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STUDIES IN THE GESNERIACEAE OF THE OLD WORLD XXXI: SOME ASPECTS OF FUNCTIONAL EVOLUTION

B. L. BURTT

ABSTRACT. A comparison is made between Old World Gesneriaceae, characterised by small seeds and an accrescent cotyledon, and other microspermous forest plants, which are usually mycorrhizal or wholly saprophytic. The early elaboration in the cotyledon of additional photosynthetic tissue, before the organization of plumule and leaf primordia, may be important in compensating for scanty food reserves. The unifoliate habit is seen as a normal kind of evolutionary development when viewed against the background of a group in which an accrescent cotyledon is already established. *Monophyllaea*, confined to rain-forest, is contrasted with *Streptocarpus* whose unifoliate species are able to survive in seasonal climates because of their ability to reduce leaf surface by formation of an abscission layer across the lamina. The evolution of the monocarpic habit in the family is briefly discussed.

An examination is made of gesneriads with actinomorphic flowers. It is reasoned that their sporadic distribution in the family makes it unlikely that all are primitively actinomorphic and evidence is presented for regarding some as being derived from zygomorphic ancestors. The terminology of floral symmetry is discussed.

The Gesneriaceae of the Old World all have numerous, very small seeds: they also nearly all have some degree of persistent growth in one of the cotyledons after germination, leading to an eventual inequality in their size. For many years the term anisocotyly has been used to describe this condition. It is an accurate descriptive term that I have used myself in this series, but it lacks the appropriate biological emphasis for the present context. It is not the final inequality of size that is important, but the occurrence of continued growth. The first point in my thesis is that small seeds, numerous seeds and an accrescent cotyledon are interlocked.

Salisbury (1942) has shown the importance of adequate seed reserves under forest conditions. Microspermy in the forest is often linked to a symbiotic association in the roots or complete saprophytism (Orchidaceae, Burmanniaceae, Gentianaceae such as *Cotylanthera*, Monotropaceae etc.). The symbiont is needed at a very early stage in the life of the seedling and must help to compensate for the lack of food reserves in the seed. Is there any such compensatory factor in Gesneriaceae? A speculative suggestion is that the continued growth of one cotyledon may act in this way, by the production of additional photosynthetic tissue before energy is required to mobilize a plumular growing point and new leaves.

The parietal placentation of Gesneriaceae, contrasting with the axile arrangement in Scrophulariaceae, parallels the evolutionary trend within Orchidaceae, that from Ericaceae through Pyrolaceae to Monotropaceae (Henderson, 1919; but cf. Pykko, 1969) and from Scrophulariaceae to the parasitic Orobanchaceae (Boeshore, 1920). In all these cases there is strong evidence that the change from axile to parietal placentation is associated with an increase in the number of ovules. In Gesneriaceae the increase is much less marked and further developments, probably connected with capsule dehiscence and seed dispersal, lead to sterilization of much of the placenta and restriction of ovule-bearing to the tips of the lamellae. This however is in turn counterbalanced by a considerable increase in ovary-length, so that the number of ovules produced is still considerable.

It may well be questioned whether an accrescent cotyledon can be regarded as an adequate compensation for impoverished seed reserves. It would seem likely that it is adequate only if there are other factors that favour the persistence of numerous small seeds rather than fewer larger ones. Two such factors may be suggested. The first is the obvious one of improved dispersal. Many terrestrial gesneriad seeds are apparently dispersed by rain-splash; almost inevitably tiny seeds will be carried in soil on the feet of passing animals, even if only for a few yards. Amongst the epiphytes (*Aeschynanthus*, *Agalmyla*) the small seeds are adorned with fine terminal hair-like processes which must permit slow descent through the air and adherence to mossy branches. In all these methods small size is important. There is another possible advantage: the lack of food reserves for the seedling also means a lack of food for insects. The small size of these gesneriad seeds may put them below the useful food-supply level. This could be particularly valuable in a group inhabiting the tropics, where biotic factors play a dominant role in evolution. It can, in fact, be viewed as another reaction to pest pressure which has been suggested as a potent cause both of unpalatability and of diversity. Certainly gesneriad fruits (with the possible exception of the indehiscent *Cyrtandra*) show singularly little sign of insect attack. Obviously field studies are needed, but the fate of small disseminules is a particularly difficult matter for observation.

The foregoing speculations may be right or wrong: at least they suggest aspects of the biology of the family on which information would be well worth having. Whatever their merit they do no more than bring us to the basic condition now existing in the Gesneriaceae—Cyrtandroideae: a group characterised by numerous small seeds and an accrescent cotyledon. It is the further evolution of this cotyledon that will now be examined.

SOME PATTERNS OF GROWTH

In its simplest manifestation, as in *Cyrtandra* or *Boea* or *Aeschynanthus* (Burtt & Woods, 1958), the duration of growth in the enlarging cotyledon is not very great; it never gets as large as a normal foliage leaf and the organization of plumular bud and the subsequent development of stem and leaves is on the usual dicotyledonous pattern.

Some species are known that normally have a well-developed accrescent cotyledon followed by a stem a foot or more high and numerous cauline leaves. Under certain conditions these plants flower and fruit with only one well-developed leaf, the accrescent cotyledon. Notes on herbarium specimens show that these conditions may be environmental (*Streptocarpus nobilis, Chirita hamosa* var *unifolia, Chirita capitis*), or they may be induced in cultivation if seed is sown during periods of short day-length; December sowing in Edinburgh has this effect on *Chirita micromusa* and *Rhynchoglossum obliquum*.

These facultative unifoliates bear witness that some caulescent species have sufficient developmental flexibility to survive in the unifoliate condition if the development of the plumular bud is inhibited. They lend support to the idea that a gesneriad with an accrescent cotyledon could become a unifoliate plant by genetic change affecting plumular development. The meristem in the accrescent cotyledon could act as a reception area for transferred growth impulses on the failure of the plumular meristem.

Given the predisposing condition of a cotyledon already provided with a basal meristem, the evolution of the unifoliate habit does not require a genetic mutation of unusual size. Its evolution does not merit the term saltatory.

The genus *Monophyllaea* belongs to the tribe *Klugieae*, as does the facultative unifoliate *Rhynchoglossum*. There are some 12 species of *Monophyllaea*, and its very close ally *Moultonia*, spread through eastern Asia from southern Thailand to New Guinea. They are essentially plants of limestone in rain forest, records on other rock are rare and many species are lime-encrusted. *M. horsfieldii* on the limestone hills around Ipoh, Perak, grows with the well-developed hypocotyl erect and the large cotyledonary lamina only slightly oblique at the top. The habitat where I saw it was a hollow which had been disturbed by working for iron ore, and *M. horsfieldii* may also grow on the limestone cliffs themselves. Certainly an allied species on the Gunong Api—Gunong Benarat limestone in Sarawak (Fourth Division) had the hypocotyl standing out nearly at a right angle from the wet limestone cliffs. However the very slender *M. beccarii*, which seems to be restricted to the shelter of limestone caves and overhangs, grows erect.

These three species all have a well-developed hypocotylar stem below the accrescent cotyledonary lamina. There are other species, however, in which the hypocotyl is quite short: one such species grew on limestone stalactites of an overhang alongside Sungei Melinau below Gunong Api (Sarawak, Fourth Division). If the erect growing unifoliates may sometimes look rather incongruous, there can be no doubt that this species is admirably adapted in its form to this particular habitat.

Moultonia singularis, another unifoliate, may be regarded as even better adapted to the limestone cliffs where it is found. All the species of *Monophyllaea* produce erect and vulnerable inflorescenses. In *Moultonia* the floral meristem is distributed along both midrib and hypocotyl and the flowers are almost sessile. The danger of inflorescences being broken by falling twigs or water is thus avoided. It looks as though a plant of *Moultonia* may live for a number of years, producing flowers and fruits throughout this meristematic area. As yet, however, we have little information about the life history of this strange plant.

To sum up, all I know of *Monophyllaea* (and the same is true of *Moultonia*) leads me to believe that it is a genus particularly well suited in its life-form to certain limestone habitats in the rain-forest to which it must also be physiologically adapted. Its range through eastern Asia and the extent of its speciation testify that within certain restricted environments it is successful: these environments are, it is true, within a climatic zone which is optimal for plant survival, but the habitats themselves are often harsh, limestone cliffs subject to drip in some cases, drought in others: they are not optimal habitats to which no adaptation is needed.

Monophyllaea does seem to be restricted to a climate without very much seasonal variation. *Streptocarpus* subgenus *Streptocarpus*, the other group that contains unifoliate species, has escaped from this restriction by an interesting, perhaps unique, device. This is the ability to effect a drastic reduction in the transpiration-surface of the leaf during the dry season by the formation of an abscission line right across the lamina. The tissue thus cut off is replaced by growth from a basal meristem in the next growing season and the cycle is repeated annually until inflorescences are produced at the base of the lamina. Normally each leaf dies after flowering, though further perennation occurs in a few cases. Growth patterns in *Streptocarpus* subgenus *Streptocarpus* may become very complicated and are dealt with more fully in a revision of the genus (Hilliard & Burtt, in press).

The distribution of subgenus *Streptocarpus* is from Ethiopia southwards to the eastern Cape, with a preponderance of its species below the tropic, in the decidedly seasonal regions of Transvaal and Natal. The picture in subgenus *Streptocarpella* is very different. This subgenus consists of caulescent plants bearing several leaves (the only exception is the subunifoliate state of *S. nobilis* mentioned above) and there is no device for surviving an unfavourable season, except that a few species (such as *S. caulescens*) develop a fleshy stem base. The distribution of this subgenus lies within the tropics, but, in contrast to subgenus *Streptocarpus*, it ranges right across the African continent to Senegambia on the Atlantic coast.

The monocarpic habit is, as has been seen, implicit in the simplest form of unifoliate growth-pattern in *Streptocarpus*, and even rosulate species are but colonies of monocarpic single-leaved units. However the monocarpic habit has also been developed elsewhere in the group, particularly in the genus *Boea*.

Species of *Boea* were cited as an example of the taxonomic importance of growth-patterns on a previous occasion (Burtt, 1964, p 13). Briefly there is a morphological series traceable: it starts with a simple type having axillary inflorescences and the terminal bud of the shoot remaining vegetative. This is the standard growth-pattern of most Gesneriaceae. In *Boea* there can then be traced a series of forms in which parts of the vegetative system die at the same time as the inflorescences they bear. Ultimately the habit is reached where a single leafy stem eventually produces a very large inflorescence, flowers and fruits and then the whole plant dies.

Species with such a monocarpic habit are *B. treubii* H. O. Forbes (Sumatra, Malay Peninsula, Sarawak), *B. paniculata* Ridl. (Malay Peninsula) and *B. havilandii* Ridl. (Sarawak). The latter grows on the limestone at Bau, some 35 miles from Kuching, and is probably the largest species. The thin woody stem is about 1 cm diameter and may reach a length of some 2 m; the inflorescence is a terminal panicle about 1·5 m high; all the fruiting specimens seen were dead or dying and no plants were observed that showed any sign of having regenerated from one that had flowered. Judging by the number of leaves present and the leaf-scars below them, this plant may grow for 15–20 years before flowering.

It is improbable that the monocarpic habit, as such, can have any selective advantage. The two obvious concomitant features are larger size and greater seed production. As these plants grow on limestone rock in places where it is not usually very densely populated, actual size is scarcely likely to be the whole reason. It is much more likely that this rather unusual and spectacular habit is the long-term result of the simple fact that the plant that produces most seed leaves behind most progeny. In situations where contrary factors are not operative evolution is towards larger plants with bigger inflorescences: monocarpy is the inevitable result. Why does this not evolve more often? It is, of course, difficult to say; it is worth remembering, however, that *Boea* has this considerable diversity of growth-patterns affecting just this very important feature—how much of the plant body dies after fruiting. It may be that such flexibility was the platform necessary for the eventual development of monocarpy. *Cyrtandra* is a much larger genus and has a much greater diversity of habit; but no variability in this particular feature and no tendency towards monocarpy. *Cyrtandra* is a genus of the rain-forest. *Boea* is one of the few gesneriads which escapes from the shelter of the rain-forest onto neighbouring limestone cliffs. *B. suffruticosus* Ridl. on the Lankawi Islands is a shrub found in the forest and shows little die back; the species which lose most growth are the rather straggling species like *B. verticillata* Ridl. from the Batu limestone near Kuala Lumpur, where it clearly suffers from seasonal drought. *B. havilandii* and *B. treubii* are usually at the forest-edge or on cliffs in forest. The whole question deserves further study.

THE OCCURRENCE OF ACTINOMORPHIC FLOWERS

The form of flower in the earliest Gesneriaceae is as uncertain as their vegetative habit. To meet our criteria for the family it must at least have had a gamopetalous corolla with epipetalous stamens, a unilocular ovary with bifid parietal placentae bearing numerous ovules and small seeds. Without these features we would scarcely recognise a gesneriad.

The nature of the inflorescence is crucial. In the Old World Gesneriaceae the axillary cyme is dominant and the cyme is of that peculiar type in which two flowers are borne at each dichotomy. These flowers open successively and are bent downwards when in bud, usually moving up to a more or less horizontal position when opening. This organization, unlike a simple cyme where the flower is solitary at each dichotomy and often erect, seems most likely to produce zygomorphic flowers. We cannot be certain that this type of inflorescence is primitive in the family, but a racemose inflorescence could be derived from it by elongation of the main axis and reduction of the inflorescences to single flowers (cf. *Verbascum* and *Celsia* in Scrophulariaceae). It may be noted that terminal racemes are chiefly found in the New World Gesnerioideae with inferior ovaries. It is concluded that there is at least a possibility that zygomorphy has been established in the gesneriaceous stock from the time it became a recognizable family.

To-day zygomorphy predominates in the family. The number of actinomorphic members is small, but their scattered distribution in the system and in the geography of the family suggests that some at least are reversions from the zygomorphic state and do not exemplify the retention of a primitive actinomorphy.

Evolutionary reversions are always interesting and it is one of the taxonomists jobs to quarry this sort of data and set it on display, for often the best examples are rarities known only from a few herbarium sheets.

Note on terminology. The use of various terms describing floral symmetry is not as clear as it should be and requires a moment's consideration. Botanists recognize three main types of symmetry in the construction of the angiosperm flower: (a) radial symmetry, equal halves being obtained when the flower is cut in any plane vertical to the top of the pedicel; the equality is, of course, only approximate in flowers having very numerous parts: (b) bilateral symmetry, when equal halves are only obtained if the section is in the median plane of the axis: (c) asymmetry, when equal halves cannot be obtained in whatever plane the flower is cut.

Radially symmetrical flowers are also said to be actinomorphic; unfortunately they are also commonly termed "regular". Of course they are no more "regular" than a bilaterally symmetrical flower: the regularity is different.

Bilaterally symmetrical flowers are also said to be zygomorphic; unfortunately they are also commonly called "irregular", which they are not. In fact a zygomorphic flower like *Antirrhinum* or *Cypripedium* exhibits much greater "regularity" than an actinomorphic one that has numerous floral parts like *Paeonia* or *Camellia*.

Finally there is the asymmetrical flower, like *Centranthus* or members of Marantaceae or Cannaceae. These might with more justification be called "irregular", but it is now too late to use this term with the added precision.

The further source of confusion in describing symmetry is the frequent failure to say what parts of the flower are under consideration. The symmetry of the ovary is most often ignored, because where carpels are fused it often requires internal examination; but this is not always so and the actinomorphy of *Ranunculus* is clearly different from the symmetry of *Saxifraga* which is actinomorphic as to calyx corolla and stamens, but zygomorphic as to ovary. The same condition applies in Gesneriaceae. Here the ovary is always zygomorphic and the following discussion on actinomorphy in the family refers only to perianth and androecium.

The examples.

The plants to be discussed are:—

Ramonda	Cyrtandroideae—Didymocarpeae
Conandron	
Tengia	
Protocyrtandra	Cyrtandroideae—Cyrtandreae
Depanthus	Gesnerioideae—Coronanthereae
Marssonia (? = *Napeanthus*)	Gesnerioideae—?

Ramonda perhaps scarcely merits inclusion, for in actual form of corolla it is seldom strictly actinomorphic: usually the lower lobes are very slightly larger than the upper and often, when they are five in number, the sinuses between the three lower ones and the two upper ones are slightly wider. Also the cone of anthers is often curved slightly downwards because the upper anthers are slightly larger than the others. However *Ramonda* is important because its fertile stamens are characteristically isomerous with the corolla-lobes, 4–6. The variability in number is unusual in the family and may occur on one plant. *Ramonda*, which consists of one species in the Iberian peninsula and two in the Balkans, is usually classed as a tertiary relic in the European flora: it is certainly marginal to the present distribution of the group.

Conandron is a monotypic genus found in Japan: it is perhaps the only member of the family that loses its leaves in winter and is a true hemicryptophyte: the growing point being protected by the backs of next year's leaves, which at this stage are densely covered with coarse brown hairs. In distribution it is peripheral to the main area of the family, as is *Ramonda*. *Conandron ramondioides* is well known in cultivation. Its floral organization is more like that of *Solanum* than of other gesneriads, for it has a 5-pointed star-shaped corolla limb and a central cone of anthers. *Conandron* clearly belongs to Didymocarpeae, of which it has the typical pod-like fruit, but it has no known close relatives.

Tengia is a monotypic genus described by W. Y. Chun (1946, p. 279) and is a native of the Chinese province of Kweichow. In habit and in the form of calyx, actinomorphic corolla and ovary it is remarkably close to another small Chinese genus *Petrocodon* Hance. It is in the androecium that the difference lies. In *Tengia* the corolla with 5 equal lobes is matched by 5 equal fertile stamens; the filaments arise near the bottom of the corolla tube and are straight; the anthers have the cells slightly divergent, the lines of dehiscence are confluent at the top forming a semicircle and the anthers are not in any way united to one another.

Petrocodon provides a sharp contrast. The corolla is just the same as in *Tengia*, but there are only two fertile stamens; the filaments are twisted so that the anthers lie face to face and the cells are widely divergent so that the line of dehiscence is straight and parallel to the length of the corolla tube. This is the androecial pattern of a zygomorphic bilabiate flower, as so commonly seen in *Didymocarpus*, *Chirita*, *Streptocarpus* etc.

It is almost impossible to imagine that a flower like that of *Tengia* should have developed a reduced and zygomorphic androecium without any visible change in the shape of the corolla. The only tenable hypothesis is that some diandrous bilabiate species, probably in the genus *Didymocarpus* in the broad sense, has reverted to actinomorphy in two steps: the first, which we know as *Petrocodon*, having a radially symmetric corolla but a bilateral androecium, the second, *Tengia*, becoming radially symmetrical in the androecium as well. It should be added that *Tengia* can scarcely be regarded as a casual peloria: it has been collected in different localities in Kweichow in 1907 and in 1935. *Petrocodon* itself has only been collected on a few occasions, in Canton province and in Hupeh. Vegetatively the two genera are not distinguishable and are characterised by leaves turning black on drying. *Didymocarpus nigrescens* Lévl. probably belongs to one of them, but as the only known specimens are in fruit it is impossible to decide to which.

Protocyrtandra is a monotypic genus of the Palau Islands in the western Pacific. Its sole species, *P. todaiensis* (Kanehira) Hosokawa (1934), was originally described in the large diandrous genus *Cyrtandra*, but was later segregated. The name given to it indicates that Hosokawa believed it to be more primitive than *Cyrtandra*.

Recently very fine material of *Protocyrtandra* has reached Dr. G. W. Gillett of the University of California, Riverside, and he has given an account of this which I have seen in manuscript (Gillett, 1969, 1970) and he has kindly permitted me to draw on his data. The important point that comes out of this new material is that although the corolla varies in having from 4 to 6 lobes the fertile stamens are isomerous with the corolla lobes. It had previously seemed that 4 out of 5 stamens were fertile, in contrast to 2 out of 5 in *Cyrtandra* proper. Furthermore the corolla lobes of *Protocyrtandra* are valvate, not imbricate as in *Cyrtandra*.

Gillett has decided that the differences do not justify generic separation of this one species, and he has reverted to the name *Cyrtandra todaiensis*. However there are some disadvantages in submerging this one actinomorphic and isomerous species amongst the 600 odd zygomorphic diandrous members of the genus and for the moment I prefer to accept this isolated species as a separate genus. Doing so permits a convenient comparison of *Protocyrtandra* and *Cyrtandra*, but it should not be taken as a carefully weighed taxonomic judgement. A workable subdivision of *Cyrtandra* may make the inclusion of *Protocyrtandra* more acceptable, but the problem must be studied from within *Cyrtandra* outwards: we cannot decide looking at *Protocyrtandra* alone.

The generic name is, of course, tendentious. Was Hosokawa right in seeing this plant as a relic of the earlier tetrandrous state of *Cyrtandra*? There is no direct evidence. We can make two general observations about *Cyrtandra*. First the range of morphological diversity is much greater in the Malay Archipelago than it is in the Pacific. Secondly the species of western Malesia have hard crustaceous fruits that do not turn soft and white at maturity as do those of the species in the Pacific. The meeting ground is in New Guinea and the Solomon Islands; here most species have western affinities but a few are allied to species from further east. The ripe fruit of *Protocyrtandra* is a soft white berry. If *Cyrtandra* has spread from the west, then the white berry is probably the more recently evolved fruit type and the actinomorphy of *Protocyrtandra* is secondary. If *Cyrtandra* has radiated from the New Guinea area, then the white fleshy fruit could be the primitive state in the genus and the actinomorphy of *Protocyrtandra* could also be primitive. On the whole the odds seem slightly in favour of *Protocyrtandra* being a reversion to isomery between androecium and corolla, but some new source of evidence is needed before we can have any confidence in this opinion.

Depanthus was extracted from the genus *Coronanthera* by S. Moore (1921) with the comment that "Neglecting some minor points, the nearly actinomorphic campanulate corollas with the five similar stamens seem fully to warrant the separation of this plant from *Coronanthera*." We are again not concerned with the niceties of the taxonomy, *Depanthus glaber* would certainly be a very isolated species in *Coronanthera* and we may accept the generic name for the time being. Here there seems to be no clue at all as to whether the actinomorphy is primitive or derived. Moore refers to the "nearly actinomorphic" corolla and to its "subequal" lobes, but the illustration does not indicate any measurable inequality enough to hint that this was derived from a zygomorphic ancestor. *Depanthus* only contributes to this study the plain fact that actinomorphy of perianth and androecium occurs in the tribe Coronanthereae, which I have placed in the subfamily Gesnerioideae rather than in Cyrtandroideae (Burtt, 1963).

Although strictly outside my title, attention may be turned for a moment to two tropical American species of the subfamily Gesnerioideae. These are *Marssonia primulina* Karst. (from Colombia) and *M. subacaulis* (Griseb.) Urban (from Trinidad and Tobago). Both these have a regular rotate corolla with five stamens. *Marssonia* is closely related to (and perhaps best included in) the genus *Napeanthus* Gardn., of which some half-dozen species with zygomorphic corollas and only four fertile stamens are known. These two genera share the curious feature of having the stomata of the leaves arranged in groups, not evenly distributed. The tribal position is uncertain.

It should perhaps be added that peloriate forms are known in a number of species of Gesneriaceae: for instance in *Sinningia speciosa*, *Rechsteineria cardinalis* and *Saintpaulia ionantha*. True breeding peloriate forms have been produced, in addition to casual occurrences.

The purpose of this catalogue is to show that actinomorphy occurs at several widely separated locations in the taxonomic plan of the Gesneriaceae. Even if one or other of these examples represents the retention of a primitive actinomorphy, this can scarcely be so in all cases. In particular *Petrocodon* gives us sound morphological grounds for believing that the actinomorphy of *Tengia* is secondary. It must also be emphasised that actinomorphy is merely a descriptive term for a certain structural plan of arrangement of floral parts. It has little biological significance. The actinomorphy of *Ramonda*, *Conandron* and *Napeanthus*, for instance, is associated with a hypocrateriform corolla and a central cluster of stamens; that of *Tengia*, *Protocyrtandra* and *Depanthus* is expressed by a tubular corolla with the stamens held around the inner circumference. This difference is perhaps another reason for thinking that not all (if any) of these examples of actinomorphy are primitive in the family.

Arguments have been produced by Robertson (1888) suggesting that certain members of Scrophulariaceae, especially *Verbascum*, are secondarily actinomorphic. His arguments, which were accepted by Pennell (1935), are based on pollination mechanisms and do not seem quite as appropriate in the Gesneriaceae, except perhaps in the case of *Ramonda*; this work is merely mentioned to call attention to the parallel problem in Scrophulariaceae.

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