Studies in the Gesneriaceae of the Old World

I.—General Introduction

BY

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The classic study of the *Gesneriaceae* of the Old World, and the foundation of all later work, is the account (under the name *Cyrtandreae*) which C. B. Clarke contributed to the Monographiae Phanerogamarum Prodromi, edited by Alphonse & Casimir de Candolle. This was published in 1883. At that time the materials available in herbaria were very scanty, for, though outlying species were well known, the great Asiatic centre of the group, S.W. China, the eastern Himalayas, Siam and the Malay Peninsula, was a territory scarcely touched by botanical explorers.

In the seventy years that have followed a great number of new species, and not a few new genera, have been described, but constructive studies in the group as a whole have been sadly lacking. K. Fritsch contributed the account of the family for Engler & Prantl's Pflanzenfamilien, but the little original work in it is negative in quality, merely involving the amalgamation of certain genera distinguished by Clarke. For the rest, only Ridley and Craib have shown any lasting interest in the group, and their studies were planned with strictly regional limitations. This is a matter for great regret, as it has led, in at least one case, to the independent restriction of a single generic name to two completely different components of the original genus. Thus, Ridley restricted Clarke's genus *Didissandra* to certain Malayan species: Craib restricted it to plants of the Himalayan region. This tangle has been resolved by the discovery that the Himalayan plants are referable to the previously monotypic genus *Corallodiscus* Batalin (Burtt, 1947 b), but is worth repeated mention as a warning that regional studies are not a suitable basis for the re-definition of genera.

If progress is to be made in the classification of *Gesneriaceae* one of the primary requisites is the provision of more accurate and more detailed descriptions. As an example, we may consider the description of the stigma of some species as "bilobed." This will frequently be found in the literature of the group, but it tells us very little of value. Four examples of bilobed stigmas may be listed:—

1. *Chirita urticifolia* & *C. Trailliana*.—Style ending in a dorso-ventrally oblique, deeply bifid, stigma (Fig. 1, a and b.).

2. *Oreocharis primuloides*.—Stigma divided in the vertical plane into two flat, more or less appressed, lobes (Fig. 1, d and e).

3. *Streptocarpus Michelmorei*.—Stigma capitate slightly bilobed in the horizontal plane, the lobes thick and standing away from one another (see Burtt, 1949 b).

4. *Didissandra sesquifolia*.—Stigma deeply and somewhat unequally divided in the horizontal plane, the lobes thin (see Clarke, 1887).

These four sorts of stigma are quite distinct from one another, and no progress can be made while they are all lumped together as "bilobed." On the other hand, the description "stigma entire" may equally well lead to the association of plants not closely allied. For example, W. W. Smith (1913, p. 41) described from Upper Burma the new species *Didymocarpus Lacei* and characterised it as a very distinct species with the habit of *Chirita pumila*, but the stigma of a *Didymocarpus*. In fact, as W. W. Smith remarked elsewhere (1912, p. 149), the general facies of *Chirita* is usually sufficient to distinguish the genus from *Didymocarpus* without the necessity of examining the stigma. At that time, *D. Lacei* appeared to be the exceptional species

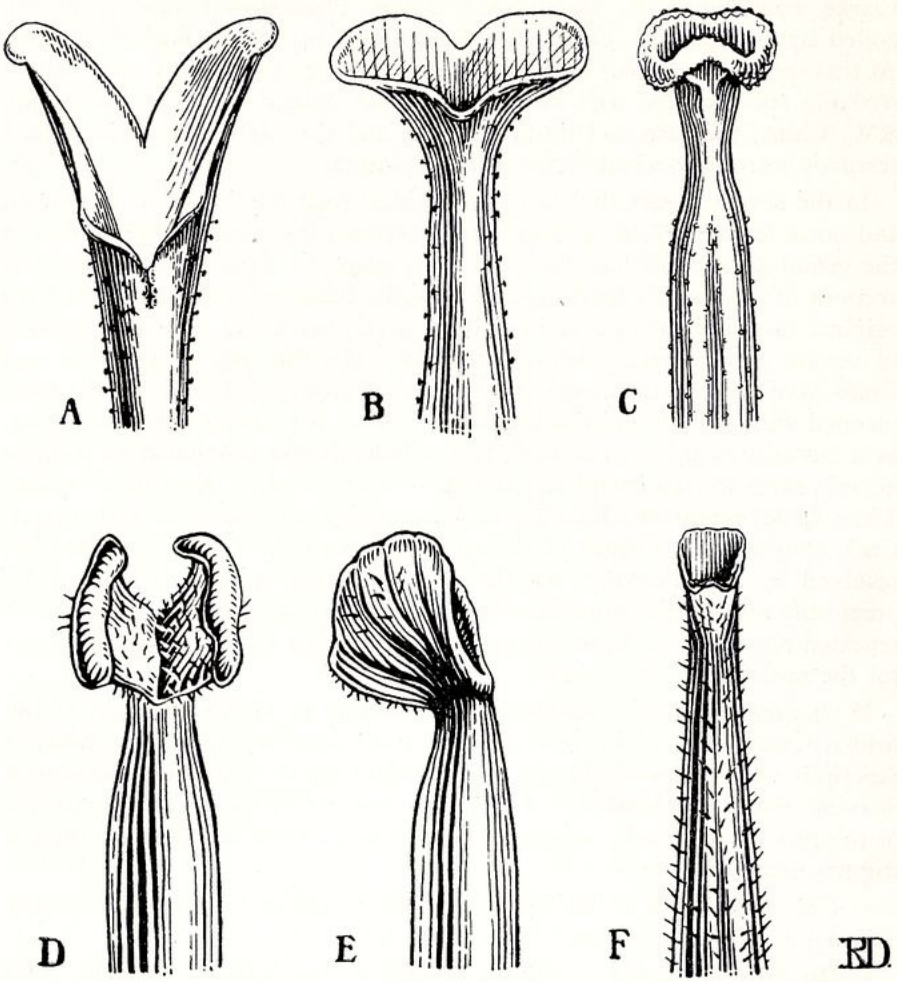

Fig. 1.

Stigmas of some Gesneriaceae. A, *Chirita urticifolia* D. Don (Cult. R.B.G. Edinburgh), from above. B, *Chirita Trailliana* W.W. Sm. (cult. R.B.G. Edinburgh), from above. C, *Didymocarpus praeteritus* Burtt & Davidson (cult. R.B.G. Edinburgh), from above. D, *Oreocharis primuloides* (Miq.) C.B.Cl. (cult. R.B.G. Edinburgh), from above. E, the same, side view. F, *Chirita Lacei* (W.W. Sm.) B.L. Burtt (Lace 4152), from above. All much enlarged.

which looked like a *Chirita* but was really a *Didymocarpus*. This view was unavoidable if *Didymocarpus* was regarded as characterised by an "entire" stigma, *Chirita* by a "bilobed" one. Now the "entire" stigma of a species of *Didymocarpus* sect. *Eudidymocarpus* is, in point of fact, a robust capitate structure (Fig. 1, c). The "bilobed" stigma of a characteristic *Chirita* is, as already described, oblique, bifid and thin (Fig. 1, a and b). The "entire" stigma of *D. Lacei* is oblique and of delicate texture, but not bifid (Fig. 1, f). It is clearly more like that of *Chirita* than that of *Didymocarpus* and, bearing in mind that the habit of *D. Lacei* is wholly that of *Chirita*, it is preferable to place it in that genus despite its entire stigma.* This is a view with which the original author of the species concurs.

Just as the description "stigma bilobed" is useless for constructive taxonomy in this group, so is the description "anthers coherent." Anthers may cohere in pairs, tip to tip, as in many tetrandrous genera such as *Corallodiscus* (cf. Burtt 1948 a), *Briggsia* (cf. Stapf, 1929); or all four may cohere together at their tips (as in *Rhabdothamnus*—see Clarke, 1883, tab. 17); or they may cohere face to face as in many diandrous genera such as *Chirita*, *Didymocarpus*, *Streptocarpus* and others. In this last condition we may say that the anthers are applanate. The taxonomic value of these features needs to be further explored, but the supreme importance of their proper description should need no emphasis.

In most genera of *Gesneriaceae* the calyx is more or less equally 5-lobed or 5-partite. In not a few instances, however, the three upper lobes are united to form a tridentate upper lip. This feature is the source of the generic name *Trisepalum*, and has resulted in other, quite unrelated, plants being placed in that genus. *Trisepalum Kingii* has already been transferred to *Petrocosmea* as *P. Kingii* (C. B. Cl.) Chatterjee, where it shares the character of bilabiate calyx with *P. Wardii* W. W. Sm. and *P. Kerrii* Craib. *Trisepalum lineicapsa* C. E. C. Fischer is in all but this one feature a normal species of *Didymocarpus* (sect. *Eudidymocarpus*) and must be transferred thereto.† Other genera which have similar bilabiate calyces are *Dichiloboea* and *Chlamydoboea*. The character also occurs in *Cyrtandra* and doubtless elsewhere in the family.

Occasions such as these, when the taxonomist is led astray by a single conspicuous feature, are particularly likely to occur in families where the classification is somewhat artificial. For when plants are consistently placed in their genera by such artificial characters as the number of fertile stamens or the division of the calyx, other features are given little attention; then suddenly an extreme example is collected and appears so distinctive as to suggest that it must be a new genus. So with the genus *Brachiostemon*, which Handel-Mazzetti (1934) described as new. This author laid great emphasis on the sterile branch of the stamen, although just such a structure is only a little less developed, but very inadequately described, in certain species of *Ornithoboea*, to which *Brachiostemon* must certainly be reduced. So too with *Ceratoscyphus*, whose horned sepals are a quite inadequate distinction from many species long rightly referred to *Chirita* (see pp. 209–212).

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* **Chirita Lacei** (W. W. Sm.), B. L. Burtt, **comb. nov.**
Syn.: *Didymocarpus Lacei* W. W. Sm. in Rec. Bot. Surv. India, vi, 41 (1913).

† **Didymocarpus lineicapsa** (C. E. C. Fischer) B. L. Burtt, **comb. nov.**
Syn.: *Trisepalum lineicapsa* C. E. C. Fischer in Kew Bull. 1928, 276.

The studies in *Gesneriaceae* made by the late Professor W. G. Craib (cf. Craib, 1918–19) represent a definite effort to break down the larger genera into associations of closely related species characterised by the possession of a carefully defined assemblage of floral characters. There is no doubt that Craib's concept of *Didissandra* (which we must now call *Corallodiscus*) is thoroughly satisfactory. The genus consists of some fifteen species with a distinctive facies and well marked technical characters in corolla, androecium and gynoecium. Of another of Craib's genera, *Tremacron*, we may say that it also represents a natural assemblage of species (only two were known to Craib, although there are probably as many as seven represented in herbaria), but the technical analysis of its characters is much more difficult than in the case of *Corallodiscus*. Craib certainly failed to distinguish it adequately from *Oreocharis*, and it is uncertain whether its generic segregation is justified. This matter will be considered in a forthcoming revision of *Oreocharis*, but one thing is already abundantly clear: there are so many anomalous species among the *Gesneriaceae* of the Old World that the recognition of each as a distinct genus would not be practical taxonomy. If *Tremacron* survives it will rather be because it represents a morphological pattern which recurs with some frequency than because the pattern itself is unusually well marked.

If we examine *Briggsia*, yet another of Craib's genera, we find a very different state of affairs. There are some fourteen species in this genus, but they are of varied habit and appearance, and are associated entirely on their floral characters: large ventricose corollas, arched filaments and anthers cohering in pairs tip to tip. Even this last feature is not quite constant, for we now have species in cultivation which have all the characteristics of *Briggsia* except that on dehiscence the anthers separate and the filaments straighten. There is, then, at full flowering, very little to separate these species from *Oreocharis*. These plants also provide a very good example of the value of being able to examine living material, for on the herbarium specimens this interesting feature is not easily observed.

The present studies are being undertaken in the belief that Craib's approach to the problem of the genera of *Gesneriaceae* was, whatever his individual errors, essentially correct. No useful purpose was served by K. Fritsch's agglomeration of *Didymocarpus*, *Chirita* and *Trachystigma* under the one name *Roettlera*, nor does C. B. Clarke's concept of the larger genera, justifiable as it was in 1883 when the number of known species was small, give a satisfactory classification. The movement, initiated independently by Ridley and Craib, towards genera based on a greater community of characters must be continued, although it seems certain that in many cases progress away from the somewhat artificial concepts employed by Clarke will be very slow.

The Old World *Gesneriaceae* are a group of manifold interest quite apart from the purely taxonomic problems which they present, and this fact is an added reason why strenuous efforts should be made to reach a more satisfactory system of classification. The morphology of the unifoliate species early aroused curiosity, and in 1860 C. W. Crocker, the Kew Propagator, reported that the single large leaf of *Streptocarpus polyanthus* Hook. fil. developed from one of the cotyledons (Crocker, 1860). He also recognised that similar unequal growth of the cotyledons took place in the rosulate species *Streptocarpus Rexii* (Hook.) Lindl. and even, to a less degree, in

Chirita Moonii from Ceylon, an apparently normal caulescent herb. Crocker realised that this curious developmental feature might be widespread, and expressed the opinion that a review of the whole group from this angle was needed. Prof. A. Dickson, Regius Keeper of the Royal Botanic Garden, Edinburgh, carried the enquiry a stage further when he showed that in *Streptocarpus caulescens* one cotyledon withers early, but the other develops into a leaf indistinguishable from the other foliage leaves of the mature plant (Dickson, 1883). The survey was considerably extended by K. Fritsch (1904), and amongst others who have studied the problem, either from seedling development or from a consideration of the mature organ, are Ridley (1906), Sir Isaac Bayley Balfour and W. W. Smith (1915), Oehlkers (1922) and Sir Arthur Hill (1938). These authors have chiefly been concerned with the problems intrinsic to the family, but Hill (1938) has attempted to bring the evidence from *Gesneriaceae* to bear upon the general problem of the monocotyledonous condition. He argued that wherever among dicotyledons only one seed leaf develops it is due to the other being suppressed or taking on a different function—never to their fusion. The evidence for this view is strong, and it is clear that there is now no proven example to support Sargant's theory that the single seed leaf of monocotyledons represents the fused seed leaves of the dicotyledons. Nevertheless, the demonstration that in many anomalous dicotyledons the two seed leaves show divergent behaviour has not yet been proved strictly relevant to the problem of the origin of the Monocotyledons. Argument from analogy must not be carried too far. In any case the *Gesneriaceae* are only on the fringe of the picture. If any dicotyledons are relevant it is others such as *Cyclamen*, *Ranunculus Ficaria* and *Peperomia*, where the suppression of one cotyledon takes place before germination, and the feature is associated with the geophilous habit.

The Old World *Gesneriaceae* lack any well-developed tap root: in unifoliate plants there seems to be a correlation between the early death of the radicle and the absence of a properly organised plumule. All genera have a shallow, fibrous root-system, and this is reflected in their ecology. Many species root in the humus which collects on cliff-ledges and among rocks; others are epiphytes, or grow on the moss of fallen trunks or on shady banks; the species which grow in open terrain at high altitudes (for example, species of *Corallodiscus*) often have a well developed rosette of radical leaves spreading flat on the ground. Species of *Gesneriaceae* are often very restricted in their distribution: for example, the limestone hills of the Malay Peninsula carry a large proportion of endemic species (cf. Henderson, 1928), while *Saintpaulia tongwensis* is confined to a single hill-top in E. Africa. Amongst a large number of very local species it is of great interest to find a few that are wide-ranging. The best example is *Boea hygrometrica* (Bunge) R. Br., known from Northern China to Australia; another is *Epithema carnosum* (G. Don) Benth., while it is by no means absolutely certain that the Central American and Asiatic members to the genus *Klugia* are specifically distinct.

Streptocarpus has proved a suitable subject for genetical work and has been investigated from the point of view of cytoplasmic inheritance and sex (Oehlkers, 1938; Goldschmidt, 1938), flower colour (Lawrence *et al.*, 1939), and sublethal genes (Lawrence, 1947). *S. Dunnii* has a curious solid granular pigment on leaves, stems and corollas, and this has been named dunnione (Price & Robinson, 1938); similar granular pigments are known to occur in

S. Pole-Evansii and in species of *Didymocarpus* and *Ornithoboea*. I do not know of their occurrence outside *Gesneriaceae*.

Cleistogamy is frequent in some species of *Streptocarpus* and Lawrence (1943) has shown that in *S. nobilis* not only cleistogamy but the whole vegetative development of the plant is dependent on the length of day.

The family limits of *Gesneriaceae* in the broader sense have chiefly come into question with regard to the position of the genus *Rehmannia*. For many years after its description by Liboschitz in 1835 this genus was shuttled to and fro between *Scrophulariaceae* and *Gesneriaceae* according to the individual views of the author concerned. During this period 3–4 other species were added to it. The problem was taken up by Solereder (1909), and his conclusions were very briefly as follows: the species which he found in *Rehmannia* were to be split up into three genera: of these the true *Rehmannia* (R. *glutinosa* and R. *angulata*) and *Titanotrichum* (based on R. *Oldhamii*) were Gesneriaceous, with the unilocular ovary typical of the family: the third genus *Triaenophora* (based on R. *rupestris*) was to remain in *Scrophulariaceae*, having a strictly bilocular ovary.

Solereder placed *Rehmannia* and *Titanotrichum* near *Napeanthus* in the *Didymocarpeae*, but Sealy (1949) has shown that *Titanotrichum* has closer affinities with genera such as *Isoloma* in the tribe *Gesnerioideae*. Not the least important point of resemblance is that *Titanotrichum* possesses scaly stolons similar to those of *Isoloma* and *Tydaea* (cf. Raunkiaer, 1934, pp. 86, 87). What of *Rehmannia* itself? This is a matter on which we must suspend judgment. It lacks the stolons and characteristic trichomes of *Titanotrichum* nor does it seem closely allied to any genera in *Didymocarpeae*. It is a normal perennial herb without any anomalous features, and this fact, together with its racemose flowers and alternate leaves, gives it, to the student of *Gesneriaceae*, an alien look. It is worth recalling that Solereder records that the nature of the secretory cells of *Rehmannia* constitutes a new anatomical feature for the *Gesneriaceae*.

Anatomical characters have not yet been greatly used in the classification of this family. It is of interest, however, that Wonisch (1909) has indicated the close affinity of *Monophyllaea*, *Klugia* and *Rhynchoglossum* from their possession of similar secretory-cavities. It will be surprising if the evidence, when available, does not also join *Moultonia* to this alliance.

Enough has been said to show the wide range of interesting topics that the very superficial studies yet made on this group have brought to light. It can scarcely be doubted that much more remains to be discovered. To the taxonomist not the least interesting point is that this group can almost be diagnosed by saying that its members nearly all show some form of anomalous behaviour. The anomalies seem to be largely absent from the American genera, and it is by no means impossible that if this tendency could be expressed in precise terms the Old World *Gesneriaceae* might once again be raised to family rank as the *Cyrtandraceae*, as was originally done by William Jack one hundred and thirty years ago (Jack, 1823). In any event it is only when these peculiarities are more fully understood, and a more satisfactory classification achieved, that the relationship of the group to neighbouring families can be properly discussed.

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