FUNCTIONAL CONSIDERATIONS AND OBSERVATIONS ON THE FLOWERS OF SOME LABIATAE

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STRUCTURAL FLOWER TYPES IN DIVERSE FAMILIES

The general *bilabiate flower type* or gullet-blossom was already recognized as functioning in diverse families by Delpino (lastly in 1887). The type seems adapted to hymenopters with precision of visits: not only by providing a lower lip as a favoured landing place with optical attraction and by ensuring co-ordination with the upper lip to limit visitor size, but also by providing precision of deposition and reception of pollen, viz. dorsally at the distal end.

I add that the bifid stigma requires contact in the median plane, not from a side. This type of stigma may be considered as a consequence of the presence of two median carpels, but it also fits the ecological requirements extremely well. It also occurs in those *Verbenaceae* that show zygomorphy, but it prevails in *Labiatae.*

The bilabiate flower structure provides the nototribic pollination (via the back of the visitor) probably favoured and mostly performed by higher bees, especially the social bees.

The *flag-(standard-)blossom,* just as good a precision instrument for bees, is also represented in diverse families. It is in many respects the opposite device, with the sexual organs ventrally (hidden or not) and the showpiece dorsally. The flag-type seems primarily adapted (as Delpino pointed out) to sternotribic pollination, where the foothold of the visitor on carina and (or) alae seems sufficient. The ventral pollination is most naturally performed by dipters as syrphids and by primitive hymenopters that are dusted all over, also by pollen-swallowing stomach-collectors or by venter-collecting bees like the *Megachilidae.*

In the sympetalous *Tubiflorae* a flag-blossom with movable parts could originate less easily (and did so less frequently) than in choripetalous families. It had to arise on top of the existing tube. Delpino indicated it in the *Scrophulariaceae* for some S. American spp. of *Collinsia.* The stamens hide their anthers in the carina-like middle lobe of the lower lip. The keel can move elastically under the weight of the visitors. These are mainly megachilid bees (*Osmia* spp.), which collect pollen and nectar.

When in the flag-type the filaments are united into a tube (as in *Papilionaceae* and in some *Labiatae*) a dorsal one should remain free or disappear to provide access to the nectar. When the flower offers pollen only, this is superfluous.

In the fourth part of this paper we shall come to the flag-type in the *Labiatae-Ocimoideae.* We remark already here that in all *Labiatae* the lower lip envelops the stamens in the bud so that the flag-type seems there neotenic. This may possibly be of evolutionary importance.

The above comparison of Delpino is criticized in Goebel's book 'Die Entfaltungsbewegungen' (p. 240) but without notion of ecology: he ascribes to both floral types the same pollinators and reduces the two types to discriminatory nutrition of either side.

Of course, the functional distinction is not absolute; bees may, and do, exchange flower types. This can be by bees receiving pollen on all parts of the body before cleaning up, by means of secondary transfer of pollen on the bodies, or by assuming a somewhat acrobatic posture by unadapted bees. This does not mean (as has also been stated by "anti-teleogists" like Goebel) that structural flower-classes arose autonomously and that a special position of and in the flower is ecologically insignificant for it. Perhaps this holds true for the feeding of the versatile honey-bee. The latter aspect is popular with entomologists. Though biological barriers and categories are rarely absolute, experience with orchids has taught that resupinate change is significant for correct pollination.

The change from the normal position promotes stealing, disturbs devices for species isolation, presents difficulties in fastness of visits and correct pollination, and causes that after failures the new technique has to be learned by the bee individually. The tendency to take nectar from a predetermined spot was clear in carpenter-bees on radial flowers with several separate nectaries. They exploited only the one situated in the position they were familiar with. The opinion that resupination is insignificant for *Xylocopa* has been disproved by van der Pijl (1954). It still survived in a paper by Schremmer (1953). This entomologist and floral ecologist investigated also illegitimate relations in some *Labiatae* (with *Bombus* spp. as legitimate pollinators). He described the trouble venter-collecting *Megachile* experienced, how short-tongued *Bombus* spp. committed nectar-robbing through punctures, how *Apis* committed pollen-theft and lepidopters nectar-theft, missing the sexual organs. The handbook of Knuth-Loew contains many more cases of illegitimate visits without proper pollination.

For pollination by birds and lepidoptera sterno- or nototriby is insignificant and the bilabiate or papilionate structure is superfluous, as is the presentation of pollen for consumption. For the structural syndromes see Faegri and van der Pijl (1971).

For the time being we leave further aside the question whether we should distinguish between directed functional adaptation and utilization of morphological polymorphism.

The acrobatics are also performed by some flowers of both types.

In the *Papilionaceae* the *Sarothamnus*-type reaches the backs and sides of bumble-bees by means of an explosive deposition of pollen. In some *Phaseolus* spp. the carina turns upwards, obtaining pleuro- or nototriby (by so-called partial resupination). In *Canavallia* the flower hangs down in a reverse, resupinate position. It functions as a bilabiate type, with the nototriby fitting its carpenter-bees (*Xylocopa*).

Orchids originally had the flag-type, but mostly changed to the gullet-type by some kind of resupination.

Though the situation in *Tubiflorae* does not support it, the question may be posed whether in some *Labiatae* a comparable change of position in the stamens occurred rather late in history concurrent with evolutionary changes in *Hymenoptera* feeding on flowers.

FLOWERS OF LABIATAE IN GENERAL

When we come to the *Labiatae* in particular, the structure of the bilabiate flower appears to be accompanied by abortion of the median, dorsal stamen. The functional significance of this disappearance seems unclear when we consider that this stamen would not have obstructed access to the nectar. Its anther would have fitted dorsally between the other ones. In his classical chapter on *Labiatae* in Engler-Prantl's 'Die natürlichen Pflanzenfamilien' (1895), Briquet thought that the disappearance might be explained mechanically as due to the early sideward fusion and contraction of the upper two petals, which made the stamen in between abort. The same reasoning would hold true for the other petals which, nevertheless, bear stamens. Moreover, the early ontogeny of the flower shows that there is plenty of room between the upper two staminal primordia. The clearly separated two petals of the upper lip in *Teucrium* support no stamen either. In most cases even peloric flowers of *Labiatae* have only four stamens.

A better argument in this direction might be that in zygomorphous *Tubiflorae* the median stamen would obstruct the all-important dorsal position of the style. On the other hand, in *Tubiflorae* lacking the dorsal stamen the style is not always appressed to the dorsal lip. This condition may be a secondary one, due to a connection with lepidoptera, as in many *Verbenaceae*.

After all, as will be adstructed later on, the bilabiate type is perhaps not necessarily basical in the *Labiatae*. This supposition will find support when we come to the *Ocimoideae* and the *Ajugoideae*.

The nectary of *Labiatae* is a discus around the base of the ovary. Its separate lobes may each be promoted functionally. As long as the secreted nectar remains accessible and located centrally, it presents no problems for the shifts in pollinators and positions discussed in the first paragraph.

The protandry of most *Labiatae* is generally considered as a protection against selfing. Many species possess, moreover, gynodioecy as a parallel device, so that some individuals have purely female flowers.

In other families too such male sterility, occurring on top of protandry, protogyny, and especially self-incompatibility, has been indicated as senseless and unexplicable.

Now in *Labiatae* the self-incompatibility is weak. The confinement of anthers and stigma (in a hood or a keel) can, moreover, make protandry void. Where this is defective, selfing usually results in seed-setting (see Knuth-Loew).

Gynodioecy has been considered from diverse viewpoints. Firstly, as a transition to (more efficient) complete dioecy. This concept does not hold true in *Labiatae* as there dioecy is very rare. Secondly, gynodioecy can be considered as functioning not just to promote cross-pollination but (also) for better fertilization in general. This concept shall be elaborated here.

Lewis and Crowe analyzed the genetic basis of gynodioecy for *Origanum* and found that the genotype of females should become gradually suppressed by that of the pollen-parent. As it persists in nature its disadvantage is obviously balanced by some advantage. This is sought by them in better seed production. In other cases female plants are more vigorous.

Another ecological viewpoint must be considered. The aggregation of flowers in inflorescences can cause dominance of geitonogamy, which makes the protandry redundant. This may be especially applicable for labiate compounds, where adjacent flowers in the dichasia may be in the male and the female phase respectively.

There are other points explaining gynodioecy as an escape, e.g. from the secondary danger of protandry. In some cases, the delay of receptivity and exposition of the stigma until the final phase may become a danger in itself. By that time the nectar is possibly exhausted or its secretion stopped; the attractivity of short-lived flowers is thus generally diminished or just altered in regard to visitors (other visitors, pollen now lacking).

Precise data on this point were not found in the literature so that detailed research seems indicated. The case of *Eriope* on p. 100 is a warning that there may be complications around protandry.

Though there is no direct connection with our case, it is necessary to point out that socalled 'unisexuality' has more aspects than avoidance of selfing. It may mean the splitting of the two functions usually combined, viz. of reception of pollen and of its deposition on agents. This aspect is often neglected. It is, however, obvious in the very unprecise anemophiles, where the two functions require different directions of pollen movement and differentiation in orientation between stigma and anthers. The opposite, utmost precision, makes in some orchids (*Catasetum*) the two functions also divorce operationally into two kinds of, entirely different, flowers. A further floral function, the production of seed, may be better executed by a specialized female flower, without exacting and caducous stamens.

The position, coherence, and mode of dehiscence of the anthers are co-adapted to the position of the androecium (dorsal or ventral), but a detailed study of this point cannot be pursued here for *Labiatae*.

The same refers to the protection of pollen against rain, a point more diligently studied by previous than by recent authors. They considered the upper lip as having a function in this respect, describing exposed anthers in some *Labiatae* as functioning in dry seasons. This, and the possible insensitivity of pollen from those *Ajugoideae* or *Ocymoideae* where the stamens are not hidden, is a different matter.

In both the flag- and gullet-type the *Labiatae* keep to didynamic stamens, the dorsal stamens being the short ones.

SOME REMARKS ON POLLINATION IN THE MAIN STOCK OF LABIATAE

It becomes now time to end generalities and to proceed to concrete cases of pollination in the *Labiatae*. I have to quote from old publications and must warn that I did not check nomenclature and generic delimitation. This paper is not a taxonomic one, but is meant to stimulate floral ecology as part of biosystematics at all levels, as a background to systematics. This explains why not only facts but also fancies and uncertainties are relevated.

We first dwell upon the groups with the convential bilabiate flower, on which Knuth-Loew already gives much information. Our main interest lies elsewhere and only the principles will be discussed in more detail, leaving specific research to future biologists, perhaps stimulated by this paper.

Briquet already pointed in the chapter mentioned above to secondary deviations from the normal type. He saw some connection with aberrant methods of pollination and already distinguished ornithophilous and psychophilous (butterfly-pollinated) shapes as described below. Flowers with total resupination were mentioned for many genera (a.o. *Salvia, Teucrium, Ajuga, Satureja*).

The ecology of the latter case is still unclear. In Schremmer (1953, p. 18) no special visitors were mentioned for two resupinate *Salvia* spp., only honey bees positioned normally with regard to the flower, that is, upside down (observed in botanic gardens). *Bombus* took its normal position in regard to space, thus an abnormal one in regard to the flower.

In southern Europe and in the tropics one can expect *Labiatae* specialized on large and strong carpenter bees. The author found in southern Yougoslavia *Phlomis fruticosa* with large yellow flowers belonging to this type and visited only infrequently by bees of bumble-bee size. These flowers have a very tough bilabiate corolla which, though possessing a swollen hinge in the upper lip, still requires much force to operate, too much for *Apis*-like bees. The claw-marks on the sides testified to this force. The anti-robbing device, usual in this class to prevent any puncturing, consisted of a dense aggregation of the hard calyces into a head, surrounded by bracts (cf. van der Pijl, 1954). The hinge and the arresting devices on the filament bases represent the reinforcements typical for *Xylocopa*-flowers. All visits were legitimate, no punctures were found. Its ecological class-companions were in this region *Acanthus mollis* and *Spartium junceum.*

The Mediterranean genus *Phlomis* probably contains more such cases, e.g. *P. russelianus* Lag., reported in Knuth-Loew as excluding even almost all species of *Bombus.*

Grant and Grant (1964) described Californian *Salvia apiana* as typically *Xylocopa*-pollinated and mechanically isolated from sympatric sister species. The flower has a lower lip to be tripped by force as the large lower lip first stands somewhat vertical, holding the stamens erect. After the downward dislodging of both, the pollen is deposited on head, wing-bases, and feet. It is remarkable that the upper lip is extremely small. This novel condition in *Salvia* may illustrate how an incidental deviation in pollination may lead to an entirely new line of evolution.

Robertson gave a review of his observations on pollination in N. American *Labiatae* (except *Ocimoideae* and *Ajugoideae*). It runs parallel to the review of literature by Briquet from the same year (1895). In some *Monarda* spp. he found transformation for pollination by butterflies (and secondarily hummingbirds). Here we see, as in other psychophilous flowers, the aggregation enabling butterflies to sit on the compound of flowers (acting as one brush-blossom) while probing. The corollas are reddish and transformed into long tubes with somewhat deviating lips. The nectar quantity is increased, as could be expected. Later observations proved (secondary?) ornithophily in this group. The change to birds as pollinators generally leads to a reduced lower lip and a long broad tube, and often to protruding sex organs. It leads to convergence (dangerous to taxonomists) in members of different groups, even polyphyletically within genera.

This point is discussed in Faegri and van der Pijl (1971) for *Salvia,* where intermediary psychophily played no role. In the tropical, red, ornithophilous *S. splendens* the sexual organs remain true to type, though the lever mechanism is degenerate. For convergent South African species see Vogel (1954). Tropical *Scutellaria* species join in.

True moth-flowers have not been reported from European *Labiatae.* One outpost there is *Melittis melissophyllum,* which has white forms possibly representing a transition to moth-flowers (cf. Knuth-Loew). Biosystematics might clear up the relation with visits of bumble-bees and sphingids, both observed.

Briquet especially emphasized the apparent radiality of corolla and stamens in *Mentha, Lycopus c.s.* as being not primitive but a regression, perhaps with convergence. This reduction and the aggregation of short-tubed flowers are connected with pollination by ill-adapted visitors as flies, beetles, and wasps.

We may add that in this group the didynamy and the one-sided position of stamens and style seem unimportant and have indeed disappeared. *Elsholtzia* has an intermediate position of the stamens. In all these forms the stigma has remained bifid.

The deviation from the general lines is not based on an incidentally deviating property, luring special visitors, but concerns a syndrome of co-adapted characters.

We find here the third case of aggregation, but each one in a different syndrome and with a different function, as described. Other cases (e.g. the pseudo-capitulae of *Hyptis* spp.) concern anticipation of the sphere of dispersal.

For further secondary modifications of the gullet flower, especially of *Salvia,* I refer to textbooks of floral ecology, as those by Faegri and van der Pijl (1971) and Kugler (1970).

THE OCIMOIDEAE

The subfamily *Ocimoideae* is not typical for temperate regions like the other ones. It has of old been considered as florally apart, less linked with higher bees. Briquet even considered its flowers as having a different morphology of the corolla, viz. four petals in the upper lip and one forming the lower lip. This 4/1 scheme is generally accepted, though some authors (also Faegri and van der Pijl, 1971) presumed a conventional $\frac{2}{3}$ scheme with total resupination of these flowers, an exchange of position between upper and lower lip. This is, however, not in agreement with the position of the other flower parts, nor with the absence of any torsion.

The four stamens only show a 'partial resupination' by bending down (like the style) along the lower lip. They remain mostly protandrous and didynamic like in *Lamium*. The style bends upwards in the second (female) flower-phase. It has conserved the bifid structure.

One might ask whether some connection exists between the aberrant morphology of the corolla and the special structure and function of the flower as a whole.

As Vogel (1954) already stated, the position of sexual organs points to sternotribic pollination as basical in the subfamily, just as in *Orchidaceae* and *Papilionaceae*. This likeness increases when the filaments fuse into a tube (as we shall see in *Coleus*) and when the lower lip becomes carina-like. Horizontally extended lip and filaments (when stiff) also allow butterflies to alight.

In *Ocimoideae* the absence of the dorsal stamen seems functional in regard to access to the nectar. In itself this point might be raised to consider the subfamily as basical in *Labiatae*.

In the New World the subfamily contains a.o. the genera *Hyptis, Eriope, Marsypianthus,* and *Peltodon*. In the Old World a.o. *Plectranthus, Hoslundia, Solenostemon, Pycnostachys, Ocimum, Coleus, Orthosiphon,* some of them with varying delimitation.

When considering actual pollination we start with the last genus. The corolla tube is long and narrow, the stamens (not appressed to the lower lip) protrude and spread far from it. This condition, together with increase of nectar and a less distinctly bilabiate shape, conforms with a butterfly — or moth — flower. For *Orthosiphon stamineus* such pollination has indeed been reported by Heide (1927) for Java. Diverse butterflies are regular visitors, but only large *Papilio* spp. are true pollinators. The anthers are versatile, nondidynamic.

The typical character of the genus *Orthosiphon*, the capitate, single stigma (instead of a bifid one), is connected with a special mode of pollination: here not median-dorsal and not precisely directed by the lepidoptera in question.

It is likely that a comparable change of shape of the stigma occurs in other psychophilous *Tubiflorae*. This is especially clear in salverform *Verbenaceae* (like *Lantana*) where the pollen is transported on the proboscis, but also in forms where the stamens are excedent for alighting or where the pollen is otherwise transported on body and feet of *Lepidoptera*.

Ocimum gratissimum was observed by Burkill (1916) in North India to be visited for nectar by *Apis indica*. It has ultimately self-pollination. In Indonesia and southern Europe several bees are visitors.

According to observations of Scott Elliot (1890/91) the genus *Plectranthus* has in South Africa two types of flowers. In one the lower lip is fixed, finally with the stamens coiling downwards around it and the style bending upwards. Examples are *P. ecklonii* Bth. and

P. melleri Bkr. Long-tongued *Bombylidae* and some *Lepidoptera* were here observed sucking nectar, whereas *Apis* collected pollen only. In the other one, having bee-blossoms, he placed a.o. *P. calycinus* Bth., *P. laxiflorus* Bth., and *P. tomentosus* E. Mey. Here the concave lower lip is hinged and depressed forcibly at each visit, swinging back elastically. At depression the sexual organs emerge from the carina, like in many papilionaceous flowers.

In this genus the nectary shows considerable enlargement of its ventral lobe, which covers the ovary (also in *Coleus*). Some species have, as a transition to *Coleus*, a sudden bend at a right angle in the corolla tube. I could not ascertain a correlation with any one of the ecological floral types mentioned. One might explain the bend as mechanically necessary to allow a horizontal flag-blossom (for hovering or alighting visitors) to be combined with a pre-existing long vertical tube. On the other hand the bend may originally have fitted a flexible lepidopteran proboscis and have excluded bees.

The dual nature of *Plectranthus* flowers was confirmed for Nepal by Burkill (1916). He saw *P. ternifolius* there visited by butterflies only, though it has a boat-shaped keel. *P. gerardianus* was visited by *Bombus*, *Apis*, and butterflies.

Considering what was found in *Orthosiphon* it now seems possible that *Plectranthus* in its evolution has developed a simple stigma. The latter was found by Robijns and Lebrun (1929) in some species originally inserted in *Plectranthus* (*P. hockii*, *P. katengense*) and transferred by them to a new genus *Holostylon*. That a hinged carina and fused filaments are present is not unreconcilable with sitting butterflies, but on the other hand this condition points more to bees and the simple stigma is also reconcilable with bees that do not execute here the precise movements prescribed in the type of *Lamium*.

One might suggest that in these forms with a long, curved tube some regression to bees has occurred without alteration of tube shape. Then the nectar had to be transported over the bend — as happens indeed, also in the real *Coleus* type.

Hamilton (1899) studied in Australia the blue, sweet-scented flowers of *P. parviflorus* Henck. These have a straight tube, the stamens free above the concave lower lip, which initially still hides style and stigma. They are visited by butterflies.

The basal spur found in some species is not unequivocal proof of psychophily (unless it is very long and narrow), but it fits this type.

Docters van Leeuwen (1933) found *P. javanicus* regularly visited by *Bombus rufipes* on a mountain in Java, where *Bombus* takes largely over from other bees. In this species the tube is straight.

Vogel (1954) published a photograph of a closely related *Syncolostemon* species, a bee-flower, in this case pollinated by a *Xylocopa*. This African species has a broad throat on the curved flower-tube, which allows even a *Xylocopa* to enter partly.

Scott Elliot observed on *Syncolostemon densiflorus* a butterfly and a bombylid species. In S. Africa the latter dipters often creep into the niche of butterflies and develop a comparably long tongue.

Robijns and Lebrun (1929) found in their material the correlation between fused filaments and a carina-like, folded lip, characterizing *Coleus*. Their mechanical explanation (compression of filaments causing them to fuse) is not satisfactory.

The genera *Coleus* and *Plectranthus* are often merged. The study of Morton (1962) shows that the criteria used to separate them are, at least in Africa, mixed in both. These are the bend, the fusion of filaments, and the shape of the lip, either carina-like or rather flat. These characters seem to reflect divergent modes of pollination in both groups. Both genera mostly prefer shady, cool habitats.

We shall see, moreover, that even in *Coleus s. str.* the 'closed' filament tube shows no real median fusion. Its function is apparently to stiffen the sexual organs when landed upon, often acting in contrast to the hinged, movable lip.

From the South American genus *Hyptis* Burkart (1937) described one species (*H. mutabilis*) showing another parallel to the papilionaceous type. The sexual organs are set free explosively from the lower lip when this is triggered downward by the right kind of bee. It is, typically, pollinated by a gastrilegic (venter collecting) bee, a *Megachile* species.

Recently Harley (1971) described the pollination of related *Eriope crassipes* in Brazil, also with small flowers. The lower lip encloses the upper part of the stamens, which burst explosively from it when a visitor triggers the lip; the latter is then bent back entirely and permanently, losing its function for alighting. This is taken over by the filaments. The colour changes. The pollen is deposited on the venters of the pollinators, mostly small gastrilegic bees. This means probably not (as is stated) pollination, but just pollen deposition in the male phase. The style (not enclosed) grows out and becomes receptive only later on, now positioned above the horizontal stamens. Its stigma is poorly bifid. Though nothing is said, the presence of nectar may be assumed as insects continued their visits to already triggered flowers. The implications of this case have already been discussed.

We now return to an Old World representative, the old genus *Coleus*, partly for the sake of an abnormality, which also occurs in second-day flowers of *Glechoma.*

Coleus frederici from Angola is figured and discussed as a partially reversed gullet flower in Faegri and van der Pijl (1971) on p. 242. The writers were puzzled by the queer blue bee-type requiring downward pressure, that has an (apparently ill-fitting) long tube, which has a sharp bend, folding the corolla down again. The lower lip is a large keel, sheltering stamens and style. The stiff, united filaments surrounding the style are fused basally with the corolla up till the hinge in the lip, but bend downwards with the latter. The distal, hinged part of the lip (or its middle lobe) forms the carina described before.

Observation of the decorative hybrid, cultivated as *Coleus hybridus* Hort., provided some answer to the puzzle. In Javanese gardens it is pollinated by bees, small *Ceratina* spp. but also the versatile large *Xylocopa latipes* (Heide, 1927). A specimen in my study showed a tremendous production of nectar, partly transported from the discus via the basal part of the corolla tube to the throat of the corolla. It is very thick and viscous. Its abundance has been indicated above as a requisite. The filaments, apparently arising from the corolla, form a stiff tube, becoming free distally of the bend in the corolla tube. Sometimes a part of the abundant nectar from a ventral lobe of the discus is conducted through the filament tube. Then it oozes out at the distal point of departure of the two lateral (upper) filaments, where these become free again.

The basal part of the filament tube is still united with the corolla base, the two upper filaments running as ridges on its side. Higher up they adhere medially but they are not connate. The ventral filaments join the tube somewhat more distally.

In some cases the viscous drop of nectar, on oozing out, remains attached at the exit between the two upper filaments. These then bend upwards destroying the sternotribic scheme. This has been said to occur naturally in other species. At least in our case it is not a natural, vital phenomenon, but an accident, probably due to plasmolysis. The adjacent sides of the two filaments become discoloured, with collapsed cells.

Observations in a more natural habitat and atmosphere may show a less concentrated and better flowing nectar. Perhaps there is a disharmony due to the hybrid nature.

The following observations on too abundant secretion may, like the former one, also have some connection with the lateness of the season.

In the dichasia only the first flowers developed fully. Others drop their corollas in the bud stage, often already before the normal flowers reach anthesis. The dropped bud-corollas seem damaged and clearly discoloured at their bases. The remaining small bud-calyces, though empty now, go on secreting. A large, viscous drop remains at their throats for 3—4 days.

Coleus tuberosus has in Java been seen pollinated by *Xylocopa aestuans*, a bee exploiting all kinds of flowers (Heide, 1923).

THE AJUGOIDEAE

The *Ajugoideae* form another subfamily with deviating flowers, neither of the bilabiate nor of the flag-type. Sometimes the group is considered as a link with, or even part of, the family *Verbenaceae* which is largely pollinated by syrphids and butterflies and shows less pronounced zygomorphy. The apical insertion of the style and a certain approach to the tube- or trumpet-like corolla of most *Verbenaceae* support this derivation. The lower lip is well developed and the tube long, the anthers are not covered.

In *Ajuga* an upper lip is absent, so that stamens and style, though situated dorsally, remain uncovered and there is open access to nectar and sexual organs. Bumble-bees are the main pollinators in Europe. *Apis* can also enter. Butterflies and long-tongued syrphids can (and do) join in here as real pollinators, especially in *A. reptans*. In this species white- or red-flowered forms exist, together with the trumpet-shape, fitting the butterfly-syndrome. It should be investigated experimentally whether these forms undergo a shift to butterflies as pollinators. This could produce isolation and speciation.

Burkill (1908) saw *Ajuga bracteosa* in mountain regions of North India systematically and exclusively visited by day-time Sphingids.

Though the genus *Teucrium* has in Europe bee-flowers, *T. africanum* (S. Africa) was described by Scott Elliot (1890/91) as butterfly-pollinated.

The access to the nectar is in most species free, so that in temperate species *Lepidoptera* can steal nectar. In Greece I saw *Macroglossa* do so in *T. flavum*.

Of the related genus *Trichostema*, Grant and Grant (1966) observed a North American species (*T. lanatum*) being truly ornithophilous though its flowers are bluish. The extremely long stamens and style arch over the entrance and block it. They are brushed by the hovering birds. The stigma is still bifid. It is desirable to investigate whether this condition can be derived from psychophily in the genus.

In *Teucrium* too, the sexual organs are freed from the narrow tube, now also by means of a dorsal split in the corolla. They bend back through it, maintaining a nototribic position. The slit allows the free movements of the style connected with protandry.

The petals forming the upper lip in the bilabiate type thus remain free in *Teucrium*. This condition is often described as a split lip, which term seems illogical when no ancestral upper lip can be assumed.

The temperate species have flowers fitting to long-tongued bees, especially bumble-bees. Their sexual organs are not much longer than the corolla and are thus brushed only when the bees enter deeply.

In *T. scorodonia* and many other species the two dorsal corolla lobes have almost

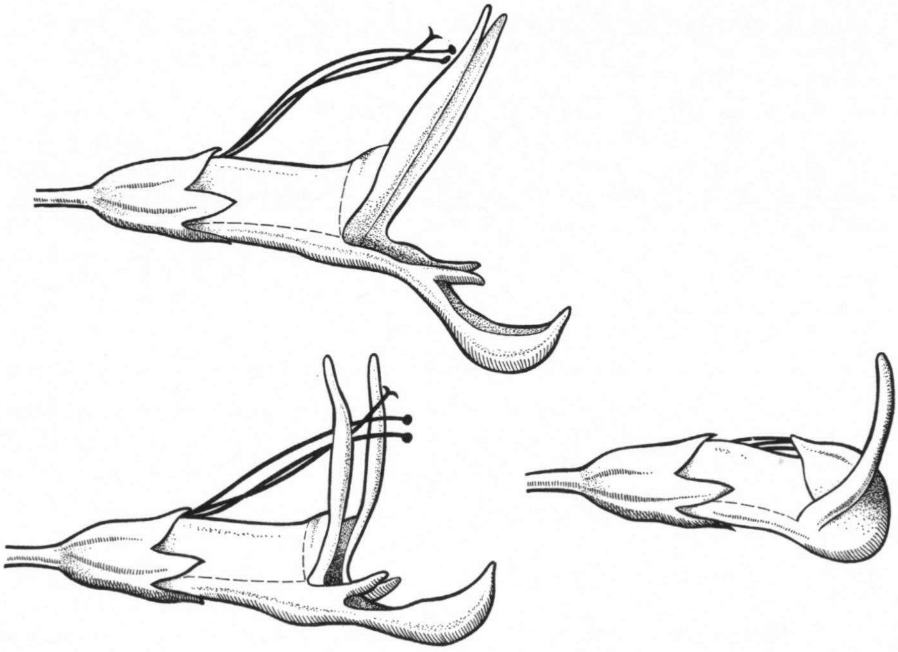

Fig. 1. *Teucrium flavum*. Left: young flower seen obliquely, before and during visit. Right: bud. — Stamens and style schematically and but partly drawn. (all × 5.3).

disappeared, in some these lobes acquired a special shape and a new function described below, viz. of excluding illegitimate visitors by a screen to be pushed first.

The handbook of Knuth-Loew contains old observations, especially those of Mac Leod (1891), on several European species.

In *T. montanum*, *Apis* can reach the nectar. Some species show homogamy and in mountainous regions the share of flies and selfing increases. In *T. pyrenaicum* the bumblebees have to push the lobes apart before their heads reach anthers and stigma and, presumably, their tongue reaches the nectar. This development is strengthened in the species discussed next.

T. flavum has been observed earlier to be pollinated by diverse kinds of bees. In Corfu I saw a.o. *Anthophora* and *Eucera* spp. The yellow-green flowers have a total length of 12 mm, of which almost two thirds concern the (partly open) tube. The anthers and the stigma seem to be out of immediate reach of visitors as they are mostly curved behind the two long lobes of the upper lip, especially in the first phase when the style is curved back further.

This split part (upper length) of the corolla tube is tough only in its ventral half by nerves in its sides. These (dotted in Fig. 1) run up into the upper lobes. The lobes themselves are sturdy too, the more so as their margins are folded double lengthwise. They look as being especially designed to receive and transmit force.

The two side lobes of the lower lip are turned inward, guiding the head of the visitor.

When the bee pushes against the two upper lobes to reach the nectar, these move sidewards bringing the sexual organs in a first contact with the head. Moreover, the whole construction of hard and flexible parts of the tube, with a dorsal split, has the curious effect that the ventral median part moves up, also moving the lower lip somewhat. The bee is thus pushed inward. Its sudden dip seems not merely caused by shifting its pressure forward.

THE CALYX

The calyx of *Labiatae* shows at least as much pluriformity as the corolla and offers special criteria for taxonomy. Its morphology has few ecological backgrounds in special floral biology. Perhaps, idealistic typologists might see the forces of 'Gestalt', working in the corolla, as shifting to the calyx. They might apply this idea to our *Coleus* (with a flag-blossom), the calyx of which is such a perfect imitation of a flag-blossom that an old inflorescence with persisting empty calyces might be taken for a papilionaceous inflorescence.

A functional consideration of labiate calyces, however, would have to be based on dispersal ecology. The functions for the latter are very varied and are often anticipated in the floral phase (see van der Pijl, 1969). This subject should be treated in a separate study of dispersal devices in the family.

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