptocarpus elongatus, Pilea tetraphylla, Pouzolzia parasitica, Lobelia heyneana* var. *inconspicua...* dans ce cortège se range aussi le *Cheilanthes farinosa,* une Fougère pantropicale, réviviscente, aux frondes subtriangulaires étalées par temps humide et recroquevillées sur elles-mêmes par temps sec; à ce moment devient visible sa face inférieure enduite d'une sécrétion cireuse blanchâtre.

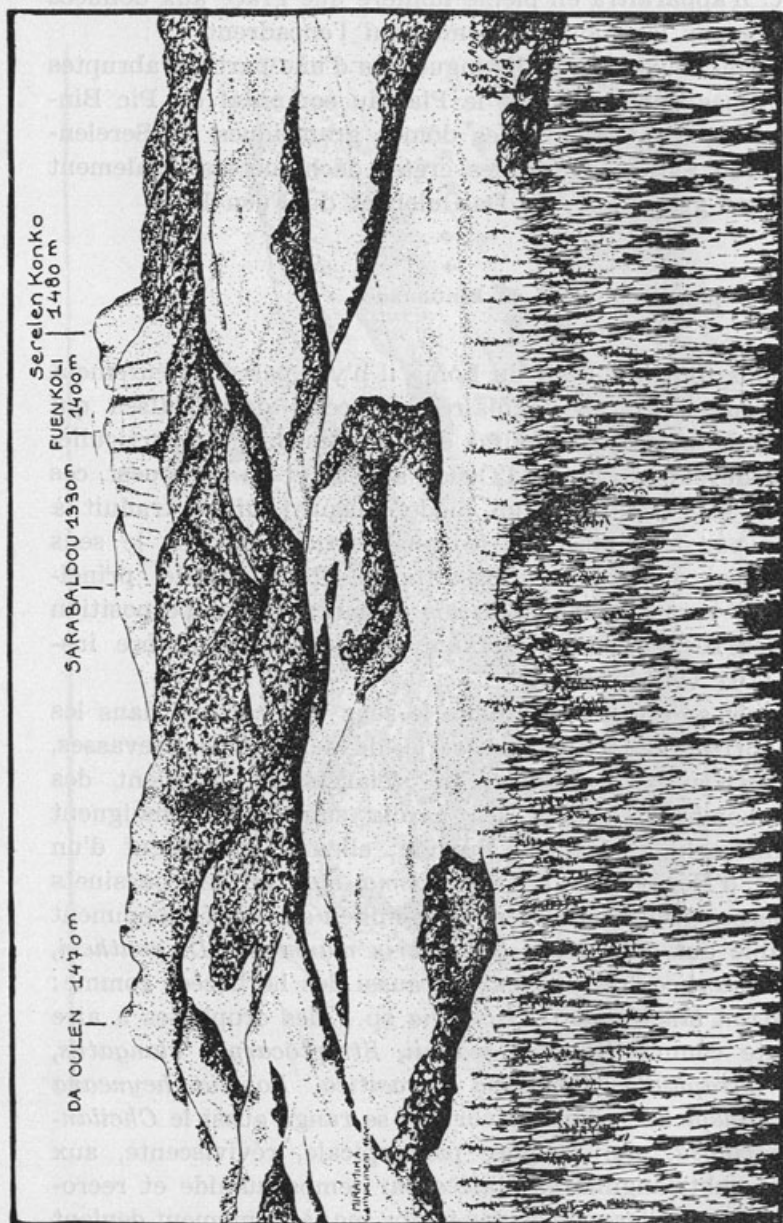Fig. 5. — Vue prise de la pente Sud du Pic Bintumane sur la fraction orientale du Plateau et sur les massifs du centre des monts Loma (J. G. ADAM dess. nov. 1965).

Fig. 6. — Vallée du Neji: vue des abords de Sekurela (piedmont E vers 600 m). Remarquer les galeries forestières d'altitude escaladant le versant Sud du Kundu-Konko; au fond la table doléritique du Pic Bintumane (J. G. ADAM dess. nov. 1965).

La formation, à divers niveaux de la falaise, de rebords subhorizontaux est propice à l'installation de saxicoles héliophiles comme *Afrotrilepis pilosa, Gladiolus aequinoctialis* var. *aequinoctialis* et d'autres orophytes comme *Gynura miniata, Conyza gigantea, Anisopappus africanus, Homalocheilos ramosissimus*...

Enfin, la falaise peut être interrompue et céder la place à des corridors herbeux à forte pente reliant le pied des escarpements à la prairie du plateau sommital; là on remarque, les plantes banales de la prairie montagnarde mises à part, des orophytes aussi significatives quant à leur répartition géographique que: *Pennisetum monostigma, Rhytachne glabra, Andropogon mannii, Tripogon major* subsp. *jaegerianus, Nerophila gentianoides*...

B) Le Bush Montagnard à Dissotis leonensis

Les hauts sommets à soubassement granitique abritent une des plus étonnantes originalités du Loma: *le Bush montagnard* à *Dissotis leonensis.* Cette Mélastomatacée se présente sous la forme d'un arbrisseau ramifié dès la base; sa couronne, quand elle se développe sans entraves, prend l'aspect d'une boule hémisphérique de 2 à 3 m de diamètre, posée à même la dalle; elle rappelle en cela les «Kugelschirmbäume», de C. TROLL (130). En peuplement, ces couronnes, serrées côte à côte, sont à l'origine de cet aspect moutonnant connu des forêts à *Parinari,* mais qui, dans le cas présent, est rendu plus frappant encore par la couleur cendrée du feuillage. En saison sèche (déc.-janv.) les feuilles, toutes insérées à la périphérie de la couronne, se colorent en un rouge vineux avant de tomber, pour être remplacées pour peu de temps, par de grandes fleurs (3 à 3,5 cm diam.) inodores, d'un rouge rosé. La richesse en épiphytes (Mousses, Usnées et autres Lichens) est une réplique à l'humidité excessive qui, en saison pluvieuse, règne sur ces hauteurs (v. photo 12).

Sur les hauts sommets au sud du Plateau, le *Dissotis leonensis* forme des fourrés à allure de maquis. Son extrême sensibilité au feu se traduit fréquemment par une dislocation
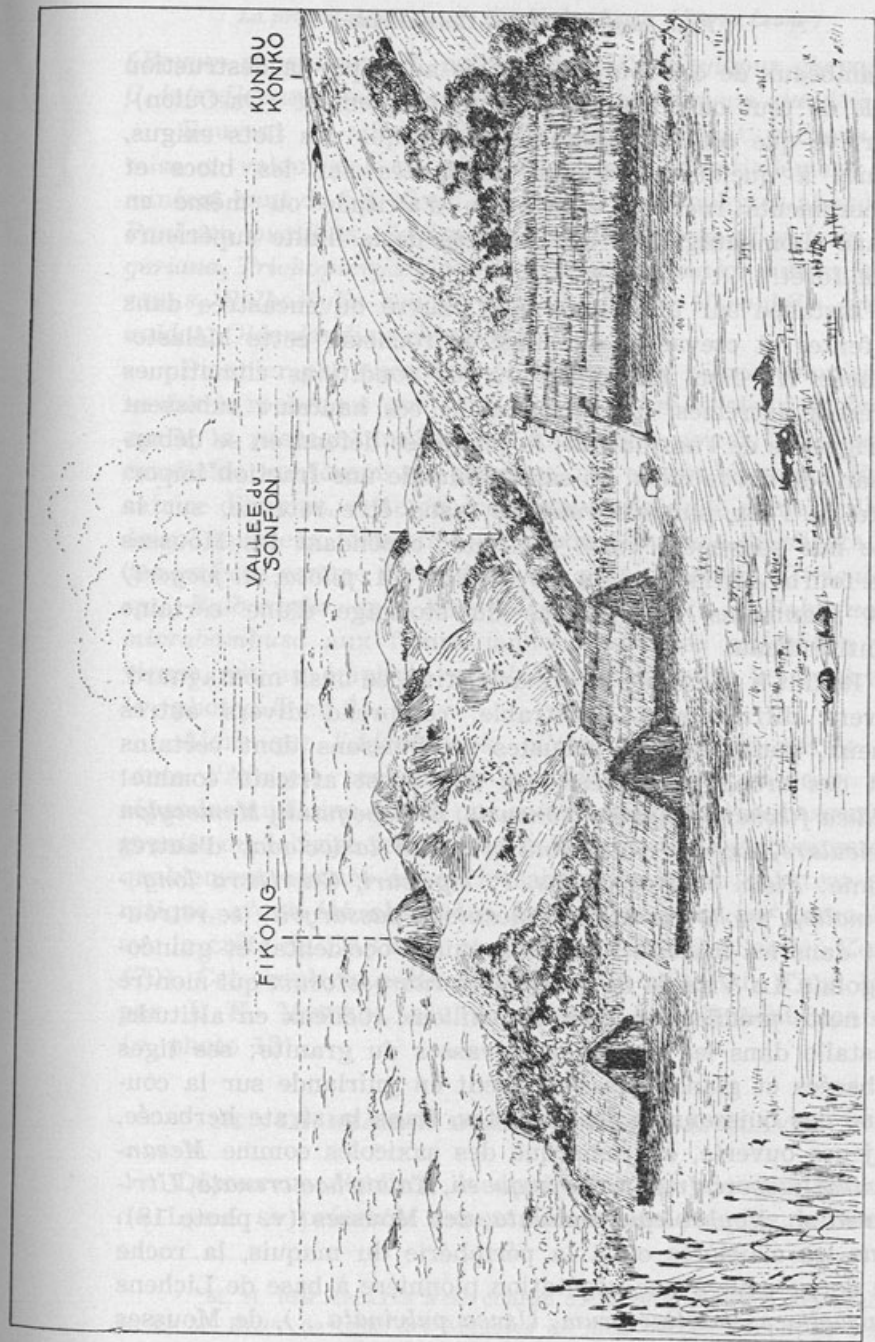
Fig. 7. — Vue de la pente herbeuse à exp. NE du Pic Bintumane (1500 m) sur une fraction de la façade N du Loma dominée par le dôme en pain de sucre du Fikong (1200 m). L'extrémité E du Kundu-Konko est séparée de la façade N par la vallée du Sonfon dont les eaux proviennent du plateau sommital du Pic Bintumane (J. G. ADAM dess. oct. 1944).

en lambeaux de ces fourrés, parfois aussi par la destruction totale de tout ou d'une partie d'un peuplement (Da-Oulen). Il arrive que cet arbrisseau ne forme que des îlots exigus, réduits à quelques individus implantés sur les blocs et affleurements rocheux en prairie d'altitude ou même en savane submontagnarde bien en-deçà de la limite supérieure de la forêt.

Installée sur un sol arénacé pauvre ou encastrée dans les fentes et crevasses du substrat rocheux, cette Mélastomatacée vit dans un milieu où les conditions climatiques s'avèrent extrêmes. En saison sèche ces hauteurs subissent les rigueurs de l'harmattan; la plante se défend en se débarrassant de ses feuilles; en saison humide une fraction importante de l'eau pluviale ruisselle, sans être retenue, sur la dalle nue souvent à forte déclivité; cependant les Mousses et la tourbe édifiée par les *Afrotrilepis (A. pilosa, A. jaegeri)* sont néanmoins responsables du stockage d'une certaine quantité d'eau.

Réduit à une seule strate arbustive, ce bush montagnard, souvent difficilement pénétrable, comprend divers autres ligneux, petits arbres, arbustes ou buissons dont certains sont des orophytes endémiques de l'ouest africain comme: *Peddiea fischeri, Eugenia leonensis, E. pobeguinii, Memecylon fasciculare, Leocus pobeguinii, Pavetta lasioclada;* d'autres comme: *Ficus eriobotryoides, F. leprieuri, Gaertnera longevaginalis, Psychotria calva, Vincentella passargei...* se retrouvent dans les massifs forestiers guinéo-occidental et guinéo-congolais. La Vitacée *Cyphostemma rubrosetosum* qui montre une nette prédilection pour les milieux rocheux en altitude, s'installe dans les fentes et crevasses du granite; ses tiges herbacées et glanduleuses s'étalent en guirlande sur la couronne des buissons et des arbustes. Dans la strate herbacée, toujours ouverte, on remarque des saxicoles comme *Mesanthemum jaegeri, Impatiens jacquesii, Kalanchoe crenata, Utricularia* sp. *Nephrolepis undulata,* des Mousses (v. photo 18). Dans les clairières ou à la périphérie du maquis, la roche nue donne asile à une végétation pionnière à base de Lichens *(Parmelia pseudotinctorum, Usnea pulvinata...),* de Mousses

(Bryum argenteum, B. petrophilum, Canphylopus chevalieri, C. introflexus, Leucoloma sericeum, Rhodobryum staudtii...)[1].

Souvent la microtopographie du substrat rocheux est mise en valeur par un minuscule gazon essentiellement graminéen, haut de 5 à 15 cm à peine où les orophytes abondent: *Panicum pusillum, Schizachyrium djalonicum, Loudetia jaegeriana, Trichopteryx glanvillei, Tripogon major* subsp. *jaegeranus, Bulbostylis congolensis, B. densa, Nerophila gentianoides, Oldenlandia echinulosa...*

Pionnier par excellence, l'*Afrotrilepis pilosa* colonise les surfaces rocheuses quel que soit le degré de leur déclivité; après le passage du feu ses touradons noircis et d'aspect coralloïde confèrent au paysage un aspect étrange. Edificatrice d'humus, cette espèce recouvre la dalle d'une pellicule de sol tourbeux, détrempé en saison pluvieuse où s'installent des espèces comme *Mesanthemum prescottianum, Utricularia* sp., *Bulbostylis* sp., *Nephrolepis undulata... Polystachya microbambusa* aux fleurs jaunes épanouies en saison pluvieuse, vit en épiphyte sur les touradons de la Cypéracée (v. photos 5 et 6).

Alors que l'*Afrotrilepis pilosa* dont l'aire s'étale sur toute l'Afrique occidentale humide est une saxicole très répandue au Loma quelle que soit la nature du soubassement, granite ou dolérite, les mottes de l'*Afrotrilepis jaegeri,* remarquablement ajustée au cycle saisonnier et au substrat granitique, n'ont été observées jusqu'à ce jour au Loma que sur la crête du Da-Oulen et sur les pentes du Serelen-Konko (70). Cet orophyte a été récolté par la suite aux Tingi Hills par J. K. Morton, seules stations actuellement connues (v. photo 15).

III — LA PRAIRIE D'ALTITUDE. SES ENCLAVES

Dépourvue d'arbres et d'arbustes, la prairie d'altitude du Loma se présente comme une vaste étendue herbeuse,

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[1] M. H. des Abbayes s'est chargé de la détermination des Lichens et M. M. Bizot de celle des Mousses de mon herbier Loma; je les en remercie très vivement.

formée essentiellement d'espèces vivaces, suffrutescentes et herbacées où les Graminées jouent la note dominante. Ces étendues sont cependant loin d'être d'une seule pièce; abstraction faite des trainées arborées à *Parinari excelsa* qui jalonnent les cours d'eau du Plateau, le tapis prairial est disloqué par de nombreuses enclaves, rocheuses ou marécageuses.

A) Les enclaves rocheuses

D'imposants blocs granitiques, isolés ou groupés, sont éparpillés à travers la prairie altimontane; et souvent le tapis végétal est dilacéré par l'affleurement de dalles rocheuses.

Les blocs granitiques, habituellement fracturés par des cassures verticales ou horizontales, donnent asile à des touffes arborées formées de buissons ou de petits arbres où, à côté de *Nuxia congesta, Hymenodictyon floribundum, Clausena anisata...* nous retrouvons de nombreux représentants du bush montagnard des sommets granitiques, à savoir: *Dissotis leonensis, Memecylon fasciculare, Eugenia leonensis, E. pobeguinii, Pavetta lasioclada...* Ces îlots, fragments minuscules du maquis à *Dissotis leonensis,* témoignent des échanges qui ont dû se faire à certaines époques, entre le «réservoir» sommital et la prairie située en contre-bas.

Blocs et dalles rocheuses donnent asile à une végétation pionnière où nous retrouvons les saxicoles héliophiles, Lichens et Mousses déjà inventoriées sur les sommets granitiques. Sur la tourbe à *Afrotrilepis pilosa,* Cypéracée tout aussi fréquente ici que sur les crêtes, on remarque la présence du *Gladiolus leonensis,* une endémique du Loma dont les fleurs blanches et penchées s'épanouissent dès les premières ondées d'avril (photo 16). Dans ce même milieu a élu domicile l'*Oxyrachis gracillima* subsp. *occidentalis,* Graminée aux feuilles capillaires et d'un vert cendré; cet orophyte, connu de l'Est africain et de Madagascar, atteint au Loma la limite occidentale de son aire de répartition.

A même le roc, et parfois sur ses parois verticales, dans un milieu d'une sécheresse extrême, s'étalent les racines du

Fig. 8. — Bloc granitique fracturé de part en part. Prairie d'altitude vers 1600 m — Mts. Loma. (K. WATRÉ dess. d'après photo P. JAEGER).

Polystachya dalzielli, dont les fleurs lilacées, très voyantes, se montrent au plus fort de la saison sèche; d'autres Orchidées comme *Bulbophyllum bifarium, B. scariosum...* ont un comportement analogue; il est vrai que pour affronter les rigueurs de la saison sèche, ces plantes disposent des réserves hydriques stockée dans leurs pseudobulbes.

Le *Gladiolus aequinoctialis* var. *aequinoctialis* profite des moindres fissures du roc pour abriter son bulbe, et il en est de même du *Polystachya bequaertii,* une endémique ouest africaine. Les fleurs très voyantes, blanches, striées de rouge, penchées et inodores de l'Iridacée sont épanouis au plus fort de la saison pluvieuse; la reproduction sexuée par graines est complétée utilement par une active multiplication végétative (bulbiles) (68) (v. fig. 12).

Les cassures horizontales de blocs rocheux (70), véritables abris ombragés et humides sont le lieu d'élection de diverses espèces à tempérament sciaphile; on y remarque des Ptéridophytes comme *Dryopteris athamantica, Nephrolepis undulata, Notholaena inaequalis* une fougère réviviscente, des *Sélaginelles;* parfois, à l'entrée même de ces crevasses se dressent, alignés en une rangée fleurie (novembre), des pieds de *Kalanchoe crenata,* l'unique Crassulacée de notre massif.

B) Les enclaves marécageuses

Parmi les dalles granitiques afleurantes il y en a qui sont suintantes; d'autres, légèrement inclinées, sont couvertes d'un film d'eau courante; d'autres enfin, à pente plus raide, sont à l'origine de cascades ou de cascadelles aux eaux torrentielles. Les dalles à forte déclivité et, partant, à courant rapide, sont favorables à l'implantation d'une Lentibulariacée remarquablement adaptée au milieu: *Utricularia tetraloba.* Cette herbe aquatique de taille minuscule (0,5 à 1 cm) est solidement amarrée au substrat rocheux par l'intermédiaire de crampons; les feuilles, toutes submergées, sont pourvues d'utricules et les fleurs, aériennes, d'un blanc crème, petites et odorantes, sont entomophiles; les graines se gélifient au contact de l'eau en une masse mucilagineuse qui adhère au

substrat. Cette Utriculaire forme de vastes colonies herbacées orientées dans le sens du courant; elles sont repérables au loin au moment de la floraison. Cette espèce endémique de l'ouest africain est proche de l'*U. rigida,* observée par nous dans les cascades du massif de Kita (Mali).

Rappelons qu'au Loma les cascades sont favorables à l'implantation des Podostémonacées. Ainsi, le *Tristicha trifaria* fut observé vers 1280 m au sommet de la grande cascade du versant ouest dans un microgazon muscinal léché par les eaux agitées, et le *Ledermanniella jaegeri* s'installe dans le lit du Miramira vers 1400 m sur des blocs granitiques temporairement exondés. Quand la déclivité de la dalle va en s'amenuisant, des coussinets de Mousses s'implantent; ils sont séparés les uns des autres par une pellicule de sol noirâtre et détrempé, véritable marécage temporaire à sec en dehors de la saison pluvieuse. Là on remarque, associé à des Algues: *Utricularia subulata, U. pubescens, Genlisea africana, Eriocaulon pulchellum, Mesanthemum auratum, Xyris festucifolia, Sebaea luteo-alba, Nemum bulbostylidoides, Panicum pusillum...* L'amenuisement de la pente se poursuivant, les coussinets muscinaux entrent en coalescence pour former un gazon continu, toujours humide, où prolifèrent des espèces hygrophiles comme: *Polygala lecardii, Swertia mannii, Utricularia* sp., *Bulbostylis densa, Eragrostis cenolepis, Schizachyrium brevifolium, Anadelphia leptocoma, Lycopodium cernuum, Osmunda regalis, Smithia ochreata ;* de là on passe, suivant les cas, à la prairie montagnarde ou à un chaos de blocs rocheux donnant asile à: *Afrotrilepis pilosa, Nerophila gentianoides, Dissotis leonensis, Leocus pobeguinii, Eugenia leonensis, Nuxia congesta, Hymenodictyon floribundum...*

Particulièrement intéressante s'avère l'étude d'une enclave marécageuse située vers l'extrémité supérieure de la galerie forestière du Miramira (1650 m). L'emplacement est marqué par la présence d'un ensemble de touradons herbeux, verdâtres, subcylindriques hauts de 50 à 75 cm, séparés les uns des autres par un intervalle subhorizontal (de 0,5 à 2 m) drainé par des filets d'eau claire et limpide;

le sol vaseux, détrempé et de couleur noire est épais de quelques centimètres à peine.

Le sommet des touradons qui représente la partie la moins détrempée est occupé par des herbacées caractéristiques des biotopes humides comme: *Pycreus nuerensis, Eragrostis cenolepis, Lipocarpha chinensis, Xyris decipiens...* Les parois subverticales des touradons de plus en plus humides à mesure qu'on s'approche de leur base et surtout la zone intermédiaire subhorizontale et fortement marécageuse, est caractérisée par la présence d'espèces héliophiles comme: *Drosera pilosa, Genlisea africana, Utricularia subulata, U. pubescens, Eriocaulon pulchellum, Xyris* sp....; de plus, les tiges flasques du *Lobelia rubescens* (proche de *L. kamerunensis*), herbe couchée-ascendante, serpentent d'un touradon à l'autre à la surface des sols spongieux et humides.

Il en est de même de celles, couleur rouille, du *Laurembergia tetrandra;* enfin, les tiges dressées aux sommets penchés du *Lycopodium cernuum* se montrent dans les espaces séparant les touradons.

Le marécage du Sonfon

Le plateau sommital du Pic Bintumane où le Sonfon prend sa source, est légèrement creusé en auge; ses pentes, très douces, sont drainées par des filets d'eau qui convergent en un thalweg médian occupé en partie par un marécage d'où s'échappent les eaux du Sonfon. Avant de dévaler les pentes herbeuses à exposition NE du Pic Bintumane, elles passent par un déversoir rocailleux marqué par la présence de: *Conyza gigantea, Otomeria cameronica, Dissotis sessilis...*

Dans le bassin sommital on voit affleurer, par endroits, des dalles doléritiques d'allure polygonale (50 à 100 cm); formant dallage, elles sont séparées les unes des autres par d'étroits sillons où s'est constitué un sol squelettique formé essentiellement de fragments doléritiques en voie d'altération, reconnaissables à leur coloration brunâtre en pain d'épice.

La surface des dalles exempte de toute altération chimique donne asile à une flore pionnière à base de Lichens,

de Mousses, de touradons d'*Afrotrilepis pilosa*... Sur les coussinets de Mousses on voit s'installer: *Cyanotis rupicola, Solenostemon* sp...; *Nerophila gentianoides* est loin d'être rare (v. photo 8).

A la fin des pluies (oct.) le marécage du Sonfon présente un sol noir détrempé, recouvert, par endroits, d'une mince pellicule d'eau. Ce groupement, encore richement fleuri à cette époque de l'année, est repérable au loin grâce à un peuplement de Cypéracées à allure joncoïde, et aux épillets d'un brun-noir luisant: *Pycreus atrorubidus, Nemum spadiceum, N. bulbostylidoides* une endémique de la dorsale Loma-Man. Au ras du sol on observe des plantes minuscules: *Eriocaulon pulchellum* (1 à 5 cm) à rosette de feuilles basales appliquées à même le sol et parfois couvertes d'un film d'eau; *Utricularia pubescens* aux fleurs d'un mauve violacé, *U. micropetala* var. *macrocheilos* aux fleurs jaunes; *Panicum* pusillum, une Graminée exiguë haute de 5 à 10 cm, *Xyris festucifolia* (10-15 cm); sont de taille plus importante: *Mesanthemum prescottianum, Scleria dieterlinii, Habenaria* sp. de la sect. *Bilabrella, Schizachyrium lomaense,* une endémique de la dorsale; à la périphérie en milieu moins humide, on note: *Swertia mannii, Cyanotis rupicola, Nerophila gentianoides, Afrotrilepis pilosa*...

Pendant les heures chaudes de la journée, le sol noir de cette cuvette marécageuse s'échauffe rapidement par rapport au milieu ambiant; cet échauffement est surtout appréciable aux emplacements où la végétation est clairsemée ou absente. Des mesures ont été réalisées le 6 Octobre 1966 par temps clair et ensoleillé, l'atmosphère étant agitée par un léger vent d'Est. La température de l'air a été mesurée au moyen du thermomètre fronde.

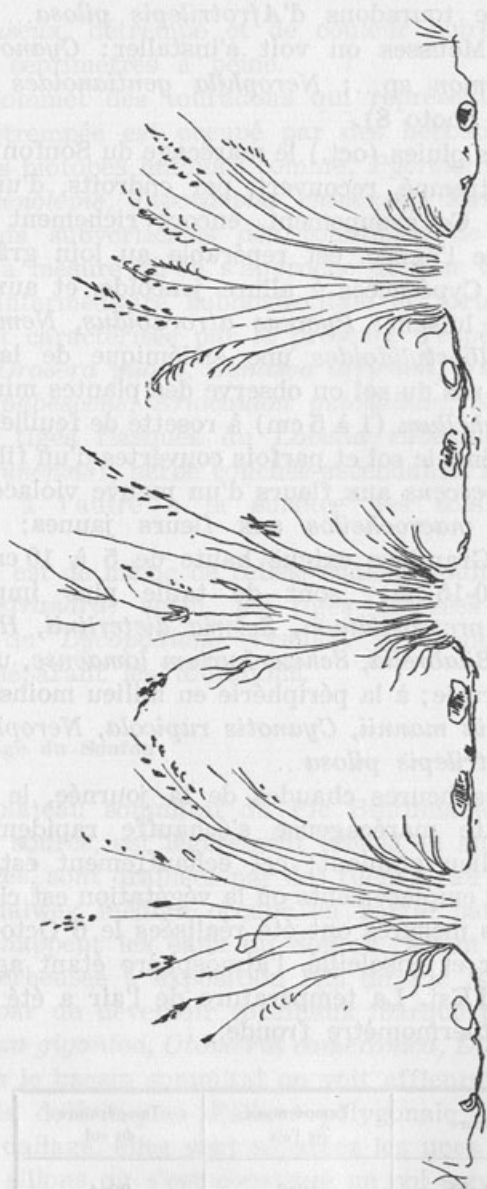| Heure	Température de l'air	Température du sol
11 00	18°8	22°4
12 45	19°4	30°6

Fig. 9. — Végétation graminéenne en touffes cespiteuses séparées les unes des autres par le sol nu persemé de cailloux ferrugineux. Prairie d'altitude du Plateau vers 1600 m (Mts. Loma).

IV — LA PRAIRIE D'ALTITUDE: DUALITÉ ÉDAPHIQUE ET FLORISTIQUE

Le tapis herbacé, essentiellement graminéen de la prairie d'altitude du Loma, abstraction faite des enclaves arborées, rocheuses ou marécageuses, est loin d'être homogène. En divers points du Plateau on remarque la présence de vastes «lambeaux cuirassés» affleurants ou subaffleurants. Nullement comparables quant à leur origine, aux cuirasses des bowé soudaniens, ces «pseudocuirasses» sont moyennement indurées et de couleur rouille; elles sont de structure alvéolaire et scoriacée avec de nombreux grains de quartz et quelques éléments ferromagnésiens, le tout amalgamé par des trainées ferrugineuses; en bref, l'ensemble se présente comme une arène granitique concrétisée par des venues ferrugineuses.

La «pseudocuirasse» et le sol squelettique chargé de concrétions qui en dérive, porte une prairie basse (50 à 70 cm), peu dense à *Loudetia Kagerensis;* les orophytes y abondent: *Cyperus nduru, Digitaria minutiflora, Panicum ecklonii, Rhytachne glabra, Protea occidentalis, Vernonia nimbaensis, Thesium tenuissimum, Sopubia mannii* var. *tenuifolia, Coreopsis camporum, Aristea angolensis, Helichrysum nudifolium* var. *leiopodium, H. mechovianum, Brachycorythis paucifolia...;* ainsi que trois des neufs endémiques appartenant en propre au Loma: *Digitaria minutiflora, D. phaeotricha* var. *patens, Loxodera strigosa* (v. fig. 11).

Côte à côte avec ces îlots cuirassés s'étalent de vastes étendues dépourvues d'horizons carapacés; les sols y sont plus profonds et pratiquement sans concrétions; la texture est sableuse (sables grossiers et fins: 65 %; limons 18,9 %, argile 9,5 %), et la valeur basse du C/N (7,3) parle en faveur d'une minéralisation active.

La strate herbacée, haute de 1,50 à 1,75 m (octobre), est constituée esentiellement de Graminées communes dans les savanes de piedmont; indifférentes à l'altitude, elles couvrent une aire souvent très vaste s'étendant ou dépassant parfois l'Afrique tropicale; citons: *Anadelphia afzeliana, Andropogon africanus, A. gayanus, A. schirensis, Beckeropsis*
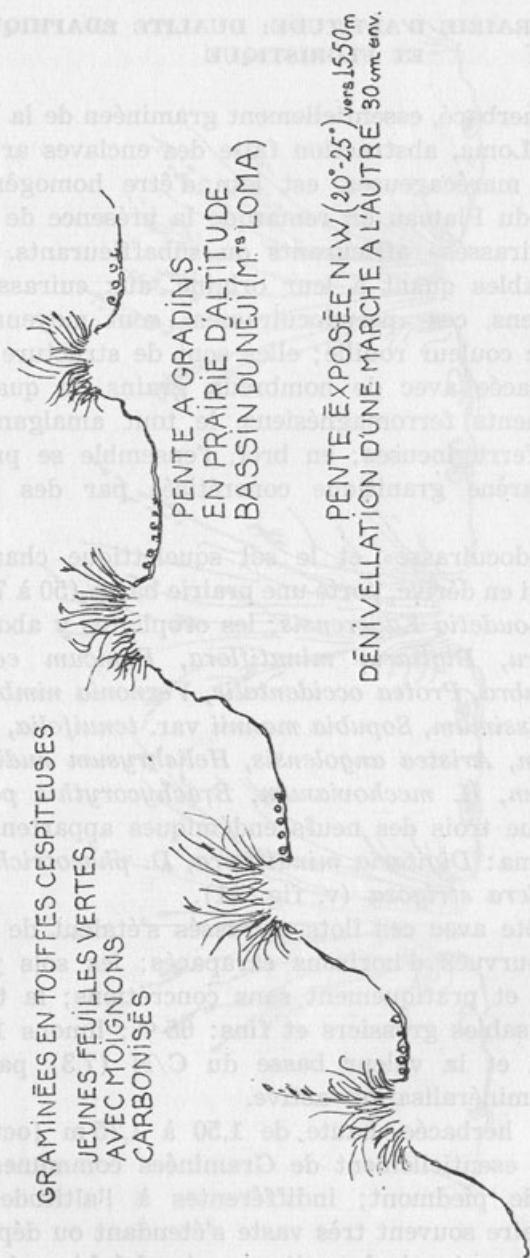
Fig. 10. — Pente à gradins en prairie d'altitude; bassin du Néji vers 1550 m (monts Loma).

uniseta, Digitaria diagonalis var. *hirsuta, Elymandra andro-phila, Hyparrhenia diplandra, H. rufa, Panicum praealtum...* Les orophytes sans être absents de ce cortège essentiellement graminéen ont, en grande partie, succombé dans la lutte contre la poussée envahissante de ces herbacées très compé-titives et grandement favorisées dans leur progression par la vague ignée.

V — LA PRAIRIE D'ALTITUDE

Origine et signification biogéographique

Pour ce qui est de ces étendues à sol profond, rien ne s'oppose, *a priori,* à l'installation de la forêt. Aussi la présence de ces vastes surfaces herbeuses, véritables enclaves dans l'étage forestier submontagnard, soulève-t-elle le problème de leur origine et de leur signification biogéographique.

Dans les monts Loma, comme dans les autres massifs de la dorsale guinéenne, la limite supérieure de la forêt se situe à une altitude inférieure à celle qu'elle occupe dans d'autres massifs montagneux plus élevés. Aussi est-il permis de penser que si les massifs de la chaîne guinéenne étaient plus hauts, la limite supérieure de leur forêt serait, elle aussi, portée à une altitude plus élevée.

Il y a cependant lieu de faire remarquer que vers leur extrémité supérieure les galeries forestières du Loma pré-sentent une physionomie qui n'est pas sans rappeler celle d'autres forêts tropicales arrivées à la limite de leur extension altitudinale. Ainsi, la similitude entre une tête de galerie faisant irruption dans la prairie montagnarde du Loma et celle, située vers 2000 m dans les monts Uluguru (Est africain), ne peut pas passer inaperçue. Dans les deux cas on passe brusquement, sans transition, de la forêt à la prairie et les arbres, surchargés d'épiphytes, aux couronnes hémis-phériques et au feuillage périphérique toujours vert, cons-tituent un type biologique — immergrüne Kugelschirmbäume de C. Troll — qui se correspond d'une région à l'autre. Cette coïncidence des types biologiques et du modelé de la forêt montagnarde parvenue à sa limite supérieure, nous

amène à supposer l'entrée en action de tout un ensemble de facteurs qui en auraient la responsabilité; ceux qui s'imposent avec le plus d'évidence seraient, à première vue, les agents climatiques exacerbés à proximité de la crête et des sommets. Au Loma, en raison de l'orientation de la chaîne, en raison aussi de son insularité, cette exacerbation semble se traduire avec un maximum d'acuité (71).

Cependant en altitude, où, en saison sèche, l'harmattan souffle avec impétuosité, ni le *Parinari excelsa,* ni la *Syzygium staudtii* n'adoptent de faciès vexillaire; mieux, contrairement à ce que l'on remarque en savane de piedmont où la plupart des essences sont défeuillées en saison sèche, ces deux arbres étonnent par la persistance de leur feuillage.

Il est communément admis que la végétation des savanes de l'Afrique intertropicale est d'origine secondaire. La végétation primitive, essentiellement forestière correspondant au *climax,* a été détruite par le feu et les défrichements c'est-à-dire par l'homme. La vague ignée en déferlant périodiquement durant des millénaires sur ces vastes étendues, a exercé une véritable sélection. N'ont survécu au traumatisme que les espèces préadaptées; parmi les ligneux, celles dont l'écorce était protégée par une épaisse couche de liège *(Karité, Bombax, Spondias...);* parmi les herbacées celles dont le cycle reproducteur était ajusté au rythme des feux, les graines étant déjà disséminées au moment de l'irruption de la vague ignée ou celles, comme les Graminées céspiteuses, dont les jeunes innovations sont protégées par un feutrage de gaines sèches; et il en est de même des bulbes, tubercules et rhizomes qui sont à l'abri sous une certaine épaisseur de sol (70).

Les non-adaptées, par contre, ont succombé à la lutte ou se sont réfugiées dans des stations inaccessibles aux feux; c'est le cas, entre autres, des peuplements de Kololo *Gilletiodendron glandulosum)* qui se sont maintenus dans les buttes gréseuses du Plateau mantingue (région de Kita) grâce à l'existence de parefeux naturels: les seuils rocheux.

Cette façon d'interpréter les faits, loin d'être une vue de l'esprit, fut défendue par des auteurs aussi avertis que Lane Poole, A. CHEVALIER, H. HUMBERT, A. AUBRÉVILLE,

CRÊTE
KUNDU-KONKO
E-W
1600m

VEGETATION CULMINALE à:
Nuxia congesta
Protea angolensis
Psorospermum alternifolium...

PSEUDO-CUIRASSE AVEC PRAIRIE-BASSE à:
Cyperus margaritaceus
Loudetia kagerensis
Lepargochloa glabra
Striga aequinoctialis...

ZONE DE LISIERE à:
Pteridium aquilinum
Maesa lanceolata
Dissotis capitata
Gleichenia linearis...

GALERIE FORESTIERE D'ALTITUDE à:
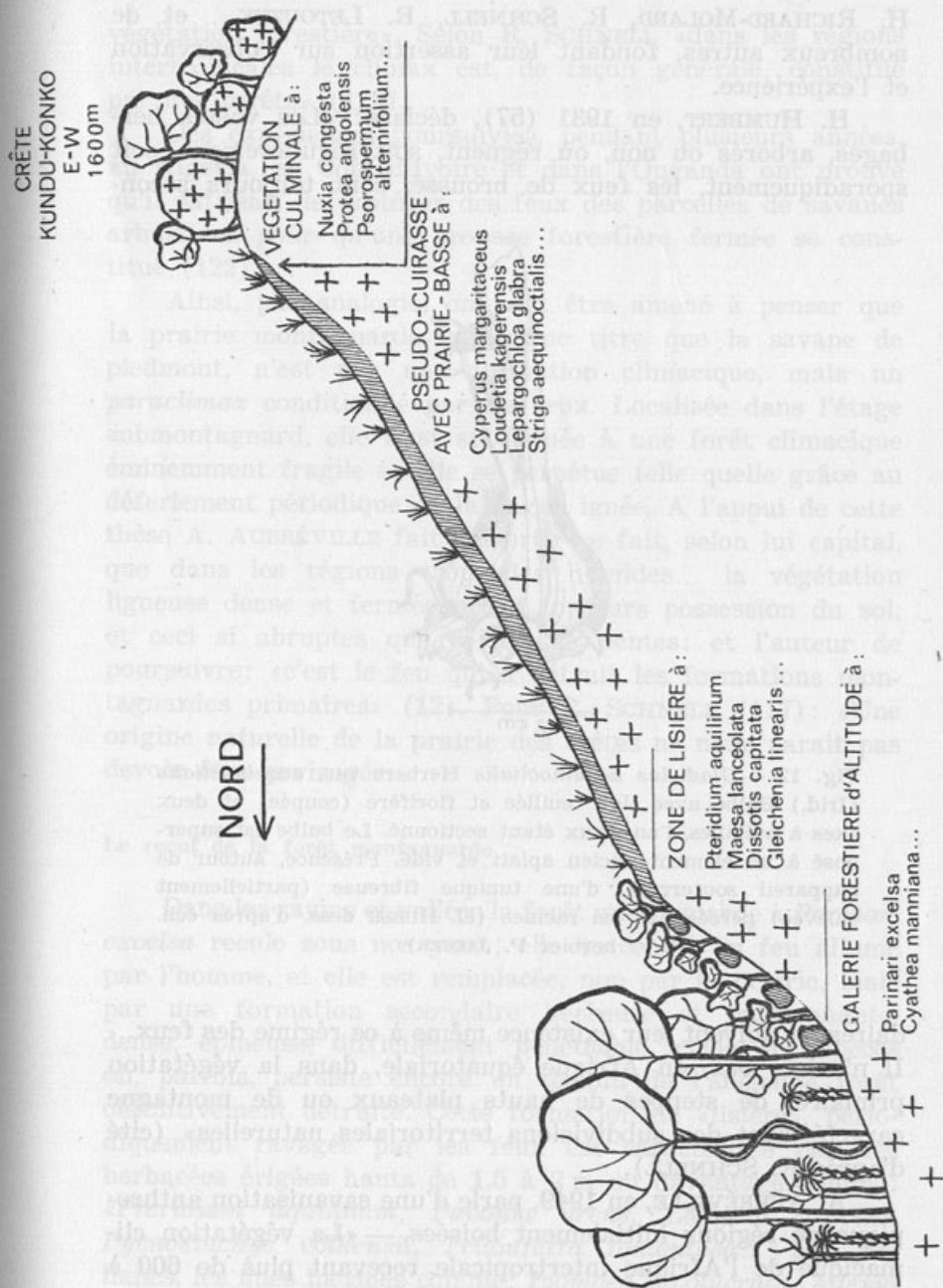Parinari excelsa
Cyathea manniana...

NORD

Fig. 11.— Transect de la crête du Kundu-Konko (éperon E du Pic Bintumane) vers une galerie forestière d'altitude du versant N, affluent du Sonfon. Remarquer l'étendue de l'horizon «cuirassé» en pente.

H. RICHARD-MOLARD, R. SCHNELL, R. LETOUZEY... et de
nombreux autres, fondant leur assertion sur l'observation
et l'expérience.

  H. HUMBERT, en 1931 (57), déclare: «Les vastes her-
bages, arborés ou non, où règnent, soit régulièrement, soit
sporadiquement, les feux de brousse, sont toujours secon-

Fig. 12. — *Gladiolus aequinoctialis* Herbert var. *aequinoctialis*
(Irid.) Bulbe avec tige feuillée et florifère (coupée) et deux
axes à bulbilles, l'un d'eux étant sectionné. Le bulbe est super-
posé à un élément ancien aplati et vidé. Présence, autour de
l'appareil souterrain, d'une tunique fibreuse (partiellement
enlevée) percée par les racines (E. HUBER dess. d'après éch.
herbier P. JAEGER).

daires, et doivent leur existence même à ce régime des feux...
Il n'existe pas, en Afrique équatoriale, dans la végétation
primaire, de steppes de hauts plateaux ou de montagne
caractérisant des subdivisions territoriales naturelles» (cité
d'après R. SCHNELL).

  A. AUBRÉVILLE, en 1949, parle d'une savanisation anthro-
pique de régions initialement boisées. — «La végétation cli-
macique de l'Afrique intertropicale recevant plus de 600 à
700 mm de pluie par an est, d'après H. RICHARD-MOLARD, une

végétation forestière». Selon R. SCHNELL «dans les régions intertropicales le climax est, de façon générale, constitué par des forêts» (122).

Des expériences poursuivies, pendant plusieurs années, au Nigeria, en Côte d'Ivoire et dans l'Ouganda ont prouvé qu'il suffisait de protéger des feux des parcelles de savanes arbustives pour qu'une brousse forestière fermée se constitue (122).

Ainsi, par analogie, on peut être amené à penser que la prairie montagnarde, au même titre que la savane de piedmont, n'est pas une formation climacique, mais un *paraclimax* conditionné par les feux. Localisée dans l'étage submontagnard, elle s'est substituée à une forêt climacique éminemment fragile et elle se perpétue telle quelle grâce au déferlement périodique de la vague ignée. A l'appui de cette thèse A. AUBRÉVILLE fait ressortir ce fait, selon lui capital, que dans les régions tropicales humides... la végétation ligneuse dense et fermée prend toujours possession du sol, et ceci si abruptes que soient les pentes: et l'auteur de poursuivre: «c'est le feu qui a détruit les formations montagnardes primaires» (12). Pour R. SCHNELL (117): «Une origine naturelle de la prairie des crêtes ne nous parait pas devoir être envisagée».

Le recul de la forêt montagnarde

Dans les ravins et vallées la forêt montagnarde à *Parinari excelsa* recule sous nos yeux; elle succombe au feu allumé par l'homme, et elle est remplacée, non par la prairie, mais par une formation secondaire herbeuse et buissonnante, dense, épineuse, difficilement pénétrable, riche en espèces où, parfois, persiste encore un témoin de l'ancienne forêt définitivement détruite. Cette formation de «lisière», périodiquement ravagée par les feux est caractérisée par des herbacées érigées hauts de 1,5 à 2 m ou davantage comme: «*Pteridium aquilinum, Pavonia urens, Laggera gracilis, Pycnostachys volkensii, Triumfetta tomentosa...* par des lianes, les unes inermes comme: *Ipomoea involucrata, Adenia lobata, Stephania abyssinica, Mikania scandens...* les autres
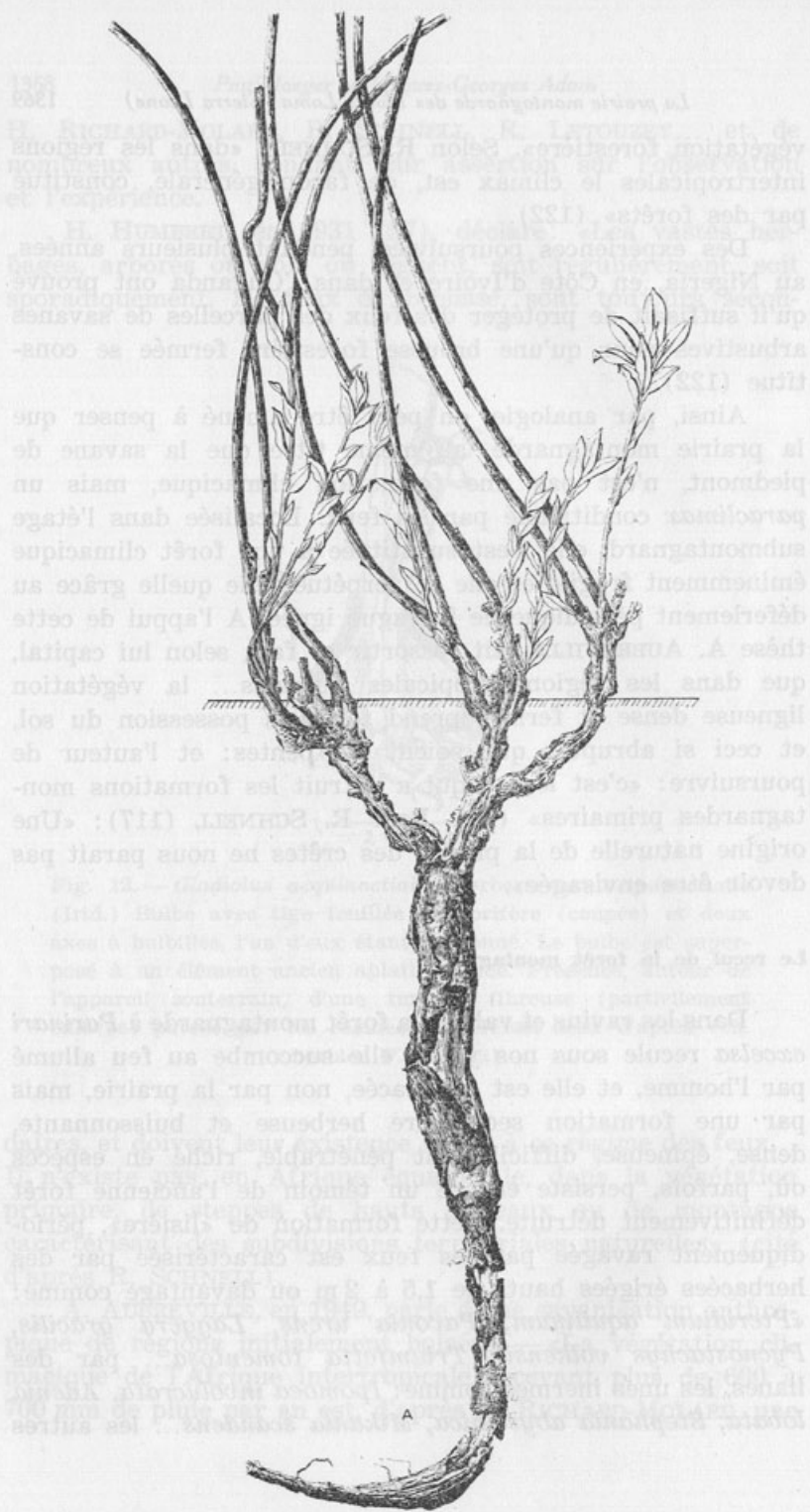
Fig. 13. — *Euphorbia depauperata*... **A** (voir légende dans
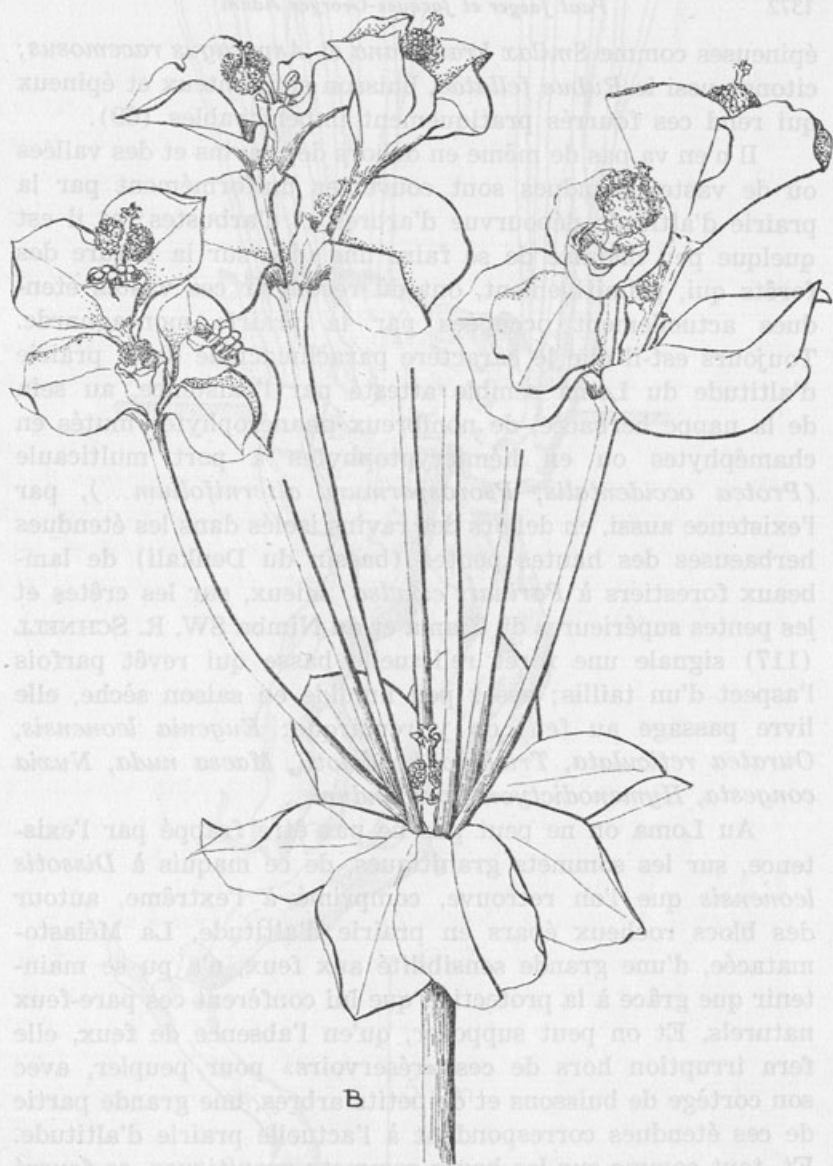la page suivante).

Fig. 13. — *Euphorbia depauperata* Hochst. ex A. Rich. (Euphorbiacées). A — Sous-arbrisseau caractérisé par son appareil souterrain napiforme. Aspect de l'appareil aérien après le passage du feu: moignons carbonisés dressés et jeunes pousses feuillées et florifères. Espèce prairiale à aire disjointe. B — Sommité fleurie (janvier) (K. WATRÉ dess.; Herbier P. JAEGER).

épineuses comme *Smilax kraussiana* et *Asparagus racemosus;*
citons aussi le *Rubus fellatae,* buisson sarmenteux et épineux
qui rend ces fourrés pratiquement impénétrables (69).

Il n'en va pas de même en dehors des ravins et des vallées
où de vastes étendues sont couvertes uniformément par la
prairie d'altitude dépourvue d'arbres et d'arbustes; et il est
quelque peu malaisé de se faire une idée sur la nature des
forêts qui, primitivement, ont dû recouvrir ces vastes éten-
dues actuellement occupées par la prairie montagnarde.
Toujours est-il que le caractère paraclimacique de la prairie
d'altitude du Loma semble attesté par l'existence, au sein
de la nappe herbacée, de nombreux phanérophytes mutés en
chaméphytes ou en hémicryptophytes à port multicaule
(Protea occidentalis, Psorospermum alternifolium...), par
l'existence aussi, en dehors des ravins isolés dans les étendues
herbaeuses des hautes pentes (bassin du Denkali) de lam-
beaux forestiers à *Parinari excelsa;* mieux, sur les crêtes et
les pentes supérieures du Ziama et du Nimba SW, R. SCHNELL
(117) signale une forêt relictuelle basse qui revêt parfois
l'aspect d'un taillis; assez peu humide en saison sèche, elle
livre passage au feu; on y remarque: *Eugenia leonensis,
Ouratea reticulata, Trichilia heudelotii, Maesa nuda, Nuxia
congesta, Hymenodictyon floribundum...*

Au Loma on ne peut pas ne pas être frappé par l'exis-
tence, sur les sommets granitiques, de ce maquis à *Dissotis
leonensis* que l'on retrouve, comprimé à l'extrême, autour
des blocs rocheux épars en prairie d'altitude. La Mélasto-
matacée, d'une grande sensibilité aux feux, n'a pu se main-
tenir que grâce à la protection que lui confèrent ces pare-feux
naturels. Et on peut supposer, qu'en l'absence de feux, elle
fera irruption hors de ces «réservoirs» pour peupler, avec
son cortège de buissons et de petits arbres, une grande partie
de ces étendues correspondant à l'actuelle prairie d'altitude.
Et, tout comme sur les hauts sommets granitiques, ce fourré
arbustif a dû être disloqué par des «clairières édaphiques»
correspondant à l'affleurement de dalles rocheuses, de sols
cuirassés... autant de stations éminement propices aux
orophytes non forestiers.

Fig. 14. — *Eupatorium africanum* Oliv. et Hiern (Composées).
Sous-arbrisseau à souche ligneuse, vivace, étalée au ras du sol
en un «plateau» hérissé de moignons carbonisés qui, après le
passage du feu, donne naissance à un faisceau de tiges dressées,
feuillées et florifères (E. HUBER dess.; Herbier P. JAEGER).

Le maquis à *Dissotis leonensis* qui, selon nous, a dû recouvrir jadis de vastes surfaces de l'étage culminal du Loma, aurait été refoulé par la vague ignée vers ces stations de repli où nous l'observons encore aujourd'hui. Ainsi, grâce au feu, la prairie en s'étendant progressivement aurait atteint sa configuration actuelle, pendant que tout un cortège d'herbacées banales à prédominance graminéenne, originaire des savanes de piedmont, faisait irruption en altitude. Hautement compétitifs et envahissants ces éléments se seraient installés au détriment de la forêt primitive, processus de savanisation guère favorable à la survie des orophytes.

Comme le feu semble être le facteur primordial responsable de la genèse, de l'extension et du maintien de la prairie d'altitude, cherchons à connaître le cycle annuel de ces espèces soumises périodiquement au traumatisme igné et aussi, si possible, leur comportement en prairie soustraite à l'action de feux.

Le cycle annuel de la végétation en prairie montagnarde soumise au feux

Dès le début de la saison sèche (novembre-décembre) quand les Graminées et autres herbacées se dessèchent, la vague ignée déferle à travers prairies et savanes laissant derrière elle un paysage de désolation. Cependant, à cette époque de l'année qui coïncide avec l'entrée en état de repos de la végétation, le dommage causé par les feux est minime, les plantes ayant pour la plupart, bouclé leur cycle reproducteur, fruits et graines étant disséminés. Contre toute attente, 15 jours ou 3 semaines après l'incendie, des jeunes pousses vertes et tendres apparaissent et, sans tarder, plusieurs vagues de floraisons se succèdent au cours de la saison sèche et même durant la saison pluvieuse suivante dont la fin est invariablement marquée par la floraison et la fructification des Graminées; et le cycle recommence (67).

L'irruption du feu a pour effet de régénérer la prairie par l'apparition d'un gazon de jeunes pousses vertes, tendres et d'une haute valeur nutritive. Aussi ces pâturages, ainsi
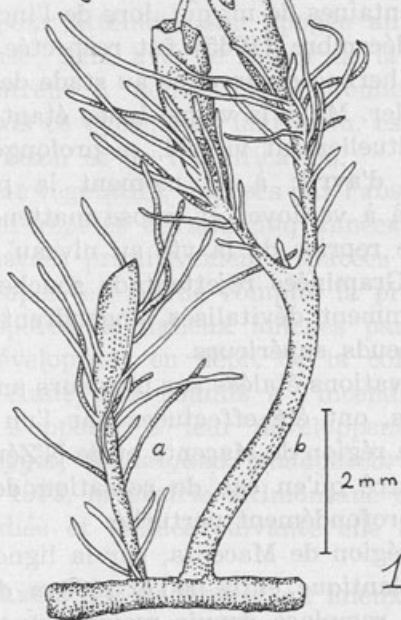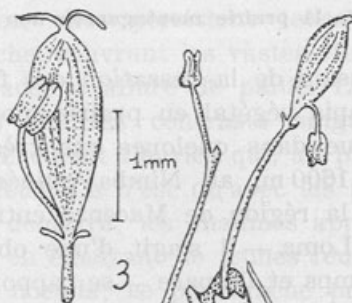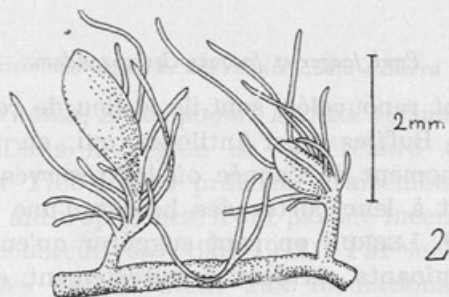
Fig. 15. — *Ledermanniella jaegeri* C. Cusset sp. nov.
(Podostémonacées).

1 — à gauche: individu jeune; à droite: individu en fleurs;
2 — individu avec boutons floraux; 3 — fleur. Lit torrentiel
du Miramira vers 1400 m (janvier) (C. CUSSET dess.;
Herbier P. JAEGER n.° 8789).

périodiquement renouvelés, sont-ils le lieu de rendez-vous de troupeaux de Buffles et d'Antilopes qui, en pleine saison sèche, à un moment de l'année où les réserves alimentaires s'épuisent, ont à leur portée des herbes d'une qualité supérieure; avec J. LEBRUN on peut suggérer qu'en l'absence de feux, les Ruminants seraient manifestement en régression sur ces hauteurs.

Le comportement de la prairie montagnarde non incendiée

La répercussion de la cessation des feux sur les comportement du tapis végétal en prairie montagnarde n'a pu être observée que dans quelques cas très peu nombreux: au Loma vers 1600 m, au Nimba guinéen entre 1000 et 1700 m et dans la région de Macenta entre 900 et 1000 m.

Le cas du Loma — il s'agit d'une observation unique, isolée dans le temps et l'espace — se rapporte à une parcelle de quelques centaines de m² qui, lors de l'incendie périodique de novembre-décembre (1965) fut respectée des feux.

La strate herbacée parvenue au stade de repos, est sèche et prête à brûler. Mais, la vague ignée étant déviée, ce stade de repos, habituellement virtuel, se prolonge jusqu'aux premières pluies d'avril; à ce moment la prairie incendiée commence déjà à verdoyer et, chose inattendue, on constate également une reprise de la vie au niveau du lambeau non incendié: les Graminées rejettent de souche et les chaumes secs, apparenmment dévitalisés, engendrent des feuilles au niveau des noeuds supérieurs.

Des observations étalées sur plusieurs années et, partant, plus complètes, ont été effectuées par l'un de nous (J. G. ADAM) dans la région de Macenta et de N'Zérékoré (Guinée); elles ont montré qu'en cas de cessation des feux le cycle annuel était profondément perturbé.

Dans la région de Macenta, sur la ligne de partage des eaux Niger-Atlantique, entre 900 et 1000 m, de vastes savanes herbeuses ont remplacé depuis moins d'un siècle l'ancienne forêt guinéenne. Ces savanes qui, pendant trois années consécutives (1947-49) n'ont pas été incendiées sont constituées principalement par des Graminées vivaces appartenant aux

genres *Hyparrhenia, Andropogon, Schizachyrium, Elymandra, Pennisetum.* Dans la région de N'Zérékoré (Mt. Nimba), entre 1000 et 1700 m des prairies, vraisemblablement très anciennement anthropogènes, n'ont pas été incendiées pendant cinq années consécutives (1967-1971). Par leur composition floristique elles s'apparentent aux formations précédentes.

A l'approche de la saison sèche les Graminées et les autres herbacées se déssèchent, mais au lieu de devenir la proie des flammes, elles persistent telles quelles durant toute la saison sèche, couvrant les vastes étendues prairiales d'une nappa herbacée à allure de paille. L'aspect terne et monotone de ces prairies contraste singulièrement avec celles, vertes et richement fleuries qui, au préalable, ont été balayées par les feux. Ce n'est qu'avec les premières pluies que la feuillaison démarre; les chaumes apparemment dévitalisés, verdissent en émettant de jeunes feuilles à leur base et au niveau des noeuds; ce phénomène prend de plus en plus d'ampleur pour atteindre son apogée au plus fort de la saison pluvieuse; puis, avec le retour de la saison sèche, ces plantes montrent à nouveau les premiers signes de flétrissement. Mais ce cycle, fait inattendu, est marqué par l'absence de floraison et de fructification.

Exclusivement végétatifs, imposés par l'absence des feux, ces cycles se sont répétés durant cinq années consécutives. Les touffes herbacées primitivement espacées se sont développées pour occuper, en fin de compte, la presque totalité du sol. Les diaspores de ligneux amenés par le vent, les animaux... se développent en dépit de la concurrence des Graminées et, n'étant plus soumis à l'incendie périodique, rien ne semble s'opposer à leur développement: *Albizzia gummifera, A. zygia, Harungana madagascariensis, Trema guineensis...* En 1972, la prairie altimontane du Nimba fut à nouveau incendiée et l'année suivante elle était émaillée de fleurs.

Parmi les plantes qui s'adaptent au mieux à ce rythme exclusivement végétatif citons: *Hyparrhenia subplumosa, Rhytachne rottboellioides, Panicum ecklonii, Cyperus tenuiculmis* var. *guineensis...*

La suppression des feux, si elle entraîne une perturbation profonde du cycle annuel de la végétation en prairie montagnarde, est cependant incapable — sans doute en raison d'une durée insuffisante de cette période de cessation des feux — de nous faire assister à une reforestation effective de ces vastes étendues herbeuses.

Aussi y a-t-il lieu d'admettre que l'existence même et la pérennité de la prairie montagnarde, la restauration des pâturages en saison sèche et, partant, la présence des herbivores, sont conditionnées par les feux. La prairie altimontane du Loma se présente comme un groupement secondaire, une enclave dans l'étage forestier montagnard, dont la stabilité serait garantie par le déferlement périodique de la vague ignée.

VI — LA FLORE MONTAGNARDE; SES ORIGINES

Le tapis végétal de la prairie d'altitude du Loma où 248 espèces, sous-espèces ou variétés ont pu être dénombrées [1], s'avère d'une réelle complexité à la fois pour ce qui est de la composition floristique et de l'origine des taxons. Comme celui du Nimba (117) le peuplement végétal de l'étage culminal du Loma se distingue par une remarquable dualité: aux orophytes inféodés aux massifs montagneux et sans affinités avec les taxons de basse altitude, s'oppose un lot d'espèces planitaires banales originaire des pays de piedmont ou de régions plus lointaines.

A) Les orophytes

Les orophytes du Loma, comme ceux des autres massifs de la dorsale sont très variés quant à leurs exigences écologiques et quant à leur origine. Suivant les cas, il peut s'agir d'espèces prairiales ou forestières, de saxicoles ou de plantes hygro- ou hélophiles. Certaines, peu nombreuses, ne se trouvent que dans le seul massif du Loma; plus nombreuses sont

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[1] Chiffre provisoire susceptible d'être modifié ultérieurement à la suite de nouvelles prospections.

celles qui sont propres à l'étage montagnard de l'ensemble des hauteurs ouest-africains allant du Fouta-Djalon à la chaîne camerounaise. Une attention spéciale méritent les
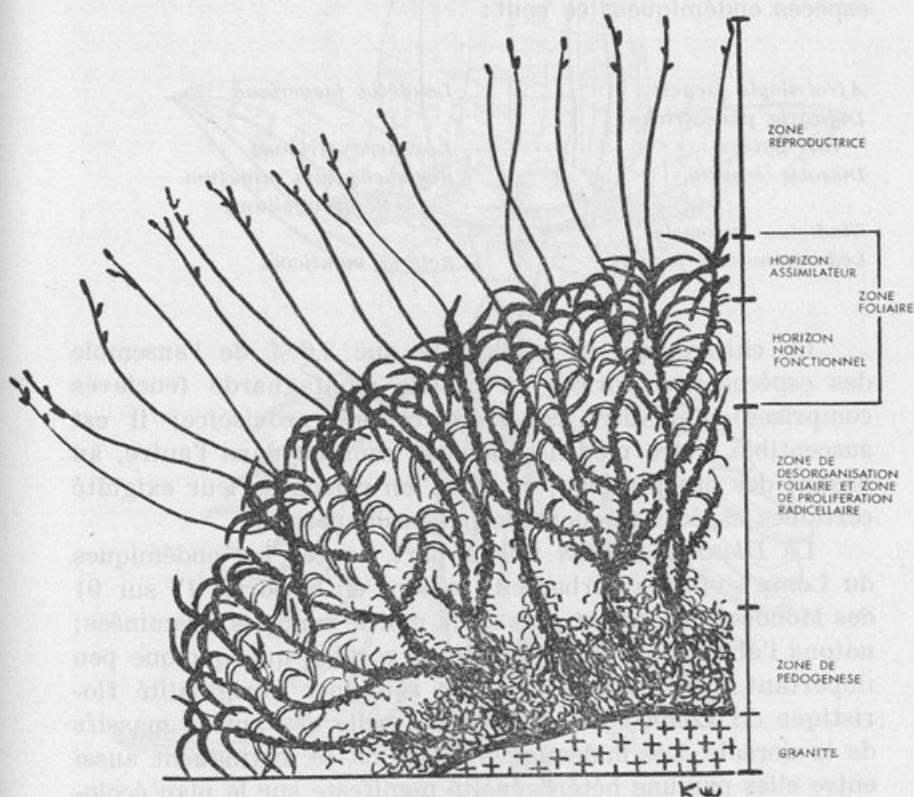
Fig. 16. — Dessin semi-schématique à travers une motte d'*Afrotrilepis jaegeri* J. Raynal (Cypéracées), orophyte saxicole, endémique des monts Loma-Tingi. Remarquer la spécialisation fonctionnelle des diverses zones disposées concentriquement (K. WATRÉ dess.; Herbier P. JAEGER).

espèces à aire disjointe que l'on trouve simultanément au Loma et, à plusieurs milliers de km de là, dans les massifs E ou SE africains.

Au Loma la forêt montagnarde à *Parinari excelsa* et, plus particulièrement les galeries forestières qui s'en détachent pour s'élancer en direction des sommets, ne recèlent

pas une seule espèce qui leur appartienne en propre; il n'en
est pas de même de la prairie ni des milieux rocheux ou
marécageux qui en dépendent où nous avons inventorié *neuf*
espèces endémiques; ce sont:

Afrotrilepis jaegeri	*Loudetia jaegeriana*
Digitaria phaeotricha	
var. *patens*	*Loxodera strigosa*
Dissotis sessilis	*Schizachyrium minutum*
	(= *S. brevifolium*)
Gladiolus leonensis	
Ledermanniella jaegeri	*Scleria monticola*

Ce chiffre, qui ne représente que 3,6 % de l'ensemble
des espèces inventoriées en prairie montagnarde (enclaves
comprises) doit être considéré comme provisoire; il est
susceptible d'être modifié, dans un sens ou dans l'autre, au
hasard des prospections; en effet, en raison de leur exiguïté
certaines espèces risquent de passer inaperçues.

Le *Dissotis sessilis* mis à part, toutes les endémiques
du Loma sont des herbacées; ce sont en majorité (7 sur 9)
des Monocotylédones et près de la moitié sont des Graminées;
notons l'absence de Fougères de ce cortège qui, quoique peu
important, permet cependant de souligner l'originalité flo-
ristique du Loma et de l'opposer à celle des autres massifs
de la dorsale. Les endémiques du Loma se distinguent aussi
entre elles par une hétérogénéité manifeste sur le plan écolo-
gique. Si le *Digitaria phaeotricha* var. *patens,* le *Loxodera
strigosa* et le *Scleria monticola* sont des prairiales typiques,
la vocation saxicole de l'*Afrotrilepis jaegeri* ne saurait être
mise en doute. Le *Gladiolus leonensis* a été observé sur la
tourbe édifiée par *Afrotrilepis pilosa* et les affinités du
Schizachyrium minutum pour les sols marécageux et tourbeux
semblent manifestes au même titre que celles du *Ledermani-
niella jaegeri* pour les eaux agitées et oxygénées des cascades
et cascadelles. Le *Dissotis sessilis*, par contre, jalonne les
ruisselets dévalant les pentes herbeuses du Pic Bintumane
et le *Loudetia jaegeriana* s'installe dans les mottes moussues
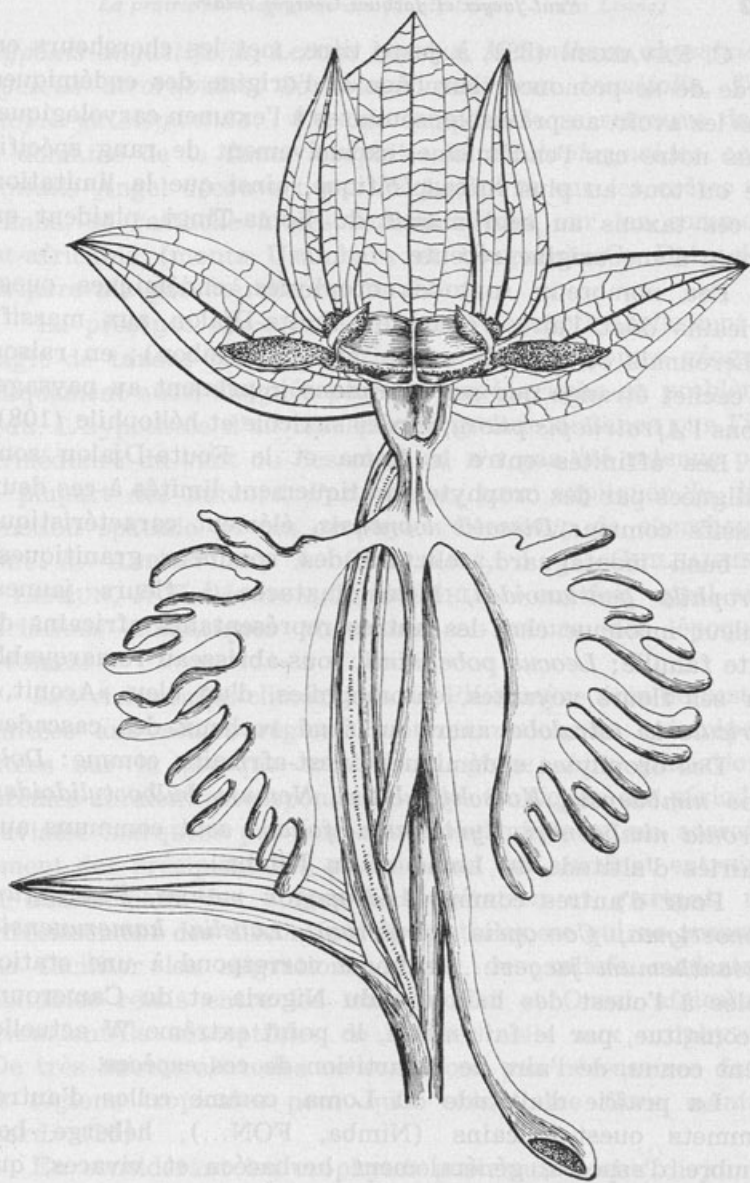accrochées aux parois rocheuses des dômes granitiques.

Fig. 17. — *Habenaria jaegeri* Summerh. (Orchidacées). Fleur vue de face; remarquer le labelle trilobé, les lobes latéraux sont profondément divisés; l'éperon (4-6 cm) est entamé à son extrémité inférieure. La plante, assez abondante en prairie d'altitude, fleurit en saison pluvieuse (K. WATRÉ dess.; Herbier P. JAEGER).

C. FAVARGER (39), à juste titre, met les chercheurs en garde de se prononcer sur l'âge et l'origine des endémiques sans les avoir, au préalable, soumises à l'examen caryologique. Dans notre cas l'endémisme, exclusivement de rang spécifique ou tout au plus infraspécifique, ainsi que la limitation de ces taxons au seul massif du Loma-Tingi, plaident en faveur d'une origine récente.

Peu nombreux sont les orophytes, endémiques ouest africains dont l'aire s'étend du Fouta-Djalon aux massifs camerounais et, parfois même, au-delà (Gabon); en raison du cachet étrange que ses touradons impriment au paysage, citons l'*Afrotrilepis pilosa,* espèce saxicole et héliophile (108).

Les affinités entre le Loma et le Fouta-Djalon sont soulignées par des orophytes pratiquement limités à ces deux massifs comme: *Dissotis leonensis,* élément caractéristique du bush montagnard relictuel des sommets granitiques; *Nerophila gentianoides,* Mélastomatacée à fleurs jaunes, couleur inconnue chez les autres représentants africains de cette famille; *Leocus pobeguinii,* sous-abrisseau remarquable par ses fleurs voyantes, entomophiles, d'un bleu «Aconit.», *Utricularia tetraloba* ancré au fond rocheux des cascades.

Des orophytes endémiques ouest-africains comme: *Dolichos nimbaensis, Kotschya lutea, Nemum bulbostylidoides, Veronia nimbaensis, Xyris festucifolia...* sont communs aux prairies d'altitude du Loma et du Nimba.

Pour d'autres comme *Andropogon mannii, Pennisetum monostigma, Coreopsis camporum, Lobelia kamerunensis, Mesanthemum jaegeri...* le Loma correspond à une station isolée à l'ouest des hauteurs du Nigeria et du Cameroun; il constitue, par le fait même, le point extrême W actuellement connu, de l'aire de répartition de ces espèces.

La prairie d'altitude du Loma, comme celles d'autres sommets ouest-africains (Nimba, FON...), héberge bon nombre d'espèces, généralement herbacées et vivaces, que l'on retrouve dans les massifs E et SE africains distants des premiers de plusieurs milliers de kilomètres; citons: *Cynanchum praecox, Disa welwitschii, Drimia zombensis, Drosera pilosa, Euphorbia depauperata, Gynura miniata, Helichrysum nudifolium* var. *leiopodium, H. mechovianum,*

Hypoxis angustifolia, Leocus lyratus, Melanthera abyssinica, Pycreus atrorubidus, Sopubia mannii var. *tenuifolia, Trichopteryx elegantula...* Un cas comparable se retrouve dans le domaine de la faune orophile: le *Nectophrynoides occidentalis* Angel découvert par M. LAMOTTE sur les crêtes du Nimba, se rattache à des formes vivant sur les sommets est-africains (monts Usambara et Uluguru). Ce Batracien vivipare n'a pas été observé au Loma.

La présence des mêmes espèces — exceptionnellement il s'agit de taxons infra-speécifiques — en des points géographiquement aussi éloignés pose au biogéographe un problème ardu. L'hypothèse d'un transport à grande distance par l'intermédiaire du vent ou des oiseaux, n'a pas été retenue par la plupart des auteurs. Par contre, pour expliquer la disjonction spatiale de ces orophytes beaucoup de chercheurs dont A. AUBRÉVILLE, A. CHEVALIER, J. L. GUILLAUMET, J. LEBRUN, J. K. MORTON, R. SCHNELL... ont fait appel aux variations climatiques survenues au cours des époques révolues.

Les vicissitudes climatiques du Pléistocène, loin de rester limitées aux seules régions septentrionales, se ont répercutées sur la presque totalité du globe. Aux glaciations boréales auraient correspondu, sous les tropiques, des périodes pluviales marquées par une chute thermique et un accroissement des précipitations, phénomènes qui auraient entrainé un abaissement des étages de végétation et, partant, un rétrécissement des discontinuités spatiales, ce qui ne pouvait que faciliter les migrations. Ainsi, des reliefs modestes, véritables relais entre les massifs Est et Ouest africains, devenaient-ils susceptibles de donner asile aux orophytes. «De très hautes altitudes ne sont donc pas nécessaires dans les régions tropicales pour qu'il existe une flore montagnard» (26).

En considérant les orophytes prairiaux à aire disjointe on est surpris par le fait que les mêmes plantes se rencontrent identiques, à l'échelon spécifique, sur divers massifs de la dorsale Loma-Man et sur certains autres de l'Est, du Centre et du S.E. africain c'est-à-dire en des points séparés par un intervalle de plusieurs milliers de kilomètres. En

raison de leur isolement géographique sur les sommets occidentaux, on aurait pu s'attendre à une diversification au moins infraspécifique.

Aussi le cas de l'*Habenaria jaegeri* Summ. déjà signalé par R. SCHNELL en 1961, est-il particulièrement suggestif à cet égard. Il s'agit d'une Orchidée des prairies montagnardes du Loma et du Fon (121); elle est très proche de l'*H. splendens* Rendle du Kilimandjaro, de l'*H. praestans* Rendle du Ruwenzori et du Mozambique et de l'*H. macrantha* Hochst. d'Abyssinie. Ces diverses espèces, très proches les unes des autres, sont caractérisées, par le même labelle lacinié-pectiné et ne diffèrent entre elles que par des variations mineures. Elles «appartiennent manifestement à un même phylum qui s'est répandu à une époque ancienne (peut-être au Tertiaire) sur les divers sommets africains» où l'isolement géographique a été particulièrement favorable aux mutations différencia-trices. La présence de la même espèce au Loma et au Fon parle en faveur d'un échange récent qui, selon cet auteur, a dû être consécutif aux variations climatiques du Quaternaire. L'absence de cette espèce au Nimba ne fait que confirmer l'individualité floristique et phytogéographique des divers massifs de la dorsale guinéenne.

Frappé par la complexité du peuplement végétal des montagnes de l'Afrique tropicale A. CHEVALIER (26) pense que «les orophiles de l'Afrique occidentale existent... aux points où nous les observons depuis un lointain passé». Et J. LEBRUN (80) d'affirmer que «le noyau de la flore orophile africaine porte... un cachet de grande ancienneté». D'après R. SCHNELL (124) la flore orophile prairiale «serait à considérer comme un témoin d'une époque ancienne plus sèche, conservé jusqu'à nos jours grâce à des conditions édaphiques favorables».

B) **Les planitiaires**

Diverses espèces, prairiales ou forestières, apparemment inféodées à l'étage culminal du Loma, se retrouvent à basse altitude en pays de piedmont, parfois même, en milieu côtier. Ainsi, au pied du Nimba libérien, dans une savane à *Rhy-*

tachne sp. vers 500 m, nous avons récolté *Phyllanthus alpestris* et *Striga aequinoctialis*. Le *Phyllanthus odontadenius* s. l., espèce à affinités montagnardes, se remarque à basse altitude à proximité des villages et le long des pistes. Des espèces qui forment de véritables peuplements au Plateau comme *Eupatorium africanus,* se retrouvent en savane de piedmont, d'autres comme *Gladiolus unguiculatus* sont largement répandues en Afrique tropicale.

De même, des plantes comme *Psorospermum alternifolium, Scutellaria paucifolia* et *Leocus lyratus* fleurissent et fructifient tout aussi bien en prairie montagnarde qu'en savane de piedmont.

Certains ligneux apparemment liés au milieu montagnard, prolifèrent tout aussi bien à basse altitude; le cas le plus spectaculaire est celui du *Parinari excelsa*. Cette Chrysobalanacée qui constitue des peuplements presque purs vers l'extrémité supérieure des galeries forestières où elle fleurit et fructifie abondamment, se retrouve en plaine, en milieu côtier (Casamance). Cette bipolarité a été particulièrement mise en relief par des auteurs comme A. AUBRÉVILLE (11), J. MIÈGE (95), et R. SCHNELL (124). Une étude cytotaxonomique des deux types, montagnard et côtier, de cette espèce, serait éminemment souhaitable.

Dans les vastes étendues herbeuses de la zone culminale du Loma on remarque aussi, quoique disséminées, des espèces endémiques de la savane ouest-africaine, comme: *Polygala cristata* et *P. baikiei*. Signalons aussi le cas du *P. lecardii,* plante commune dans tout l'ouest africain qui, en plaine et en montagne, a trouvé refuge dans les stations marécageuses.

Attirons enfin l'attention sur tout un cortège de plantes herbacées, essentiellement graminéennes, dont la pénétration en montagne est, incontestablement, l'oeuvre des feux:

Andropogon gayanus, A. schirensis, Hyparrhenia diplandra, H. rufa, Loudetia kagerensis, Panicum praealtum... et il semble qu'il en soit de même des Cypéracées de la prairie altimontane dont la moitié environ (17 sur 31) couvrent des aires très vastes dans les savanes de l'Afrique tropicale et australe:

Ascolepis protea, Bulbostylis oritrephes, Cyperus ango-
lensis, Fuirena stricta, Fimbristylis schweinfurthiana...

CONCLUSION

La Prairie d'altitude du Loma, comme celle du Nimba,
peut être considérée comme une enclave herbacée établie
au sein de l'étage submontagnard forestier. Elle correspond
à une formation secondaire, paraclimacique, qui doit son
existence et sa pérennité, non pas au climat, mais au défer-
lement périodique de la vague ignée.

Grâce au feu, la prairie se serait substituée à une forêt
basse, à un bush montagnard où le *Dissotis leonensis* domi-
nant, s'associait à tout un cortège de buissons et de petits
abres. Ce fourré, une originalité du Loma, était troué de
«clairières édaphiques», espaces non boisés, où des orophytes
non forestiers se seraient maintenus depuis une époque déjà
fort ancienne.

Cette disposition, dans son ensemble, correspond à celle
que R. SCHNELL (119) a observée au Nimba où, cependant,
la Mélastomatacée n'a pas été observée.

D'une extrême sensibilité aux feux, ce maquis a succombé
aux assauts répétés de la vague ignée; éliminé ainsi de vastes
surfaces désormais occupées par la prairie montagnarde,
cette formation n'a subsisté, à l'état relictuel, que sur les
hauts sommets granitiques où les seuils rocheux lui assurent
un certain degré de protection.

Ces hauts sommets rocheux comparables à autant d'îles
émergeant au-dessus l'océan forestier ont dû jouer, au même
titre que les «clairières édaphiques», le rôle de bastions de
refuge pour espèces relictuelles, mais aussi de creusets où,
à la suite de mutations ou d'hybridations, de nouveaux taxons
ont vu le jour. Ils ont contribué à faire du Loma un centre,
il est vrai secondaire, de repli et de diversification, voire
un réservoir d'où, à certaines périodes, se seraient écoulés,
vers la prairie voisine, des taxons jusque là maintenus à
l'abri des seuils rocheux.

A l'heure actuelle l'intensification des feux, encore attisés
sur le versant Est par le souffle de l'harmattan, accélère la

savanisation de l'étage culminal en favorisant l'irruption en altitude de tout une cortège herbacé, surtout graminéen, originaire des savanes de piedmont. Ces plantes, envahissantes et fortement compétitives risquent de mettre en péril la flore orophile déjà ancienne et d'effacer ainsi les derniers vestiges d'une documentation susceptible de nous renseigner sur l'histoire du peuplement végétal de ce massif.

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2. — Prairie d'altitude du rebord E du Plateau et de la pente Sud du Pic Bentumane, partiellement incendiées (6 déc. 65).

3. — Feu de brousse en prairie d'altitude (secteur Miramira) vers 1600 m (6 déc. 65).

4. — Prairie d'altitude près du rebord NW du Plateau; faciès à *Loudetia kagerensis* (K. Schum.) C. E. Hubb. ex Hutch. à g.: parcelle non incendiée; à dr.: parcelle incendiée et verdoyante (30 mars 65).
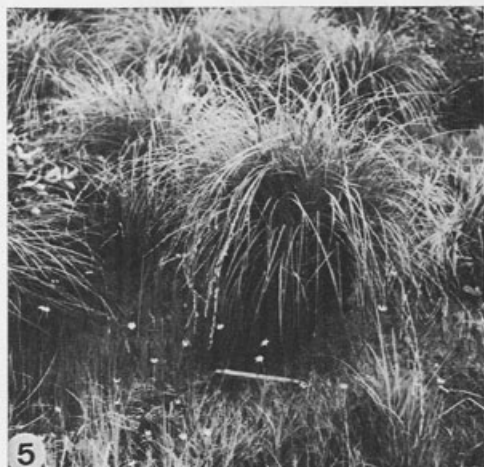
5. — *Afrotrilepis pilosa* J. Raynal (Cypéracées) en saison pluvieuse (24 sept. 64) avant le passage du feu: les touradons portent une épaisse touffe de longues feuilles retombantes; sur le sol tourbeux édifié par la Cypéracée on remarque quelques individus fleuris de *Mesanthemum prescottianum*. Corniche granitique versant W Loma vers 580 m.

6. — *Afrotrilepis pilosa* J. Raynal (Cypéracées) en saison sèche (23 déc. 65) après le passage du feu. Remarquer les touradons noirs, coralloïdes, débarrassés de la touffe foliaire. Corniche granitique du versant W du Loma vers 580 m (23 déc. 65).

7. — Touffes de *Cyperus nduru* Cherm. (Cypéracées) en fleurs après le passage du feu; versant sud du Pic Bintumane et Plateau attenant vers 1650 m, 3 février 52).

8. — Vue partielle du plateau sommital en forme d'auge du Pic Bintumane; affleurement de dalles doléritiques avec touradons noircis d'*Afrotrilepis pilosa* J. Raynal (Cypéracées); au fond à gauche point géodésique correspondant au sommet des monts Loma (26 février 66).
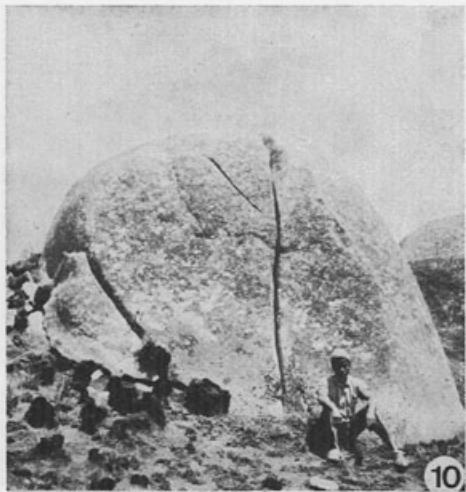
9. — Bastion rocheux à la limite des falaises à exp. Sud et Ouest du Pic Bintumane. Au 1er plan: fragment de prairie incendiée; le feu est bloqué dans sa progression par la parci rocheuse; cependant, par l'intermédiaire de couloirs herbeux il parvient au plateau sommital.

10. — Bloc granitique fracturé avec, au pied, des touradons calcinés d'*Afrotrilepis pilosa* J. Raynal (Cypéracées). Prairie d'altitude du Kundu-Konko vers 1650 m (4 mars 66).

11. — Calotte granitique du Serelen-Konko (versant N); au premier plan: la prairie d'altitude non encore incendiée (20 déc. 65).

12. — *Dissotis leonensis* Hutch. et Dalz (Mélastomatacées) chargé d'Usnées; crête sommitale du Fuen-Koli vers 1400 m (28 sept. 64).

13. — Individu isolé de *Eugenia pobeguinii* Aubrév. (Myrtacées) à la limite supérieure
     d'un lambeau de forêt montagnarde versant E du Pic Bintumane vers 1900 m.
     Remarquer l'état souffreteux de l'arbre, son port tortueux, la cime partielle-
     ment desséchée et chargée d'épiphytes (Usnées).

14. — Bush montagnard à *Eugenia pobeguini* Aubrév. (Myrtacées); buissons inclinés
     par l'action du vent. Sommet du Serelon-Konko vers 1480 m (20 déc. 65).

15. — Rocher granitique de la crête du Da-Oulen (vers 1470 m). Remarquer dans
     l'axe du personnage, accolées sur la paroi verticale à exposition sud, trois
     mottes d'*Afrotrilepis jaegeri* J. Raynal (12 déc. 65).

16. — Touffe de *Gladiolus leonensis* W. Marais (Iridacées) sur tourbe à *Afrotrilepis
     pilosa* en bordure d'une dalle granitique affleurante en prairie d'altitude du
     Plateau vers 1600 m (16 avril 66).

17. — *Dissotis sessilis* Hutch. ex. Brenan et Keay (Mélastomataceae), endémique du Loma. Plateau sommital du Pic Bintumane, dans un amoncellement de blocs doléritiques près du déversoir du Sonfon (juin 64).

18. — Peuplement de *Mesanthemum jaegeri* Jac.-Félix (Eriocaulacées), en fleurs dans le maquis à *Dissotis leonensis* au sommet du dôme granitique du Serelen-Konko vers 1480 m; orophyte ouest-africain (27 sept. 64).

19. — *Habenaria jaegeri* Summersh. (Orchidacées), en fleurs; saison pluvieuse. Prairie d'altitude du Plateau vers 1660 m (31 juillet 64).
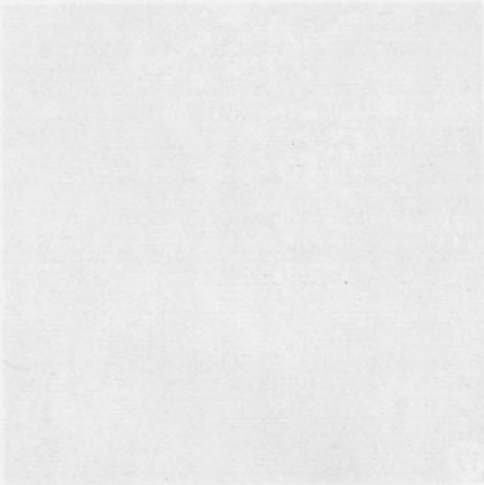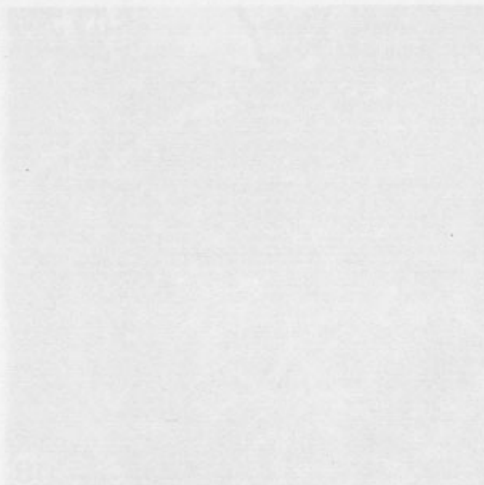
NOVA *AGAVE* SUBESPONTÂNEA
EM PORTUGAL

por

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SUMMARY

The A. found on waste calcareous places, mainly near the sea, in C. and S. Portugal, many specimens of *Agave atrovirens* Karwinski ex Salm-Dyck, which grow eubspontaneously. They are well distinguishable from the common *A. americana* L. by the broad dark green leaves, uncinate-conduplicate at apex and prolonged into a very stout spine 4-10 cm long, and by the short panicle three to five times shorter than the stout peduncle, flowers with syle twice as long as stamens and capsule oblong but contracted above into a short neck.

EM Fevereiro de 1975 notámos, em sebes nos arredores de Portimão (Algarve), que umas piteiras (*Agave* spp.) tinham as folhas verde-escuras, bastante grossas e largas, ainda que uncinado-conduplicado-sulcadas no ápice que terminava em longo espinho negro, pelo que se distinguiam sem qualquer dúvida da vulgar *Agave americana* L., também existente no sítio. Esses exemplares estavam todos reduzidos às rosetas foliares, excepto um à borda duma senda ou caminho vicinal com um escapo encimado por uma curta inflorescência paniculada, tudo já marcescente e, consequentemente, sem elementos concretos de identificação. Porém, esta inflorescência também chamou a nossa atenção pelo facto de o pedúnculo ser muito mais comprido (pelo menos, o

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* Comunicação apresentada ao «Simposio Conmemorativo del II Centenario del Nacimiento de Lagasca», Sevilha, Out. 1976.

triplo) do que a parte paniculada, esta com um contorno piramidad pouco largo.

Ao regressar a Lisboa, procurámos identificar a espécie, de certo distinta da *A. americana* L., mas a parcimónia dos elementos colhidos não nos permitiu ir longe. Em todo o caso, pareceu-nos ser ou estar próxima da *A. cochlearis* Jacobi, que mais tarde viemos a verificar não passar dum sinónimo da *A. atrovirens* Karwinski ex Salm-Dyck.

Observando com mais pormenor as piteiras que se encontram nas sebes e sítios áridos, sobretudo junto do mar, quer em Lisboa quer em toda a região que desta vai até Cascais, fomos verificando que estas piteiras de folhas verde--escuras e uncinado-conduplicadas no ápice eram muito mais frequentes do que a princípio se poderia supor. Até na própria Tapada da Ajuda, em que está situado o Instituto Superior de Agronomia em Lisboa, vários indivíduos foram detectados na encosta calcária acima do lago pequeno a Nascente do Viveiro da Silvicultura. Entre estes, também havia alguns com inflorescências marcescentes e acinzentadas, cujas panículas eram cerca de ¼ do pedúnculo. Pelos elementos agora disponíveis, ainda que poucos, fomos avolumando a convicção de poder tratar-se de *A. atrovirens* Karwiski ex Salm-Dyck.

A frequência com que estas plantas foram sendo encontradas, coadjuvada pela cor verde-escura das folhas grandes, fez-nos levantar a estranheza de que nunca nenhum botânico se lhes tivesse referido anteriormente. Esta falta supomos, no entanto, poder relevar-se pela inadequada observação minuciosa das piteiras, tidas aprioristicamente como pertencendo a *A. americana* L. ou pela simples suposição que não passariam duma forma mais verde desta última. Por outro lado, como estas espécies monocárpicas só florescem com longos intervalos de anos, também aqui certamente o motivo da sua não identificação há mais tempo.

Em Janeiro de 1976, muitas piteiras verdes da região litoral entre Santo Amaro de Oeiras e Cascais entraram em profusa floração, durando esta até Maio conforme os sítios. Não há dúvida que este ano seco de 1976 foi um ano excepcional para a abundância de floração nas piteiras, o

que também sucedeu, ainda que mais tarde (Junho e Agosto), com a *A. americana* L.

Na presença de plantas completamente floridas e frutificadas, foi-nos possível recolher todos os elementos para descrição e identificação. Consultados A. BERGER, *Die Agaven* (1915) e A. J. BREITUNG, *The Agaves* (1968), confirmámos a nossa suposição, a planta em estudo era de facto a *Agave atrovirens* Karwinski ex Salm-Dyck, e estávamos assim em presença de mais uma espécie subespontânea na região litoral calcária do Centro e Sul de Portugal. Percorridas outras regiões mais interiores do Centro de Portugal, verificámos que as piteiras nas sebes eram, de facto, só pertencentes a *A. americana* L., facilmente reconhecível pelas suas folhas glaucas rectas e panícula estreitamente oblongo-ovoide tão comprida ou um pouco mais do que o pedúnculo, além de ser planta de floração obviamente mais serôdia (Junho a Agosto, em vez de Janeiro a Maio).

A espécie *A. atrovirens* Karwinski ex Salm-Dyck é originária das regiões secas do Sul do México, onde é conhecida por «pulque». A sua boa adaptação em Portugal, com muitos indivíduos de certo já nada novos ou provenientes de propagação de outros anteriores, faz-nos supor que se trata de planta introduzida por volta dos fins do século XIX. Como certamente esta espécie não foi introduzida na Europa restritamente em Portugal em condições de ar livre, parece-nos muito provável a sua existência também em diversos pontos da região litoral do Mediterrâneo, pelo menos ocidental, isto é, da Espanha, França e Itália, incluindo provavelmente as ilhas das Baleares, Córsega, Sardenha e Sicília, onde deve proceder-se à sua busca.

Em qualquer das duas espécies que estudámos, bem como parece também suceder nas demais do género, as flores são distintamente protândricas, verificando-se um acentuado alongamento do estilete após a deiscência das anteras da própria flor.

Para facilitar o reconhecimento e identificação das piteiras que podem encontrar-se subespontâneas em Portugal, apresentamos as seguintes chaves e descrições:

Folhas glaucas, lanceolado-oblongas, rectas e terminadas em espinho de 2-3 cm; pedúnculo igual ou menor do que a panícula oblongo-ovoide; estilete subigualando por fim os estames; cápsula oblongo--obovoide, obtusa . . . . **1. A. americana**

Folhas verde-escuras, oblanceoladas ou lanceolado-acuminadas, uncinado-conduplicadas no ápice e terminadas em espinho de 4-10 cm; pedúnculo 3 a 5 × tão comprido como a curta panícula piramidal; estilete por fim exserto até ao dobro dos estames; cápsula oblonga, subcostada e contraída no cimo num colo . . . . **2. A. atrovirens**

1 **A. americana** L., *Sp. Pl.* 323 (1753).

Hemicriptófito arrosetado monocárpico muito robusto, rizomatoso-estolhoso propagando-se vegetativamente por numerosos rebentos hipógeos; caule grosso, curto, carnudo mas por fim lenhoso. Folhas com 100-200 × 15-25 cm, carnudas, glaucas, lanceolado-oblongas, rectas, subplanas apenas subconduplicadas apicalmente, um tanto contraídas junto à base dilatada, espessa e invaginante, remotamente espinhoso--dentadas com dentes de 5-10 mm; ápice terminado em espinho com 2-3 cm, anegrado, vulnerante, robusto, roliço-cónico ainda que sulcado na ½ basal na face superior. Escapo (incluindo a inflorescência) com 4-7(-10) m, erecto; pedúnculo com 8-15(-20) cm de diâmetro na base, glauco em novo, tornando-se laranja-amarelado ou avermelhado na maturação, depois marcescente e acastanhado, por fim lenhoso, do mesmo comprimento ou menor do que a panícula, revestido de numerosas brácteas estéreis foliáceas, afastadas e não imbricadas, erecto-patentes ou por fim retroflectidas, triangular-assoveladas, da mesma cor do pedúnculo, inteiras e terminadas em mucrão grosso até 1.5 cm, as proximais até 50 cm. Panícula oblongo-ovoide, frouxa, com 20-25 ramos patentes, delgados, por vezes parcialmente bulbilíferos. Flores (incluindo o ovário) com c. 7 cm e assentes em pedicelos com 10-15 mm, cilíndricos, glaucos e robustos; tubo do hipanto com c. 35 mm, verde; perianto de segmentos com 30-35 mm, oblongo-lineares, obtusos, erectos, amarelo-esverdeados, um pouco convexos no ⅓ proximal; estames muito exsertos, com os filetes de 70-80 mm, inseridos no cimo do tubo do hipanto, levemente divergentes distalmente, glabros, amarelo-esver-

1 **2**
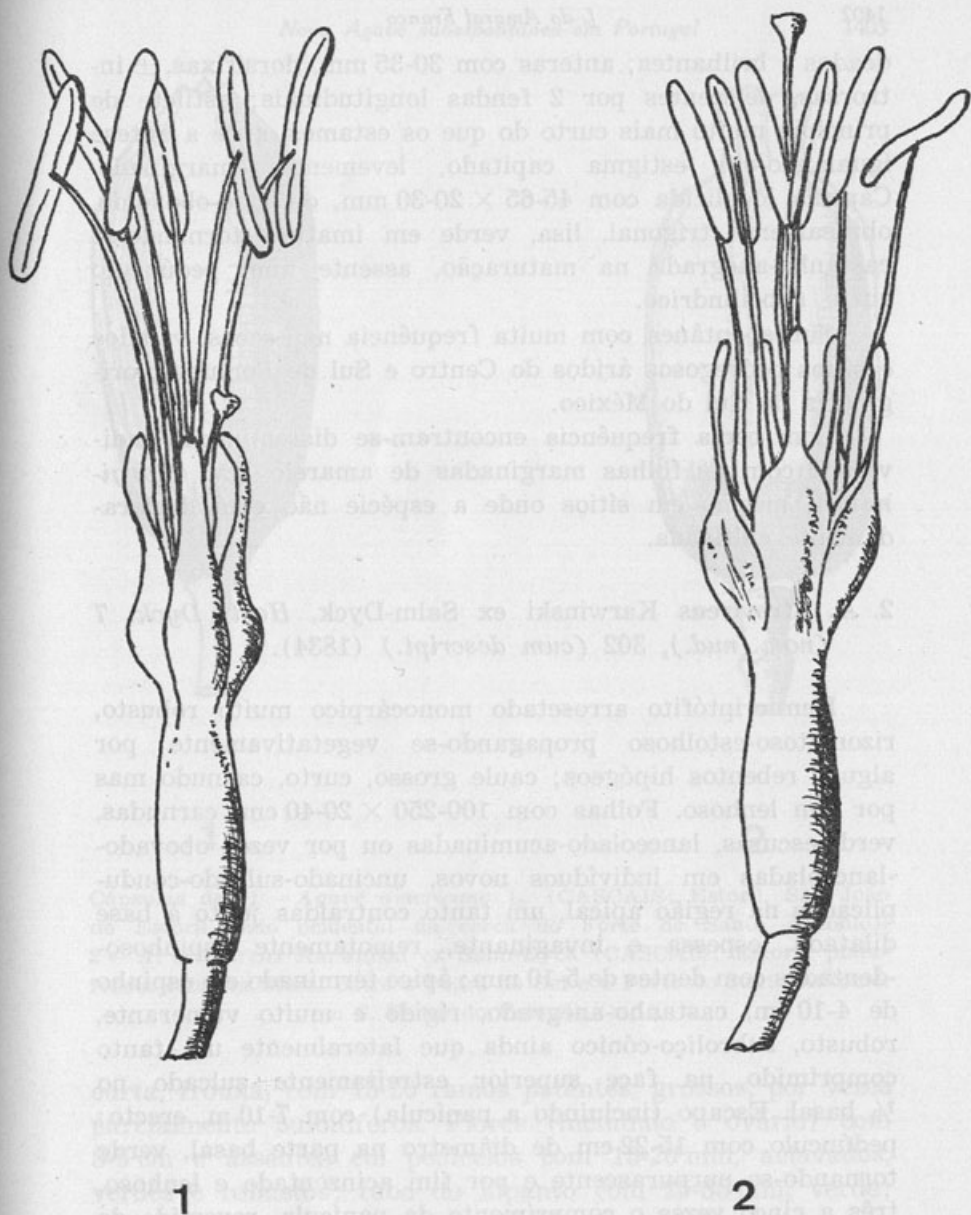
Flores de: 1 — *Agave americana* L. (SINTRA: Rio de Mouro, numa sebe a Norte da E. N. 249, pouco além do ramal para as Mercês). 2 — *A. atrovirens* Karwinski ex Salm-Dyck (CASCAIS: Estoril, plataforma calcária litoral entre a Pedra do Sal e o Forte de Santo António, em S. Pedro do Estoril) (× 1).

deados e brilhantes; anteras com 30-35 mm, dorsifixas, ± introrsas, deiscentes por 2 fendas longitudinais; estilete de princípio muito mais curto do que os estames, após a ântese igualando-os; estigma capitado, levemente emarginado. Cápsula loculicida com 45-65 × 20-30 mm, oblongo-obovoide, obtusamente trigonal, lisa, verde em imatura tornando-se castanho-anegrada na maturação, assente num pedúnculo curto subcilíndrico.

Subespontânea com muita frequência nas sebes, valados e sítios pedregosos áridos do Centro e Sul de Portugal; originária do Sul do México.

Com certa frequência encontram-se disseminados indivíduos com as folhas marginadas de amarelo (cv. *'Marginata'*), mesmo em sítios onde a espécie não está declaradamente cultivada.

2. **A. atrovirens** Karwinski ex Salm-Dyck, *Hort. Dyck.* 7 *(nom. nud.)*, 302 *(cum descript.)* (1834).

Hemicriptófito arrosetado monocárpico muito robusto, rizomatoso-estolhoso propagando-se vegetativamente por alguns rebentos hipógeos; caule grosso, curto, carnudo mas por fim lenhoso. Folhas com 100-250 × 20-40 cm, carnudas, verde-escuras, lanceolado-acuminadas ou por vezes obovado-lanceoladas em indivíduos novos, uncinado-sulcado-conduplicadas na região apical, um tanto contraídas junto à base dilatada, espessa e invaginante, remotamente espinhoso-dentadas com dentes de 5-10 mm; ápice terminado em espinho de 4-10 cm, castanho-anegrado, rígido e muito vulnerante, robusto, subroliço-cónico ainda que lateralmente um tanto comprimido, na face superior estreitamente sulcado no ⅓ basal. Escapo (incluindo a panícula) com 7-10 m, erecto; pedúnculo com 15-22 cm de diâmetro na parte basal, verde tornando-se purpurascente e por fim acinzentado e lenhoso, três a cinco vezes o comprimento da panícula, revestido de numerosas brácteas estéreis foliáceas, imbricadas e ± aplicadas (por fim retroflectidas), triangular-agudas, da mesma cor do pedúnculo, inteiras e terminadas em mucrão negro com 10-25 mm, as proximais até 75 cm. Panícula piramidal,
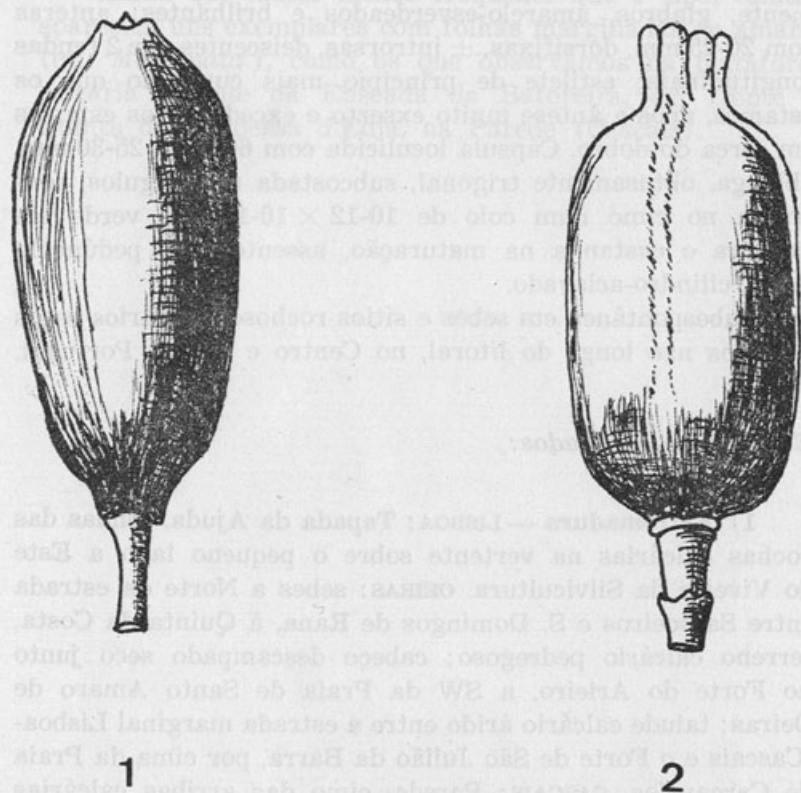
Cápsulas de: 1 — *Agave americana* L. (CASCAIS: Estoril, São João do Estoril, lado ocidental da cerca do Forte de Santo António). 2 — *A. atrovirens* Karwinski ex Salm-Dyck (CASCAIS: Estoril, plataforma calcária litoral entre a Pedra do Sal e o Forte de Santo António, em S. Pedro do Estoril) (× 1).

curta, frouxa, com 15-20 ramos patentes, grossos, por vezes parcialmente bulbilíferos. Flores (incluindo o ovário) com 8-9 cm e assentes em pedicelos com 15-20 mm, aclavados, verdes e robustos; tubo do hipanto com 25-35 mm, verde; perianto de segmentos com 25-35 mm, oblanceolados mas contraídos acima num apêndice com c. 20 mm, linear-oblongo, erectos, verde-amarelados, convexos na metade dilatada; estames muito exsertos, com os filetes de 55-65 mm, inseridos no cimo do tubo do hipanto, levemente divergentes distal-

mente, glabros, amarelo-esverdeados e brilhantes; anteras com 20-25 mm, dorsifixas, $\pm$ introrsas, deiscentes por 2 fendas longitudinais; estilete de princípio mais curto do que os estames, após a ântese muito exserto e excedendo os estames em cerca do dobro. Cápsula loculicida com 60-65 × 25-30 mm, oblonga, obtusamente trigonal, subcostada nos ângulos, contraída no cimo num colo de 10-12 × 10-12 mm, verde em imatura e castanha na maturação, assente num pedúnculo curto cilindro-aclavado.

Subespontânea em sebes e sítios rochosos calcários secos e áridos não longe do litoral, no Centro e Sul de Portugal.

Exemplares estudados:

1) **Estremadura** — LISBOA: Tapada da Ajuda, fendas das rochas calcárias na vertente sobre o pequeno lago a Este do Viveiro da Silvicultura. OEIRAS: sebes a Norte da estrada entre Sassoeiros e S. Domingos de Rana, à Quinta da Costa, terreno calcário pedregoso; cabeço descampado seco junto ao Forte do Arieiro, a SW da Praia de Santo Amaro de Oeiras; talude calcário árido entre a estrada marginal Lisboa--Cascais e o Forte de São Julião da Barra, por cima da Praia de Carcavelos. CASCAIS: Parede, cimo das arribas calcárias litorais (entre a praia da Parede ou da Água Doce e a ponta da Vigia); Estoril, plataforma calcária árida litoral (Baforeira; Pedra do Sal; Tranibeque; entre este e o Forte de Santo António; S. João do Estoril, em volta do Forte da Cadaveira, a Este da Praia da Poça, e a Oeste desta junto do Forte de S. Pedro); Cascais, plataforma calcária árida litoral (entre Oitavos e o Cabo Raso). MAFRA: Ericeira, cimo das arribas calcárias litorais, a Norte da Praia da Baleia.

2) **Algarve** — PORTIMÃO: sebe em terreno calcário junto ao ramal novo da estrada de acesso a Oeste da cidade e a Sul da ponte sobre a linha férrea; sebe em terreno calcário plano a Sul do caminho velho que segue para o Vau.

Ainda que muito menos frequente que o tipo, também aparecem uns exemplares com folhas marginadas de amarelo (cv. *'Marginata'*), como os que observámos na plataforma calcária a Este da Enseada da Baforeira, em frente da Quinta da Condessa d'Edla, na Parede (Cascais).
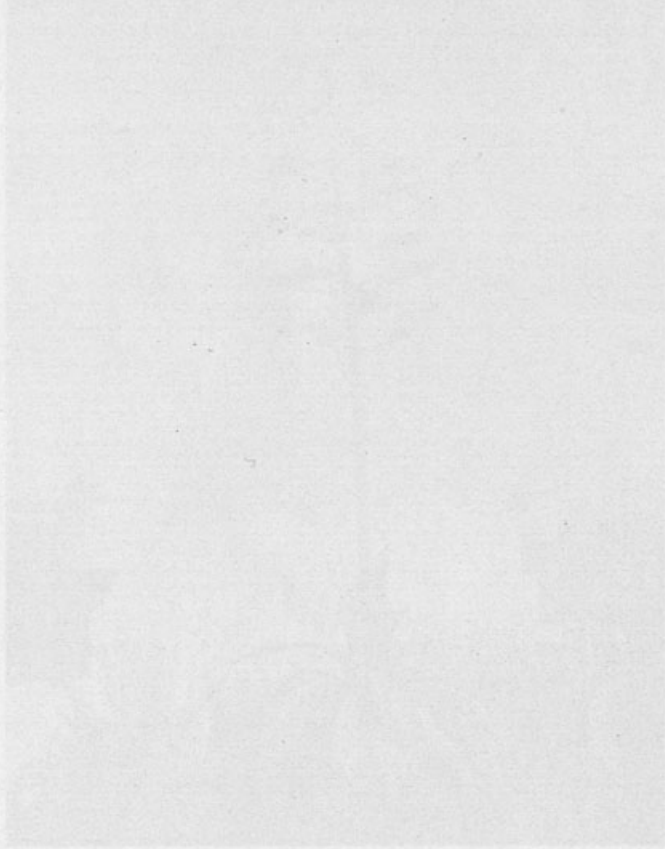
Agave americana L.

Estoril: Praia da Poça, lado W.

Agave atrovirens Karwinski ex Salm-Dyck.

S. Pedro do Estoril.

SOBRE AS RODOFÍCEAS DA RIA
DE AVEIRO

por

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INTRODUÇÃO

O estudo das Rodofíceas da costa de Portugal mereceu a atenção dos naturalistas portugueses e estrangeiros desde os princípios do século XIX. Na sua Flora Lusitanica, BROTERO (1804) enumerou as seguintes espécies: *Conferva corallina* L. (= *Ceramium rubrum* Ag.), no Tejo, pág. 432; *Fucus longissimus* Gmel. [= *Gracilaria verrucosa* (Huds.) Papenf.], junto à foz do Tejo e no litoral, entre Setúbal e Sesimbra, pág. 436; *Fucus cartilagineus* L. (= *Gelidium cartilagineum* L.) ibid., pág. 437; *Fucus laceratus* Gmel. (= *Cryptopleura lacerata* Kütz.), junto à foz do Tejo e do Douro, pág. 437; *Fucus filicinus* Wulf. (= *Grateloupia filicina* Ag.), junto à foz do Tejo, pág. 437. Não consta que BROTERO tivesse visitado a Ria de Aveiro.

Passados 44 anos (1848), WELWITSCH, de origem austríaca, colheu na Ria de Aveiro *Gracilaria confervoides* Ag. [= *Gracilaria verrucosa* (Huds.) Papenf.] e *Ceramium rubrum* (Huds.) Ag., as quais foram também colhidas por HENRIQUES, em 1874. Este continuou as suas pesquisas na Ria e em 1878 colheu *Gelidium corneum* (Turn.) Thuret. var *sesquipedale*. Além das três espécies, os ditos naturalistas colheram ainda *Pterosiphonia complanata* (Clem.) Falk., *Polysiphonia elongata* (Huds.) Harv. e *Anfeltia plicata* (Huds.) Fries. Todas estas espécies foram publicadas por HENRIQUES, em 1881, nas Contr. Fl. Crypt. Lusit.

De 1883-1911, a Sociedade Broteriana publicou as espécies que foram aparecendo em várias localidades, mas nenhuma proveniente da Ria de Aveiro.

HAUCK, em 1889, publicou um trabalho sobre Rodofíceas do Norte de Portugal, limitando, porém, os estudos a materiais colhidos na Foz do Douro, Leça e Pampolide.

Em 1912, AUGUSTO NOBRE, JAIME AFREIXO e JOSÉ DE MACEDO publicaram o «Relatório oficial do regulamento da Ria de 28 de Dezembro de 1912», em que vêm assinaladas as seguintes Rodofíceas para a Ria.

Fam. BANGIACEAE

Wildemania umbilicalis Kütz.

Fam. GELIDEACEAE

Gelidium corneum Lamour. (possivelmente vindo de outro lado).

Fam. GIGARTINACEAE

Ahnfeltia plicata Fries.

Fam. SPHOEROCOCCACEAE

Gracilaria confervoides Grev.

Fam. RHODOMELACEAE

Pterosiphonia complanata Falk.
Polysiphonia havanensis Mont. (nas estacas da Ria).

Fam. CERAMIACEAE

Ceranium rubrum Ag. (enrocamento da Barra).

O «Relatório» cita, por conseguinte, mais três espécies: *Wildemania umbilicalis* Kütz., *Gelidium corneum* Lamour. e *Polysiphonia havanensis* Mont., além das mencionadas por J. HENRIQUES nas Contr. Fl. Crypt. Lusit.

O facto de o «Relatório» referir que *Ceramium rubrum* Ag. se encontrava no «enrocamento» da Barra mostra que,

provavelmente, nessa data ainda não existiam no mesmo enrocamento *Chondrus crispus* (L.) Lyngb., nem *Gigartina stellata* (Stackh.) Batters, etc., que actualmente chamam a atenção pela sua abundância.

As condições da Ria antes de 1912 eram, portanto, muito diferentes das actuais, o que se deve à grande quantidade de blocos de pedra vermelha do Reciano, que para ali foram transportados, a fim de proteger o molhe central contra a violência das ondas nas marés cheias.

Fr. Ardré (in Portug. Acta Biol., Sér. B, **10**, 1-4: 137-555, 1969) publicou um trabalho intitulado «Contribution à l'étude des algues marines du Portugal», que nos mereceu a melhor atenção não só pela parte histórica que o acompanha, mas também pelo número de locais indicados para as Rodofíceas, obtidos a partir do estudo das colecções conservadas nos herbários de Lisboa, Porto e Coimbra, a literatura existente sobre cada espécie, etc. Verificamos, no entanto, que o número de referências à Ria de Aveiro era reduzido. Pelo contrário, o número das outras localidades e as algas existentes em cada uma delas era perfeito para a data e por isso foi para nós de muito valor a dita publicação. De acordo com ela, o ano de 1969 marca, por conseguinte, uma data em que o número de taxa de Rodofíceas inventariadas para a Ria de Aveiro era de 9 espécies.

Em 1973, o Director do Porto e Ria de Aveiro, Senhor Eng.º João de Oliveira Barrosa e o Reitor do Liceu, Senhor Dr. Orlando de Oliveira, convidaram-nos a fazer pesquisas na Ria, como vínhamos fazendo noutras localidades das margens do Vouga. Passado algum tempo, um grupo de estudantes do Liceu de Aveiro, escolhidos pelo seu Reitor para efectuar colheitas, tinha o prazer de ler, nas páginas do Bol. Soc. Brot. **51**, sér. 2: 91-106 (1977), a descrição de três Rodofíceas novas para a Ciência e uma nova para Portugal. As pesquisas continuaram e, nesta data, estão assinaladas para a Ria trinta e uma espécies de Rodofíceas, cuja descrição apresentamos em vernáculo a fim de facilitar aos estudantes o seu conhecimento.

* * *

Ao Exmo Senhor Prof. aposentado, Doutor ABÍLIO FER-NANDES, que sempre nos orientou no estudo das algas, corrigiu os nossos trabalhos e pôs ao nosso dispor livros e aparelhagem de investigação, protestamos a nossa sincera gratidão.

Ao Exmo Senhor Eng. JOÃO DE OLIVEIRA BARROSA que, por todos os meios ao seu alcance, possibilitou e facilitou as pesquisas na Ria, agradecemos a sua grande dedicação à causa do estudo da Ria, que resultou em auxílio para nós.

Ao antigo Senhor Reitor do Liceu, Dr. ORLANDO DE OLIVEIRA, que teve a amabilidade de escolher os melhores dos seus alunos para os delicados e árduos trabalhos da investigação, a nossa cordial estima e consideração.

ENUMERAÇÃO E DESCRIÇÃO DAS PLANTAS COLHIDAS

COMPSOPOGONACEAE Schmitz

Compsopogon lusitanicus P. Reis (vide Bol. Soc. Brot. 51, Sér. 2: 91, 1977). — Esteiro de Canelas, 27-VIII-1974, *P. Reis* 630 (COI).

CHANTRANSIACEAE Rabenh.

Rhodochorton purpureum (Lightf.) Rosenv. in Bot. Tidsskr. 23: 75 (1900). — De Toni, Syll. Alg.: 1510 (1903). — Gayral, Alg. Côt. Franç.: 361 (1966). — Fr. Ard. in Portug. Acta Biol., Sér. B, 10: 192 (1968).

Byssus purpurea Lightf., Fl. Scot., 2: 1000 (1792).
Conferva purpurea Dillw., Brit. Conf.: t. 43 (1809).
Callithamnion Rothii Lyngb., Hydr. Dan.: 129, t. 41 (1819).
Trentepohlia purpurea Ag., Syst. Alg.: 36 (1824). — Hook, Brit. Fl. 2: 382 (1833).
Callithamnion purpureum Harv., Man.: 116 (1841).

Talo de 1-10 mm de altura, formando um estrato ave-
ludado, subcrustáceo, mediante filamentos curtíssimos, hori-
zontais entrelaçados, emitindo filamentos erectos, simples ou
pouco ramificados, de 8-12 μ de diâmetro, constituídos por
células cilindróides, dispostas topo a topo, de comprimento
2-4 vezes o diâmetro, com plastos parietais, desprovidos de
pirenóides. Tetrasporângios 15-20 × 21-30 μ, formados em
tufos de ramúsculos.

Porto de Aveiro, 14-X-1978, *P. Reis* (COI).

Obs. Esta espécie, assinalada aqui pela primeira vez
para a Beira Litoral, foi encontrada também no DOURO
LITORAL: Foz do Douro, VII-1879, *Newton* (COI).

GELIDIACEAE Harv.

Gelidium pusilum (Stackh.) Le Jolis var. **pulvinatum**
(Ag.) Feldm. & Hamel in Rev. Alg. 9: 113, fig. 19-c (1936).
— Gayral, Alg. Côt. Franç.: 375, t. 84 (1966).

Sphaerococcus pulvinatus C. Ag., Spec. Alg.: 1: 284
(1823).

Acrocarpus pulvinatus Kütz., Sp. Alg.: 762 (1849); Tab.
Phyc. 18, t. 37, a-h (1868).

Gelidium pulvinatum Thuret in Bornet, Mém. Soc. Sci.
Nat.: 268, t. 28 (1892).

Talo reptante, roliço, com filamentos erectos de 5-15 mm
de altura e de 50-150 μ de diâmetro, de cor vermelha intensa,
irregularmente ramificado. Ramos subulados ou aclavados;
ramúsculos geralmente subfoliáceos, obovados ou ligulados,
por vezes com margem denticulada. Rizinas no centro dos
ramúsculos. Tetrasporângios distribuídos irregularmente nos
ramúsculos com 25-30 μ de diâmetro.

Próx. do farol da Barra, 17-VIII-1977, *P. Reis & M. Vieira*
707 (COI).

Esta espécie só tinha sido assinalada até hoje noutro
local da costa portuguesa: ESTREMADURA, Rio Tejo, Porto
Brandão, 11-1842, *Welwitsch* s. n. (LISU).

Gelidium pulchellum (Turn.) Kütz., Tab. Phyc. **18**, t. 53, fig. 1-f (1868). — Feldm. & Ham. in Rev. Alg. **9**: 119, fig. 23, t. 2, fig. 2 e 3 (1936). — Newton, Handb. Brit Seaw.: 263 (1931). — Gayr., Alg. Côt. Franç.: 377, t. 85 (1966). — Fr. Ard. in Portug. Acta Biol. **10**: 202 (1969).

Gelidium corneum var. *pulchellum* Turn., Fuci: 146, fig. 256 (1819).

Talo de 3-10 cm, em tufos de cor vermelha intensa, fixado ao substrato mediante rizóides. Ramificação alterna ou oposta, uni-bipinada. Filamentos geralmente com uma só ordem de pínulas curtas, semelhantes entre si (2-5 mm), nascendo ao longo dos ramos primários ou secundários, sendo uns e outros roliços ou comprimidos. Estrutura interna constituída por três estratos: cortical, muito ténue, formado por células pequeníssimas, arredondadas, de 5-6 μ de diâmetro, dispostas em filas verticais; subcortical, formado por células maiores arredondadas entre as quais existem rizinas; e central, constituído por células alongadas atenuadas nas extremidades e por algumas rizinas. Tetrasporângios esféricos com 30 μ de diâmetro, produzindo tetrásporos tetraédricos ou irregulares. Cistocarposporângios em pínulas que se tornam fusiformes.

Molhe central da Barra, 17-VII-1977, *P. Reis & M. Vieira* 700 (COI).

Esta espécie é frequente na costa portuguesa, visto ter sido colhida mais nas seguintes localidades: DOURO LITORAL: Póvoa de Varzim, VII-1878, *Newton* s. n. (COI); ibid. IX-1880, *Padrão* s. n. (COI); Leça da Palmeira, X-1848, *Welwitsch* s. n. (LISU); ibid. VIII-1872, *Henriques* s. n. (COI); Foz do Douro, 1-VIII-1878, *Lacerda* s. n. (COI). BEIRA LITORAL: Buarcos, IX-1877, *Moller* s. n. (COI); ibid., IX-1877, *Padrão* s. n. (COI); ibid., XI-1890, *G. de Carvalho* s. n. (COI; LISU); ibid., X-1929, X-1930, *T. Morais* s. n. (COI); ibid., VIII-1948, *M. de Carvalho* s. n. (COI); ibid., XI-1949, *Ernesto & Mendes* s. n. (COI); ibid., 6-IX-1953, *Rodrigues & Santos* s. n. (COI). ESTREMADURA: Ericeira, IX-1890, *Barros e Cunha* s. n. (COI);

ibid., VIII-1844, *Welwitsch* s. n. (LISU); Caxias, XI-1852, *Welwitsch* s. n. (LISU).

GRACILARIACEAE Kylin

Gracilaria verrucosa (Huds.) Papenf. in Hydrob. **2**: 195 (1950). — Gayral, Alg. Côt. Franç.: 425, t. 106 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 247 (1919).

Fucus confervoides L., Sp. Pl. ed. 2, **2**: 1629 (1763).
Fucus verrucosus Huds., Fl. Angl., ed. 2: 588 (1778).
Gracilaria confervoides (L.) Grev., Alg. Brit.: 123 (1830). — Harv., Phyc. Brit. **2**: t. 65 (1846-1851). — De-Toni, Syll. Alg. **4**, 1: 431 (1897). — Newton, Brit. Seaw.: 429, fig. 258 (1931). — Hauck in Rabenh.: 182 (1885, reimp. 1971).
Sphaerococcus confervoides (Ag.) Kütz., Sp. Alg.: 772 (1849); Tab. Phyc. **18**: t. 72 (1868).
Sphaerococcus divergens Kütz., Tab. Phyc. **18**: t. 74 (1868).

Var. **verrucosa**

Talo de 7-50 cm, de cor purpurescente, por vezes com zonas esverdeadas, simples ou em grupos, erecto ou prostrado (neste caso produzindo filamentos erectos, muito ramificados na parte inferior). Ramos alternos, dirigidos em todos os sentidos ou, por vezes, unilaterais, nus, flageliformes ou com alguns ramúsculos atenuados nas duas extremidades, fixo ao substrato mediante um pequeno disco e numerosos filamentos rizóides. Células da zona medular (observadas em secção) de paredes cada vez mais finas e diâmetro cada vez maior à medida que se aproximam do centro. Zona cortical constituída por células com 8-10 μ de diâmetro. Tetrasporângios disseminados na região cortical. Cistocarposporângios sésseis, esferóides ou ovóides.

Esteiro do Carregal, 23 e 27-VII-1973, *P. Reis* s. n. (COI).

Esta espécie já tinha sido colhida na Ria por WELWITSCH em 1848 e por HENRIQUES em 1874. Existe ainda nas seguintes localidades:

DOURO LITORAL: Póvoa de Varzim, 1878, *Padrão* s. n. (COI); ibid., 2-IV-1958, *M. Rodrigues & A. Santos* 597 (COI); Foz do Douro, I-1879, *Lima* s. n. (COI). BEIRA LITORAL: Figueira da Foz, IX-1877, *Moller* s. n. (COI); ibid., IX-1953, IX-1954, *A. Santos* s. n. (COI); Buarcos, X-1889, *J. de Carvalho* s. n. (COI); ibid., X-1939, *T. Morais* s. n. (COI); ibid., XI-1949, *Rodrigues* s. n. (COI); Cabo Mondego, XII-1939, *Lacerda,* s. n. (COI). ESTREMADURA: Lagoa de Óbidos, *Welwitsch* s. n. (LISU); Ericeira, VIII-IX-1846, *Welwitsch* s. n. (LISU); ibid., IV-1959, *Neves, M. Rodrigues, Reis & Santos* s. n. (COI); Belém, Cascais, Paço d'Arcos, Parede, Pedrouços, Tróia, Cruz Quebrada, Estoril, Oeiras, Cabo da Roca, III--VIII-IX-1841-1846, IX-XII-1849, I-IV-1850, IX-1851, I-1853, *Welwitsch* s. n. (LISU); São Julião, s. d., *Welwitsch* s. n. (LISU).

Var. **ramulosa** Kütz., Tab. Phyc. **18**: t. 72 (1868).

Esta variedade afasta-se do tipo, especialmente pelo eixo principal que é distinto e pode ultrapassar os 80 cm, com numerosos ramúsculos e alguns, poucos, compridos, nus ou quase, distribuídos no meio daqueles.

Taxon vivendo juntamente com o tipo nos vários esteiros, 27-IX-1979, *P. Reis* s. n. (COI).

Não colhida até hoje em Portugal.

Var. **procerrima** (Turn.).— Newton, Handb. Brit. Seaw.: 431 (1931).

Afasta-se do tipo pelos ramos muito longos (ca. 2,40 m), geralmente simples e quase nus.

Colhida pela primeira vez em Portugal, no esteiro do Carregal da Ria, 28-30-VIII-1980, *P. Reis* s. n. (COI).

Gracilaria vieirae P. Reis in Bol. Soc. Brot., **51**, Sér. 2: 91 (1977).

No esteiro da Costa Nova do Prado, 23-VII-1973, *M. Vieira* 692 (COI).

RHABDONIACEAE Kylin

Catenella repens (Lightf.) Batters in Journ. of Bot. **40** Suppl.: 69 (1902). — Newton, Britt. Seaw.: 119, fig. 251 (1931). — Gayral, Alg. Côt. Franç.: 437, t. 112 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 240 (1969).

Fucus repens Lightf., Fl. Scot. **2**: 961 (1792).
Fucus opuntia Good. & Woodw. in Trans. Linn. Soc. **3**: 219 (1797).
Catenella opuntia Grev., Alg. Brit.: 166, t. 17 (1830). — Harv., Phyc. Brit., t. 88 (1846-1851). — Kütz., Spec. Alg.: 724 (1849); Tab. Phyc. **16**: t. 71 (1866). — J. Ag., Sp. Alg. **3**: 588 (1876).— Hauck in Rabenh. **2**: 186 (1885, reimp. 1971).

Talo de 1-3 cm de altura, pulvinado-cespitoso. Base do talo filiforme, reptante com rizóides, emitindo ramos em di-tricotomias, sendo aquelas articuladas, por vezes fortemente constrictas nas articulações, roliças ou complanadas, de espessura irregular, de 0,5-1 mm, por vezes de 60-200 μ, frequentemente com pequenos ramúsculos. Ramos nascendo ordinariamente nas constrições. Articulações alongadas, ovóides ou claviformes, 2-10 vezes mais compridas que espessas. Tetrasporângios numerosos nos artículos dos ramúsculos curtos.

Espécie asinalada pela primeira vez para a Ria. Foi encontrada na meia laranja do molhe central da Barra, 25-XI-1978, *P. Reis & M. Vieira,* s. n. (COI). Além desta localidade, também tinha sido encontrada na Figueira da Foz, X-1929, por *T. Morais* s. n. (COI) e ainda na ESTREMADURA: Tejo salgado, Almada, Porto Brandão, X-1842, II & III--1843, *Welwitsch* (LISU).

PHYLLOPHORACEAE Nägeli

Gymnogongrus griffithsiae (Turn.) Mart., Fl. Bras. **1**: 27 (1833). —Kütz., Tab. Phyc. **19**: t. 65, fig. e-g. (1869). — Hauck in Rabenh., Crypt. Fl. **2**: 139, fig. 56 (1885). — De--Toni, Syll. Alg. **4**, 1: 242 (1897). — Newton, Handb. Brit.

Seaw.: 412, fig. 245 (1931). — Chemin. in Bull. Soc. Bot.
Franç.; 755, t. 6-7, fig. 1-3 (1933). — Gayral, Alg. Côt.
Franç.: 457, t. 120, fig. 58c (1966). — Schott. in Bull. Inst.
Ocean.: 62, fig. 35-36 (1968).

Fucus griffithsiae Turn., Hist. Fuc.: t. 37 (1808).
Sphaerococcus griffithsiae Ag., Sp. Alg. **1**: 316.

Talo cespitoso, pulviniforme, de 2-5 cm de altura, de cor
avermelhado-acastanhada, cartilaginoso, roliço ou subcom-
primido, indiviso próximo da base e em seguida irregular-
mente ramificado, fixado ao substrato mediante um disco.
Ramificação dicotómica, densa, por vezes fasciculado-poli-
cótoma. Segmentos filiformes, curtos ou longos, sendo os
terminais, quer alongados, quer curtíssimos e acuminados
ou subulados ou ainda obtusos e então, muitas vezes, com-
primidos. Nematécias dispersas irregularmente pelos ramos,
nascendo muitas vezes nas axilas, esferoidais, finalmente
extensas e amplexicaules.

Espécie encontrada pela primeira vez na Ria, 17-VIII-
1977, *P. Reis & M. Vieira* 696 (COI) e pela segunda na BEIRA
LITORAL, onde já era conhecida: Buarcos, X-1929, *T. Mo-
rais* (COI). DOURO LITORAL: Póvoa de Varzim, IX-1881, *Padrão*
(PO, COI, LISU); Foz do Douro, 27-VII-1879, *Newton* (PO).
ESTREMADURA: rio Tejo, pr. Caxias, III-1849, *Welwitsch*
(LISU); Santa Catarina de Ribamar, 27 & 28-I-1853, *Welwi-
tsch* (LISU); Tejo pr. Cruz Quebrada, XII-1849, *Welwitsch*
(LISU).

Gymnogongrus norvegicus (Gunn.) J. Ag., Sp. Alg., **2**,
1: 320 (1851-1863). — Chemin. in Bull. Soc. Bot. Franç. **71**:
305, fig. 1-2 (1929). — Seoane in Inv. Pesquis. **29**: 126, fig. 33,
6-7 (1965). — Gayral, Alg. Côt. Franç.: 455, fig. 58 (1966). —
Schotter in Bull. Inst. Océanogr.: 47, fig. 23-27 (1868). —
De-Toni, Syll. Alg.: 246 (1897).

Fucus norvegicus Gunn., Fl. Norv.: t. 3, fig. 4 (1766-
-1772). — Turn., Syn. Fuc. **2**: 222 (1802); Esp. Icon. Fuc.:
t. 153, fig. 1-4 (1797-1808).

Condrus norvegicus (Gunn) Lamour., Essai: 39 (1813).

Sphaerococcus norvegicus (Gunn) Ag., Sp. Alg.: 255 (1823).

Oncotylus norvegicus (Gunn) Kütz., Phyc. Gen.: 411 (1843); Sp. Alg.: 789 (1849).

Talo de 3-5 cm, de cor coccíneo-purpúrea, cespitoso, arredondado na base, comprimido na parte superior e em seguida plano, de ramificação dicotómica. Axilas muitas vezes um tanto agudas. Ramos lineares, de 2-5 mm de largura, com os últimos segmentos obtusos, arredondados ou emarginados no ápice. Pseudo-nematécias hemisféricas, salientes nas duas páginas, medindo cerca de 1-2 mm de diâmetro.

Molhe central, pr. farol, 17-VII-1977, *P. Reis & M. Vieira* 697 & 698 (COI).

Encontra-se também no DOURO LITORAL: Leça da Palmeira, VIII-1872, *Henriques* (COI). BEIRA LITORAL: Buarcos, IX-1977, *Moller* s. n. (COI); Figueira da Foz, Buarcos 7-IX--1953, *A. Santos* (COI). ESTREMADURA: Praia das Maçãs, VIII-1840, *Welwitsch* (LISU); Portinho d'Arrábida, 14-XII--1851, *Welwitsch* (LISU); Oceano Atlântico nas rochas pr. Oeiras, 1-XI-1851, *Welwitsch* (LISU); Caxias, XI-1849, *Welwitsch* (LISU).

GIGARTINACEAE Hauck

Gigartina acicularis (Wulf.) Lamour. in Ann. Mus. Hist. Nat. Paris, 20: 44 (1813). — J. Ag., Sp. Alg. 2: 263 (1851). — Kütz., Tab. Phyc. 18: t. 1c-e (1868). — Harv., Phyc. Brit., 3: t. 104 (1846-1851). — De-Toni, Syll. Alg. 4, 1: 198 (1897). — Hauck in Rabenh., Meersalg.: 136 (1885). — Newton, Br. Seaw.: 406 (1931). — Gayral, Alg. Côt. Franç.: 470 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, 10: 258 (1969).

Fucus acicularis Wulf., Crypt. Aquat. 3: n.º 50 (1803).

Sphaerococus acicularis (Wulf.) Ag., Sp. Alg. 2: 322 (1885).

Talo de 4-10 cm, vermelho-acastanhado, purpúreo ou violáceo-escuro, quando seco, roliço, cartilagíneo, com cerca de 1 mm de espessura, irregularmente ramificado em todos os sentidos, disposto em tufos. Ramos divaricados, curvos, ponteagudos, com ramúsculos ± curtos, patentes ou curvados, subulados, subatenuados na base. Cistocarpos quase esféricos, 1-4 nos ramúsculos, muitas vezes unilaterais. Tetrasporângios em ramúsculos um tanto engrossados.

Espécie muito frequente na costa portuguesa, mas assinalada pela primeira vez para a Ria, no molhe central pr. farol, 14-X-1976) *P. Reis & M. Vieira* (COI). Foi também colhida em:

DOURO LITORAL: Porto, Douro, *Newton* (COI); Apúlia pr. Póvoa de Varzim, 22-IV-1958, *M. Rodrigues & A. Santos* 662 (COI); ibid., IX-1880, *Padrão* (COI); Figueira da Foz, entre Buarcos e o Cabo Mondego, 8-IX-1953, *A. Santos,* 19 (COI); Buarcos, IX-1877, *Moller* (COI); ibid., VIII-1948, *J. Montezuma de Carvalho* (COI). ESTREMADURA, Cascais, 6-IX-1843, *Welwitsch* (COI).

Gigartina teedii (Roth.) Lamour. var. **lusitanica** M. Rodrigues in Bol. Soc. Brot., sér. 2, 32: 91 (1958). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 262 (1969).

Talo de 5-20 cm, vermelho-acastanhado, cartilaginoso, aplanado, de 3-10 mm de largura, densamente ramificado, com pínulas subhorizontais, patentes, simples, agudas, subespinicentes, inseridas nas margens dos eixos e dos ramos, muito raramente na superfície de uns e outros. Exemplares férteis produzindo cistocarpos muito numerosos.

Este taxon tem sido citado como *Gigartina teedii* (Roth.) Lamour., mas não há dúvida que ele constitui uma boa variedade, como M. RODRIGUES notou. É vulgaríssima na costa portuguesa, mas não tinha sido ainda assinalada para a Ria. Foi colhida no molhe central, 17-VIII-1977, *P. Reis & M. Vieira* 694 (COI). É conhecida ainda de:

DOURO LITORAL: Póvoa de Varzim, Aguçadora, 22-IV-
-1958, *M. Rodrigues & A. Santos* 606 (COI) ; Póvoa de Var-
zim, IX-1877, *Padrão*. ESTREMADURA: Cascais, 6-IX-1843,
Welwitsch (COI) ; Tejo salgado, pr. Caxias, X-1851, *Welwitsch*
(LISU) ; Foz do Tejo, pr. S. Julião, 7-1850, *Welwitsch*; entre
Cascais e Cabo da Roca, II-1840, *Welwitsch* 61 (LISU) ;
S. Julião da Barra e Oeiras, VIII-1845, *Welwitsch* (LISU) ;
Cabo da Roca, II-1840, *Welwitsch* (LISU) ; entre Cruz Que-
brada e Caxias, IV-1843, *Welwitsch* (LISU) ; Oeiras, XI-1851,
Welwitsch (LISU) ; Oeiras, XI-1851, *Welwitsch* (LISU).

Gigartina stellata (Stackh.) Batters in Journ. of Bot.
40, Suppl.: 64 (1902). — Newton, Handb. Brit. Seaw. 408,
fig. 242 (1931). — Rosenving, Mar. Alg. Denmark, Rhodoph.
4: 509, figs. 474-476 (1931). — Gayral, Alg. Côt. Franç.: 467,
t. 125 (1966).

Fucus stellatus Stackh., Ner. Brit.: t. 12 (1795).
Fucus mamillosus Good. & Woodw. in Trans. Linn. Soc.
3: 174 (1797).
Sphaeroccocus mamillosus C. Ag., Sp. Alg. 1: 260 (1823).
Chondrus mamillosus Grev., Alg. Brit.: 127 (1830).
Mastocarpus mamillosus Kütz., Phyc. Gen.: 398, t. 76,
fig. 3 (1843), Sp. Alg.: 733 (1840) ; Tab. Phyc. 17: t. 39
(1867).
Gigartina mamillosa Hauck in Rabenh., Krypt. Fl. 2: 137,
fig. 55 (1885). — De-Toni, Syll. Alg. 4, 1: 218 (1897).

Talo de 6-15 cm, de cor purpurascente ou vermelha
intensa, cartilagíneo, plano ou canaliculado, roliço na base
e fixado ao substrato mediante um disco, dicotomicamente
ramificado, formando céspedes hemisféricas. Ramos patentes.
Segmentos quer todos semelhantes, lineares, de 2-4 mm de
largura, quer todos acunheados de 2-8 mm de largura ou os
inferiores lineares e os superiores acunheados, os terminais
emarginados ou bífidos, subacuminados ou muitas vezes um
tanto obtusos. Papilas na parte superior da fronde e no
disco, quer raras, quer numerosas curtas ou alongadas.
Cistocarposporângios com pericarpo ovóide, de 2-5 mm de
comprimento, curta ou longamente pedicelados.

Espécie muito abundante no molhe central da Ria, 17-VIII-1977, *P. Reis & M. Vieira* 695 (COI). Em 1912, porém, ainda ali não fora encontrada. Foi colhida também nas seguintes localidades:

DOURO LITORAL: Foz do Douro, s. d. *Newton* (PO). BEIRA LITORAL: Buarcos, XI-1889, *Goltz de Carvalho* (PO).

Chondrus crispus (L.) Stackh., Ner. Brit. XXIV (1997).— Lyngb., Hydr. Dam.: 15, t. 5A-B (1819). — Grev., Alg. Brit.: 129, t. 15 (1830). — Harv., Phyc. Brit.: t. 63 (1846-1851). — Kütz.*, Sp. Alg.: 735 (1849); Tab. Phyc., **17**: t. 49 (1867). — J. Ag., Sp. Alg. **2**: 246 (1851). — De-Toni, Syll. Alg. **4**, **1**: 180 (1897). — Newton*, Handb. Seaw.: 404, fig. 241 (1931). — Gayral*, Alg. Côt. Franç.: 471, t. 127 (1966). — Fr. Ardré* in Portug. Acta Biol., Sér. B, 256 (1969).

Fucus crispus L., Syst. Nat. **2**: 718 (1767); Mant. Plant.: 134 (1767).
Fucus filiformis Huds., Fl. Angl.: 585, ed. 2 (1778).
Sphaerococcus crispus C. Ag., Sp. Alg. **1**, **2**: 256 (1822); Syst. Alg.: 219 (1824).
Chondrus incurvatus Kütz., Phyc. Gen.: 399, t. 73, fig. 2 (1843); Sp. Alg.: 735 (1849); Tab. Phyc. **17**: t. 50 (1867).

Talo erecto, de 8-15 cm, de cor violácea ou purpúreo-lívida, cartilagíneo, plano, filiforme na base, aderente ao substrato mediante um disco, de onde se elevam várias frondes. Ramificação dicótomo-flabeliforme. Dicotomias ± numerosas. Segmentos de largura muito variável (estreitos, lineares ou largos e acunheados), com ápices agudos ou obtusos, estreitos ou largamente arredondados; margens encrespadas, nuas ou com proliferações liguladas. Cistocarposporângios impressos no disco ou nas proliferações, quase ovais, de 2-2,2 mm de diâmetro. Tetrasporângios formando manchas semelhantes a carposporângios, na região cortical dos segmentos terminais.

Como *Gigartina stellata* (Stackh.) Batters, também *C. crispus* C. Ag. é muito vulgar no molhe central da Ria,

mas só em 17-VIII-1977 ali foi colhida pela primeira vez por *P. Reis & M. Vieira* 712 (COI). Foi herborizada ainda nas seguintes localidades:

DOURO LITORAL: Foz do Douro, I-1878, *Lima* (COI); ibid. 1879, *Newton* (COI). BEIRA LITORAL: Cabo Mondego, XII-1939, *Lacerda* (COI); ibid., IX-1953, *A. Santos* (COI); Buarcos, IX-1877, *Moller* (COI); ibid., IX-1877, *Moller* (COI); ibid., X-1929, *T. Morais* (COI); ibid., VIII-1949, *M. de Carvalho* (COI); ibid., VIII-IX-1953, *A. Santos* (COI). ESTREMADURA: S. Martinho do Porto, V-1958, *M. Rodrigues & A. Santos* (COI); Ericeira, IV-1959, *Neves, M. Rodrigues, Reis & Santos* (COI); Paço d'Arcos, IX-1878, *Welwitsch* (COI); Cruz Quebrada: Cascais, II-III-IX-1872, s. n., *Welwitsch* (LISU).

Obs. Os autores assinalados com asterisco atribuem a combinação a LYNGBYE, mas KYLIN atribui-a a STACKHOUSE.

LOMENTARIACEAE Nägeli

Lomentaria articulata (Huds.) Lyngb., var. **linearis** Zanardi, Syn Alg. Adriat.: 97 (1841); Saggio: 50 (1843). — De-Toni, Syll. Alg. 4, 1: 554 (1897).

Lomentaria phalligera J. Ag., Alg. Med.: 110 (1842); Sp. Alg. 2: 727 (1852), non Kütz.

Lomentaria linearis Zanardi, Icon. Phyc. Adriat. 2: 161, t. 79 (1865). — Kütz., Sp. Alg.: 863 (1849); Tab. Phyc. 15, t. 85 (1865).

Chylocladia phalligera J. Ag., Sp. Alg. 3: 300 (1876).

Chylocladia articulata (Huds.) Grev. var. *linearis* (Zanardi) Hauck in Rabenh., Krypt. Fl. 2: 156 (1885, reimp. 1971).

Fronde erecta, de 3-12 cm de altura, róseo-purpúrea, empalidecendo no seco, irregularmente ramificada. Ramos primários um pouco contraídos na base, divididos frequentemente por dicotomias. Ramos secundários com ramúsculos opostos nas extremidades. Artículos roliços ou um pouco aplanados, tubulosos, de 4-6 vezes o diâmetro ou de 1-2 mm de largura, os terminais acuminados ou obtusos. Estrutura

interna constituída por duas zonas: a periférica formada
por células muito pequenas e arredondadas, a subjacente
por células grandes e irregulares. Tetrásporos tetraédricos,
dispostos em torno de pequenas depressões corticais. Cisto-
carpos 1-3, ordenados em filas transversais.

Esta variedade, assinalada pela primeira vez para a Ria,
no molhe central, 17-VIII-1977, *P. Reis & M. Vieira* (COI),
é vulgar noutras localidades da costa portuguesa:

MINHO: Apúlia, Aguçadora, 22-IV-1958, *M. Rodrigues
& Santos* (625 (COI). DOURO LITORAL: Foz do Douro, 27-VII-
-1879, *Newton* (PO, COI); Póvoa de Varzim, 27-IX-1881,
Padrão (PO, COI, LISU). BEIRA LITORAL: Buarcos, X-1929,
T. Morais (COI); Cabo Mondego, I-XII-1939, *Lacerda* s. n.
(COI). ESTREMADURA: São Martinho do Porto, V-1958, *M. Ro-
drigues & Santos* 718 (COI); Santa Catarina de Ribamar,
27 e 28-I-1853, *Welwitsch* (LISU); Tejo, pr. Cascais, III-1849,
Welwitsch (LISU).

CERAMIACEAE Reichenb.

Ceramium ciliatum (Ellis) Ducluz., Essai Conferv. Mont-
pellier: 64, t. 53, fig. 1-4 (1905). — Lyngb., Hydroph. Dan.:
121, t. 37 (1819). — Harv., Phyc. Brit. 129 (1847). — J. Ag.,
Sp. Alg. **2**: 133 (1851). — Ardiss., Phyc. Medit. **1**: 117 (1883).
— Hauck, Meersalg. **2**: 110 (1885, reimpr. 1971). — De-Toni,
Syll. Alg. **4**, 2: 1473 (1903). — Gayral, Alg. Côt. Franç.: 529,
t. 156 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B,
10: 280 (1969).

Conferva ciliata Ellis in Phil. Trans. **57**: 425, t. 18, fig. h
(1776); Lightf., Fl. Scot. **2**: 998 (1792); Dillw., Brit. Confer.:
77, t. 53 (1809).
    Echinoceras ciliatum Kütz., Phyc. Gen.: 380 (1843).

Talo delicado, de 5-10 cm, de cor vermelha intensa,
regularmente dicotómico, com segmentos patentes e as extre-
midades encurvadas em forma de torquez. Artículos dos
ramos principais 2-4 vezes o diâmetro. Nós corticados, sepa-
rados por espaços iguais ao diâmetro ou ultrapassando-o,

providos de uma coroa de espinhos, constituídos por 3 células, sendo os da parte inferior menores. Entrenós incolores. Tetrasporângios verticilados, ± proeminentes, muitas vezes alternando com os espinhos. Gonimoblastos laterais, frequentemente inseridos em proliferações e cercados de ramúsculos, 3-4 vezes mais longos, servindo-lhes de invólucro.

A Beira Litoral é assinalada pela primeira vez para esta espécie, 30-IX & 25-XI-1978, *P. Reis & M. Vieira* 720 (COI). Foi colhida ainda nas seguintes localidades: ESTREMADURA: S. Martinho do Porto, 1-V-1958, *A. Santos & M. Rodrigues* (COI); Tejo salgado, IV-1849, *Welwitsch* (LISU). ALGARVE: Cabo de S. Vicente, VI-1847, *Welwitsch* (LISU); Lagos, VI-1847, *Welwitsch* (LISU).

Ceramium flabelligerum J. Ag., Syst. Alg. Advers.: 27 (1844). — Harv., Phyc. Brit. 3: t. 144 (1847). — Kütz., Sp. Alg. 688 (1849); Tab. Phyc. 13: t. 14, fig. f-j (1863). — De--Toni, Syll. Alg. 4, 2: 1482 (1903). — F. Miranda in Bol. Real Soc. Esp. Hist. Nat.: t. 29 (1929). — Newton, Handb. Brit. Seaw. 401 (1931). — Seoane-Camba in Inv. Pesquis.: 133, fig. 37 (1965). — Gayral, Alg. Côt. Franç.: 531 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 282 (1969).

Ceramium spiniferum Kütz., Sp. Alg., 688 (1849).

Talo de 4-10 cm, de cor purpúrea. Eixos principais ramificados dicotomicamente. Ramos alternos, quase dísticos, ramificados em forma de leque ou flabelado-corimbosos na parte superior. Segmentos erecto-patentes, terminando em forma de torquez aberta, com uma espícula articulada e colorida, no lado externo de cada artículo. Artículos dos ramos principais de comprimento uma vez e meia maior que o diâmetro, sendo o dos ramos superiores igual a cerca de metade do diâmetro. Corticação geral. Tetrasporângios salientes da corticação, formando verticilos e tornando os artículos nodosos nas regiões terminais frutíferas. Gonimoblastos dispostos nos ramos superiores em grupos de dois a três, cercados de ramúsculos curtos que lhes servem de invólucro.

Molhe central da Barra, 17-VIII-1977, *P. Reis & M. Vieira* 713 (COI). Encontra-se, além disso, nas seguintes províncias: DOURO LITORAL: Foz do Douro, VIII-1789, *J. Newton* (PO); Leça da Palmeira, IX-1880, *Newton* (COI, PO). ESTREMADURA: Rio Tejo, nas rochas basálticas, 9-III-1852, *Welwitsch* (LISU); Tejo salgado, pr. Caxias, 22-II-1952, *Welwitsch* (LISU); Tejo, pr. Caxias, sobre as frondes de *Fucus vesiculosus*, 9-III-1952, *Welwitsch* (LISU).

Ceramium arborescens J. Ag., Analecta Algol. **2**: 33 (1894). — De-Toni, Syll. Alg. **4**, 2: 1472 (1903). — Newton, Handb. Seaw.: 399 (1931).

Talo arboriforme, de 8-9 cm, de cor intensamente vermelha. Eixos principais muito desenvolvidos. Ramificação dicotómica com os ramos progressivamente mais delicados, sendo os últimos quase capilares e corimbosos. Extremidades dos ramos principais geralmente alongadas e ligeiramente curvas. Proliferações numerosas. Corticação presente, formada a partir das duas margens (superior e inferior) de cada nó, sobre os respectivos entrenós e deixando uma zona nos artículos da parte superior do talo; na inferior corticação total. Artículos do ápice não corticados. Nós inferiores distantes, os superiores próximos. Artículos inferiores iguais a 2-3 vezes o diâmetro. Tetrasporângios verticilados, em série simples e imersos. Gonimoblastos raros.

BEIRA LITORAL: Aveiro, no molhe central da Barra, 17-VIII-1977, *P. Reis & M. Vieira* 711 (COI).

Obs. Esta espécie é assinalada pela primeira vez para Portugal.

Ceramium rubrum (Huds.) Ag., Syn.: 60 (1817); Sp. Alg. **2**: 146 (1828). — Lyngb., Hydr. Dan.: 118, t. 62b, fig. 1 (1819). — Harv., Phyc. Brit.: t. 181 (1848). — Mart., Fl. Bras.: 14 (1833). — Derb. & Sol., Mém. Physiol. Alg.: 71, t. 18, fig. 9-11 (1856). — Kütz., Tab. Phy. **13**: t. 4 (1863). — J. Ag., Epicr.: 100 (1876); Fl. Morphol.: t. 3, fig. 21-23 (1879); Anal. Algol. **2**: 37 (1892). — Ardiss., Phyc. Med.

1: 113 (1883). — De-Toni, Syll. Alg. **4**, 2: 1476 (1903). — Gayral, Alg. Côt. Franç.: 535 (1966). — Fr. Ardr. in Portug. Acta Biol., Sér. B, **10**: 289 (1969).

Conferva rubra Huds., Fl. Angl., ed. 2: 600 (1778). — Dillw., Brit. Conferva: t. 34 (1809).

Conferva tubulosa Huds., Fl. Angl., ed. 2: 660 (1778). *Boryna variabilis* Bonnem. in Mém. Mus. **16**: 53 (1828).

Talo de 20-25 cm, de cor intensamente vermelha, ramificado subdicotomicamente, totalmente corticado, inerme, subnoduloso. Extremidades dos ramos ligeiramente curvas ou rectas, afiladas. Artículos cilíndrico-elipsóidais, translúcidos na parte média da fronde. Nós obscuros e muitas vezes contraídos. Tetrasporângios mergulhados no estrato cortical em torno dos nós, dispostos em 1-2 séries transversais. Gonimoblastos 1-2, nascendo nos próprios segmentos ou muitas vezes em raminhos cercados de 3-5 ramúsculos encurvados, igualando ou ultrapassando os cistocarposporângios.

Trata-se de uma espécie vulgaríssima em toda a costa portuguesa, publicada por HENRIQUES in Contr. Fl. Crypt. Lusit.: 25 (1881) por quem tinha sido herborizada em 1876, depois por MOLLER (1877) e por T. MORAIS (1929).

DOURO LITORAL: Póvoa de Varzim, VIII-1879, *Newton* (COI); ibid., IX-1880, *Padrão* (COI); Leça da Palmeira, VIII-1872, *Henriques* (COI); São João da Foz, VII-VIII-1858, *Henriques* (COI); Foz do Douro, VIII-1878, VII-VIII-1879, *Newton* (COI). BEIRA LITORAL: Buarcos, IX-1877, *Moller* (COI); ibid., VIII-1879, *Henriques* (COI); ibid., X-1929, *T. Morais* (COI). ESTREMADURA: S. Martinho do Porto, V-1958, *A. Santos* (COI); Ericeira, IV-1959, *Neves, M. Rodrigues, Reis & Santos* (COI); Pedrouços, Caxias, Cruz Quebrada, Tróia, VI-VIII-1849, *Welwitsch* (LISU); Porto Brandão, II-1843, *Welwitsch;* Arrábida, VI-1852, *Welwitsch* (LISU). ALGARVE: Faro, V-1847, *Welwitsch* (LISU).

SPYRIDIA Harv.

Spyridia filamentosa (Wulf.) Harv. in Hook., Brit. Fl. **2**: 336 (1833); Phyc. Brit.; t. 46 (1846).

Vide P. REIS in Bol. Soc. Brot. **51**, Sér. 2: 94 (1977).

Callithamnion tetragonum (Wither) C. Ag., Sp. Alg. **2**:
176 (1823, reimp. 1969). — Harv., Phyc. Brit.: **3**: t. 136
(1847). — Kütz., Tab. Phyc. **12**: t. 3, fig. c-d (1862). —
Ardiss., Phyc. Med. **1**: 74 (1883). — Hauck, Meeresalg.: 81
(1885, reimp. 1971). — Kylin, Stud. Algenpl.: 158 (1907). —
Boerg., Mar. Alg. Canary Isl. **3**: 46, fig. 17 (1930). — De-
Toni, Syll. Alg. **4**, 2: 1320 (1903). — Feldm. Céram. Medit.:
473 (1940). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**:
309 (1969).

Conferva tetragona Wither., Arrang. Brit. Pl. **5**: 405
(1818).
Ceramium brachiatum Bonnem., Ess. Hydr. ed. 2: 87
(1828).
Phlebothamnion tetragonum Kütz., Sp. Alg.: 654 (1849).
Dorythamnion tetragonum Nägeli, Beitr. Morph. Syst.
Ceram.: 344 (1861).

Talo erecto, de 6-8 cm de altura, de cor intensamente
vermelha, cespitoso, subquadrangular na base, fixo ao
substrato mediante rizóides. Eixos principais cobertos de
ramos inseridos em espiral, alternos e pinados, os quais
são igualmente cobertos de ramúsculos, que lhes dão um
aspecto cilindróide. Pínulas encurvadas para a ráquis e
apiculadas. Base dos eixos principais inteiramente corticada
com cerca de 360 μ de diâmetro; ramos com 110-190 μ; os
ramúsculos com 60-80 μ e as células terminais com 15-20 μ
de diâmetro. Artículos de comprimento 2-3 vezes o diâmetro.
Artículos dos ramúsculos cilindróides, igualando o diâmetro.
Gonimoblastos inseridos nos ramos superiores. Tetrasporân-
gio no lado anterior das últimas pínulas.

Apesar de pouco vulgar, herborizou-se no molhe central
da Barra em 17-VIII-1977, *P. Reis & M. Vieira* 719 (COI).
Foi encontrado também nas seguintes localidades:
MINHO: Apúlia, Aguçadora, IV-1958, *M. Rodrigues &
Santos* s. n. (COI). DOURO LITORAL: Leça da Palmeira, VIII-
-1872, *Padrão* s. n. (COI); Foz do Douro, 1880, *Newton* s. n.

(COI). ESTREMADURA: Cabo da Roca, Parede, II-1842, IV-1850, *Welwitsch* s. n. (LISU).

DELESSERIACEAE Nägeli

Hypoglossum woodwardii Kütz., Phyc. Gen.: 65, fig. 1 (1843); Sp. Alg. 875 (1849); Tab. Phyc. **16**: t. 11 fig. a-c (1866). — J. Ag., Sp. Alg. 3, 3: 189 (1898). — De-Toni, Syll. Alg. 4, 1: 694 (1897). — Gayral, Alg. Côt. Franç.: 539, t. 161 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 311 (1969).

Fucus hypoglossum Woodward. in Trans. Linn. Soc. 2: 30, t. 7 (1794). — Lamour., Ess. Thalassioph.: 39 (1813). — Grev., Alg. Brit.: 75, t. 12 (1830). — C. Ag., Sp. Alg.: 176 (1869). — J. Ag., Sp. Gen. Ord. Alg. 3, 1: 489 (1876). — Ardiss. in Phyc. Med. **1**: 260 (1883).

Fucus hypoglossoides Stackh., Ner. Brit. ed. 2: tab. 13 (1816).

Delesseria hypoglossum (Woodward) C. Ag., Sp. Alg. 1: 176 (1823, reimp. 1969).

Delesseria lingulata Duby, Bot. Gall.: 946 (1830).

Talo de 6-8 cm, foliáceo, membranoso, de cor coccínea, vagamente ramificado, com proliferações nascendo das nervuras, fixado ao substrato por um disco comum a várias frondes. Ramos de 2-4 cm, lanceolado-lineares, acuminados numa e outra extremidade, de 1-3 mm de largura, inteiros. Nervuras cingidas muitas vezes por uma asa estreita, mesmo na parte inferior, raramente nuas. Nervuras secundárias ausentes. Lâmina formada por uma única camada de células. Cistocarporângios sésseis sobre a nervura, sub-esféricos, por fim apiculados. Tetrasporângios formando soros ao longo das nervuras.

Herborizou-se pela primeira vez no molhe central da Barra, 17-VIII-1977, *P. Reis & M. Vieira* 718 (COI). Aparece, no entanto, em toda a costa portuguesa.

MINHO: Montedor, 25-III-1963, *Fr. Ardré;* 18-X-1963, *Fr. Ardré;* Viana, 24-III-1963, *Fr. Ardré.* DOURO LITORAL:

Póvoa, 1881, *Henriques* (COI); Foz do Douro, São João da Foz, VIII-1871, *Newton* s. n. (COI). BEIRA LITORAL: Buarcos, VIII-1879, *Henriques* s. n. (COI). ESTREMADURA: Nazaré (COI); Tejo salgado, Pedrouços, Caxias, Praia das Maçãs, Trafaria, II-1841, II-1942, 8-1849-VI-1853, *Welwitsch* s. n. (LISU), Arrábida, III-VII-1852, *Welwitsch* s. n. (LISU); ibid., 1958, *Palminha;* ibid., IV-1959, *Neves, Reis & Santos,* s. n. (COI). ALGARVE: Sagres, 27-28-II-1960, 25-IV-1963; Lagos, 26-II--1960; Praia da Rocha, 25-II-1960, 27-IV-1963; Carvoeiro, 26-IV-1963; Albufeira, 15-VIII-1960, *Feldmann.*

Cryptopleura ramosa (Huds.) Kylin ex Newton, Brit. Seaw.: 332, fig. 205 (1931). — Gayral, Alg. Côt. Franç.: 547, fig. 165 (1966). — Fr. Ardré in Portug. Acta Biol., Sér. B, **10**: 319 (1969).

Ulva ramosa Huds., Fl. Angl.: 476 (1762).
Fucus laceratus Gmel., Hist. Fuc.: 179, t. 21, fig. 4 (1768).
Nitophyllum laceratum (Gmel.) Grev., Alg. Brit.: 83 (1830). — Harv., Phyc. Brit. **2**, **1**: t. 267 (1846-1851). — J. Ag., Sp. Alg. **3**, **3**: 658 (1898). — De-Toni, Syll. Alg. **4**, **1**: 663 (1897).
Cryptopleura lacerata (Gmel.) Kütz., Phyc. Gen.: 444 (1843); Sp. Alg.: 870 (1849); Tab. Phyc. **16**: t. 25, fig. a-d (1866). — Kylin, Stud. Deless.: 86 (1924).

Talo de 6-12 cm, de cor vinoso-coccínea, plano, membranáceo, irregularmente ramificado e atenuado na base em estipe curto, de poucos milímetros de altura, fixo ao substrato mediante um disco. Ramificação pseudo-dicótoma ou, raro, penatiforme. Segmentos ondulados na margem ou subfimbriados. Lobos supremos arredondados ou emarginado--crenulados. Nervura do estipe grossa, formada por numerosas vénulas que, na parte inferior do talo, se separam irradiando e depois se aproximam, formando anastomoses ao longo da fronde. Vénulas simples, constituídas por uma única fiada de células cilíndricas, dispostas topo a topo, só perceptível por transparência com o auxílio do microscópio.

Cistocarporângios hemisféricos, com orifício na parte superior, distribuídos ao longo das margens dos segmentos e dos lobos. Tetrasporângios agrupados em soros arredondados, independentes ou em linhas confluentes ao longo das margens dos segmentos e dos lobos.

É pouco frequente, mas existe em toda a costa, com excepção da zona do Cabo de S. Vicente a Vila Real de Santo António.

Encontrada no molhe central da Barra, 15-VIII-1977, *P. Reis & M. Vieira* 709 (COI).

Outras localidades:

MINHO: Ofir, Apúlia, IV-1958, *M. Rodrigues & Santos* s. n. (COI). DOURO LITORAL: Póvoa de Varzim, 14-VII-1878, *Newton* (PO); ibid., IX-1879, *Padrão,* s. n. (COI); Leça da Palmeira, VIII-1872, *Henriques* s. n. (COI); ibid., VIII-1879, *Newton* (COI); Foz do Douro, VIII-1879, *Newton* (COI); Foz do Douro, VIII-1879, *Newton* (COI). BEIRA LITORAL: Buarcos, IX-1877, *Moller,* s. n. (COI); ibid., VIII-1879, *Henriques.* ESTREMADURA: Peniche, X-1884, *Mendonça* s. n. (COI); Ericeira, V-1842, III-1844, *Welwitsch* s. n. (LISU); Tejo salgado, Paço d'Arcos, Cruz Quebrada, Belém, Cascais, 1841, 1842, 1847, 1850, 1852, *Welwitsch* (LISU); Arrábida, I-1958, *Vieira* s. n. (COI); ibid., IV-1959, *Neves, M. Rodrigues, Reis & Santos* (COI).

RHODOMELACEAE Harv.

Polysiphonia elongata (Huds.) Harv. in Hook., Br. Fl., 2: 333 (1833). — J. Ag., Sp. Alg. 2, 3: 1004 (1863). — Kütz., Phyc. Gen.: 428, t. 50, fig. 5 (1843); Sp. Alg.: 828 (1849); Tab. Phyc. 14, t. 4 (1864). — Ardiss., Phyc. Med. 1: 416 (1883). — Hauck in Rabenh., Meeresalg.: 227 (1885). — Falkenb., Rhodom.: 126, t. 21, fig. 6-9 (1901). — De-Toni, Syll. Alg. 4, 2: 903 (1903). — Gayral, Alg. Côt. Franç.: 589 (1966).

Conferva elongata Huds., Fl. Angl.: 599 (1762).
Corradoria elongata (Huds.) Mart., Fl. Bras. 1: 16 (1883).

Hutchinsia elongata (Huds.) Ag., Sp. Alg. 2: 82 (1823).

Gramitia elongata (Huds.) Bonnem., Hydry. Loc. 16: 22 (1828).

Polysiphonia stenocarpa Kütz., Sp. Alg.: 830 (1849); Tab. Phyc. 14: t. 11, fig. d-f (1864).

Polysiphonia chalarophlaea Kütz., Sp. Alg.: 831 (1849); Tab. Phyc. 14, t. 12, fig. d-f (1849).

Polysiphonia clavigera Kütz., Sp. Alg.: 831 (1849); Tab. Phyc. 14, fig. a-d (1849).

Hutchinsia strictoides Lyngb., Hydr. Dan.: 114, t. 35 (1819).

Talo de 10-20 cm de altura, de cor vermelho-purpúrea nos ramúsculos jovens e acastanhada nos antigos. Eixos principais perfeitamente distintos, ramificados alternadamente em todos os sentidos, corticados até à ponta dos ramos, com 1-2 mm de diâmetro. Ramúsculos de última ordem nus, com 40-80 μ de diâmetro e quatro células pericentrais, cercadas de outras quatro mais pequenas (nos ramos mais antigos oito células terciárias envolvem as oito precedentes e são cercadas pelas células corticais).

Apesar de muito rara foi, no entanto colhida por MOLLER e HENRIQUES, na Ria, em 1876 e ultimamente em 17-VIII-1977, no molhe central da Barra, por *P. Reis & Vieira* s. n. (COI).

Na zona entre S. Vicente e Vila Real de Santo António não foi ainda encontrada, mas existe em outras localidades.

MINHO: Montedor, 5-III-1963, *Fr. Ardré*. DOURO LITORAL: Póvoa de Varzim, VII-1878, *Newton* s. n. (COI); Leça da Palmeira, VIII-1872, *Henriques* s. n. (COI); Foz do Douro, VII-1879, *Newton* s. n. (COI); ibid., I-1879, *Lima* s. n. (COI). BEIRA LITORAL: Buarcos, VII-1953, IX-1954, *Santos* (COI); ibid., IX-1877, *Moller* (COI); Figueira da Foz, I-1870, *Simões* (COI). ESTREMADURA: Cascais, Paço d'Arcos, Caxias, II-III--1843, X-1849, III-1852, *Welwitsch* s. n. (LISU); Tróia, III-IV--1850, *Welwitsch;* Arrábida, V-1958, *Neves, M. Rodrigues, Reis & Santos* (COI).

Polysiphonia havanensis Mont. in Ramon de la Sagra, Hist. Nat. Cuba 9: 34, t. 5, fig. 3 (1834).

Talo de 5 cm, cespitoso, intensamente ruivo-acastanhado. Filamentos primários prostrados, reptantes, constituídos por artículos de comprimento igual a ½ do diâmetro, inflados nos genículos, produzindo filamentos secundários, inseridos em ângulo mais ou menos recto, decompostos em subdicotomias (raras na parte inferior), longamente atenuados, pouco ou muito ténues nos ápices, descorticados, mais ou menos providos de ramos compostos e de ramúsculos simples, uns e outros constituídos por artículos 4-sifonados, de comprimento irregular, desde 1,5 até quase o triplo do diâmetro; genículos dilatados especialmente na parte inferior do talo. Ramos distantes na parte inferior, semelhantes aos filamentos secundários, e aproximados na parte superior, misturados com ramúsculos um tanto mais simples longos ou curtos atenuados na base, por vezes muito curtos. Tetrasporângios ovóides, muito raros, um ou poucos (2-3) em cada ramúsculo.

Ria de Aveiro, nas estacas do porto da Vista Alegre, 3-IX-1975, *P. Reis* s. n. (COI).

Obs. Transcrição da Revista I. D. E. S. O. **4**: 41 (1975).

Polysiphonia pulvinata J. Alg., Alg. Med.: 124 (1842); Sp. Alg. 2, 3: 957 (1865).

Talo de 5 cm, em céspedes densíssimas, fusco-purpúreas. Filamentos primários prostrados, densamente entrelaçados, radicantes, constituídos por artículos cujo comprimento é igual ao diâmetro ou ½ deste, produzindo filamentos secundários mais ou menos erectos, com dicotomias raras, muitas vezes cobertos de ramúsculos de segunda ordem, sendo uns e outros articulados desde a base, 4-sifonados. Ápices fasciculado-tricoblastíferos. Ramúsculos inferiores alongados, mais ou menos patentes, sendo os superiores muitas vezes mais densos, patentes ou ascendentes. Artículos descorticados, sendo o comprimento igual ao diâmetro na parte inferior e até ao triplo na superior dos espécimes mais desenvolvidos; genículos dilatados especialmente na metade inferior dos eixos principais. Tetrasporângios dispostos em

série até 4-5 nos filamentos torulosos, abaixo dos ápices. Cistocarpos urceolados ou subpiriformes, raros.

Habita na Ria de Aveiro, nas águas tranquilas da praia do Carregal a cerca de 20 cm de altura de água, 25-VIII--1975, *P. Reis* 718 (COI).

Assinalada também para o DOURO LITORAL: Foz do Douro, VIII-1879, *Newton* s. n. (COI). ESTREMADURA: Cascais, Estoril e Parede, I-1850, *Welwitsch* s. n. (LISU).

Obs. Transcrição da Revista I. D. E. S. O., 4: 42 (1975).

Polysiphonia fernandesiana P. Reis in Bol. Soc. Brot. 51, Sér. 2: 99 (1977).

Vide descript. loc. cit.

Ria de Aveiro, 11-VI-1972, *P. Reis* 652A (COI).

Bostrychia scorpioides (Gmel.) Mont., Hist. Bot. Cuba: 39 (1838). — Harv., Phyc. Brit., 2: Tab. 48 (1846). — Batters in Journ. Bot. London (Supl.: 77, 1902). — De-Toni, Syll. Alg. 4, 2: 1164 (1903). — Newton, Brit. Seaw.: 332 (1931). — Fr. Ardré, in Portug. Acta Biol., Sér. B, 10: 344 (1969).

Fucus scorpioides Gmel., Hist. Fuc.: 135 (1768).
Fucus amphibius Huds., Fl. Angl. ed. 2: 590 (1778).
Rhodomela scorpioides (Gmel.) Ag., Sp. Alg. 1: 380 (1822). — Grev., Alg. Brit.: 105 (1830). — Hook., Brit. Fl. 2: 294 (1833).
Alsidium scorpioides (Gmel.) J. Ag. in Linnea 15: 28 (1841).
Helicothamnion scorpioides (Gmel.) Kütz., Phyc. Gen.: 433, t. 43V (1843).

Talo de 5-10 cm, formando tufos de cor acastanhada, por vezes negra, aderindo às raízes de halófitos mediante rizóides. Eixo primordial ramificado irregularmente. Eixos secundários unilaterais, alternos ou dicótomos. Ápices em forma de cauda de escorpião. Sifão central estreito, cercado

de várias camadas de células de parede espessa, sendo estas envolvidas por 1-2 camadas de células semelhantes, mais pequenas e assimiladoras. Tetrasporângios tetraédricos, dispostos em verticilos sobre estiquídias fusiformes. Cistocarposporângios ovóides sobre os últimos ramúsculos.

Assinalada pela primeira vez para a BEIRA LITORAL: esteiro de Mira, a sul da Costa Nova do Prado, 2-IX-1979, *P. Reis* 725 (COI).

Existe também no DOURO LITORAL: Foz do Douro, 1889, *Hauck* s. n., na ESTREMADURA: Seixal, Portimão, pr. Setúbal, 7-VIII-1847, VI-1852, *Welwitsch* s. n. (LISU) e em Faro, 1963, *Ginsburg-Ardré* s. n. in Contr. Etud. Alg. Mar. Port.

Laurencia pinnatifida (Gmel.) Lamour., Essai: 42 (1813). — Grev., Alg. Brit.: t. 14, fig. 1-5 (1830). — Ardiss., Phyc. Med. **1**: 332 (1833). — Harv., Phyc. Brit. **2**: t. 55 (1846). — Kütz., Sp. Alg.: 856 (1849); Tab. Phyc. **15**: t. 66, fig. a-e (1865). — J. Ag., Sp. Gen. Ord. Alg. **2**: 764 (1852): **3**: 656 (1876). — Hauck in Rabenh. Krypt. Fl. **2**: 208 (1885). — De-Toni, Syll. Alg. **4**, **2**: 798 (1903). — Gayral Alg. Côt. Franç.: 563 (1966). — Fr. Ardré, in Portug. Acta Biol., Sér. B, **10**: 357 (1069).

Fucus pinnatifidus Gmel., Syst. Nat. **2**: 1385 (1768); Hist. Fuc.: 156, t. 16, fig. 3 (1768).
Condria pinnatifida (Gmel.) Ag., Sp. Alg. **1**: 337 (1822).

Talo de 5-10 cm de altura, de cor vermelho-escura ou acastanhado-esverdeada, conforme a intensidade luminosa do ambiente, cespitoso, fixado ao substrato mediante um disco acompanhado de filamentos rizóidais. Ramificação 2-4-fida, alterna, muito raramente oposta ou unilateral. Ramos primários distantes ou aproximados, ± comprimidos, frequentemente de base adelgaçada e os ápices arredondados ou lobados. Ramúsculos numerosos, distintos, pinados. Pínulas ínfimas mais longas, as superiores mais curtas e as supremas confluentes com o ápice crenado. Ráquis principal quase roliça na base com 1-4 mm de largura, de ápice obtuso,

arredondado ou lobado; últimas ramificações com pínulas de 0,5-1 mm de largura. Tetrasporângios mergulhados na região cortical dos ramúsculos. Cistocarposporângios em forma de urna com poro apical, fixados lateralmente nos últimos ramúsculos. Carpósporos piriformes.

Frequente no molhe central da Barra, onde foi colhido pela primeira vez, em 17-VIII-1977, por P. REIS & V. VIEIRA 707 (COI).

Outras localidades:

MINHO: Apúlia, Aguçadora, IV-1958, *M. Rodrigues & Santos* (COI). DOURO LITORAL: Póvoa, IX-1877, *Padrão* (COI); Leça da Palmeira, XIII-1872, *Henriques* s. n. (COI). S. João da Foz, I-1879, *Newton* (COI). BEIRA LITORAL: Cabo Mondego, XII-1939, *Lacerda* (COI); Buarcos, 1822, *Moller* s. n. (COI); ibid., IV-1930, *T. Morais* (COI); ibid., VIII-1948, *M. de Carvalho* s. n. (COI); Figueira da Foz, XI-1949, *M. Rodrigues* (COI); ibid., IX-1953, IX-1954, *Santos* s. n. (COI). ESTREMADURA: Nazaré, XI-1883, *Padrão* s. n. (COI); S. Martinho do Porto, Ericeira, IV-1950, *Neves, M. Rodrigues, Reis & Santos* s. n. (COI); Tejo salgado, Cabo da Roca, Cascais, Caxias, XI-1849, II-XII-1851, 1852, *Welwitsch* (LISU). ALENTEJO: Arrábida, 1958, *Palminha;* Vila Nova de Milfontes 1954, *Dizerbo.*

DISTRIBUIÇÃO DAS ESPÉCIES DE RODOFÍCEAS DA RIA, NAS LOCALIDADES DA COSTA DE PORTUGAL

Na primeira parte deste trabalho, a introdução, expôs-se a história das pesquisas sobre as Rodofíceas da Ria de Aveiro. Na segunda, apresentou-se a descrição em português das espécies, a fim de facilitar aos estudiosos do grupo o seu conhecimento. Nesta terceira parte, pretende-se mostrar quais são as espécies da Ria representadas em cada uma das 56 localidades, onde, até à data, se têm efectuado colheitas de Rodofíceas; a média de espécies existentes nas principais zonas da costa; a maior frequência de algumas espécies; as que existem só na Ria; as que se encontram

em toda a extensão da costa portuguesa; as que não existem na zona norte, mas ocorrem nas outras e as que se estendem desde o norte só até várias localidades.

Por conseguinte, não se pretende saber qual é a localidade da costa de Portugal que tem maior ou menor número de espécies de Rodofíceas, nem mesmo se o número delas, em geral, aumenta ou diminui do norte para o sul. Só interessa a representação das Rodofíceas da Ria nas várias localidades e média de cada região; a sua presença em toda a costa portuguesa ou só dentro de certos limites.

De harmonia com o referido plano, a análise do quadro anexo mostra o seguinte:

1.º — Que o número de espécies assinalado para cada localidade é muito variável: vai de 1 espécie em Lagoa de Albufeira e no Cabo de S. Vicente até 31 na Ria de Aveiro.

2.º — A média das espécies pelas principais zonas da costa é de 10,2 do Rio Minho ao Douro; de 16,5 do Douro ao Mondego; de 7,9 do Mondego ao Tejo; de 6,6 do Tejo ao Cabo de S. Vicente e deste até Vila Real de Santo António é de 5,7.

Por conseguinte a média dos números médios de espécies das algas Rodofíceas da Ria de Aveiro, representados nas cinco zonas vai diminuindo para o sul e no rio Mondego encontra-se a máxima (16,5) ao norte e a maior (7,9) ao sul.

3.º — Em relação à frequência nota-se que as espécies correspondentes aos números 11-16 inclusive apresentam uma frequência de 3,9 para a 1.ª zona; 5,2 para a 2.ª; 2,9 para a 3.ª; 2,5 para a 4.ª e 1,1 para a 5.ª. As frequências restantes afastam-se pouco destas.

Também neste aspecto a Ria representa frequência mais alta que as outras quatro localidades.

A presença varia de 20 para *Chondrus crispus* (L.) Lyngb., a 45 para *Gigartina acicularis* (Wulf. Lamour. dentro

das 56 localidades, para as espécies de maior frequência ou
seja 11-16. A presença das restantes está compreendida entre
19 e 43 ou é mais baixa que 19.

4.º — Existem espécies (n.ᵒˢ 1, 9, 18, 21, 26 e 29) que
     só são assinaladas para a Ria de Aveiro. Trata-se
     de espécies descritas recentemente que poderão
     existir noutras localidades, onde não poderão ter
     sido ainda colhidas ou ter sido consideradas como
     outras espécies.

5.º — A maior parte das espécies (n.ᵒˢ 2, 4, 6, 7, 11, 13,
     16, 17, 19, 20, 22, 23 e 25) encontram-se em toda
     a extensão da costa portuguesa (costa ocidental
     e sul).

6.º — Há espécies (n.ᵒˢ 8, 12, 14, 15, 24, 27 e 31) que se
     estendem desde o norte até à zona do Tejo ao Cabo
     de S. Vicente inclusive. Outras só atingem a zona
     do Mondego ao Tejo inclusive (n.ᵒˢ 3, 10 e 28).
     A única espécie que não existe na zona do norte,
     mas atinge a zona do Mondego ao Tejo é a n.º 5.

7.º — A n.º 30 só foi encontrada na 1.ª, 2.ª e 5.ª zonas.

MAPA DA DISTRIBUIÇÃO DE RODOFÍCEAS EXISTENTES NA RIA DE AVEIRO

Géneros dispostos segundo a ordem de Kylin		
	31	Laurencia pinnatifida (Huds.) Mont.
	30	Bostrychia scorpioides (Huds.) Mont.
	29	Polysiphonia havanensis Mont.
	28	P. pulvinata J. Ag.
	27	P. elongata (Huds.) Harvey
	26	P. fernandesiana P. Reis
	25	Pterosiphonia complanata (Clemen.) Falken.
	24	Cryptopleura ramosa (Huds.) Kylin ex Newton
	23	Hypoglossum woodwardii Kütz.
	22	Callitamnion tetragonum (Withering.) C. Ag.
	21	Spyridia filamentosa (Wulfen.) C. Ag.
	20	Ceramium rubrum (Huds.) C. Ag.
	19	C. flabelligerum J. Ag.
	18	C. arborescens J. Ag.
	17	C. ciliatum (Ellis) Duclus.
	16	Lomentaria articulata (Huds.) Lyngb.
	15	Gigartina teedii (Roth) Lamour. var. lusitanica M. Rodrigues
	14	G. stellata (Stack.) Batters
	13	G. acicularis (Wulfen.) Lamour.
	12	Chondrus crispus (L.) Lyngb.
	11	Gymnogongrus norvegicus (Grun.) J. Ag.
	10	G. griffithsiae (Turn.) Martins
	9	Gracilaria vieirae P. Reis
	8	G. verrucosa Papenfus.
	7	Catenella repens (Lightf.) Batters
	6	Gelidium sesquipedale (Turner) Thuret
	5	G. corneum Lamour. var. corneum
	4	G. pusillum (Stackh.) Le Jolis
	3	G. pulchellum (Turn.) Kütz.
	2	Rhodochorton purpureum (Lightf.) Rosen.
	1	Compsopogon lusitanicus P. Reis

I. DO RIO MINHO AO DOURO

LOCALIDADES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T.	média de espécies
Âncora					+							+	+	+	+	+	+			+						+					+	10	
Montedor		+			+	+		+	+	+	+	+	+	+			+			+		+	+		+		+				+	16	
Viana		+	+		+	+	+		+	+	+	+	+	+	+	+			+			+	+				+	17	
Ofir					+								+											+							+	4	10.2
Apúlia						+				+	+	+	+	+						+	+							+	9	
Aguçadora					+				+	+		+	+						+								+	7	
Póvoa de Varzim		+			+		+	+	+	+			+			+			+	+	+	+		+				+	15	
Vila do Conde								+	+															+	3	
Leixões			+					+	+	+				+	+								+	7	
Leça		+					+		+		+		+				+	+					+	9	
S. João da Foz			+			+				+							+							+	5	
Foz do Douro	+	+			+	+	+		+	+	+	+	+	+		+	+		+	+	+	+		+	+	+	+	+	21	

II. DO RIO DOURO AO MONDEGO

LOCALIDADES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T.	m. e.
Ria de Aveiro	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	31	
Cabo Mondego												+	+	+	+	+										+				+		7	16.5
Buarcos					+		+			+	+	+	+			+				+	+		+	+	+		+			+	+	17	
Figueira da Foz			+				+	+			+		+	+			+								+				+	+	11	

III. DO RIO MONDEGO AO TEJO

LOCALIDADES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T.	m. e.
Nazaré												+							+		+									+	4	
S. Martinho do Porto				+						+	+	+	+	+	+	+			+		+		+						+	12	
Lagar de Óbidos						+					+	+																+	4	
Baleal			+		+	+			+		+	+	+	+					+	+	+							+	12	
Berlengas					+					+				+														+	4	
Peniche				+				+		+	+	+	+	+	+		+		+	+	+							+	12	
Cabo Carvoeiro	+		+	+	+			+				+	+		+			+	+									+	12	
Ericeira								+	+	+	+			+	+											+	8	
Magoito		+				+			+	+	+	+	+	+	+		+	+		+							+	13	
Azenhas do Mar										+							+	+										+	4	
Praia das Maçãs										+							+											+	3	7.9
Cabo da Roca						+				+	+	+					+											+	6	
Cabo Raso		+	+		+			+	+	+	+	+	+					+		+								+	13	
Cascais			+		+			+	+	+						+	+			+	+							+	11	
Estoril			+		+			+															+					+	5	
Parede		+		+	+	+		+	+	+	+	+	+	+	+		+	+		+	+			+				+	18	
Cruz del Rei			+		+		+		+	+																		+	6	
S. Julião da Barra								+		+																		+	3	
Oeiras				+		+			+	+	+						+											+	7	
Paço d'Arcos						+			+	+						+			+		+							+	6	
Caxias					+	+				+	+	+				+	+		+		+							+	8	
Cruz Quebrada			+		+		+			+	+	+				+	+		+									+	9	
Pedrouços			+		+	+		+		+							+		+									+	7	
Belém					+						+																	+	4	

IV. DO TEJO AO CABO DE S. VICENTE

LOCALIDADES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T.	m. e.
Lagoa de Albufeira																														+		1	
Cabo Espichel																	+							+							2	
Sesimbra			+		+	+	+				+	+	+	+	+	+		+			+			+				+	13	
Arrábida	+				+	+			+	+	+	+	+	+	+	+		+	+			+	+	+				+	17	6.6
Outão			+		+							+																+	3	
Tróia											+					+												+	2	
Sines			+		+					+	+		+	+			+			+	+			+				+	11	
Vila Nova de Milfontes											+	+		+														+		4	
Carrapateira			+								+			+	+					+	+		+					+	7	

V. DO CABO DE S. VICENTE A VILA REAL DE SANTO ANTÓNIO

LOCALIDADES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T.	m. e.
Cabo de S. Vicente												+																				1	
Sagres			+		+					+				+	+	+				+									7	
Lagos	+		+		+										+					+									5	
Praia da Rocha			+		+	+				+										+	+								7	5.7
Carvoeiro	+		+		+	+	+			+			+	+					+	+									11	
Albufeira													+							+	+								3	
Faro	+					+					+									+					+			+			6	

INTROGRESSION IN WEST AFRICAN ORCHIDS OF THE GENUS *EULOPHIA*

by

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SUMMARY

Eulophia cristata Steud. and *E. millsoni* Summerhayes are two commonly occurring ground orchids in west Africa. They differ in their ecological preferences, but on the coastal plains of Ghana, which have been considerably distributed through shifting peasant agriculture, both species intermingle and hybrid swarms occur. These species differ markedly in such characters as flower colour and morphology, number of flowers in the spike, and height of the inflorescence. Using these characters, hybrid indices and pictorial scatter diagrams have been produced for several populations to demonstrate the extent of introgression. It is a noteworthy feature of these populations that introgression is unilateral, for though backcrosses with the *E. millsoni* parent abound, none involving the *E. cristata* parent have been encountered.

INTRODUCTION

T HE genus *Eulophia* consists of large terrestrial orchids. In West Africa it contains 34 species (SUMMERHAYES in HEPPER, 1968). Most of these have large, colourful and often very beautiful flowers. They differ considerably from each other in details of flower structure and colour and do not, in West Africa, form a taxonomically critical genus of closely allied species, though in southern Africa several species complexes occur (HALL, 1965). Hence the discovery in 1956 of hybridization and apparent introgression between two of the commonly occurring species on the coastal plains

of Ghana was unexpected. The two species concerned (see Plate 1) are the pink and purple-flowered *E. cristata* (Sw.) Steud. and *E. millsoni* (Rolfe) Summerhayes which has cream coloured flowers with an orange tip to the spur. A subsequent examination of the literature and of herbarium specimens revealed that similar hybrids, between these species, had been collected by earlier workers and described as separate species. Following the discovery of the hybrids in 1956, a survey of the populations of these orchids on the coastal plains of Ghana revealed the occurrence of introgression in most of the populations. A detailed study of these populations was undertaken and demonstrated an unusual situation in which introgression is occurring in one direction only, from *E. cristata* into *E. millsoni*. Introgression is affecting this latter species in a variety of ways, including ecological adaptation, time of flowering and general morphology. The significance of these effects is considered in relation to the present day distribution of this species and its future evolution.

DISTRIBUTION

Both *E. cristata* and *E. millsoni* have a wide distribution in the savanna regions of tropical Africa. The range of *E. cristata* extends across West Africa from Senegal to the Cameroons, south into Zaire and east into Uganda, the Sudan and Ethiopia. *E. millsoni* occurs from the Ivory Coast to the Cameroons, east into Uganda and the Sudan, and from there south to Zimbabwi and Mozambique.

Location of hybrid populations

All the hybrid populations which I have encountered occur on the coastal plains of Ghana (the Accra Plains). Three such population were studied in detail. Also, populations located where only one of the species is present were examined for purposes of comparison with the hybrid populations. The three populations in which introgression was studied are situated in the coastal grasslands of Ghana:

1) *The Nsawam road colony* is situated about 750 m. west of the main road from Accra to Nsawam, about 16 km. from Accra.

2) *The Adantan colony* is situated on the Accra to Aburi road on the east side about 400 m. south of the village of Adantan, in a shallow valley on the Accra side of the village.

3) *The Aboadi colony* is situated around the lagoon at the back of the sandbar on the Sekondi side of Aboadi.

The first two colonies are only a few kilometres apart in the continuous grassland area of the Accra Plains, whilst the Aboadi colony occupies a small enclave of grassland about 190 km. to the west.

Ecology

Both species grow in the savanna regions of Africa but they occur in quite distinct habitats. *E. cristata* grows in well drained soils. In almost all the localities where I have seen it in West Africa it has been growing on laterite. This is the case on the coastal grasslands of Ghana where it is absent from the extensive areas of clay, but abundant over most of the laterite. *E. millsoni,* on the other hand, favours seasonally waterlogged grassland. It grows in valleys and depressions in the laterite areas where alluvial deposits of sand and silt have accumulated, overlying an impervious base. Also, it occurs scattered across the broad expanse of clay soils on the coastal plains of Ghana on either side of the Volta River (the Akuse clays). During the rainy season these habitats become waterlogged, but for the remainder of the year they are very dry, resulting in unfavourable conditions for most species of plants. These areas support a short and impoverished grassland which is dominated by the grass *Brachiaria falcifera* (Trin.) Stapf. Also characteristic of these situations are many geophytes including *Anthericum warneckei* Engl., *Murdannia simplex* (Vahl) Brenan, *Crinum ornatum* (Ait.) Bury, *Urginea ensifolia* (Thonn.) Hepper and *Curculigo pilosa* (Schum. & Thonn.) Engl.

Hybrid plants occupy a wide range of habitats intermediate between and including those of the parents. Usually they grow in the *E. millsoni* populations but in the western part of the Accra Plains, and around Winneba and Elmina, the hybrids occur scattered over the rolling grassland. In the Aboadi and Adantan localities the two types of habitat, laterite and alluvial depressions, adjoin and there is little intermediate habitat. In these situations the hybrids occur alongside *E. millsoni* but do not extend onto the laterite where only *E. cristata* grows. During this study F_1 hybrids were only encountered on four occasions, in each case growing in an intermediate type of habitat where a thin overlay of silt covered the laterite. In the Nsawam road colony there is a broad area of transitional habitat on the lower slopes of the hillside where the laterite is covered by silt. *E. millsoni* abounds in the lowlying seasonally waterlogged valley and in the transitional zone on the lower slopes. *E. cristata* is abundant on the laterite and also in this transitional area. Hence the conditions are ideal for the development of a hybrid population. The F_1 plants and considerable numbers of introgressed forms of *E. millsoni* occur in this transitional area.

Reproductive biology

Flowering in these orchids, as with many plants in the savanna regions of Africa, is stimulated by the effects of the annual fires which sweep through the grasslands during the dry season, and by the early rains which fall towards the end of that season. Flowering takes place between late February and May, after the first rains have occurred. The abundance of flowering spikes varies considerably in different years. For instance, 1956 and 1959 were years when flowering occurred in great profusion, whereas the intervening years were very poor with few visible spikes. In the two favourable years *E. cristata* was so abundant that it coloured the landscape in many of the grassland areas of the Accra Plains, and children from nearby villages gathered them by the armful for sale along the roadsides. The reasons for these

major fluctuations in flowering are not known. However, local changes in abundance due to the effects of burning were observed. Areas of grassland which did not burn in a particular year produced very few flowering spikes, whereas adjacent burnt areas produced a much larger number of spikes. Heavy rain is necessary to initiate the development of the dormant underground flowering shoots. On the Accra Plains the time, distribution and amount of the early rains, which occur towards the end of the dry season, is very variable and uncertain. On occasions an early local storm may initiate flowering, sometimes in areas which were not burnt that year. If the storm is followed by another dry spell, late burning will destroy the flowering shoots of these orchids in that year. I frequently observed this to happen on very localized areas of the Accra Plains. However, on these occasions a second flowering sometimes occurred.

These orchids, particularly *E. cristata* and the F_1 hybrids, reproduce rapidly by vegetative means. The rootstock consists of a branched chain of angular tubers about 4×3 cm. and 2.5 cm. thick. A new tuber is produced every year at the end of each branch. Hence a clone of plants rapidly develops, occupying a square metre or more of ground. Some idea of the rate of development of these clones can be gauged from observations on an albino plant which was discovered in 1956 in the Nsawan road colony. In this plant the pink and purple pigment was completely lacking from the flowers and inflorescence, so that the flowers were pure white with a green lip. In 1956 there were only three flowering spikes occupying an area about $\frac{1}{2}$ m. in diameter. By 1959 there were eight flowering spikes occupying an area about 1.75 m. in diameter.

These orchids are adapted to pollination by large insects. The cap on the column is about 3 mm. broad and requires appreciable pressure to push it off. Each pollen mass on the pollinium is slightly over 1 mm. in diameter, hence, only large insects can bring about pollination. Each flower on the spike remains open for several days [LOCK & PROFITA (1975) give a mean duration of 10-14 days in *E. cristata*] and each spike lasts for up to three weeks. The flowers of

both species are only slighty scented. During the day the scent is, at most, barely noticable, but after dark *E. cristata* produces a weak, pleasant sweet aroma, whilst that of *E. millsoni,* though still weak, is more pungent and not particularly pleasant. Visits were paid to several of the flowering colonies on the Accra Plains at various times of the day and night in order to collect and observe pollinating insects but remarkably few insect visitors were found. The only species which I observed freely visiting the flowers of both orchids was a large beetle belonging to the *Meloidae — Coryna hermanniae* L. This was often found at rest on the flowers and was frequently eating them. It flies freely in the sun, particularly when the winds are calm. It favours the flowers of *E. millsoni* but was also found on those of *E. cristata.* On two occasions these beetles were observed with pollinia sticking to the back of the thorax. Most of the flowers of *E. millsoni* in which the ovary had been fertilized and was swelling had the column partially eaten by these beetles. There seems little doubt that they are the main pollinating agent of *E. millsoni,* at least on the Accra Plains of Ghana where this orchid sets seed freely, with most of the flowers producing a capsule.

The situation in *E. cristata* is less clear. On the Accra Plains few flowers develop capsules. Many spikes are completely sterile, whilst those that are fertile rarely have more than 1 or 2 capsules, even though the spikes bear between 20 and 30 flowers. Insects were only rarely observed to visit the flowers of this species on the coastal plains and the pollinia and cap in fading flowers were usually intact, indicating that they had not been pollinated. In 1959 this orchid flowered about three weeks earlier than usual (it was in full flower on March 1st) and in great profusion. However, flowering occurred before the *Coryna* beetles emerged and even fewer capsules than usual were formed. Similar observations on this species, made in Guinea savanna localities in Ghana, showed that pollination occurred more frequently and that each spike usually had 5 or more developing capsules.

Since these observations were made, LOCK & PROFITA (1975) have reported on a study of pollination in *E. cristata* on the Accra Plains. They concluded that carpenter bees of the genus *Xylocopa* (especially *X. olivacea*) pollinate this orchid. They were able to observe pollination on four occasions and found that in 31 % of the 203 flowers that they examined pollinia have been removed, presumably by visiting insects. They concluded that the bees were attracted by the colour of the flowers, as no nectar appeared to be produced.

Pollination experiments (see Table 1) carried out on wild plants showed that both self and cross pollinations are sucessful. Also, crosses between the two species could readily be made and produced normal capsules.

TABLE 1

Pollination experiments on *Eulophia* orchids

	No pollination – spikes bagged	Selfed	Cross pollinated	Pollinated with *E. millsoni*	Pollinated with *E. cristata*
E. cristata	6 (0)	10 (10)	16 (16)	4 (4)	—
E. millsoni	6 (0)	7 (7)	6 (6)	—	4 (2)

Figures in parenthesis indicate number of resulting capsules.

Germination tests on the seed resulting from these crosses were not carried out. LOCK & PROFITA (1975) obtained similar results. They found that both cross and self pollinatio resulted in a somewhat reduced seed fertility (67 % and 65 % in selfed flowers and 96 % in cross pollinated flowers).

Chromosome number

The karyotype of these two orchids was examined in root tips using low temperature treatment (CHINNAPPA & MORTON, 1978) and in pollinia, using the method described by HALL (1965) — see Table 2. The most suitable stage in which to examine the chromosomes proved to be the metaphase of the pollen grain nucleus leading to the formation

of the generative and tube nuclei. This, of course, gives the gametic chromosome number and the chromosomes are relatively distinct, well spread and of reasonable size. *E. millsoni* has a gametic number of 21 chromosomes, all very similar in size and shape. *E. cristata*, on the other hand, appears to have a gametic number of 27 chromosomes. Of these, 21 are large and similar to those of *E. millsoni*,

TABLE 2

Chromosome numbers in *Eulophia* orchids

	2n	n	Voucher	Locality
E. cristata	56		s.n. (JKM)	Legon, Ghana
» »		c.27	s.n. (GC, JKM)	Achimota to Pokoasi Rd., Ghana
» »		27	SL1234 (SL, K, GC, JKM)	Lunsar junct. to Port Loko, Sierra Leone
E. millsoni		21	s.n. (GC, JKM)	Accra to Elmina Rd., Ghana
» »		21	GC 38109 (GC)	Ayikuma near Dodawa, Ghana

whereas 6 are smaller in size. Many nuclei of *E. cristata* were not easy to interpret and in several there was a possibility of there being more than 6 small chromosomes, giving a gametic number in excess of 27. Whether these small chromosomes are supernumerary of β chromosomes is not clear at this stage. Root tips proved difficult to work with, but an excellent mitotic plate of *E. cristata* showed 56 chromosomes. However, ar-RUSHDI (1971) reports a sporyphytic chromosome number of 46 in this species in Nigeria. This is the only published chromosome count for either of these species. HALL (1965) gives chromosome numbers for 21 species of *Eulophia* from southern Africa. In these the gametic numbers range from 20 to 60 with 21 and 27 the most commonly occurring numbers. Clearly, further work is required on the cytology of *E. cristata*. No information on the cytology of the hybrids is available.

Populations analysis

a) *Sampling.* The main purpose of this investigation was to demonstrate that introgression is occurring, and the direction in which gene flow is taking place. A random sampling of the orchid population, across a large tract of these coastal grasslands, would have been of little value because of the great difference in abundance of the two species and their hybrids. *E. cristata* vastly out numbers both *E. millsoni* and its hybrids, which are usually confined to restricted areas of suitable habitat. Also, only 4 small groups of F_1 hybrids were encountered. Hence, sampling was limited to areas occupied by hybrid populations and all individuals flowering that particular year (1956) were scored in the three populations selected for study.

b) *Scoring.* As these two orchids differ considerably in the colour of their flowers (see Plate 1), this provides a very suitable and convenient method of assessing hybridity. *E. millsoni* has entirely cream flowers, apart from the tip of the spur which is bright orange. No trace of purple or green colouration has been observed in the flowers of plants growing in pure colonies of this species. In hybrid plants the flowers frequently have purple veins on the lip, are pink or purple flushed, or have a pronounced greenish colouration. The two species differ in many other ways besides flower colour and several morphological characters were also scored. A condition normal to *E. millsoni* was scored as 0, and to *E. cristata* as 2; any intermediate stage as 1. The normal condition in each species was determined after examination of pure colonies from several localities remote from areas of hybridization. The following 10 characters were scored, and used both in the construction of the hybrid index and pictorial and scatter diagrams.

1) Height of inflorescence from ground to tip. 0 = below 66 cm. 1 = 66 to 90 cm. 2 = over 90 cm.
2) Number of flowers in the inflorescence. 0 = below 9. 1 = 9 to 16. 2 = over 16.
3) Angle of lateral sepals to the ovary. 0 = over 120°. 1 = 46° to 120°. 2 = under 46°.

4) Angle of lateral lobes of the lip to the horizontal. 0 = below 91°. 1 = 91° to 110°. 2 = over 110°.
5) Colour of perianth wings. 0 = cream. 1 = cream tinged with pink to salmon pink. 2 = pure pink.
6) Colour of lateral lobes of the lip. 0 = cream. 1 = a pronounced greenish tinge or traces of pink or mauve. 2 = olive.
7) Colour of spur. 0 = bright orange. 2 = pink. 1 = a pronounced greenish colouration with the reduction of absence of the orange tip, or a pink colouration superimposed on the normal *E. millsoni* condition.
8) Ground colour of lip. 0 = cream. 2 = pale purple. 1 = cream with a pink or mauve tinge, to bright salmon coloured.
9) Colour of veins of lip. 0 = cream. 2 = deep purple. 1 = pale purple to mauve tinged ,or a pronounced greenish colouration.
10) Height of veins (calli) at base of the lip. 0 = under 0.7 mm. 1 = 0.7 to 1.4 mm. 2 = 1.5 mm. and over.

Analysis of results

The two methods which have been used to analyze the data are hybrid indices and pictorial scatter diagrams. These are simple to produce and provide an effective means of portraying the results.

The Hybrid Index of a plant consists of the sum of the values for the 10 characteristics which were scored. Thus *E. millsoni* normally has a value of 0 and *E. cristata* of 20. The hybrid indices have been plotted as histograms (Figs. 2-4) which show their frequency in each of the three populations. Colonies of each of the species were examined in areas where only one occurred and where no signs of hybridization were apparent. In these colonies *E. cristata* had an index within the range 19-20 with 87 % of the plants scoring 20. The colonies were situated near Nsawam on the coastal plains, near Ajena and Gambaga in the Guinea savanna regions of Ghana, and near Port Loko in Sierra Leone. Colonies of *E. millsoni* were examined near Dawa

and north of Adidome on the coastal plans of Ghana. The plants all had an index of 0 or 1 with 78 % of them scoring 0.

In the Pictorial Scatter Diagrams (Figs. 5-7) the characters used for the two axes are number of flowers in the inflorescence for the horizontal axis, and the heigh of the
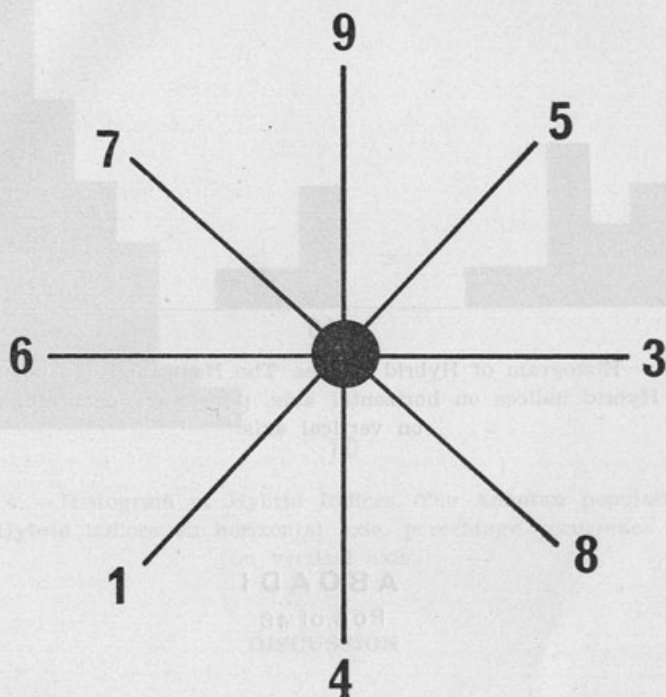
Fig. 1. — Symbol used in Pictorial Scatter Diagrams.
For explanation see text.

veins at the base of the lip for the vertical axis. Each plant is represented by a dot, to which lines are attached to indicate the presence of the remaining characters. Absence of a line indicates an *E. milssoni* character, a short line an intermediate character, and a full length line an *E. cristata* cracter. The significance of each of the lines used in the symbols is shown in Figure 1 in which the numbers refer to the list of characters scored (see above).
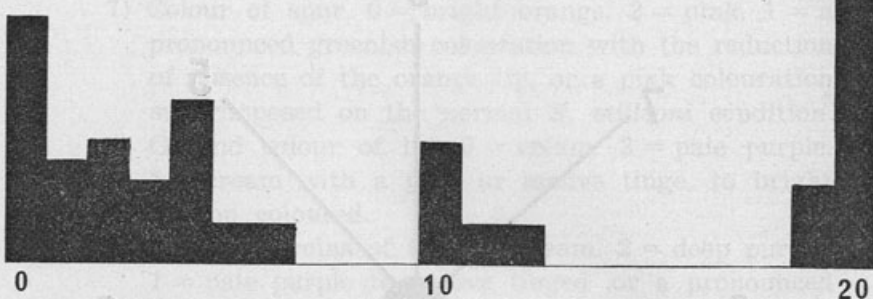
Fig. 2.— Histogram of Hybrid Indices. The Nsawam Road population.
Hybrid indices on horizontal axis, percentage occurrence
on vertical axis.
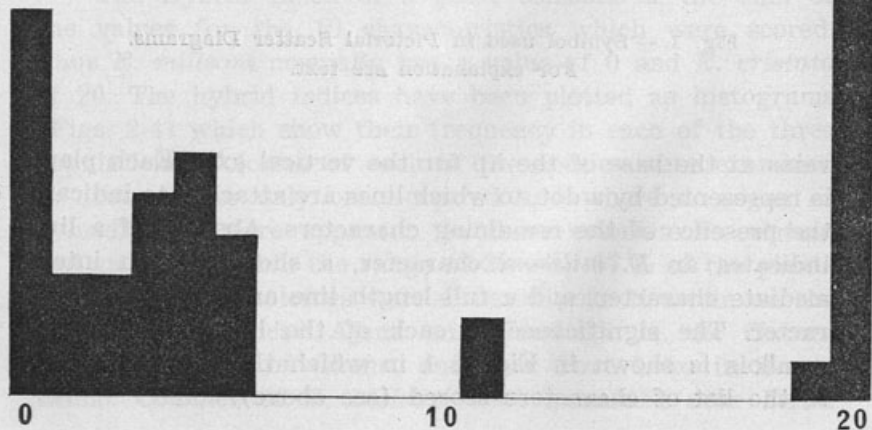
Fig. 3. — Histogram of Hybrid Indices. The Aboadi population.
Hybrid indices on horizontal axis, percentage occurrence
on vertical axis.
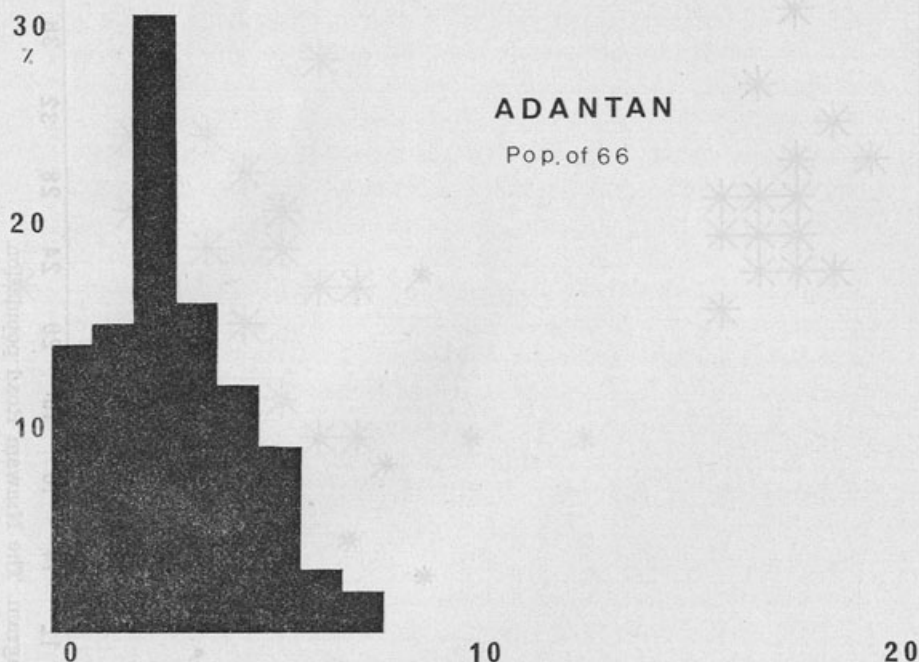
Fig. 4. — Histogram of Hybrid Indices. The Adantan population.
Hybrid indices on horizontal axis, percentage occurrence
on vertical axis.

DISCUSSION

These *Eulophia* hybrids provide an interesting example
of unilateral introgression in which gene flow is in one
direction only, leaving the donar species *(E. cristata)* unaf-
fected (see Figs. 2-7). In the Aboadi and Nsawam road
(Figs. 3,6 and 2,5 respectively) populations both species
are present together with F_1 hybrids. The flow of *E. cristata*
genes into *E. millsoni* is apparent. The Adantan population
(Figs. 4 & 7) consists of introgressed forms of *E. millsoni*
without either F_1 hybrids or the *E. cristata* parent. However,
this species is present in the colony but was not flowering
during the year when the population was sampled. Several
flowering spikes were noted in a subsequent year.
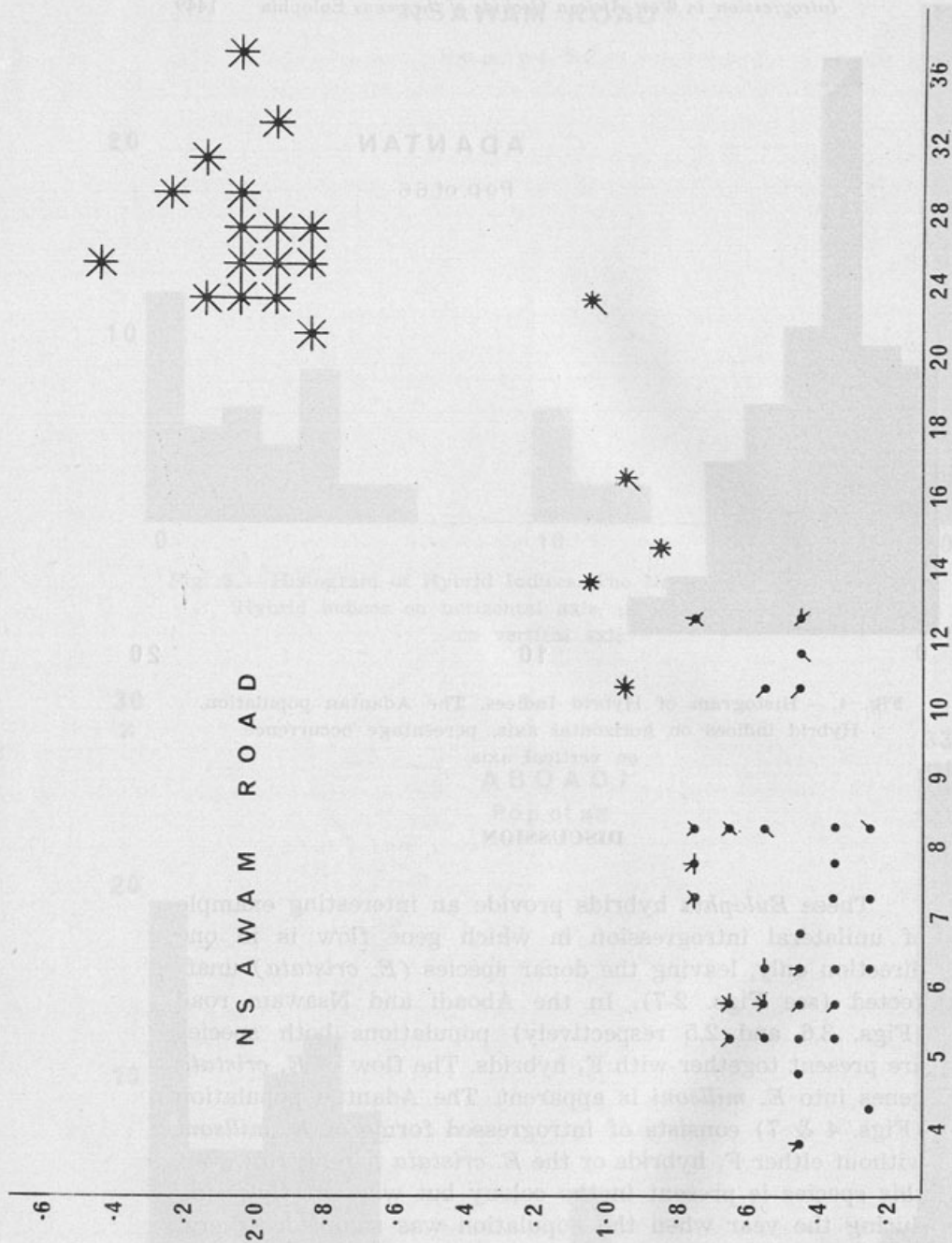
Fig. 5. — Pictorial Scatter Diagram. The Nsawam Road population.
Horizontal axis represents number of flowers in the spike. Vertical axis represents the height of the veins (calli) at the base of the lip petal.
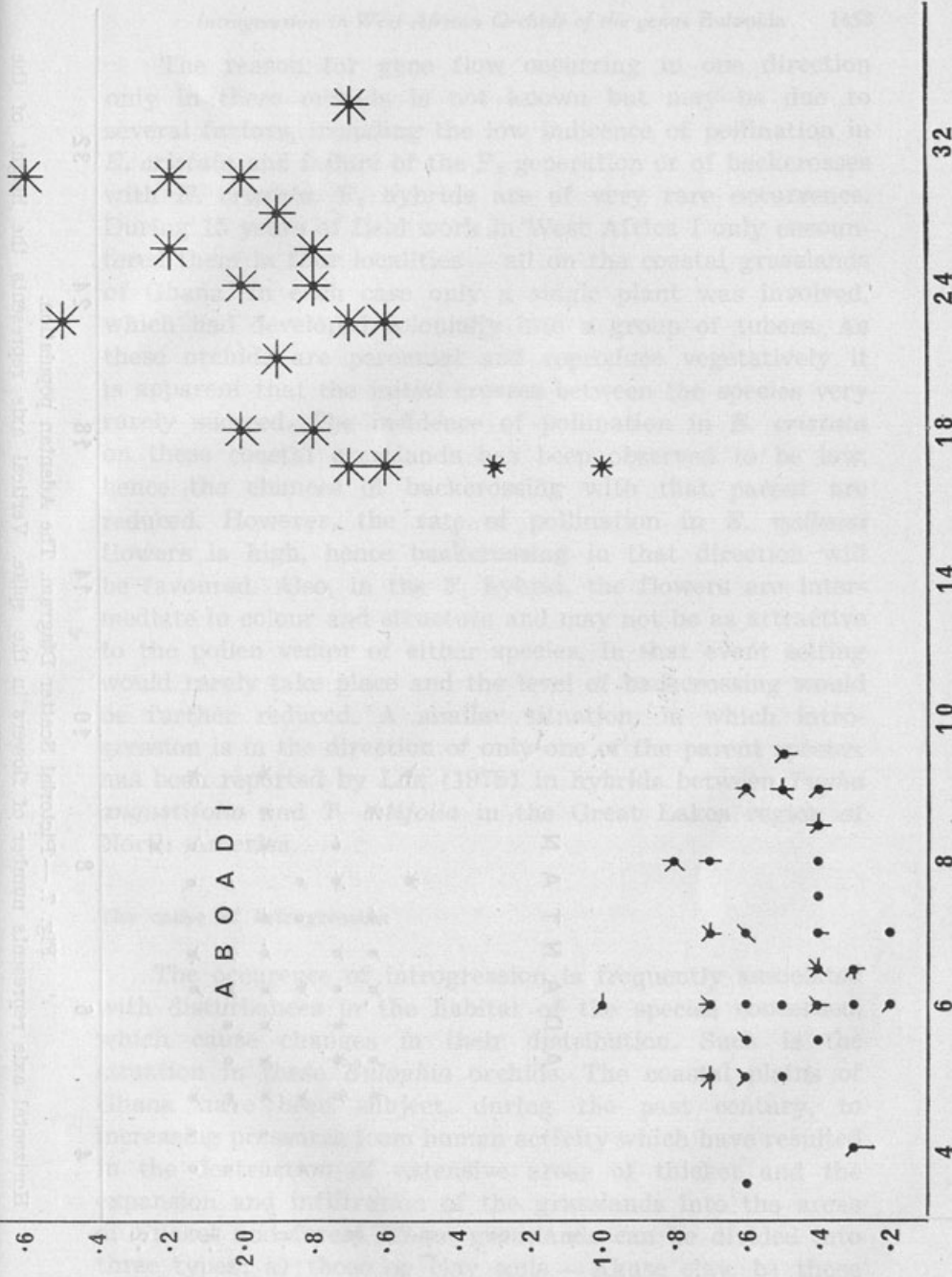
ABOADI

Fig. 6.— Pictorial Scatter Diagram. The Aboadi population.

Horizontal axis represents number of flowers in the spike. Vertical axis represents the height of the veins (calli) at the base of the lip petal.
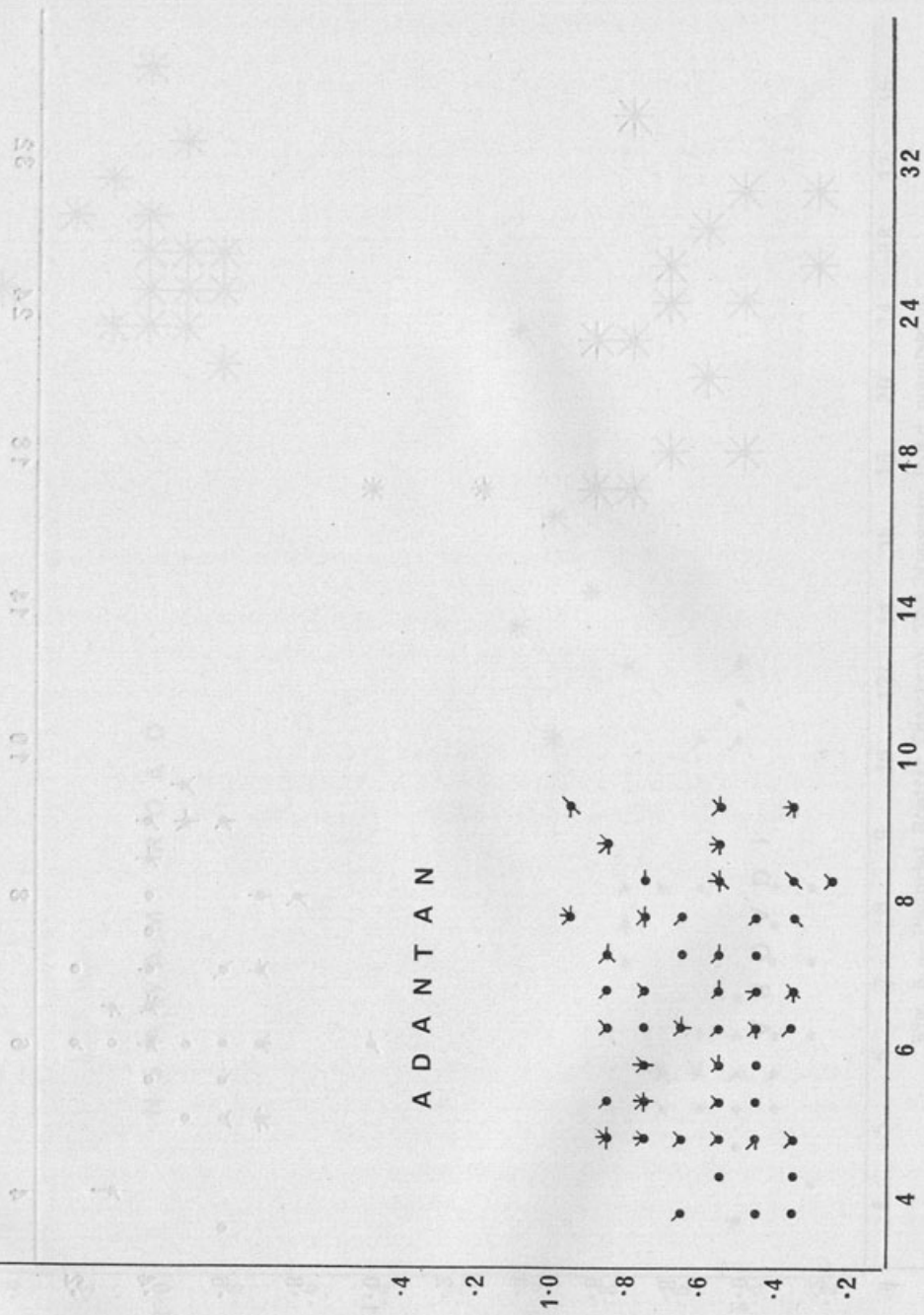
Fig. 7. — Pictorial Scatter Diagram. The Adantan population.

Horizontal axis represents number of flowers in the spike. Vertical axis represents the height of the veins (calli) at the base of the lip petal.

The reason for gene flow occurring in one direction only in these orchids is not known but may be due to several factors, including the low indicence of pollination in *E. cristata* and failure of the F_2 generation or of backcrosses with *E. cristata*. F_1 hybrids are of very rare occurrence. During 15 years of field work in West Africa I only encountered them in four localities — all on the coastal grasslands of Ghana. In each case only a single plant was involved, which had developed colonially into a group of tubers. As these orchids are perennial and reproduce vegetatively it is apparent that the initial crosses between the species very rarely succeed. The incidence of pollination in *E. cristata* on these coastal grasslands has been observed to be low, hence the chances of backcrossing with that parent are reduced. However, the rate of pollination in *E. millsoni* flowers is high, hence backcrossing in that direction will be favoured. Also, in the F_1 hybrid, the flowers are intermediate in colour and structure and may not be as attractive to the pollen vector of either species. In that event selfing would rarely take place and the level of backcrossing would be further reduced. A similar situation, in which introgression is in the direction of only one of the parent species, has been reported by LEE (1975) in hybrids between *Typha angustifolia* and *T. latifolia* in the Great Lakes region of North America.

The cause of introgression

The occurence of introgression is frequently associated with disturbances in the habitat of the species concerned, which cause changes in their distribution. Such is the situation in these *Eulophia* orchids. The coastal plains of Ghana have been subject, during the past century, to increasing pressures from human activity which have resulted in the destruction of extensive areas of thicket and the expansion and infiltration of the grasslands into the areas of thicket and forest. These grasslands can be divided into three types: a) those on clay soils — Akuse clay, b) those on the laterite, and c) those occurring on and immediately

behind the coastal strand and around lagoons. The first and the last of these types represent natural climaxes due to adaphic and climatic factors. Most of the grassland on the laterite, however, appears to be derived from the breakdown of more or less continuous vegetation of thicket and dry forest. The soil in this area is suitable for village farming in which the shifting pattern of agriculture, involving «slash and burn» methods of cultivation, has destroyed large areas of natural vegetation and favoured the development of grassland. When these farms are abandoned, due to declining soil fertility, they are rapidly colonized by grass. This burns annually as a result of both natural and man made fires. Regeneration of the thicket and forest is slowed down by the improverished soil, and in many areas it is completely prevented by the annual fires which sweep across the plains and frequently encroach on the remaining areas of thicket and forest. In years of severe burning the rate of encroachment can be considerable. 1959 was one such year. In the Nsawam road population the edge of the thicket was marked by metal stakes at the beginning of this study in 1956. No change had occurred between then and 1959, but in that year the thicket was driven back 84 m. in the area facing the severe wind-driven fires. Several thicket clumps were completely destroyed and others were considerably reduced in size.

Neither of these orchids can grow in areas of continuous thicket and forest. They require grassland or grassy enclaves. *E. cristata* is abundant in the grasslands on the laterite, especially in areas recently derived from thicket, but it is rare or absent from large areas on the clay soils, except at their northern tip where this species is again abundant. In this area the grasslands of the Accra Plains are now in contact with those of the Guinea savanna through the «Volta Gap» where the Volta River breaches the forested range of hills separating the Guinea savanna of the interior from the coastal grassland. This area of forest was only about 20 km. wide, but extensive felling associated with farming and construction of the Akosombo Dam have destroyed much of it and permitted the migration of Guinea savanna species onto the coastal plains. *E. cristata* occurs in the

Guinea savanna. The origin of the extensive colonies of this orchid on the coastal plains appears to be by migration from the Guinea savanna through the Volta Gap. This occurred when suitable habitats were created by the destruction of thicket and forest and the development of farms. *E. cristata* is also abundant in small areas of grassland at the back of the coastal strand and around lagoons. Several of these colonies, e. g. at Senya Beraku, Winneba, Elmina and Aboadi, are in isolated grassy enclaves separated by many kilometres of thicket and forest from the grassland of the Accra Plains. Hence it is probable that they are of different and older origin. However ,the low incidence of pollination in this species throughout the coastal plains, suggests that it is a recent arrival in an area where its pollinator does not occur.

Pure colonies of *E. millsoni* are confined to the grassland on the clay soils. This species also occurs along the coast in seasonally flooded areas behind the strand. However, *E. cristata* also grows in these locations and all the colonies show signs of introgression. *E. millsoni* appears to have followed the recession of the thicket and forest on the laterite soil. Again, most of these colonies show evidence of hybridization. Hybrid colonies occur on the coastal grasslands wherever the two species come into close contact. This occurs throughout the grassland areas on the laterite, in the enclaves of grassland behind the coast, and around the edge of the grassland on the clay.

The significance of introgression

Introgression may have a significant influence on future evolution in these orchids. As long as there is a barrier to the formation of backcrosses with the *E. cristata* parent, this species will not be affected, but certain effects on the *E. millsoni* populations are already apparent. The introgression of *E. cristata* characters into *E. millsoni* has produced changes in morphology, flower colour, ecological adaptation and time of flowering. It is difficult to asses the selective value of changes in morphology and flower

colour, but the effects of other changes are more apparent. Introgressed forms of *E. millsoni* are frequently encountered away from the lowlying seasonally marshy land to which this species is normally confined. On the undulating grasslands which lie inland from Winneba, this species and its hybrids occur scattered over the whole area. Similarly, they are to be found on the higher ground of the Accra Plains around Achimota and Legon. Hence it is apparent that introgression has enabled *E. millsoni* to extend its area either by an increase in ecological tolerance or by a change in competitive efficiency.

Though both these species of *Eulophia* flower at approximately the same time of year, many of the hybrids come into flower several weeks later and are frequently only just opening when the remainder of the colony is past its peak flowering period. The selective importance of this may be considerable in an area subject to annual burning. These orchids flower soon after the annual fires which sweep the plains, and on a number of occasions I have observed flowering colonies badly damaged by late burning. Hence a delay in the time of flowering prevents damage from fires and increases reproductive success.

Nomenclature

The name *E. flavopurpurea* (Rchb. f.) Rolfe has replaced *E. millsoni* as an earlier homonym in recent literature (SUMMERHAYES in HEPPER, 1968). However, it is apparent both from the name and the type description of *E. flavopurpurea* that it is a hybrid between *E. millsoni* and *E. cristata,* hence the name *E. millsoni* should be retained for this species. The following is a partial synomy of *E. millsoni* and its hybrids with *E. cristata.*

E. millsoni (Rolfe) Summerhayes in Flora of West Tropical Africa ed. I. 2: 446 (1936). *Lissochilus millsoni* Rolfe in Flora of Tropical Africa 7: 79 (1897) — Type Millson 86 (K) from Ilorin in Nigeria (Rowland s. n. from Ilorin, in Herb. Kew and cited by Rolfe under this species is

a hybrid with *E. cristata*). *L. lacteus* Kraenzl. in Engler
Bot. Jahrb. 43: (1908) — type Beauman 24 (K) from
Misahöe in Togo.

E. cristata × E. millsoni. *E. flavopurpurea* (Rchb. f.) Rolfe
in Flora of Tropical Africa 7: 65 (1897). *Cyrtopera
flavopurpurea* Reichenbach in Beit. Syst. Pflanz. 5: 68
(1871) — type Schweinfurthe 3546 (sketch in K) from
the Sudan — *«Labellum dilute purpureostriatum, calcor
apice flavium, petala etc. flavidovirescentia». Lissochilus
johnsoni* Rolfe in Kew Bull. 1910: 160 — type Johnson
854 (K) from the Accra Plains of Ghana appears to be
the F_1 hybrid. *L. andersoni* Rolfe l. c. 159 (1910) —)type
Anderson from Aburi in Ghana — this plant is illus-
trated in Bot. Mag. t. 8470. The illustration shows mauve
stripes on the lip and greenish sepals and petals — clearly
one of the backcrosses or segregates verging towards
the *E. millsoni* parent.

ACKNOWLEDGEMENTS

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        Can. J. Genet. Cytol. **20**: 475-481.
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    1965 Studies of the South African species of *Eupholia*. *J. South
        African Bot.* suppl. **5**: 248 pp.
HEPPER, F. N.
    1968 Flora of West Tropical Africa ed. 2. **3**, 1: 276 pp. Crown
        Agents, London.

LEE, D. W.
  1975 Population variation and introgression in North American *Typha. Taxon* 24: 633-641.
LOCK, J. M. & PROFITA, J. C.
  1975 Pollination of *Eulophia cristata* (Sw.) Steud. (Orchidaceae) in southern Ghana. *Acta Bot. Neefl.* 24, 2: 135-138.

PLATE I
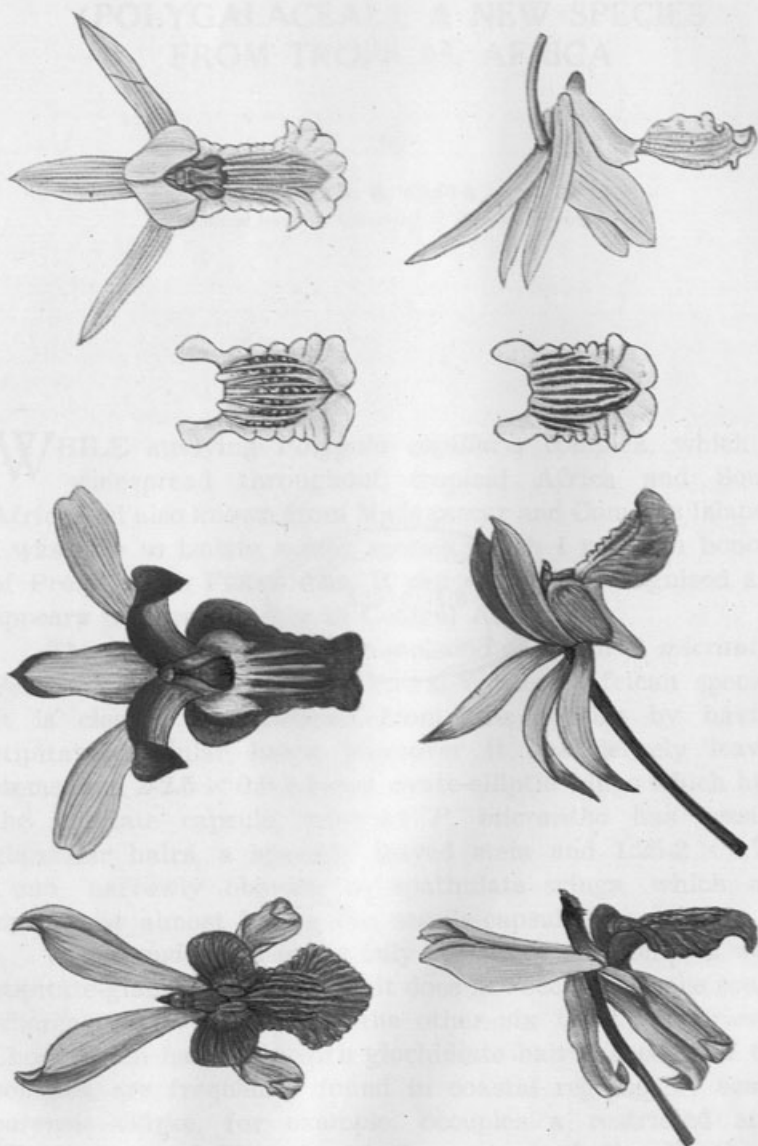
Flowers of *Eulophia*.

Left to right: *E. cristata, E. cristata* X *E. millsoni* F1 hybrid, lip petals of segregates,
E. millsoni. All X 2.

LUCE, D. W.
1975 Population dynamics and distribution in Sierra [...]
Canada. Taxon 24: 423-441.

LUCE, J. M. & FROST, L. C.
1978 [...]
in Southern [...] Acta Bot. Neerl. 25: 3: [...]
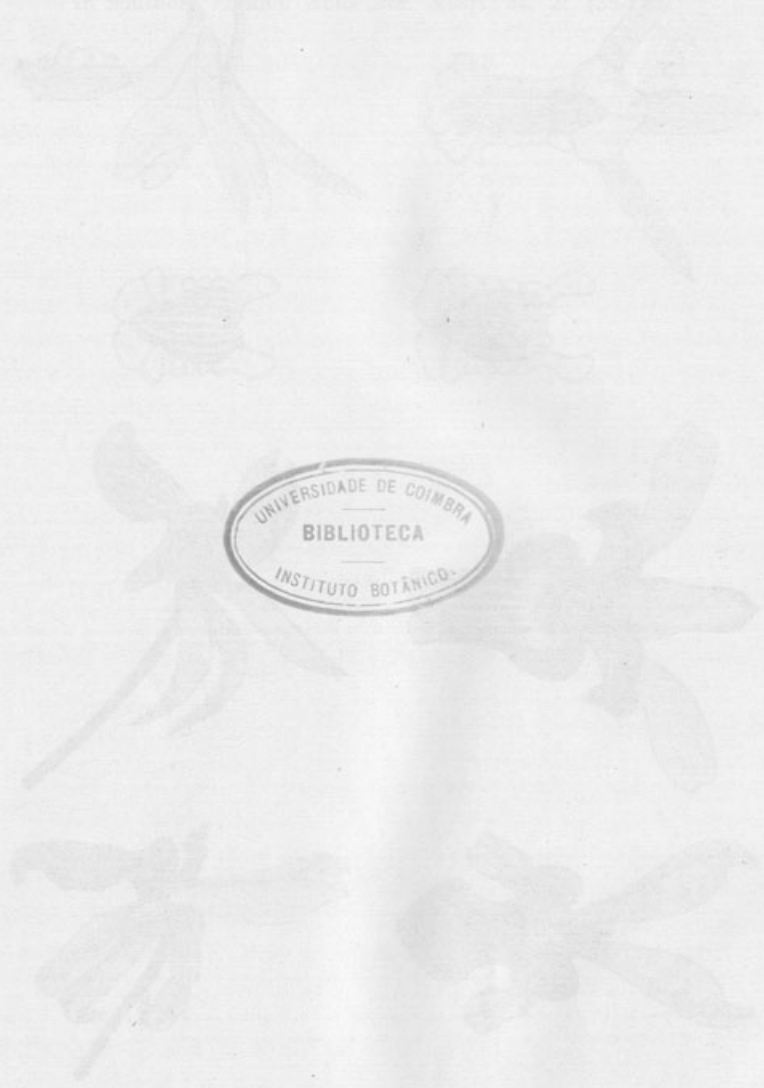
POLYGALA FERNANDESIANA (POLYGALACEAE), A NEW SPECIES FROM TROPICAL AFRICA

by

J. A. R. PAIVA

Botanical Institute, University of Coimbra, Portugal

WHILE studying *Polygala capillaris* complex, which is widespread throughout tropical Africa and South Africa and also known from Madagascar and Comores Islands, I was able to isolate a new species which I name in honour of Prof. ABÍLIO FERNANDES. It can easily be recognised and appears to occur mainly in Central Africa.

The new species has been included so far in *P. micrantha* Perr. & Guill., which is a Central-Western African species. It is clearly distinguished from this species by having stipitate-glandular hairs. Moreover it has densely leaved stems, and 2-2.5 × 0.9-1.2 mm, ovate-elliptic wings which hide the stipitate capsule, whereas *P. micrantha* has sessile-glandular hairs, a sparsely leaved stem and 1.25-2 × 0.75-1 mm, narrowly obovate to spathulate wings, which are shorter or almost hiding the sessile-capsule.

P. fernandesiana is the only species of the complex with stipitate-glandular hairs, and it does not occur near the coast, whereas *P. micrantha* and the other six (excl. *P. africana* Chod. which has seeds with glochidiate hairs) species of the complex are frequently found in coastal regions. *P. sansibarensis* Gürke, for example, occupies a restricted area (East coast of Kenya and Tanzania and the North of Mozambique) along the coast.

Polygala fernandesiana J. Paiva, sp. nov.

Herba annua, caule erecto, ramoso, gracili, generaliter-4-angulato, 10-25 cm alto, pilis stipitato-glandulosis instructo. Folia alterna, breviter petiolata, petiolo c. 0.5 mm longo, glabro vel sparse stipitato-glanduloso piloso; lamina linearis vel lineari-lanceolata, 5-15 × 0.5-1.25 mm, apice acuta, interdum recurvata, basi cuneata, glabra, costa supra impressa, subtus conspicua. Flores lilacinei vel rosei, pedicellati, pedicellis c. 0.8 mm longis, glabris, in racemos terminales, raro laterales, rhachidi striata, glabra, 2.5-10 cm longa (pedunculo 5-16 mm longo, semper $^1/_5$-$^1/_6$ racemi tanquam longo, stipitato-glanduloso piloso) dispositi; bractea lanceolato-linearis, c. 1 mm longa, glabra, caduca; bracteolae lineares, c. 0.5 mm longae, glabrae, caducae. Sepalum posterius lineare, 1.25-1.5 mm longum, glabrum; alae ovato-ellipticae, 2-2.5 × 0.9-1.2 mm, glabrae, capsulam complete opertentes (generaliter quam capsula duplo longiores); sepala anteriora libera, linearia, 0.75-1 mm longa, glabra. Petala superiora obovata, 1.5-1.75 × 0.5 mm, carinam aequantia aut longiora; carina 1.5 × 0.5 mm, cristata, crista c. 0.5 mm longa. Stamina 8, parte libera filamentorum 0.2 mm longa, tubo 0.4-0.5 mm longo, glabro; antherae 0.1-0.2 mm longae. Ovarium aplanato-ellipsoideum, 0.3 × 0.25 mm; stylus 0.1-0.2 mm longus, ramo anteriore stigmatifero. Capsula 1.25-1.5 × 0.75 mm, subgloboso-ellipsoidea, stipitata, glabra. Semina ovoidea vel ellipsoidea, 0.75-0.8 × 0.4 mm, breviter pubescentia, ecarunculata.

Habitat in Africa Centrali (in regionibus vulgo dictis Chad, Nigeria, Cameroon, Central African Republic).

Typus: Cameroon, prope Nagaou Ndéré Plateau, 20.IX. 1967, *Jacques-Félix* 82220 (P, holotypus; YA, isotypus).

Affinis *P. micranthae* a qua caulibus pilis stipitato-glandulosis instructis et floribus majoribus (alae 2-2.5 × 0.9-1.2 mm nec 1.25-2 × 0.75-1 mm) praecipue differt.

Species in honorem praeclarissimi Prof. Dr. Abilii Fernandis, Botanicae eximii cultoris, dicata.

Polygala fernandesiana J. Paiva

Annual densely leafy herb, 10-25 cm tall, often much branched from the base; stems slender, 4-angled and covered with stipitate-glandular hairs. Leaves petiolate (petiole c. 0.5 mm long, glabrous or with slightly stipitate-glandular hairs); lamina 5.15×0.5-1.25 mm, linear-lanceolate, acute at the apex, cuneate at the base, sometimes arcuate, glabrous. Flowers pink or lilac, rarely whitish, arranged in terminal (occasionally some lateral) racemes, 2.5-10 cm long, with a glabrous, striate rachis (peduncle 5-16 mm long, always $^1/_5$-$^1/_6$ as long as the racemes, stipitate-glandular hairy), early caducous bracts (1 mm long, lanceolate-linear, glabrous) and bracteoles (0.5 mm long, linear, glabrous); pedicels (c. 0.8 mm long, glabrous. Posterior sepal 1.25-1.5 mm long, linear, glabrous; wing-sepals 2-2.5×0.9-1.2 mm, ovate-elliptic, glabrous and completely hiding the capsule (usually twice longer than the capsule); anterior sepals 0.75-1 mm long, linear, glabrous, free. Upper petals 1.5-1.75×0.5 mm, obovate, longer or as long as the carina; carina 1.5×0.5 mm, crest c. 0.5 mm long. Stamens 8, free part of filaments 0.2 mm long, staminal tube 0.4-0.5 mm long, glabrous; anthers 0.1-0.2 mm long. Ovary flattened-ellipsoid, 0.3×0.5 mm; style 0.1-0.2 mm long, anterior branch stigmatic. Capsule 1.25-1.5×0.75 mm, subglobose-ellipsoid, stipitate, glabrous, neither winged nor emarginate. Seeds 0.75-0.8×0.4 mm, ovoid-ellipsoid, rugose, with white or brownish short hairs, not carunculate.

CHAD: Folle, Mussopys, 13.III.1964, *Andru* 1199 (K); Lake Chad, IX.1902, *Chevalier* 5391 (P); Lake Chad, Mboukou, 24.IX.1902, *Chevalier* 5527 (K; P); Lake Chad, between Kenio and Tomi, 22.IX.1902, *Chevalier* 5693 (P); Lake Chad, Ungourras Plateau, 13.IV.1902, *Chevalier* 6116 (K; P); Lake Chad, Ungourras Plateau, 14.XI.1902, *Chevalier* 6117 (P); Lake Chad, IX.1957, *Koechlin* 4709 (P).

NIGERIA: Northern Region, Sardauna Prov., Mambilla Plateau, 4.VIII.1973, *Chapman* 52 (K); Adamawa Prov.,

Mambilla Plateau, Dorofi, VI.1958, *Chapman* 65 (K; P);
Southern Region, Bamenda, N. of Bum, *Maitland* 1397 (K).

CAMEROON: Mango Distr., 7 km S. of Poli, 29.VII.1974,
Fotius 2209 (P; YA); N. of Nagaou Ndéré Plateau, 20.IX.1967,
Jacques-Félix 8220 (P; YA); Mbepit Distr., near Foimbot,
Letouzey 1611 (P); Maka, 40 km N. of Tibati, 21.IX.1963,
Letouzey 5874 (K; P; YA); Grand Yoli, near, Mayo Darlé,
19.VI.1967, *Letouzey* 8665 (P; YA); Massif du Mbepit, 9.VIII.
1932, *Letouzey* 11611 (P; YA); W. loc. *Mildbraed* 10161 (P);
15 km N. of Bouat Laterita, VIII.1966, *Lebrun* 14162 (P);
Mt. Ngamba, E. of Ngaou Ndéré, *Piot* 38 (P); Njen Tibati,
6.IX.1914, *Tessmann* 2723 (K).

CENTRAL AFRICAN REPUBLIC: Yalinga, 4.VIII.1921, *Le
Testu* 2998 (BM; P); Zako, 18.XI.1922, *Le Testu* 4343 (BM; P);
Waka, Kaga Mbigo, 60 km N. of Bambari, 13.IX.1922, *Tisserant* 56 (BM; P).
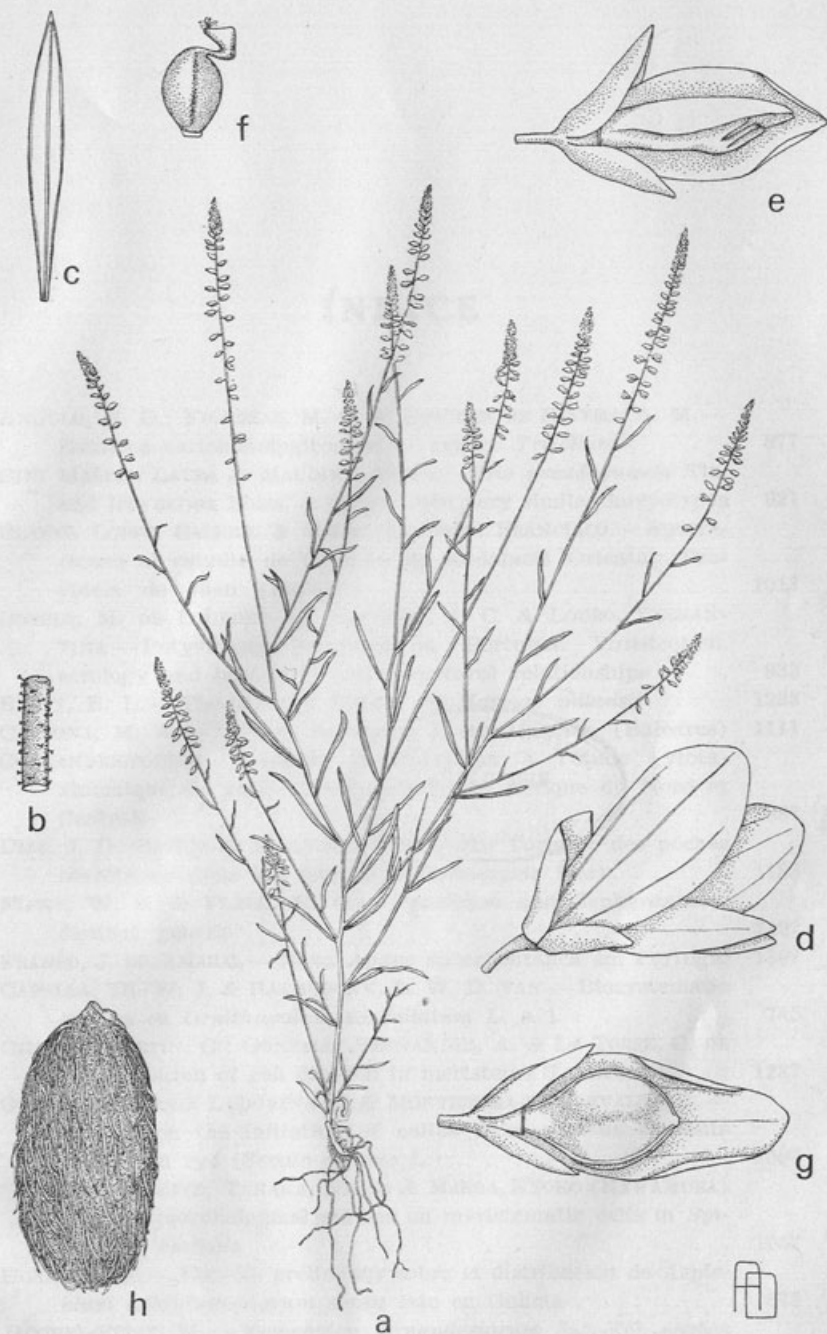
Polygala fernandesiana J. Paiva

a) habit (× ½); b) part of branch (× 7.5); c) leaf (× 2); d) flower
(× 10); e) flower with upper petal removed (× 10); f) ovary (× 10);
g) developing fruit (× 12); h) seed (× 30). All from *Fotius* 2209 (P).

ÍNDICE

INSTRUÇÕES AOS COLABORADORES

1. O *Boletim da Sociedade Broteriana* é uma revista destinada à publicação de artigos originais em todos os domínios da Botânica. No entanto, artigos muito extensos sobre florística, fitogeografia e fitossociologia são publicados geralmente nas *Memórias,* enquanto que os trabalhos de divulgação científica e os referentes à história da Botânica são reservados para o *Anuário* — as duas outras revistas da Sociedade.

2. Destinado principalmente à publicação dos artigos elaborados pelo pessoal científico do Instituto Botânico de Coimbra, nele se inserem todavia trabalhos da autoria de membros da Sociedade, bem como os de outros investigadores, quer portugueses, quer de outras nacionalidades. A publicação de qualquer artigo, porém, está na dependência da aprovação da Comissão Redactorial.

3. Os manuscritos entregues para publicação devem ser dactilografados a dois espaços e possuir uma margem da largura habitual. Poderão ser escritos em português, inglês, francês, alemão, italiano ou espanhol. O nome do autor (ou autores) deverá figurar na primeira página, bem como o endereço da Instituição em que trabalha. Um resumo não excedendo aproximadamente 300 palavras, preferivelmente em inglês, deverá iniciar o artigo.

4. Os nomes latinos dos géneros, espécies e categorias infraspecíficas que figurarem no texto devem ser sublinhados uma só vez, enquanto que os nomes dos autores, quando não escritos em maiúsculas, devem ser sublinhados com um traço ondulado. As palavras em negro devem ser sublinhadas duas vezes. Os nomes dos autores citados no texto devem ser seguidos pela data da publicação entre parênteses.

5. No que respeita à ordenação e disposição da bibliografia, seguir as normas utilizadas em um dos volumes recentes desta publicação.

6. As figuras a intercalar no texto, geralmente reproduzidas em zincogravura, não deverão exceder a mancha tipográfica. As estampas *hors-texte* (em regra fotogravuras) serão impressas em papel *couché* e não deverão ultrapassar 13 × 18 cm. Sempre que as figuras sejam de pequenas dimensões, aconselha-se a sua reunião em estampas com as dimensões acima indicadas.

7. Cada autor (ou grupo de autores) receberá 50 separatas grátis, sendo as excedentes que pretender fornecidas ao preço do custo e pagas directamente à Tipografia.

INSTRUCTIONS AUX COLLABORATEURS

1. Le *Boletim da Sociedade Broteriana* est un périodique destiné à la publication d'articles originaux concernant tous les domaines de la Botanique. Cependant, des articles très longs sur floristique, phytogéographie et phytosociologie sont en général publiés dans les *Memórias,* tandis que les travaux de divulgation scientifique et ceux concernant l'histoire de la Botanique sont réservés au *Anuário* — les deux autres revues de la Société.

2. Ayant particulièrement pour but la publication des articles élaborés par le personnel scientifique de l'Institut Botanique de Coimbra, ce périodique publie aussi les travaux des membres de la Société, ainsi que ceux d'autres botanistes, soit portugais, soit de quelque autre nationalité. Toutefois, la publication des articles est sous la dépendance de l'avis de la Commission de Rédaction.

3. Les manuscrits doivent être dactylographiés à deux espaces et avoir une marge. Ils peuvent être rédigés en portugais, anglais, français, allemand, italien ou espagnol. Le nom de l'auteur (ou des auteurs) devra figurer à la première page après le titre du travail, ainsi que l'adresse de l'Institution où il travaille. Un résumé ne dépassant pas 300 mots, de préférence en anglais, devra ouvrir l'article.

4. Les noms latins des genres, des espèces et des catégories infraspécifiques devront être soulignés une fois, tandis que les noms des auteurs, quand non dactylographiés en lettres majuscules, doivent être soulignés par une ligne ondulée. Les noms des auteurs cités dans le texte doivent être suivis de la date de la publication mise entre parenthèses.

5. En ce qui concerne la bibliographie, voir quelque volume récent du *Boletim.*

6. Les figures du texte, en général des dessins à l'encre de Chine, ne doivent pas, avec les légendes, dépasser 10,5 × 18 cm. Les planches hors-texte ne devront pas dépasser 13 × 18 cm. Les figures à petites dimensions doivent être réunies dans des planches aux dimensions ci-dessus mentionnées.

7. Chaque auteur (ou groupe d'auteurs) recevra 50 tirages à part gratuits, tandis que l'excédent de ce nombre lui seront fournis au prix du coût et devront être payés directement à l'Imprimerie.