The Gentians : Notes and Queries.

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(PLATE II.)

I HAPPENED to spend some six weeks, from the end of July to the beginning of September 1886, at Arolla (a locality situated at the head of one of the southern offshoots of the valley of the Rhone near Sion), 6400 feet above the level of the sea. During my wanderings about the woods and pastures which clothe the sides of the valley from this level to the snow-line, a couple of thousand feet higher, my attention was attracted by the characteristically alpine vegetation, and more especially by the Gentians, of which some species, such as *Gentiana purpurea* and *G. campestris*, were very abundant. *G. verna* and *G. acaulis* were also by no means uncommon; but the latter had almost ceased to flower.

It is well-nigh forty years since I occupied myself with systematic botany; and I had no works of reference at hand except Gremlin's 'Flore analytique,' which I happened to have bought at Lausanne, and Rapin's 'Guide des Botanistes dans le Canton de Vaud,' which a fellow-traveller was kind enough to lend me. But the extraordinary amount of variation which presented itself when I compared considerable suites of specimens with the diagnoses and descriptions in these works struck me so much that, all "unanoited and unannealed" as I was in systematic work, I was tempted to see what I could make out of the facts for myself. In truth, the Gentians took hold of me rather than I of them; and I have been more or less their bondservant ever since. Beginning with *Gentiana purpurea*, I found that I could not understand that form without knowing something about the rest of the species of *Gentiana*; and, by a parity of reasoning, a knowledge of *Gentiana* involved that of the other genera of the Gentianeæ. So that, since my return to England, I have been led to make a rapid survey of the whole Order; and it is the broad results of that survey that I wish to lay before the Linnean Society.

I have to thank the Director of Kew Gardens for the free use of the splendid herbarium under his charge. It affords the means of carrying out the investigation I have attempted much more thoroughly; and I am well aware of the incompleteness of the

observations I venture to offer. But, at present, it is needful for me to turn my attention to other things; and if I venture to bring forward so imperfect a piece of work, it is in the hope that it may be taken up and finished by more competent hands.

Every botanist is aware that the Gentianæ constitute one of the most natural and well-defined of the Orders of plants. The type of structure which runs through the five or six hundred species included in the Order undergoes but few and, for the most part, inconsiderable modifications. There are no trees and but few shrubs among them; a few are climbers; and there are a few saprophytes. The opposition, entirety, and palmate-venation of the leaves have but few exceptions; and it is very rarely that the flower departs from typical regularity. The chief distinctive characters of the groups into which the Order is at present divided lie in the flower, and indeed in the corolla; since the form and proportion of the calyx, the occasional synanthery, and the greater or less intrusion of the placenta are characters which vary greatly from genus to genus.

Under these circumstances, I have confined myself almost entirely to the study of the structure of the flower. I find that some seven or eight modifications of that structure are distinguishable; and that these again fall into two series, each of which is characterized by a peculiar disposition of the nectarial organs, and presents a gradation of forms of the corolla from the rotate, or rather stellate, condition, through the campanulate to the extreme infundibulate character.

In one of these series the nectarial cells are situated on the inner surface of the cup, from the edge of which the lobes of the corolla proceed, and towards its basal end. They are aggregated in such a manner as to form either a single patch, bisected by the vein which becomes the median vein of a corolla-lobe; or two patches, one on each side of that vein. I term the Gentianæ of this series *Perimelitæ*.

In the other series there are no such patches of secreting-cells visible on the corolla; but in many members of the series there is a zone of such cells, which encircles the base of the ovary, and is therefore furnished by the outer faces of the carpellary phylomes, which are often raised into tubercles. In others, I have not been able to make sure of the existence of nectarial cells, either on the surface of the ovary or on the stemono-carpellary internode, which forms the actual bottom of the flower-cup. But

dried plants are very unfavourable subjects for the determination of points of this kind; and as many of these flowers, which have no apparent nectaries, are known to be visited by honey-sucking insects, I shall for the present assume that honey-secreting surfaces exist on the central parts of the flower. In contradistinction to the *Perimelitæ*, the Gentianæ of this series may be termed *Mesomelitæ*.

In the series of the *Perimelitæ* four modifications of floral structure are discernible. To these I propose to give the names of *Actinanthæ*, *Keratanthæ*, *Lophanthæ*, and *Stephananthæ*.

I. *Actinanthæ*.

The corolla is rotate*, or, if it is more or less campanulate, the sinuses which separate the lobes are very deep. The nectarial arcæ are single or double, and often concave inwardly. There is no distinct gynophore; but the ovary is occasionally "stipitate;" that is to say, its basal moiety, which then contains no ovules and remains very narrow, constitutes an apparent stalk on which the dilated ovuligerous moiety is supported. The margins of the lobes of the corolla may be produced into longer or shorter denticulations or laciniæ; but there are no filamentous appendages developed on the inner face of the corolla. The stigmatic surfaces are oblong-ovate.

The species in which I have found this type of floral structure are :—

A.	B.	E.
Gentiana	Gentiana	Gentiana
aurca.	primulæfolia.	saxosa.
umbellata.	vaginalis.	cerina.
Moocroftiana.	nummularifolia.	
detonsa.	saxicola.	
	multicaulis.	
Jacschkea.	incurva.	
Pleurogyne.	Grisebachii.	
Exadenus.	gracilis.	
	monieroides.	
	ericoides.	
	magellanica.	
	patagonica.	

* This term appears to me to be often employed ambiguously. It is applied, on the one hand, to corollæ in which the cup appears to be formed merely by the confluence or connation of the bases of the lobes, and is not in any way marked off from the latter; and, on the other hand, to corollæ in

In *Exadenus* the nectarial surfaces are hemispherically depressed and bulge outwards, so that their positions are marked externally by convexities of the corolla. Dr. Grisebach ('Genera et Species Gentianearum,' p. 322) says of each "fovea glandulifera," that it is "extus tantum conspicua, intus per petali substantiam clausa;" but the real state of the case appears to me to be as I have stated it. *Exadenus*, in fact, represents the first stage of a transition from *Actinanthæ* to the next type.

II. *Keratanthæ*.

This differs from the preceding in no essential respect, except in the deepening of the nectarial concavities, in such a manner that their external walls project as long horns or spurs, which are sometimes directed downwards and sometimes upwards. Moreover, the lobes are relatively shorter, and the corolla is more or less campanulate. It is very possible, and indeed probable, that further inquiry may bring to light forms constituting a complete transition between *Actinanthæ* and *Keratanthæ*.

The genus *Halenia* is the only representative of this type.

III. *Lophanthæ*.

Here, again, the corolla has fundamentally the same characters as in *Actinanthæ*; and the only essential difference lies in the development of filamentous appendages, or fimbriæ, from the inner surface of its cup. These fimbriæ occur in different positions: sometimes they are *parastemonal*; that is to say, they arise singly or in groups from a common base, along, or close to, the line of symphysis of the filaments of the stamens with the cup of the corolla. In this case they are sometimes so minute as to be distinguishable only by the aid of the microscope; sometimes, on the other hand, they are so long as to extend across the interval between one series and another, and thus to form a more or less complete barrier across the interval between the ovary and the corolla. These fimbriæ have already been noticed in some of the species in which they occur; but

which the cup more or less closely embraces the ovary, and is even narrower at the summit than the middle. The physiological import of the two forms is very different; and, morphologically, the latter are really hypocrateriform corollæ with very long lobes. I use the term "rotate" in the first sense.

they have been described as appendages of the filaments of the stamens. I have looked into this point with considerable care; and, in all cases, I find that the fimbriæ cohere with the corolla and not with the filaments, if sufficient care is taken in separating the two. If the filaments are roughly torn away, on the other hand, some of the fimbriæ may come with them, attached by flakes of the corolline epidermis. In order to remove all possible doubt, it would of course be necessary to study the development of the fimbriæ.

In other exemplifications of the *Lophanthe* type the fimbriæ are *perinectarial*; that is to say, they are developed, not in longitudinal series parallel with and close to the stemono-petaline symphyses, but in close relation with the margins of the nectarial area.

The species in which I have met with the *Lophanthe* modification are:—

1. With *parastemonal* fimbriæ.

A.	B.	D.	E.
Gentiana	Gentiana	Gentiana	Gentiana
ciliata.	foliosa.	montana.	montana.
crinita.	rupicola.	diemensis.	concinna.
barbatula.	Hookeri.	pleurogynoides.	
	fastigiata.		
	cerastioides.		
	cernua.		
	Jamesonii.		
	radicata.		
	limoselloides.		
	diffusa.		

2. With *perinectarial* fimbriæ.

Swertia (Ophelia).
Frasera.

The fimbriæ of *Swertia* and *Frasera* are well known. In the *Gentianæ* proper the only distinct account of them which I have met with is that given by Müller ('Alpenblumen,' p. 343, *G. ciliata*). The disposition of the fimbriæ in the various species in which they occur is well worthy of a more careful and detailed study than it has yet received. In some species (e. g. *Gentiana montana*, *pleurogynoides*, and *rupicola*) the parastemonal fimbriæ are so minute as to suggest that they may be absent in some varieties, which would thus effect a transition between *Lophanthe* and *Actinanthæ*. Sir J. Hooker ('Flora of New Zealand') has

already suggested that *G. concinna*, *saxosa*, and *pleurogynoides* may be varieties of *G. montana*. Perhaps it may be as well to mention that the mycelia of fungi, not infrequent in dried flowers, occasionally resemble fimbriæ.

IV. *Stephananthe*.

The corolla is elongated, campanulate, or infundibulate; the relatively short lobes becoming deflexed at right angles to the elongated "cup" in the fully expanded flower. Just below the junction of each lobe with the cup, the inner wall of the corolla is produced into a transverse ridge, the free, slightly convex, edge of which becomes divided into a number of broad flat unequal lobes, and these, again, subdivide into approximately equal, flat, elongated and pointed pectinations. The longitudinal axis of these (in the species which I have examined) is traversed by a vascular bundle derived from the veins of the corolla; and, in this respect, they differ from the fimbriæ of *Lophanthe*, in which I have found no vascular bundles. For the sake of distinguishing them from the fimbriæ, I propose to call these structures, which constitute the well-known "corona," *pectines*.

It is easy to imagine that the *pectines* may have been derived from parastemonal fimbriæ, by the transverse extension of the upper ends of the two series of such fimbriæ until they met in the middle line, while the longitudinal part of each series became aborted; but I have met with no indication of the transitional forms between *Lophanthe* and *Stephananthe* which, on this hypothesis, must have existed. In *Frasera* there are transversely disposed rows of fimbriæ which have a certain, though not very close, resemblance to the pectines; but they are situated on the basal side of the nectaries and close to them, while the pectines are on the opposite side and far away from the nectaries. In the expanded flower, the pectines are directed upwards and inwards, sometimes more in the one direction, sometimes more in the other. It would be very interesting to ascertain whether their position does, or does not, vary according to the state of development of the pollen and the stigmatic surfaces.

The following species are referable to this type. Those marked with an asterisk are placed here on the authority of Grisebach or of Weddell.

A.	B.
Gentiana	Gentiana
Amarella.	liniflora.
campestris.	nitida.
germanica.	*inflata.
tenella.	*thyrsoides.
*auriculata.	*crassolæma.
*nana.	*trichostemma.
*livonica.	*scopulosa.
*acuta.	*filamentosa.
*floribunda.	*Ringii.
*mexicana.	

These are all the types of floral structure which I have met with in the Perimelitous series. It will be observed that, looking at them broadly, they present a general progress, so far as the shape of the corolla is concerned, from the stellate form with deeply divided lobes in, e. g., *G. aurea*, to the infundibulate form with sharply deflexed lobes in, e. g., *G. campestris*; and, so far as the difficulty of access to the nectaries is concerned, from the openness to all comers in the first case, to the hiding away at the end of horns in *Keratanthe*, the partial barring of the road in *Lophanthe*, and the more complete obstruction offered by the corona in *Stephananthe*.

In the series of the *Mesomelitæ* the following modifications have presented themselves:—

V. *Asteranthe*.

The corolla is rotate, the cup being very short and the lobes very long. There are no plicæ, fimbriæ, or other appendages, and the expanded flower is widely open.

I find this structure only in the genus *Eustoma* and in *Gentiana lutea*. I am unable to say anything definite about the nectarial surfaces in the former, except that there are none discoverable on the corolla. In the latter, they are well known to form a zone round the base of the ovary. Neither *Eustoma* nor *Gentiana lutea* are, theoretically speaking, satisfactory representatives of the least modified forms of the Mesomelitous series. For this purpose a Gentian with a flower like that of *G. saxosa*, but with the nectaries ovarian, is wanted; and I have not been able to find any which fulfils this requirement. In *Eustoma* the calyx and the ovary are specialized in the direction of the

type which I shall describe under the head of *Lissanthe*; and in *Gentiana lutea* in the direction of *Ptychanthe*. The spathe calyx and the ovary of *Gentiana lutea* present points of strong resemblance to those of *G. purpurea*; and the free hybridization, under natural conditions, of the two last-mentioned species is asserted upon apparently strong evidence. In my opinion, however, that evidence is by no means so conclusive as it looks at first sight; and the facts of the case require careful and experimental re-examination.

It is of course possible that *G. lutea* may be an ally of *G. purpurea* which has reverted to a less modified condition; but at present I see no sufficient grounds for adopting that hypothesis.

VI. *Limnanthe*.

The corolla is rotate and devoid of nectaries. The margins of the lobes may be lacinated; or their surfaces may be beset with longitudinal rows of fimbriæ (*Menyanthes*). Five, apparently glandular "hypogynous" tubercles are commonly developed at the junction of the walls of the ovary with the perianthial cup, which is more or less adherent to the base of the ovary.

A.	B.	C.
Menyanthes.		
Limnanthemum.	Limnanthemum.	Limnanthemum.
		Villarsia.
D.		E.
Liparophyllum.		Liparophyllum.
Limnanthemum.		
Villarsia.		

All systematic botanists recognize the aberrant character of the *Menyantheæ*. But I do not find in the works which I have consulted any notice of the circumstance that some of them, at any rate, present a more or less marked perigyny. I have examined only *Limnanthemum indicum*, *Menyanthes trifoliata*, *Villarsia capensis*, and *Liparophyllum Gunnii*; but in all these the perianth adheres to the base of the ovary, and the adhesion becomes more and more extensive in the order in which the species have been named.

VII. *Lissanthe*.

The corolla is devoid of nectaries. Sometimes there are distinct, apparently nectarial, tubercles on the base of the ovary;

but, in the great majority, the presence or absence of nectarial surfaces has yet to be determined. Many are said to have "rotate" corollæ; but in all such which have come under my observation the corollæ are really hypocrateriform. Usually, the corolla varies from campanulate to long-tubed infundibulate forms; and the cup or tube is thin-walled, elastic, and pretty closely embraces the ovary. The filaments are inserted, sometimes very low down, and sometimes very high up in the tube. In some cases the anthers are united round the style, and the stigmas form a circular disk above the synantherous staminal ring (*Voyria*).

α. Corollæ short-tubed (hypocrateriform).

Lapitheæ, Exacum, Chironia, Sabbatia, Dejanira.

β. Corollæ long-tubed (infundibulate).

Chlora, Erythræa, Canscora, Coutoubea, Prepusa, Lisianthus, Tachiadenus, Belmontia, Voyria.

Here, as in preceding cases, the principle of the observed modification is obviously the interposition of obstacles in the way of access to the deep-seated portions of the cavity of the flower. In this respect, the flowers of *Voyria* and those of the long-tubed *Lisianthus* and *Tachiadenus* are models of obstructiveness.

I have examined species of the following genera:—

A.	B.	C.	D.	E.
Erythræa.	Erythræa.	Erythræa.	Erythræa.	Erythræa.
Chlora.				
Sabbatia.	Sabbatia.	Exacum.		
	Dejanira.	Sebæa.	Sebæa.	Sebæa.
	Coutoubea.	Belmontia.		
	Prepusa.	Tachiadenus.		
	Tachia.	Chironia.		
	Lisianthus.	Canscora.	Canscora.	
	Voyria.			

The nature of the cup-like "hypogynous disk" of some of the "Lisyanthæ" of Grisebach requires investigation. In the only species presenting this structure which I have examined, it appears to be formed by the coalescence of expansions of the bases of the filaments.

VIII. *Ptychanthe*.

The corolla is campanulate or infundibulate, never rotate. The wall of the tube, between the interlobular sinuses and the insertion of the filaments, is produced into a series of longitudinal plications or "interlobes," the folded edges of which project into the throat of the tube, and more or less completely divide it into a corresponding number of longitudinal passages. The free margins of the interlobes may extend as far as those of the lobes, and they may be provided with long laciniae. In some species the anthers cohere into a ring round the style, below the stigma, which last may take the form of a disk. Very often, the stemono-corolline symphyses are produced into strong longitudinal ridges, which continue the direction of the interlobular folds, and, by abutting against the ovary, subdivide the basal moiety of the cavity of the flower into passages which continue those in its marginal half. The base of the ovary is often tuberculate and clearly nectarigenous. The basal portion of its cavity is often devoid of ovules; and, sometimes, is elongated into a narrow stipes, which, in certain cases (e. g. *Crawfurdia*), attains a great length.

This type of structure is found exclusively in those species of the genus *Gentiana* which are included by Grisebach under the heads of *Celanthæ*, *Tretorhiza*, *Cyane*, *Chondrophyllum*, *Thylacites*; in some of the *Andicola*; and in the genus *Crawfurdia*.

I have specially examined the following out of the numerous species which exhibit this type of structure, several in the fresh state :—

A.	B.	C.
<i>Gentiana</i>	<i>Gentiana</i>	<i>Gentiana</i>
verna.	sedifolia.	pedicellata.
prostrata.	prostrata.	zeylanica.
squarrosa.	spathacea.	Loureirii.
asclepiadea.	adsurgens.	
Andrewsii.	ramosissima.	
affinis.	Gayi.	
acaulis.		
purpurea.		
Burseri.		
punctata.		
cruciata.		
nikoensis.		
Bucgeri.		
Thunbergii.		
japonica.		
<i>Crawfurdia</i> .		

Such are the types or leading modifications of floral structure which I have met with; and such the evidence, taken together with the extant descriptions of the forms I have not examined personally, on which I base the conclusion that they embrace all the most important morphological modifications of the corolla which the Gentianæ offer. It will be observed that, unfortunately, they do not exhibit any particular relation to the received family, or even generic, groups. The accepted genus *Gentiana*, for example, exhibits no fewer than five of the eight types of floral structure; while the *Lissanthe* type is exhibited by some five-and-thirty accepted "genera." If *Frasera* and *Swertia* are to be regarded as generically distinct from *Gentiana*, I fail to see on what principle *G. amarella* and *G. purpurea*, which differ at least as much from one another as *Swertia*, *Frasera*, and *Gentiana* do, can be grouped into one genus. Considerations of this kind, which might be multiplied indefinitely, obviously suggest a thorough revision of the taxonomy of the Order—a task which I certainly shall not presume to attempt, but which will, I hope, be executed by some one more fitted to take such a large and difficult piece of work in hand.

Another important conclusion, which is naturally suggested by the facts to which I have drawn attention, is that the several types in each of the two series bear a certain progressive relation to one another. It is obvious that *Actinanthæ* and *Asteranthæ* are the simplest and least modified forms in each series; that *Stephananthæ* is the most differentiated of the *Perimelitæ*; that *Ptychanthæ* and the more specialized forms of *Lissanthe* are the most differentiated of the *Mesomelitæ*; while *Lophanthæ* and *Keratanthæ* in the one series, *Limnanthe* in the other, constitute lower grades of differentiation, though they are nowise to be regarded as transitional between any of the others.

Thus, on purely morphological grounds and as a mere generalization of the facts, without the introduction of any speculative considerations, the relations of the various types may be represented thus:—

Or, to put the facts in another way, the several types in each series may be regarded as modifications of a common plan, of which the simplest exemplification is to be found in *Actinanthé* and *Asteranthe* respectively. If so, it is an easy step to the conclusion that both these are slightly diverse modifications of a still more simple, but, at present, purely hypothetical, common form, having the main features of *Actinanthé* and *Asteranthe*, but with the nectarial surfaces either feebly developed on both ovarian and corolline surfaces, or entirely absent. I will call this hypothetical "Ur-gentian," *Haplanthe*.

Thus far I have endeavoured to travel no hair's breadth beyond matters of observation and their obvious relations. It is plain that, even if all the five hundred and odd species of Gentianæ had been created separately and raised in pots in the Garden of Eden, their morphological relations would have been exactly what they are. But, to a believer in evolution, the significance of these facts is unmistakable. With whatever caution one may be inclined to regard phylogenic speculations, it is hard, in such a case as this, to resist the force of the suggestion, that these morphological relations do really indicate the path which the evolution of the plants composing the Order has followed. At any rate, the evidence is strong enough to justify us in accepting this conception as a good working hypothesis. And there is the more justification for doing so, that, if we regard the morphological facts by the light of Sprengel and Darwin's theory of the origin of flowers, they at once become intelligible.

In foraging for information about the Gentians, immediately after my return to England, I took up Müller's 'Alpenblumen'; and I was exceedingly struck by the views put forward in the remarkable page and a quarter which he devotes to a "Rückblick auf die Gentianarten" (p. 348), and which I here translate:—

"The genus *Gentiana* is fitter than almost any other to furnish a biological explanation, from the arrangements in regard to fertilization, of the systematic grouping based on morphological indications; and to dispose the subdivisions of the system as branches of a parent stem. It is primarily divisible into two main branches, of which the one secretes honey from the lowest part of the ovary, the other from the lowest part of the corolla. If, then, two kinds of nectarial structure have arisen from an original uniform nectarial structure, the common ancestor of these two groups must have secreted honey, both from the base of the ovary and from that of the corolla, as is the case, *e. g.*, in *Saxifraga oppositifolia*; and thus, in the one group the one half, and in the other the other half, must have been specially developed, to the exclusion of its fellow. But it is also conceivable that the ancestors of *Gentiana* were honeyless, and that the two forms of nectary have been developed independently.

"Of the one of the two main branches, we have a lateral twig remaining in *G. lutea*, which stands low down in point of development, and is certainly nearest the common stem. Like *G. lutea*, without doubt, the ancestors of the genus had fully open flowers, with almost free petals, and tempted the appetite of their fertilizers, either with perfectly accessible honey, in the angle between the ovary and the corolla, or only with pollen. In any case, they were open to the visits of very various insects, which therefore subserved cross-fertilization irregularly and, as it were, accidentally (as in *G. lutea*), so that the occurrence of such fertilization was by no means assured, and spontaneous self-fertilization in case of need could not be dispensed with.

"After the development of the nectaries, Bees, and especially Humble-bees, proved the most effective cross-fertilizers; and campanulate flowers adapted to them became developed. In the one branch, unbidden guests were excluded by the formation of deep passages (*Saftlöcher*); and, by the coalescence of the anthers into a ring round the style, cross-fertilization by Humble-bees was assured (*Cœlanthe**). In the other branch, fimbriæ of the

* *Ptychanthe* (mihi).

petals, at first, afforded an imperfect defence against useless visitors, and narrowing of the flower ensured the contact of the Bees with the stigmas as well as with the anthers (*Crosso-petalum**).

"Subsequently, in the one main branch, under the conditions already indicated, the *Cælanthe*-form, adapted to Humble-bees, was bred into the *Cyclostigma*-type†, adapted to Butterflies; whilst in a particular offshoot of the other main branch, the development of the pectines and the narrowing of the corolla around the ovary brought Butterflies as well as Humble-bees into service as cross-fertilizers (*Endotricha* ‡).

"The original yellow colour of the flowers (as in *G. lutea*) was gradually changed into blue by the selective action of Humble-bees; and instructive intermediate stages of this process are seen in the species of *Cælanthe*. But after the blue coloration was once fixed, the colour maintained itself throughout the process by which Butterflies, by unconscious selection, bred *Cælanthe* into *Cyclostigma*."§

I confess that, when I first read this uncompromising application of the theory of flowers, originated by Sprengel and Darwin, to the case of the Alpine Gentians, I thought it somewhat rash, and gave it a very cool and sceptical reception. It occurred to me that if it was a valid explanation of the morphological characters of the flowers at all, it ought to be applicable not only to those of the Alpine *Gentianæ*, but to the whole genus; and, if to the genus, then why not to the whole order? And the chief motive which has led me to spend a good deal of time and trouble in working over a considerable proportion of the species of *Gentiana* and of the genera of *Gentianæ*, was the obvious importance of arriving at some conclusion respecting this question.

I do not profess to have settled it; but, so far as I have gone, I have found nothing that conflicts with Müller's extremely in-

* *Lophanthe* (mihi).

† *Ptychanthe* (mihi).

‡ *Stephananthe* (mihi).

§ Sir Joseph Hooker ('Flora of New Zealand') observes that the pure blue of the European and Himalayan Gentians is unknown in the Arctic regions and the higher latitudes of the Andes. The widespread *G. montana* has pale whitish-yellow flowers streaked with red or blue. These facts are interesting in relation to the primitive character of the Novo-Zelanian, Australian, and Austro-Columbian Gentians.

genious speculation. On the contrary, everything confirms it. As I have already remarked, the principle which underlies the progressive modification of the flower, in each of my series, is the gradual interposition of more and more obstacles in the way of easy access to the nectaries. Yet these obstacles, whether they arise out of a mere narrowing and elongation of the tube of the corolla, as in *Lissanthe*, or out of the development of fimbriæ and pectines (as in *Lophanthe* and *Stephananthe*), or of interlobes, synanthery, and discoidal stigmata (as in *Ptychanthe*), are always of such a nature that they afford no effectual hindrance to the passage of a thin and flexible organ, like the haustrium of a suctorial insect, but only just sufficient obstacle to make the insect an efficient agent in cross-fertilization.

Few inquiries would be more interesting and profitable (though undoubtedly few more difficult) than the working out of the geographical distribution of the Gentianæ in relation to the Insect Faunæ of the several regions in which they occur.

I merely note that those Gentianæ which have remarkably long infundibulate corollæ are found in regions, such as Madagascar and Guiana, which are tenanted by large Lepidoptera provided with long haustria.

Müller's doctrine respecting the origin of the forms of the flower in the Alpine *Gentianæ* appears to me to be equally applicable to the whole of the Order, and to supply a true cause whereby the morphological facts may be correlated and explained.

I do not suggest that the interaction of cross-fertilizing insects with the variation in the structure of the corolla accounts for all the characters by which the five hundred species of Gentianæ differ from one another. Why one species is annual and another has a rhizome; why the great majority have opposite palmati-veined leaves, while some have alternate or pennati-veined leaves; why the majority have a single-celled ovary, and yet, in many, the ovary is more or less completely two-celled*; why most are herbaceous, while some are bushy and

* The partially, or wholly, two-celled ovary appears to be generally regarded as the result of the gradual introrsion of the margins of the carpellary phyllomes into the cavity of a primitively one-celled ovary. But had "*Haplanthe*" a one-celled ovary? Must not the apocarpous condition precede the syncarpous? Does not the state of the ovary in Apocynæ and Asclepiadæ rather suggest that the primitive Gentians (or perhaps, I should rather say, the primitive stock of all these orders) had an ovary like that of a hypogynous Saxifrage?

some are climbers, are problems hardly to be solved by the consideration of the causes which have brought about the modification of the corolla. But I have little doubt that, with larger knowledge, analogous causes will be found to be operative in all these cases. One of the great lessons which Darwin has taught us is faith in the doctrine of sufficient causes; and consequently hesitation in assuming that any structure, however slight or unimportant in appearance, is devoid of significance in relation to either present or past conditions of existence, the chiefest of these being the struggle for existence with competitors, while climate and station probably occupy a very secondary place.

Even in respect of geographical distribution—upon which climate and station are usually assumed to exercise so great an influence,—facts which have come under my notice in studying the Gentians have led me to be a little sceptical as to the extent of that influence.

At Arolla I never met with a specimen of *Gentiana acaulis* anywhere except in the region between the pine-woods and the snow-line. Yet this same species grows so freely in some parts of Southern England, as to be used for the borders of beds in a kitchen-garden*. The genus *Erythræa*, which is notorious for the slightness of the differences between its "species," is of world-wide distribution. It occurs all over Europe, in the Sinaitic Desert, in Egypt, in Hindostan, in the hottest parts of Australia, and in the moist temperate climate of New Zealand. Mr. Gunn, in a note appended to specimens of *Gentiana montana* in the Kew Herbarium, says that this species occurs everywhere, from the shore to the summit of the mountains. *Gentiana campestris* is said by Hooker and Arnott to be "abundant in Scotland, especially near the sea." It was no less abundant at Arolla from 6400 feet to the snow-line.

In studying, with some care, the geographical distribution of various large and widespread groups of closely allied animals, such as the *Canidae*, the *Astacomorpha*, and freshwater Fishes, I have been much impressed by the necessity of a most minute study of their morphology as a preliminary to any attempt to deal with the facts of distribution. I think there is no greater mistake than to suppose that distribution, or indeed any other large biological question, can be studied to good purpose by those

* Lady Elizabeth Cust informed me that this was the case at Cobham Park in her childhood.

who lack either the opportunity or the inclination to go through what they are pleased to term the drudgery of exhaustive anatomical, embryological, and physiological preparation.

Elaborate works on Distribution have been published which are of little more value than catalogues of reference, because their authors have been unaware of this necessity. And I may point my remarks by showing that even such a brief and imperfect sketch of the minuter morphological characters of the Gentianæ as is here presented is fruitful of suggestions in regard to their Distribution.

My studies of Animal Distribution have led me to the belief that the division of the land-surface of the globe into large areas, which corresponds most nearly with the broader facts, may be stated as follows. Europe, Africa, Asia, and North America as far as Mexico form one great province—ARCTOGÆA; in which Ultra-Saharal Africa, Madagascar, Hindostan, and Indo-China are more or less distinctly characterized as subprovinces. For my present purpose it will suffice to speak collectively of the latter as the Southern Arctogæa, in contradistinction to the rest of the province as Northern Arctogæa. South America, with the Isthmus, as far as Mexico, constitutes a second great province, AUSTRO-COLUMBIA; Australia with the adjacent islands a third; while New Zealand and the neighbouring islets may be most conveniently regarded as a fourth.

In mentioning the species of the various types of Gentianæ which I have examined, I have arranged them under the heads of A, for Northern ARCTOGÆA; B, AUSTRO-COLUMBIA; C, Southern ARCTOGÆA; D, AUSTRALASIA; E, NOVO-ZELANIA.

Adopting this scheme of four great distributional provinces, one of which is subdivided into two regions, the following propositions appear to me to hold good of the Gentianæ:—

1. Species of the Order are found in all five regions. They flourish within the Arctic Circle and up to the limit of perpetual snow in mountain-ranges. They also abound in sundry tropical climates, both moist and dry. The *Limnanthe* type, represented exclusively by marsh- or water-plants, occurs in all the regions, and will not be further mentioned.

2. The head-quarters of the Order (if we consider the number of types represented) are in the North Arctogæal and the Austro-Columbian regions, both of which contain representatives of all the types.

3. The Australasian, South Arctogæal, and Novo-Zelanian regions are all poorer in types. South Arctogæa contains only three, *Lophanthe*, *Lissanthe*, and *Ptychanthe*; Australasia two, *Lophanthe* and *Lissanthe* (perhaps *Actinanthé*); Novo-Zelania three, *Actinanthé*, *Lophanthe*, and *Lissanthe*.

4. The Australasian and Novo-Zelanian provinces have very few species; in the Northern and Southern Arctogæal regions they are very much more numerous. Their numbers are greatest in Austro-Columbia.

5. Only one species is certainly known to be common to any large extent of two provinces, namely *Gentiana prostrata*, which extends from the Eastern Alps of Europe, by way of Northern Asia and America, to the southern extremity of South America.

6. The only types which certainly occur in all five regions are *Lophanthe*, *Limnanthe*, and *Lissanthe*. *Actinanthé* is known in three; namely the Northern Arctogæal, the Austro-Columbian, and the Novo-Zelanian. I think it probable, however, that it may yet be found in Australia. *Keratanthe* and *Stephananthe* occur in two, Northern Arctogæa and Austro-Columbia; *Ptychanthe* in three, Northern and Southern Arctogæa and Austro-Columbia.

7. Notwithstanding the general similarity of the climatal conditions in the mountain-chains of Northern Arctogæa and Austro-Columbia, and the abundance of Gentians in both, their Gentian Floræ are fundamentally different. In the Pyrenees, the Alps, and the Himalayas, the *Ptychanthe* type is largely represented in relation to the *Actinanthé*, *Lophanthe*, and *Stephananthe* types.

In the Andes it is just the other way. Gentians of the *Actinanthé* and *Lophanthe* types abound, and *Stephananthe* is well represented; while I cannot make sure of more than six representatives of *Ptychanthe*, though this type is so easily recognized that there is little chance of its being overlooked or mistaken. Out of more than 60 species of South-American *Gentianæ*, enumerated in Grisebach's 'Genera' and Weddell's 'Chloris,' it appears that nine, namely, *G. nitida*, *liniflora*, *inflata*, *thyrsoides*, *crossolæma*, *trichostemma*, *scopulosa*, *filamentosa*, and *Ringii*, belong to *Stephananthe*, and six to *Ptychanthe*; while the rest all belong either to *Actinanthé* or to *Lophanthe*. Judging from the proportion of those which have examined, it seems probable that there are nearly as many of *Lophanthe* as of *Actinanthé*.

And when it is considered that only one species is common to

the highlands of Northern Arctogæa and of Austro-Columbia, the contrast between the Gentian Floræ of the two becomes still more striking.

In Sir Joseph Hooker's well-known paper "On the Distribution of Arctic Plants" (Transactions Linn. Society, vol. xxiii.), the following twelve Gentianæ are stated to occur north of the Arctic Circle:—*Gentiana aurea*, *propinqua*, *detonsa*, *arctophila*, *Amarella*, *tenella*, *glauca*, *prostrata*, *nivalis*, *verna*; *Pleurogyne rotata*, *Menyanthes trifoliata*.

I have not examined *Gentiana arctophila*; but I believe it to belong, like *G. aurea*, *propinqua*, and *detonsa*, to the *Actinanthæ* type. In this case the components of the Gentian Flora of the Arctic regions may be classified as follows:—

Actinanthæ.	Keratanthæ.	Lophanthæ.	Stephananthæ.
5	0	0	2
Limnanthæ.	Asteranthæ.	Lissanthæ.	Ptychanthæ.
1	0	0	4

In the Flora of the European Alps I can find no representative of the *Actinanthæ* type except *Pleurogyne carinthiaca*. On the other hand, two of its Gentianæ, *Gentiana ciliata* and *Swertia perennis*, belong to *Lophanthæ*.

Passing to the *Stephananthæ* type, *Gentiana tenella* is admittedly common to the Alps and the Arctic regions; but the former have *G. germanica*, *campestris*, and *nana* in place of *G. amarella*. How far any real distinction is to be drawn between *G. amarella* and *G. germanica* is a question for future examination.

Limnanthæ is represented by *Menyanthes trifoliata* in both the Arctic and the Alpine regions; *Asteranthæ* only in the Alpine; *Lissanthæ* in neither.

The ordinarily recognized species of *Ptychanthæ* in the proper Alpine region of Europe are some eighteen or nineteen in number. Three of these, namely, *G. verna*, *nivalis*, and *prostrata*, are also Arctic; but the Gentians of the *acaulis* group, which flourish, along with *verna* and *nivalis*, in the Alps, are unknown in the Arctic regions. Again, the Gentians of the *purpurea* group, though they occur in Southern Scandinavia and Kamtschatka, stop short of the Arctic Circle.

It appears to me that these facts are very difficult to reconcile with the view that the high Alps have been peopled with their Gentianæ from the Arctic regions or *vice versâ*. The abundance

of Gentians of the *Actinanthæ* type in the Andes indicates their adaptability to alpine conditions; yet they are absent in the Alps, while well represented in the Arctic regions.

It must be understood that I deal only with the broad facts of the case. Some attempts which I made to study the few forms which abounded at Arolla, with a view of distinguishing the book-species among them, became unsuccessful exactly in proportion to the number of specimens I examined; and I left off with the conviction that I had no means of knowing whether *G. purpurea* was distinct from *G. punctata*, *G. campestris* from *G. germanica*, or *G. verna* from three or four other "species." In *G. campestris* the number of varieties in size, habit, foliation, form, number of parts and colour of the flower, were really astonishing; and I met with the strangest monstrosities. In *G. verna* the range of variation was quite as remarkable. If all the species of *Gentianæ* are in this case, it is perilous to attempt numerical estimates on the foundation of ordinary collections.

DISTRIBUTIONAL DIAGRAM.

NORTH ARCTOGÆA.

Actinanthæ.

Keratanthæ.

Lophanthæ.

Stephananthæ.

Asteranthæ.

Limnanthæ.

Lissanthæ.

Ptychanthæ.

AUSTRO-COLUMBIA.

AUSTRALASIA. NOVO-ZELANIA.

SOUTH ARCTOGÆA.

Actinanthæ.		(?)	Actinanthæ.
Keratanthæ.			
Lophanthæ.	Lophanthæ.	Lophanthæ.	Lophanthæ.
Stephananthæ.			
Asteranthæ.			
Limnanthæ.	Limnanthæ.	Limnanthæ.	Limnanthæ.
Lissanthæ.	Lissanthæ.	Lissanthæ.	Lissanthæ.
Ptychanthæ.	Ptychanthæ.		

The names printed in black letters are those of strongly dominant types in the several regions.

If the facts of distribution of the Gentianæ are adequately stated in the above propositions, one conclusion appears to me to be very clear; and that is, that they are not to be accounted for by migration from any "centre of diffusion," to which a locality can be assigned in the present condition of the world. If the *Gentianæ* of the Andean range had been derived from those of Northern Arctogæa, or *vice versâ*, it seems unaccountable that the proportion of representatives of the types should be so different in the two assemblages; and, still more, that there should be only one species common to both.

There is a well-known case of zoological distribution which presents a certain parallelism with that of the *Gentianæ*. The genus *Tapirus* is represented by certain species in South America, and by another in the Indo-Malayan region. And palæontology furnishes the explanation of the fact by proving the existence of Tapirine animals, which have since died out, over the vast intermediate area in the Middle Tertiary epoch. There has been no migration, but simply local modification of the genus at opposite ends of its primitively continuous area of distribution, with subsequent extirpation over the intermediate space.

I am not aware that any fossil remains of Gentianæ have been brought to light; but it is known that many of the plants of the Middle Tertiary epoch were extremely similar to those which now exist. Furthermore, it is certain that the great elevated areas of both the Old and the New Worlds existed, and had attained a considerable height, possibly even greater than that which they at present possess, during the Pliocene epoch. Under these circumstances, I see no reason to object to the supposition that species of the genus *Gentiana* itself, closely similar to our existing species, may have, at that time, occupied pretty much the same regions and stations as those in which they are now found, and had already adjusted themselves to their hard conditions of existence. If so, the changes in the physical geography of the world, which preceded and accompanied the Glacial Epoch, must undoubtedly have narrowed the range, and probably extirpated a good many of the pre-Glacial species of *Gentiana*. But the remainder would have as readily found secure refuge in sheltered nooks and valleys, as the existing species do; and, as the climate improved with the passing away of the Glacial epoch, they would start afresh from their fastnesses to compete with other immigrants for the possession of the new localities laid open to them.

Gentiana prostrata may have had its present distribution before the Glacial epoch. In fact, I am more surprised to find only one species widely spread over both the Northern Arctogeal and the Austro-Columbian provinces, than I should be if there were several; and I am not a little disposed to think that a serious critical comparison of the two Floræ, with due attention to the range of variation of the species in each, may bring about a considerable alteration of our views on this subject.

The supposition that the distribution of the Gentianeæ in Pliocene or in Miocene times was substantially similar to what it is now, is of course no solution of the problem of their distribution; it is simply driving the search for that solution further back. Is it possible to fix any anterior limit to this retrogression?

I suppose it would be, if one could fix the age of the first appearance of Diptera, Hymenoptera, and Lepidoptera provided with long haustria. For, upon Müller's hypothesis, the existence of the *Keratanthe*, *Stephananthe*, *Lissanthe*, and *Ptychanthe* types presupposes that of such insects. Unfortunately, we are, as yet, hardly in a position to speak positively on this point. The most that can be said is that there is no evidence that they were abundant before the middle of the Mesozoic epoch, or that they existed in Palæozoic times. Free play, therefore, is left to speculation; and I do not think any good grounds could be given for denying the existence of even the more specialized Gentianeæ in the Cretaceous epoch; while the "Ur-Gentian," the hypothetical anemophilous *Haplanthe*, may be dated back almost as much further as probabilities permit us to carry the existence of flowering plants. For it is obvious that a very slight further modification, in the direction of simplicity in *Haplanthe*, would bring about a form of flower which might serve as the starting-point for those of almost all the Orders of Dicotyledons. But speculation as to when or where the hypothetical *Haplanthe* may have originated is, for the present, idle. "Ignoramus" and, I fear, for a long while, "ignorabimus."

Considering how slight the morphological differences between the eight types really are, and that (according to the hypothesis) they have been brought about by the selective operation of agencies of the same order, it seems to me that it would be rash to deny that species belonging to the same type may have arisen in different

localities. I do not think it probable that the process of modification and the materials it works upon would be so similar in widely different localities as to give rise to the close similarities which lead us to group individuals in the same species; but the polygeny of genera, and still more of larger groups, appears to me to be highly probable*.

We are very much in the habit of tacitly assuming that because certain plants and certain animals exist only under certain climatal conditions, there is something in what we vaguely call the "constitution" of the plants or animals which binds them to these conditions, and renders it impossible for them to live elsewhere. I wish we could get rid of this word "constitution;" for I take it to be one of the many verbal anodynes by which the discomfort of ignorance is dulled. If it means any thing definite, it merely signifies that there is some morphological or physiological impediment to the existence of the plant or animal, outside the defined conditions; and our business is to find out what that impediment is. When I was at Arolla I was extremely astonished by the distribution of two very common species of *Epilobium* (*E. spicatum* and *E. Fleischeri*), which were flowering at the same time. There was any quantity of the latter among the boulders of the bed of the stream at the bottom of the valley; but nowhere else. And there was any quantity of *E. spicatum* growing on the lateral walls of the valley, from 30 or 40 feet above its bed upwards, but nowhere else. I used to amuse myself by looking for trespassers of either species in the province of the other; but I never could find any. Everybody knows that the seeds of the *Epilobia* are abundant and provided with special aids to distribution by the winds; and there certainly is no failure of breezes in the valley. Every year, therefore, millions of seeds of each species must be scattered over the territory of the other. Why does one thrive, and the other die?

To say this depends on the "constitution" of the two species, is simply to wrap up the fact in another form of words. And I can conceive of no investigation more likely to lead to results of far-reaching importance, than that which should get to the bottom of this, or any analogous case.

Finally, I may put another question. Is anybody in a posi-

* I find weighty remarks on this topic in Engler's "Versuch einer Entwicklungsgeschichte der Pflanzenwelt," 2 Theil, p. 318.

tion to deny that, in the absence of all other phænogamous vegetation, the Gentians might have occupied every region and station on the earth's surface in which flowering plants can exist? Is there any ground for seeking the causes of their distribution elsewhere than in the competition with other plants which they have undergone and are undergoing, and in the course of which it has often happened that the success of a given form in adapting itself to certain conditions has involved a corresponding diminution of the faculty of adapting itself to others?

Such are the observations I have to offer. I call them "Notes and Queries;" and I am afraid there are more queries than notes. My hope in offering them to the Society is to stimulate those who are better qualified than I am to carry through a serious botanical inquiry, and who have more time before them than I have to take up the subject. I believe that the systematic and exhaustive study of a single well-chosen Order, and of all the biological problems which it presents, would inaugurate a new era in the progress of Botany. The amount of patient and sagaciously directed labour which is embodied in our standard systematic works is astounding; and the deepest gratitude is due to those who have thus brought the data of Vegetable Morphology and Distribution into a shape in which they can be dealt with. But from the point of view of the Evolution doctrine, it is obvious that Taxonomy and Distribution have to be subjected to a process of revision, which will hardly fail to revolutionize both.

DESCRIPTION OF PLATE II.

A scheme to illustrate the morphology of the flower of the *Gentianææ*.