Corrections and Additions to the Book 'Morphology of Seed-Plants'

By

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With 13 Figures

Summary

Guédès M. 1981. Corrections and additions to the book 'Morphology of Seed-Plants'. — Phyton (Austria) 21 (2): 261—287. — English with German summary.

In an effort to correct mistakes in the author's "Morphology of Seed-Plants" (Cramer 1979, Vaduz) and to present further facts and interpretations, some notes are given here. Mainly roots, life form, axillary buds, unifacial leaf portions, floral phyllotaxis and gynoecia are considered.

Zusammenfassung

Guédès M. 1981. Korrekturen und Ergänzungen zum Buch „Morphology of Seed-Plants". — Phyton (Austria) 21 (2): 261—287. — Englisch mit deutscher Zusammenfassung.

In dem Bestreben, in dem Buch „Morphology of Seed-Plants" (Cramer 1979, Vaduz) enthaltene Fehler zu verbessern sowie weitere Fakten und Interpretationen darzustellen, bespricht der Autor eine Anzahl morphologischer Themen. Im besonderen werden Wurzeln, Lebensformen, Axillarknospen, unifaziale Blattabschnitte, florale Phyllotaxis, Fragen der Gynözeum-Morphologie u. a. behandelt.

The additions and corrections presented here are related to the author's book 'Morphology of Seed-Plants' (8°, 326 pages, 30 figures), which is published by J. Cramer (Vaduz 1979). References to the page numbers are given in relation to this book.

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Root branching (p. 21 and p. 24)

Lateral roots of most Monocots arise opposite xylem bundles, as with Dicots (VAN TIEGHEM & DOULIOT 1888). They are initiated opposite phloem bundles in the *Gramineae* and *Cyperaceae*, but in e. g. corn (*Zea*) they may also appear in front of xylem bundles. CLOWES 1978 recently confirmed the occurrence of an endodermal pouch around rootlet primordia in corn. This is multilayered and indistinguishable from a root-cap, but is later replaced by a true cap from the dermatogen of the lateral root itself.

Regeneration of root apex (p. 30)

As early as 1933, GAUTHERET had shown that in *Zea mays* isolated root tips including the root-cap and at least part of the proximal meristem with what is now called the quiescent center, could regenerate a whole root. When too little meristem remained with the cap, only anarchic growth occurred. Distal portions of roots whose tip had been excised regenerated a cap and apparently a quiescent center from their remaining meristem. The latter fact had been known since PRANTL's work in 1874.

Detailed experiments on root regeneration in *Zea* have recently been carried out by FELDMANN 1979. He found that regeneration (of decapitated roots) is possible from the meristem proximal to the quiescent center. The meristem then regenerated a quiescent center and root-cap. Furthermore, roots could be regenerated directly, i. e. through direct elongation of the explant along the same axis as in the intact root rather than through development of an adventitious root from a callus, from cultivated meristematic portions excised just proximal to the quiescent center, and without the latter. The meristem used in the latter experiments was 300—350 μm in length. When the quiescent center remained attached to it, regeneration was also possible.

Since direct regeneration is possible from either the quiescent center, the adjacent upper meristem or both, it is all too clear that such experiments tell little or nothing about the actual initiating role of cells from these two regions in the normal, intact root.

Root chimeras (p. 31)

I noticed that work should be done on root chimeras, if any, to clear up the functioning of root apices. It must be mentioned that there already are at least two papers on such chimeras. BRUMFIELD 1943, by irradiating seedlings of *Crepis capillaris* (L.) WALLR. (*Compositae*) and *Vicia faba* L. (*Papilionaceae*), obtained sectorial chimeras, a sector being detectable by chromosomal abnormalities in many of its cells, and being apparently produced by a single initial. There seemed to be three sectors, each of which was comprised of a third of the root-cap, the cortex and the stele. The moment the roots were irradiated, they appear to have possessed three

initials for the whole of their tissues. RICKARD 1952, however, who also X-rayed *Crepis*, got three sectors in the cortex only of a single root, so he believed that there were three initials to the cortex, three to the cap and three to the stele. It is obvious that much further work is needed in this line.

Closed-type roots (p. 32)

The origin and functioning of cortical initials in the root of *Cyperus fuscus* L. (*Cyperaceae*) is described by JUGUET & VALLADE 1979.

Summer and winter annuals (p. 39)

Although it is not a morphologic one, the distinction may be mentioned between summer annuals which germinate, flower and die within the same calendar years, and winter annuals, which germinate in fall, to flower and die next year. As is well-known, the same species may behave both ways depending on the strain. Wheat is normally a winter annual, but certain cultivars are summer annuals, because they need no vernalization.

Multi-articled sympodia within a season in woody plants (p. 45)

In temperate woody plants with sympodial development, only one article develops within a season, but there are exceptions especially in vines such as *Wisteria sinensis* (SIMS) SWEET (p. 47). Also in *Citrus* (*Rutaceae*) two or three sympodial articles generally develop during each season, the second from the first and the third from the second. Sympodization here is through apex death, not apex flowering (SCHROEDER 1951). In *Cornus alba* L. (*Cornaceae*) where sympodization occurs as a result of the development of terminal inflorescences three articles at least may develop within a season (GUÉDÈS, unpubl.).

Trees and shrubs (p. 48)

The acrotonous condition is not sufficient for a woody perennial to become a tree. A trunk must appear at least below. As a rule, the lower portion of the trunk, from ground level up, is naked, which implies the lack or early disappearance of most lateral branches in the early life of the plant. On the other hand, in a basitonous woody perennial, if only one or a few main shoots arise from the lower zone of the previous year's shoot, and each develops some sort of a trunk, this being mono- or sympodial, a polycormic tree may result, i. e. a tree with several trunks diverging from near ground level. This may be seen in the elder (*Sambucus nigra* L., *Caprifoliaceae*) or in *Cotoneaster salicifolia* FRANCH. (*Rosaceae*). In these plants, sprouts arisen in a basitonous way are themselves mesotonous, more or less plagiotropic and commonly sympodial in their development. Several oblique undulate trunks may thus appear in old plants, and one of them may survive singly as a small tortuous tree.

264

I have prepared a morphologic system of tree and shrub architecture (GUÉDÈS, in press), suggesting to restrict the term shrub (true shrubs) to colonial woody perennials with basitonous branching, other 'shrubs' in effect being dwarf trees. The various constitutions of trunk and branches of trees, respecting their sympodial or monopodial structure, the occurence of short shoots etc. enabled me to define ten main morphological types of architecture with several variants in most of them. It is hoped that this system is morphologically more consistent than HALLÉ, OLDEMAN & TOMLINSON's one (1978); perhaps I may also refer the reader to my review of the latter (GUÉDÈS 1980a).

Iterative innovation (p. 50)

An axillary shoot developed at ground level by a determinate shoot (and similar to the latter as in rhizomatous irises [p. 43] or grasses) may be called an innovation. In perennial plants innovations may remain vegetative for one or more years before they flower (more years e. g. *Aconitum* sect. *Lycoctonum*, *Ranunculaceae*: SEREBRIAKOVA & POLYNTSEVA 1974). Their production is a kind of sympodization as explained. When innovations are flowering they themselves develop innovations of the next higher order. I mentioned on p. 50 that young, not yet flowering *Asparagus officinalis* L. plants give rise to several such 'generations' within the same season. This is also true of the adult flowering plant of this species. TROLL 1964: 325—331 spoke of iterative innovation in such instances, innovation then meaning development of innovation shoots. Up to 10 flowering innovations develop within the same season in adult *Asparagus officinalis*, all or most of whose buds are formed in the previous fall. Iterative innovation according TROLL l. c. also occurs in *Canna indica* L. (*Cannaceae*), *Juncus subnodulosus* SCHRANK (*Juncaceae*), *Nardus stricta* L. (*Gramineae*), *Carex arenaria* L. (*Cyperaceae*). In annual grasses, or annual shoots (innovations) of perennial grasses, severals orders of innovations commonly develop, the process being called tillering. Every tiller comes from a lower axillary bud of the main shoot (first-order tillers) or of a previous-order tiller. Tillering is different from iterative innovation insofar as, even in perennial grasses the ultimate generation of tillers will not give rise to next year's main shoot(s). The latter will be originated by a lower axillary bud of the current year's shoot, as was the first generation of the current year's tillers.

Apical growth of stem (p. 53)

I may have stated by mistake that Gymnosperms may have GW (green-white) chimeras. Only WG (white-green) chimeras seem to be known, although GW ones certainly are a possibility. Also the epidermis (TI = first tunica layer) rarely proliferates at the margins of leaves in Gymno-

sperms, so that my statement that there are white margins to leaves of WG chimeras is erroneous.

Attention must be called to the work of STEFFENSEN 1968 (see also COE & NEUFFER 1978) on the shoot apex of *Zea mays* L., where radiation-induced sectoring is very carefully related to a histogenetic study of the apex. The corn apex appears to have a few initials, probably often two, to each of its histogens. TI-TIII initials make up two vertical series each of which originates one half of the plant (one half means here one side of the plant divided by a plane cutting through stem and midribs of the leaves).

As the shoot is already well developed in the mature seed, to get a completely half-mutated plant, one must irradiate a very young embryo, 36—40 h after fertilization. It is known that at this time the first periclinal division occurs in the terminal cell of the filamentous embryo, establishing its bilateral symmetry. Half-mutated plants appear when one of the two cells then produced mutates. This cell must give rise to the three histogen initials on one side and consequently these are all mutated. Later irradiation leads to more and more upwardly located sectors, limited to one histogen. If mature seeds are irradiated and one of the initials of an histogen is induced to mutate, the mutation is found at tassel level, in the form or a ½ or ¼ sector. If sectors occur below in such plants, they are narrower, because they come from mutated cells that were below the initials. In the mature seed, the initials have already produced the whole of the cells from which leaves and bracts have been or will be initiated. So if there are two initials for each histogen, no irradiation at this stage can lead to a ½ sector at the vegetative level. The tassel, on the other hand, is still to be laid down by the initials at the mature seed stage, so half mutated tassels may occur from irradiated seeds. As initials may be more than two in each histogen, or because they have already begun dividing to initiate the tassel, narrower sectors also are found in mutated tassels from irradiated seeds.

The midrib plane of corn is a boundary that is often trespassed on by cell progenies, i. e. one sector of a two-sectored plant may cross the midrib of a leaf while not reaching that of the leaf below on the other orthostichy. Thus adjustments are constantly being made between cell progenies, some of which may become temporarily or progressively wider, while others are accordingly restricted so that the specific form is maintained.

Half-rosette plants (p. 65)

Half-rosette plants may be annual, their rosette elongating into a flowering shoot within the year after germination. This is seen in e. g. *Capsella bursapastoris* L. (*Cruciferae*). TROLL 1937: 223—236 believed that a plant is still a rosette rather than a half-rosette one if the rosette apex elongates into an inflorescence stalk bearing no true leaves. If this is accepted it is hard, as TROLL acknowledged, to draw a line between such rosette plants and those half-rosette ones with leaves only down their elongated

stem. This is why I prefer to restrict the use of the term rosette plant for plants which never elongate their rosette axis and develop inflorescences or flowers laterally. Such plants belong to "rosette plants with indefinite main axis" in TROLL's terminology. In my view all plants with a rosette whose axis elongates into a stalk, whether or not leafy, are half-rosette plants.

Axillary buds: rarer locations. Con- and recaulescence, anaphysis (p. 66)

When recaulescence occurs between a leaf and its axillary bud, it might be that no independent bud trace is detectable in the dual lower portion common to both. This could occur when the bud arises at the axil but its traces depart from leaf ones as they are already outside the stem. Subsequent intercalary growth just against the axil then might lead to a recaulescent zone including the leaf and a merely cortical portion of the bud (Fig. 4).

A similar condition might occur in buds axillary at first but owing their later concaulescent condition to an intercalary growth zone between their subtending leaf and the merging point of their traces with the stele of the supporting shoot (Fig. 3). Discreteness of vascular supply thus is no telling evidence of con- or recaulescence. Morphologic examination is required to detect the possible occurence of bud tissue along the stem or leaf before eliminating these possibilities when no discrete strands are seen to the displaced bud.

When discrete strands occur to the bud, they may be integrated with a leaf trace which becomes centric below bud insertion as opposed to colla- teral above, where it is purely foliar, as in *Saururus* bracts bearing an inflorescence (TUCKER 1975, 1976).

If intercalary growth involves the whole of the petiole at its insertion and above the departure zone of the leaf trace(s) the node becomes elongated with the petiole congenitally adnate to the stem along their zone of concrescence (joint elongation, Fig. 5). When elongation takes place above the closure of the gap of a leaf trace, this will be seen parallel to, and outside the stele before passing into the leaf (Fig. 5), as with lateral traces of such displaced leaves subtending lower inflorescence branches in *Cornus sericea* L. (BARABÉ & VIETH 1980). If elongation occurs at the level of the gap, this itself becomes stretched the whole length of the concrescent zone (Fig. 6), as is the gap of the median trace of the *Cornus* leaves just alluded to. Such displacements of leaf apparent insertion may be called anaphysis (see also TROLL 1964: 131—133).

When leaves displaced through anaphysis have axillary buds, these of course are also displaced to become seemingly inserted at the new axil (Fig. 7), being at the same time con- and recaulescent. The elongated nodal

zone is made up of the stem and basal portions of the axillary bud and leaf when intercalary growth occurs at the level of bud insertion involving the basal portion of the leaf at the same time. *Cornus sericea* often has such displaced leaves or bracts at the level of its two lowermost inflorescence branches, the latter being involved in the displacement process (Fig. 7). Lower inflorescence branches in this *Cornus* may also be merely con- or recaulescent. When bracts are very reduced their trace may not enter the appendage itself, remaining in the stele gap of the supporting axis, or there may be a gap with no trace whatever. Upper inflorescence branches are always concaulescent and lack bracts. Con- and recaulescence as well as anaphysis were studied in this plant by BARABÉ & VIETH 1980 in an illuminating paper.

<center>Lateral and leaf-opposed serial buds (p. 68)</center>

As indicated, serial buds may be collateral, i. e. in a tangential row within each axil, in some Monocots. It may happen that only one bud in the series occurs in an axil, without being the median one. In the palm *Plectocomiopsis corneri* FURTADO the only bud in each leaf axil is 30—40° away from the midrib zone of the leaf base (FISHER & DRANSFIELD 1979). When leaves enwrap the stem, leaf axils in fact circle the latter, and collateral buds might occur all around. In vegetative plagiotropic stems of *Musa* (*Musaceae*) the leaves have a single 'axillary' bud but it is inserted 180° away from the median leaf region i. e. above the meeting point of both margins of the leaf base on the side opposite the midrib (FISHER 1978). The same is seen in vegetative leaves or certain species of *Daemonorops* (*Palmae*), whereas in *Korthalsia rigida* BLUME, another palm, the axillary bud is 130° from the midrib (FISHER & DRANSFIELD 1979). Inflorescence buds are normal axillary buds in these palms, and in *Daemonorops* transitional leaves between vegetative and fertile zones often subtend both a conventional inflorescence bud and a leaf-opposed vegetative bud. In my view all these palm leaves potentially have a circling series of axillary buds, vegetative or sexualized, among which only two opposite or near-opposite ones are developed, singly or both at the same time. Bracts of *Musa* do not encircle the peduncle and subtend two superimposed collateral series of flower buds. Two species of *Dracontium* (*Araceae*) seem to have many circling series of collateral buds in the axils of their enwrapping bulb scales (TROLL 1937: 538, 539).

A lateral bud such as that of *Korthalsia* thus seems to be one of a potential circling series of serial collateral buds. It must be carefully distinguished from extra-axillary lateral buds (p. 325), which are basically conventional axillary buds somewhat displaced laterally owing to their developing a bulky axillary bud to their own prophyll (*Cucurbitaceae*; TROLL 1939: 1976—1979).

Is dichotomy in seed plants a really true one ? (p. 72)

As initials appear to be present at the apex of stems of seed plants, one would expect that in the rare instances of true dichotomy, they are apportioned between the two daughter apices. Each half of them would go to each apex and regenerate the whole initial complement. Initials in fact are hard to locate histogenetically, but at least one would see the apex proper become split into two. Now it seems that in dichotomizing apices the apex proper ceases growing and two new apices differentiate on its flanks. Since these apices bear no relation to any leaf axil, they may be called adventitious, and dichotomy would thus be subapical adventitious budding.

Lammas shoots (p. 131)

When the apical bud of a woody plant breaks several times within the same season, the supplementary flushes besides the spring one give rise to lammas shoots, the term applying especially to the second flush, which may take place about the lammas (August 1). As a lammas shoot proper is elongating from the terminal bud, lateral lammas shoots may develop from axillary buds on the stem segment below, whether it is from the previous season or the previous flush in the same season. I studied such a case in *Choisya ternata* KUNTH (*Rutaceae*; GUÉDÈS, 1980 b).

Multinodal pines develop lammas shoots. Their winter bud may be made up of the first flush only before its elongation, so the lammas shoots are not preformed. Other such pines have a multi-storied apical bud including the consecutive flushes of the season (see LANNER 1976, 1978). Lammas shoots are apparently not preformed within apical buds of broad-leaved trees.

Intermediary apical buds formed during the short resting periods between the seasonal flushes may be imperfect, much in the way of incipient buds of the avocado (p. 131). If they are lacking altogether, there is a protracted growth period all through the season instead of several flushes with intervening periods of rest. Flushing and continuously growing shoots occur on the same individual. On conventional shoots of temperate woody plants, elongation of course occurs during the sole spring flush.

Cauliflory

Flowers or inflorescences sometimes seem to appear on ripened shoots more than a year old, with no very clear connection to former leaf axils, at first sight at least. It is often thought, and sometimes stated in print, that they are adventitious. This is unlikely in view of the rarity of adventitious normal shoots above cotyledons. Cauliflory has rarely been studied in enough detail. Some studies are quoted by HALLÉ & al. 1978. In the Judas-tree (*Cercis siliquastrum* L., *Caesalpiniaceae*) cauliflory is from serial

buds that develop on succeeding years in leaf axils. Most of the latter produce inflorescences for some years only, after fall of the corresponding leaves. Some axils, however, may 'awake' after a many years' dormancy, and again send out flowers, their supporting shoot having become more or less bulky in the meantime. No inflorescence is adventitious (GuÉDÈS, unpubl.).

In *Gleditsia triacanthos* L. (*Caesalpiniaceae*) long shoots bear axillary short determinate shoots with no elongated internodes, that live only one year. Commonly, after fall of its first determinate shoot, so two years after fall of its subtending leaf, an axil develops new determinate shoots from serial buds on succeeding years. Two or three serial shorts may appear in the same axil within the same season. These shoots in effect are 'caulifolious' vegetative short shoots. Inflorescences of *Gleditsia* arise in the leaf axils of one-year-old shoots, exactly as determinate vegetative shoots. Leaves are formed at the bottom of the inflorescent axis, and a sterile determinate shoot is homologous with the sterile lower portion of an inflorescence axis. True cauliflory does not seem to occur in *Gleditsia triacanthos*, i. e. axils more than a year old develop only vegetative determinate shoots, not inflorescence (GuÉDÈS, unpubl.).

Locally multilayered epidermis (T I) and leaf initiation (p. 91)

Rather than occur in the young leaf primordium, periclinal divisions of TI (dermatogen or first tunica layer) that lead to the invasion of TII (second tunica layer) by daughters of TI cells may occur laterally on the stem apex, above the youngest leaf primordium. TI then is locally two or three cells thick, and when this region takes part in producing a leaf primordium, the latter may be entirely made up of cells that are genetically TI if the whole of its cell rows is produced by the multilayered TI. In certain chimeras of *Tradescantia fluminensis* VELL. (*Commelinaceae*, THIELKE 1957), whose leaves develop from the second and third layers, TI becomes partly two- or three-layered and leaf tissues normally derived from TII or TIII are genetically TI in those leaf regions that come from apex zones with two- or three-layered TI.

Morphology and architecture of unifacial leaf portions (p. 105)

Although forerunner tips (p. 103) generally are epiunifacial, i. e. with their morphologically lower surface all around, some instances have been quoted by VOGEL 1966 of orchid tepals with hypounifacial tips. The extremity of such phyllomes is then outrolled, and they have their morphologically upper (ventral) surface all around.

With respect to the morphology of the upper cross-zone of their petioles. leaves with unifacial petioles are of two kinds. (The word cross-zone means here the meeting zone of both right and left leaf margins, as well as the more

Fig. 1—13. — Schemes. — Fig. 1. Formation of a funnel-shaped structure through pinching of an inside proliferation of the cross-zone of the unifacial claw of a tepal. Ventral view of the tepal. Fig. 1a. Cross-section of similar structure, pinching perfect, so the inner tube is closed, broken lines indicate upper margins of unifacial claw. — Fig. 2. Formation of a funnel-shaped nectary through ventral proliferation (arrows) of a circular margin portion arisen through meeting of two loops from ventral margin on both sides of the cross-zone. Ventral view of petaloid stamen, with a ventral lobe on the left, bearing a ventral pollen sac. Dorsal pollen sac on the same side. After LEINFELLNER's (1959) data. Fig. 2a. Cross-section of such a nectary.
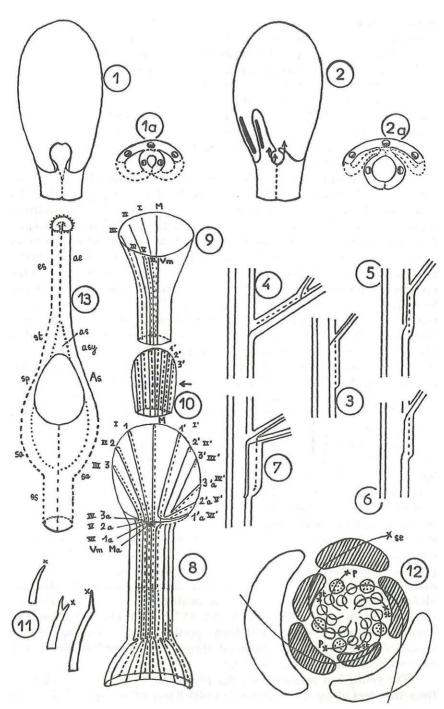
Fig. 3—7. Displacement of apparent insertion of leaves and axillary shoots through intercalary growth. — Fig. 3. Anaphysis. Leaf trace joins stele at level of apparent insertion. — Fig. 4. Recaulescence with shoot trace inserted on leaf trace. — Fig. 5. Anaphysis, leaf trace joins the stele at the level of morphologic insertion. — Fig. 6. Same, but the stele gap is elongated as a result of intercalary growth at its level. — Fig. 7. Anaphysis of leaf with con- and recaulescence of axillary bud. Stele gap elongated.

Fig. 8. Cellular architecture of a leaf with unifacial petiole. Between base and petiole, cross-zone arises through bulging of ventral cell rows. Between petiole and blade, cross zone either arises in the same way (left) or (right) is marked by the subhorizontal courses of cell rows making up the lower blade on this side. Representative cell rows from TII are marked M, 1, 2, 3, 1', 2', 3', their bulges at cross-zone level Ma, 1a, 2a, 3a, 1'a, 2'a, 3'a. Ventral view with ventral shanks of cell rows as solid lines, dorsal ones as broken lines. M, I, II, III, IV, V, VI; I', ... VI', Vm denote bundles of the petiole and blade. These are not drawn but would differentiate at the levels of cell rows and their loops. Note that IV—VI do not occur in the blade on the left, whereas they do on the right. They would be ventral petiole bundles on both side. — Fig. 9. Asciidiate leaf with unifacial petiole and no base. Ventral view. Dorsal bundles as solid lines, ventral ones as broken lines. Bundles drawn only on the left. — Fig. 10. Leaf primordium, ventral view, with representative cell rows from TII. Arrow indicate level of proliferation to give rise to a cross-zone or ligule.

Fig. 11. From a leaf primordium (in longitudinal section, ventral side on the right) drawn on the left, a dorsal spur may develop through proliferation on its back below apex (middle scheme) or an epiunifacial point may arise if dorsal proliferation involves its apex (right scheme). Crosses denote leaf apex.

Fig. 12. Phyllotaxis of flower of *Ranunculus repens*. Redrawn from MEICENHEIMER 1979. Bracts white crescents outside, sepals hatched, petals dotted, stamens white circles. Contact parastichies are drawn, those appearing at the level of each floral whorl begin with a cross and se(sepals), p(petals), st(stamens).

Fig. 13. Generalized scheme of a carpel constituent of a syncarpous gynoecium. Ventral view. Broken lines indicate zones of congenital fusion either within the carpel itself (ventral suture) or with its adjoining carpels in the gynoecium. Zones of the syncarpous gynoecium to which such a carpel would take part are indicated as follows: ae anepisynsolid, As asymplicate, asy asyntubular, es episynsolid, sa synascidiate, sp symplicate, ss synsolid, st syntubular; as apical septum.

272

or less horizontal margin segments just adjoining this meeting zone, or cross-zone proper, on the ventral side of the petiole). Either the ventral, inverted bundles of the petiole stop at the cross-zone and do not serve the blade (Fig. 8, left) or (same, right) they proceed into the lower zone of the blade. In the latter instance, the nearer a ventral bundle to the median line of the petiole, the lower does it become located in the blade. If there is a ventro-median, half of it becomes the lowest main blade bundle (VI' in fig. 8). The first kind of leaf may be exemplified by those of some of the *Dioscoreaceae* (GUÉDÈS 1967) and the second kind by those of *Pelargonium* × *hortorum* L. H. BAILEY.

When a leaf of the first kind becomes peltate-ascidiate, the upper cross-zone of its petiole proliferates in such a way that the ventral petiole bundles now proceed into a superadded ventral blade portion. On the contrary, when a leaf of the second kind becomes peltate or ascidiate, there is no further proliferation of the cross-zone, for this already develops the lower blade portions on both sides of the normal leaf blade. To become peltate-ascidiate, the latter kind of leaf merely undergoes a rearrangement of the products of its upper petiole cross-zone: instead of being split into two lateral halves, one on each lower side of the blade, they are now continuous medio-ventrally. In other words, both lateral halves of the blade are now folded ventrally and congenitally merged at their former lowermost margins. There is no superadded tissue in the peltate-ascidiate leaf when this is compared to the normal one. It will perhaps be clear from Fig. 8 that on the left (first kind) a mere ventral flange marks the cross-zone, while on the right (second kind) the cross-zone has originated the lower portion of the blade, giving rise to bundles IV', V', VI'. On the left bundles IV, V, VI of the petiole do not proceed beyond the cross-zone.

Architecturally, in a leaf built from TI-TIII layers of the apex, cell rows of the TII layer continue ventrally (Fig. 8, solid lines) from the petiole into the blade, developing shallow bulges at the cross-zone (Fig. 8, on the left) in leaves of the first kind, while in the second kind of leaf (Fig. 8, right), ventral TII rows, reaching the cross-zone, depart into the dorsal (lower) region of the lower blade zone, then back on the ventral region of the same zone, before they ascend again the ventral portion of the main blade. This course will be obvious for rows 1', 2', 3' whose cross-zone loops in lower blade portion are numbered 3'a, 2'a, 1'a. In both kinds of leaves, TII rows, having reached the brim of the blade (1, 2, 3, 1', 2', 3') go down dorsally along the blade and petiole (broken lines). When ascidiate, both kinds of leaves are similiar (Fig. 9, with bundles IV, V, VI, IV', V', VI' either developed de novo in the superadded ventral blade portion, and as prolongations of petiole ventral bundles, or displaced through blade inrolling from their former lateral position in the blade).

The young leaf primordium (Fig. 10) has its TII rows vertical, going from the stem along its ventral side (solid lines) till its upper brim, then

back along its dorsal surface (broken lines). During ontogeny of leaves with unifacial petioles, a ventral proliferation takes place atop the latter (arrow level) to either originate a cross-zone bulge, or proliferate into the lower blade portion. If the leaf is to become peltate-ascidiate that zone develops the ventral portion of the ascidium or peltate blade.

Histogenetically the development of a shallow cross-zone playing no part in forming the blade is similar to the development of a ventral ligule. Unifaciality of the petiole, however, becomes obvious in the first instance, even if it remains flat, through the orientation of its vascular bundles.

In the same fashion, the histogenetic development of an epiunifacial forerunner tip (Fig. 11) is similar to that of a dorsal spur. The only difference is that the proliferation originating the forerunner tip occurs dorsally very near the phyllome apex so as to involve it and displace it atop the forerunner tip. Hypounifacial forerunner tips develop as ventral proliferations again involving the phyllome apex.

Between the bifacial leaf-base, if such occurs, and the unifacial petiole is a cross-zone (Fig. 8). As explained (p. 92, fig. 13/2) the most lateral cell rows in the leaf-base may not reach the petiole. Lateral rows of the petiole prolong outmost or near-outmost rows in the base (Fig. 8). As outmost bundles cross the base to merge into a ventro-median, or become very near each other, they have to cross cell rows nearer to the median zone. Again architecture at the junction between base and petiole is the same whether the leaf has a unifacial petiole or a conventional one with a ligule: in both instances cell rows emit transversal outgrowths ventrally (often limited to the epidermis if a ligule is to be formed). Morphological significance of the structure becomes obvious as differentiation goes on.

Although most leaves with unifacial petioles have bifacial leaf-bases, the latter may be lacking, as in *Ginkgo biloba* (p. 109, fig. 16/9). It needs not to be admitted that a virtual base occurs in such leaves. Cell rows of the stem apex may well develop a unifacial petiole as depicted in Fig. 9.

Equitant Iris leaves (p. 118)

When presenting BUGNON's view on equitant *Iris* leaves I stressed that it had been reached as a result of direct histogenetic studies, and as these are very difficult it should be tested by means of chimeras. I have now done this myself by studying cvs. "variegata" of *I. pallida* and *I. foetidissima* (GUÉDÈS 1980 a). These are GWG chimeras where frequent periclinal divisions send epidermal (TI) or TIII cells, both genetically green, among the white cells of the TII layer. The progenies of so displaced cells are green patches among white tissue. As these patches may be elongated the whole length of the leaf, I was unable to support BUGNON's concept. Cell divisions originating the *Iris* leaf give rise to longitudinal cell families whose orientation parallels that of main nerves, rather than crossing them. As in other

Monocots (STEWART & DERMEN 1979) leaf architecture is closely reflected by vascularization, and is as the classical view had long had it. Since equitant *Iris* leaves are merely grass-like leaves congenitally folded at blade level along their midrib, it becomes quite natural that *Iris* subgen. *Scorpiris*, in contradistinction to other irises, has non-equitant, conventional ribbon leaves.

Histogeny of leaves in the *Gramineae* (p. 118)

In the *Gramineae* it would seem that the leaf not rarely has a blade made up of TI ('epidermal') cells while its sheath mostly comes from TII. This was demonstrated in a bamboo by studying a chimera (THIELKE 1961) and confirmed histogenetically by BUGNON 1979 in other grasses.

Leaflets and stipules (p. 121)

Stipules are the first and only basipetal leaflet pair in *Ailanthus altissima*. They are the lowermost pair of acropetal leaflets in other taxa (see WEBERLING & LEENHOUTS 1965, they believed this is also true of *Ailanthus*, but their own figures seem to point to the view here suggested).

Leaflet development (p. 121)

Citation of *Clematis* as an example of a leaf with basipetal leaflets is a lapsus. *Clematis* is described by TROLL 1939: 1530 and TEPFER 1960 as with acropetal leaflets to its leaves. *Polemonium* (*Polemoniaceae*) and *Lycopersicon* (*Solanaceae*, COLEMAN & GREYSON 1976) afford true examples of basipetal leaflets. Leaflets of the *Papilionaceae* are acropetal in their development.

When all leaflets are acropetal, the whole of them correspond to the compound terminal leaflet of those leaves whose first-developed leaflets are midway up the rachis.

Syncotyly and the origin of Monocots (p. 132)

HAINES & LYE 1979 have reviewed the subject of syncotyly and tried to support the interpretation of the single cotyledon of Monocots as originated through fusion of the two in Dicots. In *Impatiens glandulifera* ROYLE (*Balsaminaceae*) and *Daucus carota* L. (*Umbelliferae*) there may be only one cotyledon. In intermediate stages in *Impatiens* it is clear that the two cotyledons are more or less completely fused along their adjoining edges, their axillary buds also becoming merged into one. In other words the embryo may form the usual two cotyledons, a single lateral cotyledon, or a bivalent lateral cotyledon. Such monocotyledonous seedlings in Dicots may be induced experimentally in *Eranthis hyemalis* (L.) SALISB. (*Ranunculaceae*, HACCIUS & TROMPETER 1960). In these cases there is a switch in seedling phyllotaxy from the whorled to the alternate condition, in exactly

the same way as sometimes in vegetative stems of e. g. the Labiatae (p. 132) where intermediate stages with a bivalent leaf at every node are also known. If phyllotaxy is wholly modified the leaf or cotyledon is actually univalent, exhibiting no indication of duality. In some genera of the *Umbelliferae* (*Bunium, Conopodium*) and in certain species of *Peperomia* (*Piperaceae*), *Corydalis* (*Papaveraceae*) and *Ranunculus* (*R. ficaria* L.; *Ranunculaceae*) the seedling has a single univalent cotyledon and this no doubt must be considered as phylogenetically arisen from the usual pair, as seen in terato-logic *Impatiens* seedlings just alluded to. Such solitary cotyledons occur in genera or species of otherwise dicotyledonous taxa.

It then is a possibility that the sole cotyledon of Monocots, though at present univalent, also arose in this way from the two cotyledons of dicotyledonous ancestors. As nothing very precise is known about origin of Monocots, and no unquestionable reversion to any putative ancestral dicotyledonous state seems to have been described in seedlings of Monocots, this is a mere hypothesis. In any case the cotyledon of Monocots now is a single phyllome.

The petioles of the two cotyledons are united into a tube in many *Umbelliferae* (HACCIUS 1952) and species of *Rheum* (*Polygonaceae*, HUSS 1980: 20—21) and of *Anemone* (*Ranunculaceae*). This parallels gamophylly in the adult state in such plants as *Dipsacus fullonum* (p. 134; see also HACCIUS 1952: 501, TROLL 1937: 249).

Leafs with protracted apical growth (p. 137)

Often-quoted are pinnate leaves of several *Meliaceae* (*Guarea, Chisoch-eton, Dysoxylum, Cabralea*) which are said to display a very protracted apical activity, behaving much as shoots, and to develop their pinnae continuously or sometimes (*Chisocheton*) in flushes of several leaflets with intervening resting periods. The apex of these leaves in fact has nothing to do with a shoot bud, for its meristematic activity is actually very short, as in all leaves of seed plants. As early as 1887, SONNTAG found that meristematic activity soon ceases at the apex of *Guarea* leaves, and leaflets are initiated acropetally. Then the leaflet and rachis grow to their full length in two flushes. At the end of the first, apical leaflets remain in a primordial state as a spurious bud atop this lower flush. Leaflet initiation, however, is per-fectly conventional, the whole of the acropetal series appearing after early cessation of apical activity in the leaf primordium.

Inflorescences in woody plants (p. 146)

BRIGGS & JOHNSON 1979 published a very important paper on inflores-cences in the *Myrtaceae*. This will have to be used in future studies on inflorescences of woody plants. The authors recognize the importance of proliferous inflorescences, which they call auxotelic. Auxotelic inflore-

276

scences are said to be conflorescences, being made up of uniflorescen-
ces, the latter often reduced to single floweis. Conflorescences may be
aggregated into auxotelic superconflorescences. The authors also have
other useful terms such as metaxyphyll for Zwischenblatt. They do not
seem to have met with the case of flower peduncles with one or two vege-
tative shoots in the axils of their prophylls. They acknowledge that attempts
by English-speaking authors to account for inflorescences have often been
'inadequate, and indeed vapid'.

Branching and inflorescences in *Prunus* subgen. *Amygdalus* (p. 149)

I stated in error that in *Prunus* subgen. *Amygdalus* there are axillary
inflorescences whose prophylls subtend vegetative buds. I unfortunately
was led to this misstatement by the description in Flora Europaea 2:
78 which reads 'each flower-bud flanked by 2 leaf-buds'. Actually, the
axillary bud is vegetative with one or both of its prophylls subtending a
solitary flower. The situation is correctly stated by REHDER 1949 when he
writes of "buds three in each axil, the lateral ones flowers buds". In *Prunus
triloba* LINDL., of the same subgenus, it seems that the axillary bud may
sometimes be a flower whose prophylls are then 'sterile'. In *P.* subgen.
Amygdalus, there are no conventional inflorescences, but the prophyllary
flower(s) may be considered a proliferous (auxotelic) inflorescence, often
with a single flower.

Acer negundo (p. 150)

It must be mentioned that my description refers to female inflores-
cences, which were observed in the cv. 'variegatum'. Living male trees
were unavailable to me.

True and false umbels in *Umbelliferae* (p. 151)

In the *Saniculoideae* (FROEBE 1964), apparently simple umbellules are
compound ones, being themselves built of umbellules each of which basically
has a central female flower with peripheral male flowers Abortion of one
or the other flower kind, reductions, condensations lead to the deceptive
normal condition. In e. g. *Sanicula europaea* L. the umbellules comprise
false umbels in which some umbellules are inserted on the very shortened
peduncles of the others, there being two orders of umbellules. Such false
umbels are then reminiscent of those of the *Cornaceae*.

In the *Hydrocotyloideae*, inflorescences are basically thyrses (compound
racemes of dichasia) that are often impoverished and condensed into umbels
of false umbellules, i. e. umbellules with flowers of two or more successive
orders. If only first order flowers develop, a true umbel is originated (FROEBE
1979). This has a terminal flower, topping the main axis of the original
thyrse. Umbels and umbellules in the *Apioideae* are true ones, generally
without a terminal flower, although this occurs in more than 30 genera.

Apopetalous flowers (p. 162)

Apopetaly is generally a phylogenetic, and hypothetic, process. It may however be postgenital, that is, petals are initiated, then very soon cease growing, with the result that they are not to be found in the adult state. Although the genus *Scleranthus* (*Caryophyllaceae*) is believed to be apetalous by taxonomists, it has long been known that in *S. annuus* L. five petal primordia arise, only to become immediately arrested in their development (PAYER 1857).

Floral phyllotaxis (p. 163)

The subject of flower phyllotaxis is further discussed in DUPUY & GUÉDÈS 1980 where attention is called to the possibility of floral phyllomes developing, in many instances, each at the limit divergence angle from the previous one in the phyllotactic spiral. This was suggested by HIRMER and accepted by HIEPKO in many cases in the *Ranales*. Although it probably cannot be generalized it might be useful to keep this concept in mind when studying phyllotaxis of flower buds. Later rearrangements would lead to the 2/5 or other phyllotaxis of the adult flower. Spiral sequence of initiation is probably more widespread in flowers than previously believed. For instance, perianth and androecium members appear in spiral sequence in *Humulus lupulus* L. (*Cannabaceae*, LEINS & ORTH 1979). As stamens are opposite tepals the spiral sequence is continuous and regular, and judging from fig. 5 in LEINS & ORTH's paper, it may well be that at initiation the divergence angle is the limit angle, with the result that stamens at first are not exactly opposite tepals. Continuous spiral sequence is also apparent during perianth and androecium initiation of *Cannabis* (*Cannabaceae*) and *Laportea* (*Urticaceae*, SATTLER 1973). Remarkably stamens and carpels in *Silene coeli-rosa* (L.) GODRON (*Caryophyllaceae*) are initiated spirally. When the plant is cultivated at lower temperatures, petals are also spiral in their initiation. Floral phyllomes in *Silene coeli-rosa*, however, appear in their adult location, and hardly any limit divergence angle is to be measured between any of them at any time (LYNDON, 1978a—b).

Contact parastichies may be detected in truly polymerous androecia and gynoecia such as those of *Ranunculus* and other *Ranunculaceae*. I stated on p. 169 that it is generally hard to connect the parastichies (or orthostichies) of androecium, gynoecium and tepals where they are spiral. Studying *Ranunculus acris* L., SATTLER 1973 wrote that 'the number of vertical pistil rows is not necessarily the same as that of the stamens. But often the pistil primordia continue the vertical stamen rows'. EICHLER 1878 on the other hand spoke in several instances of a continuous spiral pervading the perianth, androecium and gynoecium, often with phyllotactic changes between two kinds of phyllomes. Androecia and gynoecia in the *Ranunculaceae* might display ortho- or spirostichies. If the same phyllotaxis were retained between the two, ortho- or spirostichies were

continuous throughout the whole of the androecium and gynoecium. They might also include the petals. Phyllotaxis, however, often changed between the three sets, ortho- or spirostichies being added or deleted between two sets. According to EICHLER, among the *Ranunculaceae*, in *Adonis aestivalis* L. there are at most 8 petals, whereas there are 13 stamen spirostichies. In *Eranthus hymealis* there are as a rule 6 petals and generally 12 stamen spirostichies. The 3 carpels are seated atop three evenly spaced spirostichies among those of the androecium. In *Ranunculus acris, R. bulbosus* L., EICHLER found divergence angles of about 8/21 or 13/34 in the androecium and gynoecium, also probably 5/13 in the latter. He stressed that there is no discontinuity from the androecium to the gynoecium, meaning that 13 of the spirostichies in the former proceed into the latter. He also believed, out of comparison with *Adonis*, that the corolla was also basically spiral in *Ranunculus*. In these observations and reasonings, he was following WYDLER 1859.

In a recent interesting paper, MEICENHEIMER 1979 indicated that in *Ranunculus repens* L. sepals are arranged in a 3/8 phyllotaxis, which is changed to 5/13 when petals are initiated, as a whorl. Then phyllotaxis shifts to 8/21 as stamens, then carpels appear spirally. Phyllotaxis is 2/5 below the calyx, so one may draw a pair of contact parastichies among the bracts. On reaching the calyx, three sepals are found along these parastichies, and a further parastichy is needed to accommodate the remaining sepal, as their phyllotaxis is 3/8. The 3 now extant parastichies, then, reach 3 of the petals, and 2 further parastichies must be added for the two remaining petals of the 5/13 corolla. The 5 parastichies now reach 5 of the stamens, and 3 further parastichies appear in the androecium. So phyllomes are initiated along 8 parastichies in the androecium, and these proceed into the gynoecium.

I have redrawn MEICENHEIMER's fig. 19 (Fig. 12) adding the parastichies. I believe this way of presenting the data to be clearer to the rank and file morphologist than the author's so elaborate mathematical description. In fact, all this merely means that the apex is producing relatively smaller primordia nearer to one another in space and time as initiation of floral phyllomes proceeds. It is interesting that MEICENHEIMER found the calyx and corolla with a 3/8 and 5/13 phyllotaxis respectively, though both have 5 members. This means that sepals and petals are initiated nearer to the limit divergence angle than is supposed in the classical concept of a 2/5 calyx and alternating corolla. HIRMER 1931 and SCHÖFFEL 1932 believed that in the *Ranunculus* flower all phyllomes are initiated spirally with the limit divergence angle between them.

Contorted corolla and phyllotactic sequence in the calyx (p. 167)

Besides some of the *Theaceae* it must be mentioned that the *Oxalidaceae, Linaceae, Malvaceae* normally have contorted corollas winding in the direc-

tion of the calyx spiral. Such corollas again are at the same time metatopic and apparently controlled by calyx aestivation in the arrangement of their petals. There are of course as many flowers with clockwise and anticlockwise corollas in the same species, as with calyces.

In this connection, mention must be made of the curious results of Ghosh & Davis 1978. They found that as expected clockwise and anticlockwise shoots predominantly produce axillary flowers with anticlockwise and clockwise corollas respectively, flowers being heterodromous with respect to their supporting axis. The rarer homodromous flowers, however, gave fruits with a greater proportion of normal seeds.

Sympetaly (p. 188)

The subject of petal fusion has been discussed in great detail by Nishino 1978, Sattler 1978 and Daniel & Sattler 1978. Sattler contemplated several possibilities for a continuous tube to arise below free lobes, and wondered what, if anything, could be called fusion when there is no true, postgenital fusion, as in such usual instances as the corolla in the *Solanaceae*. He believed one might speak of meristematic fusion when marginal meristems are seen at primordium margins, then those of adjoining margins come to meet each other between the lobes, with the issuing intervening meristem responsible for the development of the interlobular portions of the corolla tube. When a circular meristem develops below the lobes and in the interlobular zones to originate the floral tube, no fusion could be contemplated.

In my view, even with these somewhat different ontogenies the tube is anyway plurivalent, i. e. corresponds to the whole of the petal claws of a choripetalous corolla. In vegetative leaves, too, marginal meristems are more or less obvious, leaves remaining homologous. When an interlobular portion seems to come from a meristem that did not originate from fusion of adjacent marginal meristems, the problem is that of knowing what its cells are building. If morphology reveals its product is petaline and part and parcel of neighboring sublobular regions, then it indeed belongs to both petals. Not all petals need arise in precisely the same way, no more than they need be vascularized in precisely the same fashion. In any case as a petal extends on both sides, more and more cells of the floral apex become involved in its development, more and more cells of the apex flank giving rise to cell rows of the petal. When cell rows of neighboring petals of sympetalous corollas come to meet each other, meristematic activity may or may not be obvious at the margins of the original lobes, i. e. first-elongated cell-rows making up the median zones of the petals. Even when marginal meristems were present in the beginning they may have faded away before or during tangential extension of petals, i. e. formation of new cell rows from apical cells adjacent to the young petal. Marginal meristems may also not yet be

differentiated during tangential extension of the lobes. When the floral apex is building the corolla tube, it may divide its cells below the lobes to further lengthen the cell rows that make them up, or the lower cells of the lobes may proliferate to the same effect. These are interesting growth modalities that detract nothing from the petaline and plurivalent character of the resulting corolla.

It may also be that in corollas, and especially in androecia and gynoecia, a continuous tore is developed by the apex, with the free lobes appearing only later from its rim. The tore is plurivalent and its constitution is revealed by lobe development later, and further differentiation within the whole structure. Fused compound stamens of some of the *Malvaceae* and gynoecia of some of the *Primulaceae* were found to develop in this way.

Stamens of Gymnosperms (p. 202)

It was remarked by SPORNE 1980 that the word "stamen" used for Gymnosperm microsporophylls would shock Anglo-saxon morphologists. But are microsporophylls anything else than stamens, a word used by English-speaking taxonomists of Gymnosperms (see e. g. DALLIMORE & JACKSON 1966)?

A more disturbing problem is the interpretation of stamens in the *Pinaceae*. When they are transformed into bracts as in hermaphrodite cones, their blade becomes the bract one, with their pollen sacs vanishing. It is thus impossible to consider the main staminal blade as the ventral one of a peltate phyllome, as I did. Were it so, the dorsal, polliniferous blade would become the bract one rather than disappear (the bract is normally oriented with respect to the cone axis). Since the stamen nonetheless is peltate according to DLUHOSH's studies, it must be hypopeltate (p. 108) with a cross-zone on its back, developing the polliniferous blade, appressed on the main blade. The polliniferous blade no longer occurs in modified stamens which are left with their main blade only, now the bract blade. As an example of studies on hermaphrodite cones, one may quote STENZEL's 1876 paper.

On reinvestigating the development of the glands in the *Ginkgo* stamen, AMEELE 1980 found that it differs widely from the development of a pollen sac. He does not necessarily dismiss their homology with pollen sacs, however, so my stand may be maintained for at least the time being.

Duality of cross-zone ovules (p. 209)

Attention is called to a paper by KSHETRAPAL & TIAGI 1970 where dual vascularization of cross-zone ovules is demonstrated in certain *Oleaceae*, although the authors seem to be unaware of the peltate carpel concept. Such a duality, however, is far more common than suggested by them. It is seen also in *Triosteum* (*Caprifoliaceae*; WILKINSON 1948).

Typology of syncarpous gynoecia (p. 212)

A more comprehensive type of the syncarpous gynoecium would be comprised of the following portions, from the bottom upward:

— unifacial carpel stipes congenitally fused into a synsolid portion. (Stipes may also be merged postgenitally at least above, in which case no portion of the gynoecium above the stipes is congenitally fused, although postgenital fusion of course remains possible.)

— congenitally closed zones of peltate carpels merged congenitally into the synasciadiate portion. (Upper portions of the same closed zones may be postgenitally fused, or free, as an asynascidiate portion, then no carpel parts above can be congenitally fused.)

— lower regions of open or postgenitally closed carpel zones fused congenitally into a symplicate portion.

— upper region of open or postgenitally closed carpel portions postgenitally fused (or free) into an asymplicate portion.

— above their basically open zone, carpels often develop unifacial or hollow styles. These carpellary styles may be congenitally fused into the episynsolid or syntubular (hollow styles) portion of the gynoecium. This can happen only where there is no asymplicate, asynascidiate or asynsolid portion.

Unifacial or hollow styles may be postgenitally fused or free at least above as the anepisynsolid, or asyntubular portion of the gynoecium. They are necessarily so if the gynoecium has an asymplicate, asynascidiate or asynsolid portion.

A hollow style of a single carpel, whether isolated or part of a compound style, may have its ventral surface lining its cavity and then be bifacial, or its cavity may be lined by its morphologically outer surface, the style at the same time being hollow and unifacial. Stylar canals of compound styles may be lineadby the ventral surfaces of bifacial carpellary styles, or the outer surfaces of unifacial styles.

Compound styles whose constituent styles are not congenitally closed or unifacial belong to the symplicate or asymplicate portion of the gynoecium.

The whole of this concept is summed up 'tant bien que mal' in Fig. 13.

When there is an apical septum, if styles are postgenitally fused as in the *Convolvulaceae*, it develops from the postgenitally appressed cross-zones of the styles as explained on p. 222. I however stated in error that styles are postgenitally fused in the *Scrophulariaceae*, *Solanaceae* and *Labiatae* (p. 214). In these, as in many other families, styles are congenitally fused into an episynsolid portion. When there is an apical septum in the *Labiatae*, *Scrophulariaceae*, *Solanaceae*, *Ericaceae*, *Myrtaceae* with such episynsolid styles, it develops from congenitally fused lower cross-zones of congenitally merged unifacial styles.

Ovule orientation (p. 213)

When cross-zone ovules are bent downward (their raphe above) they are apotropous, whereas they are epitropous if bent upward, their raphe below. In both cases, they may be erect or pendant. The same orientations are seen in marginal ovules near the cross-zone on each side of it. Two such ovules are epitropous in e. g. the *Geraniaceae*, while they are apotropous in the *Labiatae*. It may happen that a cross-zone ovule is apotropous and is flanked with two epitropous ovules as in *Sphaeralcea angustifolia* (Cav.) G. Don (*Malvaceae*).

Although as stated on p. 213, the common condition for marginal anatropous ovules on a placenta is to have their micropyles sideways and toward the inner carpel surfaces, such ovules are sometimes apotropous with their micropyles clearly downward (*Hibiscus syriacus* L., *Malvaceae*). It may be that instances occur of marginal rows of epitropous ovules.

Anatropous ovules inserted on the suture of the congenitally closed portion of peltate carpels may be lateral as on free margins, or sometimes epitropous (*Oxalis, Oxalidaceae*), or else apotropous (*Impatiens, Balsaminaceae*).

Chalazogamy (p. 232)

The description respecting chalazogamy must be replaced with the following: It seems that in all cases of apparent chalazogamy, the pollen tube travels within the ovule in such a way as to reach the embryo sac at its micropylar end, so that fertilization is always effected via the synergides.

Ovule interpretation (p. 237)

Attention may perhaps be called in this connection to teratologic leaflets in *Caragana sinica* (Buc'hoz) Rehd. (*Papilionaceae*, Guédès & Dupuy 1980). Leaves of this shrub have 4 leaflets, and each of the upper two often bears a dorsal ascidium, or is itself turned into an ascidium in exactly the same way as foliarized ovules. From a plant teratologist's point of view it seems highly interesting to point out this similarity. *Caragana* leaflets behave as *Codiaeum* leaves alluded to in the book.

Tubular nectaries in peltate petals (p. 242)

I had followed Leinfellner 1959 in stating that those *Ranunculus* petals with a tubular nectary are basically normal *Ranunculus* petals with a very short unifacial claw whose ventral upper margin develops a nectariferous scale, the latter becoming the ventral wall of the nectariferous cup, whose closure occurs dorsally through the development of a ligular outgrowth of the ventral surface of the main blade of the petal. In view of

LEINFELLNER's own fig. IV/9 in his 1959 paper, concerning a *Ranunculus sceleratus* L. phyllome. I now believe that the whole of the wall of the nectary cup comes from the ventral upper margin of the unifacial claw, as depicted on Fig. 2. That margin makes loops on each side, both loops meeting in the middle. A circular margin zone is thus delimited and its proliferates as indicated by arrows on Fig. 2. If this tubular nectary were vascularized, its bundles would be normally oriented (Fig. 2a). Development of vascular bundles in such nectary tubes might probably be induced by means of growth-promoting substances.

The ventral margins of unifacial petal or tepal stalks may also become folded medianly and inwardly as explained in Fig. 1. This is known as teratological occurences in *Ranunculus* petals and *Narcissus* tepals (see DUPUY & GUÉDÈS 1980). The resultant tubular structure then has its bundles inversely oriented (Fig. 1a).

Homology, ontogeny, histogeny (p. 245)

Plant scientists are advised to ponder the zoological situation which has long revealed that nothing is to be made of the origin from one or another germ-layer in deciphering morphologic meaning of structures. At the very same time that classical homologies were negated or at least questioned between floral phyllomes on the ground of their coming from different apex layers, DE BEER 1947 was demonstrating that the ectodermal (today: mesectodermal) layer of the newt gave rise to cartilages of the jaws and visceral arches as well as dermal bones of the skull, all supposed to be always derived from the mesoderm. In fact it had already long been known that during regeneration or asexual multiplication tissues are differentiated by another layer than the one they come from in normal ontogeny. Now the regenerated organs are homologous with normal ones, and the newt skull is homologous with vertebrate skulls with less or no cells from the ectoderm. And although not the same somites take part in forming limbs in various vertebrates, vertebrates limbs are homologous.

As recalled by DE BEER 1971 it had been keenly stressed by WILSON as early as 1894 that "embryological development does not in itself afford at present any absolute criterion whatever for the determination of homology ... comparative anatomy, not comparative embryology, is the primary standard for the study of homologies". For this problem see also the important paper of OSCHE 1973.

Evolution takes place in the genomes of gametes or asexual germs. Then all adult cells are potentially alike and may actualize any portion of their genome. Taxa or organisms use one or more of these cells from various sources to build organs that are homologous when similar portions of the genomes of their constituent cells are used, wherever these come from.

284

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