# On the Relation between the "Bloom" on Leaves and the Distribution of the Stomata. By Francis Darwin, F.R.S., F.L.S.

[Read 4th February, 1886.]

Sachs* has pointed out that there is a connection between the distribution of stomata on leaves and their protection from wet by the wax-like coating commonly known as "bloom."

He says:—"It is especially the surfaces of leaves that are well provided with stomata which seem to be protected against the adherence of water. The leaves of water-plants such as the Nymphæaceæ, *Polygonum amphibium*, *Hydrocharis*, &c., are thoroughly wetted on their lower surfaces, which have no stomata; but water runs off in round drops from the upper surface, where the stomata occur. The meaning of this fact in the economy of the plant is evident; the mouths of the stomata would be closed by prolonged contact with water, and would thus prevent the rapid ingress and egress of gas."†

In the year 1878 my father was engaged in studying the bloom on leaves, and it fell to my share to follow up the suggestion of Sachs—that one function of bloom is to be found in the protection of the stomata from wet. The mere fact that stomata close when the leaf is wetted might lead us to expect that water interferes with their function, even if we had no theoretical reasons for believing so. Barthélemy (as quoted in the Botan. Centralblatt, vol. xix.) has recorded a fact demonstrating the closure of stomata by water. The leaves of *Nelumbium* give out bubbles of gas when immersed in water and exposed to sunshine, but the production of bubbles ceases if the "bloom" is removed so that water comes into contact with the stomata. The conclusion that the closure of the stomata is due to contact with water must, however, be cautiously received, for it seems probable, as Garreau‡ states, that the act of washing

* 'Physiologie Végétale' (French translation), 1868, p. 178.

† In Lundström's interesting paper, "Die Anpassungen der Pflanzen an Regen und Thau" (Nova Acta Reg. Soc. Sci. Upsal. 1884), the author points out that in *Trifolium repens* the *under* surface of the leaflets is wetted by rain, while the upper bloom-protected surface remains dry. He connects this fact with the occurrence of stomata on the upper surface.

‡ Ann. Sci. Nat. 1850.

off the bloom stops up the stomata. There are certain facts which go to show that stomata tend to be developed in parts protected from rain. The well-known fact that in a large number of leaves the stomata are exclusively on the lower surface, where they are not so likely to be wetted, is in accordance with this statement. In vertical leaves, as is well known, the stomata are equally distributed on the two surfaces*, and in most such leaves the surfaces would be equally wetted. An interesting confirmation of this view may be found in the fact mentioned by Haberlandt† that lenticels are "fairly equally distributed all round vertical branches, while on horizontal branches they are much more numerous on the lower than on the upper side. We might expect that the function of lenticels would be interfered with by wetting in the same way as applies to stomata, and it is therefore of interest to find that (at least in young branches, according to Haberlandt) they tend to be developed chiefly on the underside, where they are more or less protected. In young leaves, which are often more nearly vertical than the adult leaves of the same species, we may perhaps believe that stomata are protected by not being open at first, but whether the opening of the stomata corresponds with the assumption of the horizontal position I cannot say. Von Höhnel has shown that the cuticular transpiration of young leaves is very large, so that even with closed stomata they may transpire sufficiently.

The idea that the tendency to accumulation of stomata on the under surface of leaves is an arrangement by which they are protected against rain, is in accordance with Hohnfeldt's observations‡. He found that in underground leaves the stomata show no marked tendency to accumulate on the under surface; indeed the contrary is often the case. This is precisely what might be expected on the theory that they are developed on the under surface of aerial leaves as a protective against rain, &c., since the underground leaves are of course not exposed to such dangers. Hohnfeldt quotes Caruel's remarks on

* In the nearly vertical leaves of *Lactuca Scariola* I found the stomata on the morphologically lower side to be the most numerous—exceeding those on the other side in about the proportion of 140 : 100.

† Physiolog. Pflanzenanatomie, p. 317.—Haberlandt gives no explanation of the fact.

‡ As reported in the Botan. Centralblatt, 1880, p. 1161.

*Passerina hirsuta*: the upper surfaces only of the leaves have stomata, and these surfaces are protected by being pressed closely to the stem or against other leaves.

With regard to the kind of wetting which is prevented by the bloom on leaves, it is probable that it is more effective against rain than against dew, since at least some bloom-protected leaves are easily covered with a coating of dew in very finely divided drops. It is curious to observe the effect of immersion on such a leaf—which may be plunged into water still retaining its coating of dew, and will be found to be perfectly dry on being removed from the water—so that the readiest way of drying such a leaf is to dip it into water. Another fact may perhaps be mentioned as tending, as far as it goes, to confirm the view here advocated—namely, that bloom is frequently absent from the projecting nervatures, though present on other parts of leaves—the nervatures being the parts of leaves on which stomata are not developed.

Finally, it must be remembered, since bloom certainly has other functions besides the protection of leaves from wetting, that it cannot be expected that every species should show a correspondence in the distribution of bloom and stomata. Lundström's essay, above alluded to, is of interest in this connection He shows that in some species arrangements exist for the collection and distribution and absorption of rain as it falls on the leaves; and here the surfaces are so modified, by secretions &c., that they are wetted with especial ease. This class of cases must no doubt have a bearing on the subject of the present paper. Such cases as those of *Trifolium repens* and *Vaccinium Vitis-idæa*, where the *lower* surface of the leaf is especially wetted by rain, are of much interest.

The case of *Lobelia Erinus* also conveys a caution. Here, according to Lundström, there are small scale-leaves at the base of the flower-stalk which collect the rain on their upper surfaces; yet it is on these surfaces that the stomata exclusively occur. This case is not in reality opposed to my results, since the stomata function as organs of absorption.

The results here obtained were worked out in the year 1878, and it was intended to publish them in a work of my father's to be devoted to the subject of bloom. I shall on another occasion give some account of my father's results, and of some further work of my own in the same direction. The present paper, with the exception of the introductory remarks, is written entirely from my notes of 1878.

Through the kindness of Sir J. D. Hooker I was enabled to carry out the work in the Jodrell Laboratory in the Royal Gardens at Kew. I was thus enabled to obtain a large supply of fresh material, a necessary condition to the success of my investigation. It is a pleasure to me to express my sincere thanks for the opportunity which he so kindly placed at my disposal. I wish also to express my thanks to Mr. R. Irwin Lynch, now Curator of the Cambridge Botanic Gardens, but who at that time held a post at Kew. Through Mr. Lynch's kind assistance I was able to obtain good specimens of the many species which I required.

I first made a list of species of which the number of stomata on the leaves have been determined, using for this purpose the works of

Czech (Botan. Zeitung, 1865).
Kareltschikoff (Bull. de la Soc. des Naturalistes de Moscou, 1866).
Morren (Bull. de l'Académie R. de Belgique, t. xvi.).
Weiss (Pringsheim's Jahrb. vol. iv.).

This list I gave to Mr. Lynch, asking him to supply me with specimens of species chosen at random from among those in my list; I hoped in this way to get some idea of the number of plants which have bloom-protected leaves. But I was obliged to supplement the list with leaves selected as having bloom, so that no accurate conclusions of this kind can be drawn from my tables. In these cases, as well as in many others, I made use of my own observations on the number of stomata.

Having obtained my specimens, I had merely to note the distribution of bloom on the surface of the leaves. This is not so easy as it might seem, since many leaves occur which are perfectly dry after immersion, and which, nevertheless, have no true bloom. In the following tables the leaves noted as having bloom are such as examination with the naked eye sufficed to classify among "bloom" leaves. Bloom is here used to mean a coating of minute particles of a waxy character which is removable either by warm water (about 40° C.) or in any case by ether. Leaves occur which emerge from water dry on the lower surface, but which have no bloom in the above sense.

Between leaves such as these and those which are completely wetted, a number of gradations occur. We find more or less perfect developments of a certain character of the surface—which may be called greasiness. The water coating the surface shrinks into patches or drops, leaving large areas dry. The leaf, in fact, behaves towards water like certain metallic or grease-coated surfaces. The degree of greasiness varies a good deal, some leaves exhibiting it in great perfection, while others do so only when the leaf is shaken. The stomata of many of this kind of leaf must, no doubt, be protected against wet; but as they graduate into those which are easily wetted, I have placed them (except those mentioned on p. 108) in the class having no bloom. I am inclined to think that immersion in water is not a thoroughly satisfactory test of the leaf's capacity of resisting natural sources of wet, since some of the "greasy" or "metallic" class of leaf seem to be much more completely wetted by rain than by a single immersion in water. This is a further reason for keeping the best protected leaves, those which have a true bloom, in a separate class. Leaves such as *Hydrangea quercifolia* and the Raspberry have their lower surfaces almost perfectly protected against wetting, but this is due to a fine coating of hairs. As such cases do not bear on the function of bloom proper, but only on the general question of the protection of stomata, they are excluded from my tables.

It must be remembered that bloom is in many cases easily injured, and that in old leaves it is sometimes washed off by rain or removed by rubbing against other leaves, &c. It is therefore possible that some leaves noted as having no bloom may show this coating under other circumstances; I can only say that I have been aware of, and tried to avoid, this error.

In dealing with the results I have been obliged to use a few simple symbols. The number of the stomata on a leaf is expressed as a fraction, of which the numerator expresses the number of stomata on the upper surface and the denominator the number on the lower. Thus $\frac{100}{150}$ would mean that the upper stomata are to the lower as 100 to 150. My figures being taken from different sources cannot be taken to represent any absolute number of stomata per square millimetre, but merely the proportion between the stomata on the upper and lower surfaces.

When there are no* stomata on the upper surface the state of things is expressed by $\frac{0}{S}$, the letter S being employed in the denominator to show that the symbol expresses the distribution of the *stomata* and not of the *bloom*, in which latter case the letter B is employed. According to this plan the floating leaves of water-plants would be symbolized by $\frac{S}{0}$:—no stomata on the under surface. Precisely similar symbols are used to express the distribution of bloom:—

$\frac{B}{B}$=Bloom on the upper as well as on the lower surface.

$\frac{0}{B}$=Bloom on the lower surface only.

$\frac{B}{0}$=Bloom on the upper surface only.

$\frac{0}{0}$=No bloom on either surface.

The leaves examined are divided into four classes according to the distribution of the bloom, and each class is analysed into groups according to the distribution of the stomata.

The leaves forming Class $\frac{0}{0}$ have no bloom on either surface; and those in Group 1 have no stomata on the upper surface.

## Class $\frac{0}{0}$.—No bloom on either surface.

### Group 1.—Stomata=$\frac{0}{S}$. 75 species.

Acer platanoides.
Aconitum Napellus.
A. lycoctonum.
Actæa spicata.
Ægopodium Podagraria.
Æsculus Hippocastanum.
Amygdalus communis.
A. persica.
Andromeda speciosa.
Anemone japonica.
Araucaria Bidwellii.
Asarum europæum.
Asclepias curassavica.
Begonia hydrocotylifolia.
B. quinquifolia.
Betula alba.
Brexia madagascariensis.
Broussonettia papyrifera.
Buxus sempervirens.
Camellia japonica.

* In leaves usually described as having no stomata on the upper surface, there are often a few scattered ones, especially near the veins.

Carpinus betulus.
Celtis occidentalis.
Cerasus Mahaleb.
C. vulgaris.
Citrus Aurantium.
Clematis Viticella.
Cratægus oxyacantha.
Fagus sylvatica.
Ficus benjamina.
F. cordata.
F. elastica.
Fraxinus excelsior.
Gastonia palmata.
Gentiana cruciata.
Girondia manicata.
Gleditschia triacantha.
Goldfussia glomerata.
Hedera Helix.
Helleborus niger.
Hydrangea hortensis.
H. quercifolia.
Ilex Aquifolium.
Juglans regia.
Kalmia latifolia.
Lilium speciosum.
Maclura aurantiaca.
Mahonia Aquifolium.
Maianthemum bifolium.
Mercurialis perennis.
Morus alba.
Negundo fraxinifolia.
Olea europea.
Philadelphus coronarius.
Piper magnoliæfolium.
Pittosporum Tobira.
Platanus occidentalis.
Pæonia sp.
Pritzelia zebrina.
Prunus domestica.
P. Laurocerasus.
Pyrus communis.
P. Malus.
Rhodea japonica.
Rhododendron hirsutum.
R. ponticum.
Ribes aureum.
Rubia tinctorum.
Salisburia adiantifolia.
Solanum tuberosum.
Syringa vulgaris.
Taxus baccata.
Theophrasta Jussieui.
Trollius europæus.
Vinca major.
Vitis vinifera.

Group 2.—Stomatal formula between $\frac{0}{S}$ and $\frac{1}{2}$; that is to say, one third, or less than one third of all the stomata are on the upper surface. 29 species.

| | |
|---|---|
| Antirrhinum majus | $\frac{2}{120}$ |
| Apium Petroselinum | $\frac{27}{61}$ |
| Asclepias incarnata | $\frac{67}{191}$ |
| Aster chinensis | $\frac{16}{40}$ |
| Atropa Belladonna | $\frac{55}{227}$ |
| Brassica Rapa | $\frac{21}{61}$ |
| Campanula persicifolia | $\frac{3}{210}$ |
| C. urticæfolia | $\frac{6}{65}$ |
| Capsella Bursa pastoris | $\frac{33}{114}$ |
| Centaurea phrygia | $\frac{23}{78}$ |
| Convolvulus arvensis | $\frac{21}{43}$ |
| Dianthus barbatus | $\frac{12}{47}$ |
| D. deltoides | $\frac{47}{110}$ |
| Galium boreale | $\frac{10}{129}$ |
| Geum urbanum | $\frac{20}{193}$ |
| Gratiola officinalis | $\frac{4}{57}$ |

| | |
|---|---|
| Impatiens parviflorum | $\frac{9}{46}$ |
| Levisticum officinale | $\frac{48}{97}$ |
| Menyanthes trifoliata | $\frac{8}{40}$ |
| Orobus vernus | $\frac{1}{38}$ |
| Papaver Rhœas | $\frac{9}{37}$ |
| Phaseolus multiflorus | $\frac{18}{103}$ |
| Plumbago Larpentæ | $\frac{41}{101}$ |
| Populus dilatata | $\frac{55}{270}$ |
| P. nigra | $\frac{54}{313}$ |
| P. pyramidalis | $\frac{11 \cdot 2}{40 \cdot 6}$ |
| Saponaria officinalis | $\frac{14}{74}$ |
| Senecio vulgaris | $\frac{20}{78}$ |
| Tradescantia subaspera | $\frac{7}{28}$ |

Group 3.—Stomatal formula $\frac{1}{2}$ to $\frac{1}{1}$ (excluding $\frac{1}{2}$, including $\frac{1}{1}$).

The stomata on the upper surface form more than a third, but not more than half, of the whole number of stomata. 30 species.

| | |
|---|---|
| Amarantus caudatus | $\frac{171}{193}$ |
| Aster pyrenæus | $\frac{35}{88}$ |
| Atraphaxis spinosa | $\frac{112}{157}$ |
| Barbarea vulgaris | $\frac{129}{189}$ |
| Bidens tripartita | $\frac{55}{82}$ |
| Calendula officinalis | $\frac{18}{22}$ |
| Chenopodium Bonus-Henricus | $\frac{47}{69}$ |
| Chrysanthemum Leucanthemum | $\frac{42}{49}$ |
| Convolvulus tricolor | $\frac{20}{39}$ |
| Dianthus Seguierii | $\frac{7 \cdot 4}{9 \cdot 2}$ |
| Helianthus annuus | $\frac{175}{325}$ |
| Isatis tinctoria | $\frac{214}{231}$ |
| Lepidium ruderale | $\frac{16}{16}$ |
| Lychnis Viscaria | $\frac{59}{91}$ |
| Pentstemon barbatus | $\frac{185}{233}$ |
| Plantago lanceolata | $\frac{76}{117}$ |
| P. media | $\frac{64}{105}$ |
| Populus Carolinæ | $\frac{263}{405}$ |
| P. monilifera | $\frac{89}{131}$ |
| Rhipsalis crispata (Succulent.) | $\frac{10}{12}$ |
| Rumex Acetosa | $\frac{16}{28}$ |
| Scabiosa arvensis | $\frac{43}{59}$ |
| Silene inflata | $\frac{33}{60}$ |
| Statice latifolia | $\frac{98}{106}$ |
| Tanacetum vulgare | $\frac{72}{82}$ |
| Valeriana Phu | $\frac{69}{95}$ |
| Viscum album | $\frac{1}{1}$ |
| Yucca aloifolia (Thick and leathery.) | $\frac{7 \cdot 6}{8 \cdot 2}$ |
| Zea Mays | $\frac{94}{158}$ |
| Zinnia elegans | $\frac{31}{55}$ |

Group 4.—More stomata on the upper surface than on the lower: stomatal formula greater than $\frac{1}{1}$. 9 species.

| | | |
|---|---|---|
| Acacia decipiens | $\frac{103}{96}$ | Vertical. |
| Achillea Millefolium | $\frac{61}{12}$ | |
| Alisma Plantago | $\frac{135}{100}$ | |
| Araucaria imbricata | $\frac{46}{45}$ | |
| Ranunculus Flammula | $\frac{46}{23}$ | Some leaves have bloom above. |
| Sedum acre | $\frac{6}{4}$ | Succulent. |
| S. album | $\frac{14}{7}$ | Succulent. |
| Sempervivum tectorum | $\frac{107}{60}$ | Succulent. |
| Statice incana | $\frac{75}{60}$ | |

Among the above 143 plants are some which cannot fairly be compared with the rest, from their different structure. These are :—

| | Stomata. |
|---|---|
| Acacia decipiens | $\frac{103}{96}$ |
| Rhipsalis crispata | $\frac{10}{12}$ |
| Sedum acre | $\frac{6}{4}$ |
| S. album | $\frac{14}{7}$ |
| Sempervivum tectorum | $\frac{3}{4}$ |
| Yucca aloifolia | $\frac{76}{8{\cdot}2}$ |

*Acacia* is excluded because of the vertical position of its leaves. The succulents are obviously not comparable with ordinary leaves in the matter of stomata distribution. In a thick fleshy leaf, with relatively few stomata, the few that do exist may be necessarily more evenly distributed than in a thin leaf.

If we divide the species into two sets—(A) in which the stomata on the upper surface are one third or less than one third of the whole number of stomata; (B) where they are more than one third of the whole—we have :—

104 out of 137 species, or 76 per cent., in Class A.
34 out of 137 species, or 24 per cent., in Class B.

These results show clearly that, in leaves with no bloom on either surface, there is a strong tendency towards accumulation of stomata in the lower surface. This is also shown by the fact that, out of the 137 species, 75 (or 55 per cent.) have *no* stomata on the upper surface; that is, in Class $\frac{0}{0}$ (bloom $\frac{0}{0}$), the group $\frac{0}{S}$ are 54 per cent.

## Class $\frac{0}{B}$.

### Leaves with bloom on the lower surface only.

Here are included a few plants of which the lower surface is of such a character as to come out very dry, though not actually covered with bloom; such as *Cobæa scandens*, *Geranium Robertianum*, *Solanum Dulcamara*, &c. 19 species.

| | Stomata. | Remarks. |
|---|---|---|
| Abies canadensis | $\frac{0}{S}$ | |
| A. pectinata | $\frac{0}{S}$ | |
| Acer Pseudoplatanus | $\frac{0}{S}$ | |
| Arauja serifera | $\frac{0}{S}$ | |
| Ailanthus glandulosus | $\frac{0}{S}$ | |
| Cassia floribunda | $\frac{0}{S}$ | |
| Cobæa scandens | $\frac{0}{S}$ | |
| Daphne Mezereum | $\frac{0}{S}$ | Young leaves have bloom above. |
| Geranium Robertianum | $\frac{0}{S}$ | |
| Humulus Lupulus | $\frac{0}{S}$ | |
| Pharus latifolius | $\frac{0}{S}$ | This twisted grass-leaf has its physically upper side free from stomata. (The physically upper side is morphologically the lower side.)* |
| Polygonatum multiflorum | $\frac{0}{S}$ | |
| Primula farinosa | $\frac{13}{103}$ | Mealy underneath. |
| Quercus pedunculata | $\frac{0}{S}$ | |

* M. A. de Candolle has been so good as to call my attention to the fact that Juniper, according to Dutrochet (Mémoire, ii. p. 100), has stomata only on the upper surfaces of the leaves, and the branches hang down so that the upper surface of the leaves is downwards.

| | Stomata. | Remarks. |
|---|---|---|
| Salix babylonica ........................ | $\frac{0}{S}$ | |
| Solanum Dulcamara..................... | $\frac{60}{263}$ | |
| Sophora japonica ........................ | $\frac{0}{S}$ | Young leaves are $\frac{B}{B}$. |
| Tradescantia virginica ................. | $\frac{1\cdot8}{6\cdot4}$ | |

The number of species is small; nevertheless it comes out fairly clearly that where the under surface is protected against wet the tendency of the stomata to accumulate on the lower surface is stronger than in the class where bloom is absent altogether.

Fifteen leaves, or 83 per cent., have stomata exclusively on the lower surface; whereas in Class $\frac{0}{0}$ only 55 per cent. were in this condition.

It will be seen that in the three leaves that have any stomata above, their number does not exceed one fourth of the whole number of stomata.

Two leaves may be mentioned in which a coating of hairs on the lower surface serves almost as well as "bloom" to keep the leaf dry during immersion in water, and in which the stomata are chiefly or exclusively on the lower surface. These are the Raspberry and *Hydrangea quercifolia*.

## Class $\frac{B}{0}$.

### Leaves which have bloom only on the upper surface.

| | Stomata. | |
|---|---|---|
| Convallaria majalis ..................... | $\frac{2\cdot4}{3\cdot1}$ | |
| Lathyrus pratensis ..................... | $\frac{38}{41}$ | |
| Primula Auricula ........................ | $\frac{S}{0}$ | |
| Ranunculus Flammula................. | $\frac{46}{23}$ | Some leaves have no bloom. |
| Trifolium repens ........................ | $\frac{160}{98}$ | |
| Vicia Cracca .............................. | $\frac{65}{22}$ | |
| V. sativa.................................... | $\frac{100}{32}$ | |

Seven species*: of which one has all its stomata on the upper

* It was thought fairer to include only one species of *Primula* and of *Trifolium*.

surface, four have at least twice as many stomata above as below, while the remaining two leaves have the formula $\frac{38}{41}\left(\frac{93}{100}\right)$ and $\frac{2\cdot4}{3\cdot1}\left(\frac{77}{100}\right)$.

## Class $\frac{B}{B}$.

### Leaves with bloom on both surfaces.

Group $\frac{0}{S}$; or those in which the stomata are exclusively on the lower surface. They are 16, or 38 per cent.

Alstrœmeria aurantiaca.
(The stomata are on the physically lower, but morphologically upper side.)
Aquilegia vulgaris.
Berberis sp.
Bomarea Caldasii.
Chelidonium majus.
Corydalis capnoides.
Cytisus Laburnum.
Euphorbia Cyparissias.
Hypericum calycinum.
(Bad bloom above.)
Linaria vulgaris*.
Oxalis sp.
Poinsettia sp.
Poterium Sanguisorba*.
Rhus sp.
Robinia Pseudacacia.
Rosa sp.

Group $\frac{0}{S}$ to $\frac{1}{1}$.

The next group comprises those in which there are stomata on the upper surface, but in which they never equal those on the lower surface in number. They are 14 in number, or 33 per cent. of the whole Class $\frac{B}{B}$.

| | | | |
|---|---|---|---|
| Brassica oleracea | $\frac{219}{301}$ | Pelargonium glaucum | $\frac{8\cdot2}{8\cdot4}$ |
| Caladium sp. | $\frac{6}{10}$ | Ruta graveolens | $\frac{1}{6}$ |
| Chlora perfoliata | $\frac{1\cdot4}{3\cdot1}$ | Sonchus oleraceus | $\frac{17}{80}$ |
| Crambe maritima | $\frac{12}{16}$ | Thalia dealbata | $\frac{6}{18}$ |
| Erythrina cristata | $\frac{0\cdot7}{16}$ | Trifolium pratense | $\frac{95}{97}$ or $\frac{565}{913}$ |
| Glaucium sp. | $\frac{5\cdot5}{8}$ | Tritonia sp. | $\frac{4\cdot7}{5\cdot1}$ |
| Mimosa pudica | $\frac{138}{302}$ | Tropæolum (about) | $\frac{15}{30}$ |

Lastly, there is the Group $\frac{1}{1}$ to $\frac{1+x}{1}$, or those in which the

* These species are placed in Group $\frac{0}{S}$, as the stomata on the lower surface are so much more numerous than those on the upper.

stomata on the upper surface are equal to or more in number than the lower stomata. They are 12, or 29 per cent.

| | | | |
|---|---|---|---|
| Artemisia Dracunculus | $\frac{42}{41}$ | Lotus corniculatus | $\frac{68}{49}$ |
| Crinum capense | $\frac{4 \cdot 5}{4 \cdot 5}$ | Lathyrus sylvestris | $\frac{79}{53}$ |
| Desmodium gyrans ...... (about) | $\frac{15}{15}$ | Medicago lupulina | $\frac{118}{100}$ |
| Dianthus sp. | $\frac{7 \cdot 8}{6 \cdot 6}$ | Melilotus officinalis | $\frac{83}{61}$ |
| Gypsophila perfoliata | $\frac{103}{98}$ | Nicotiana glauca | $\frac{10}{9 \cdot 6}$ |
| Linum flavum | $\frac{5 \cdot 8}{5 \cdot 4}$ | Triticum sativum | $\frac{121}{86}$ |

The Class $\frac{B}{B}$ is thus divided into—

$\frac{0}{S}$ .................. 38 per cent.,

$\frac{0}{S}$ to $\frac{1}{1}$ ........... 33 „

$\frac{1}{1}$ and over........ 29 „

or they may be arranged thus :—

Those in which upper stomata are fewer than lower 71 per cent.
Those in which upper stomata are equal to or *more numerous* than the lower stomata.................... 29 „

It is well known that succulent plants tend to be covered with bloom. The following plants are excluded from comparison in the matter of stomata :—

| | |
|---|---|
| Aloe arborescens | $\frac{20}{29}$ |
| Beschorneria Tornellii | $\frac{5 \cdot 5}{6 \cdot 2}$ |
| Calanthe crenata | $\frac{3 \cdot 9}{4 \cdot 3}$ |
| Cotyledon bracteosum | $\frac{2 \cdot 3}{1 \cdot 3}$ |

*Nelumbium speciosum*, with stomata only above, and *Marsilea*, with more above than below, are also excluded, having the leaves of a water-plant. It is obvious that if these leaves were included in the above groups, they would favour my conclusions unfairly.

The three following tables give the results of the analysis of the above 204 species :—

| | | | | |
|---|---|---|---|---|
| **1st Comparison.** | | | | |
| | Bloom $=\frac{0}{0}$. | Bloom $=\frac{0}{B}$. | Bloom $=\frac{B}{0}$. | Bloom $=\frac{B}{B}$. |
| No stomata above............ | 55 per cent. | 83 per cent. | 0 per cent. | 38 per cent. |
| With stomata above......... | 45 ,, | 17 ,, | 100 ,, | 62 ,, |
| **2nd Comparison.** | | | | |
| Upper stomata equal to or more numerous than lower.............. | 5 per cent. | 0 per cent. | 71 per cent. | 29 per cent. |
| Upper stomata *less* frequent than the lower . | 95 ,, | 100 ,, | 29 ,, | 71 ,, |
| **3rd Comparison.** | | | | |
| Stomatal formula $\frac{1}{2}$ or less | 76 per cent. | 100 per cent. | 0 per cent. | 52 per cent. |
| Formula greater than $\frac{1}{2}$ ... | 24 | 0 ,, | 100 ,, | 48 ,, |

*Remarks on the Comparisons.*

Comparing Class $\frac{0}{0}$ with Class $\frac{0}{B}$, we see that where, as in $\frac{0}{B}$, the stomata on the under side of the leaf have the double protection of position and bloom, the percentage of leaves with stomata exclusively on the lower surface is decidedly greater—83 per cent. compared with 55 per cent.

Comparing Class $\frac{B}{B}$ with Class $\frac{0}{0}$, we find the number of leaves having stomata above to be 62 per cent., instead of 45 per cent. That is, more leaves have *some* stomata above when the upper surface is protected by bloom. But it is remarkable that so many (38 per cent.) of Class $\frac{B}{B}$ should have all their stomata below*. This may, perhaps, be explained by the fact that bloom is in some cases removed by rain, rubbing of other leaves, &c.; so that, even where there is bloom above, the lower surface remains the safest position for the stomata. Nevertheless, we see that in $\frac{B}{B}$ there are more species with some stomata on the upper surface than without any on that surface; whereas in Classes $\frac{0}{0}$ and $\frac{0}{B}$ the reverse is the case.

* These leaves seem, on the whole, to be thin delicate leaves; so that one might imagine that stomata on one surface would suffice, and if so, the under surface would, as suggested, be the best place.

If we look at the Second Comparison, and compare again Class $\frac{B}{B}$ with $\frac{0}{0}$ or $\frac{0}{B}$, we see the influence of bloom on the upper surface determining the distribution of the stomata; for 29 per cent. in $\frac{B}{B}$ have the upper stomata equal in number to, or more numerous than, the lower stomata, as compared with 5 per cent. in $\frac{0}{0}$, or 0 per cent. in $\frac{0}{B}$.

To put it in another way. In Class $\frac{0}{0}$ 45 per cent. have some stomata on the upper surface; but only one ninth of these have the number of upper stomata equal to or greater than the number of lower stomata. In Class $\frac{B}{B}$ 62 per cent. have some stomata above, and nearly half of these have the upper stomata equal in number to, or greater than, the number of the lower ones.

Looking at the third Comparison, and comparing Class $\frac{0}{0}$ with Class $\frac{0}{B}$, we see the same accumulation of stomata on the lower surface, especially when this surface is bloom-protected. Comparing Class $\frac{0}{B}$ with Class $\frac{B}{B}$, we see that this tendency disappears when bloom appears on the upper surface. Lastly, in $\frac{B}{0}$ we see accumulation of stomata on the *upper* surface when this is the *only* surface which is bloom-protected.

The number of species in Class $\frac{B}{0}$ is too few to draw any trustworthy conclusions from. The great tendency to accumulation of stomata on the upper surface is remarkable, especially when this fact is taken in connection with what we know of Class $\frac{B}{B}$, where the upper surface is likewise bloom-protected, but where the tendency to accumulation on the upper surface is much smaller. It is possible that the distribution of stomata is determined in this class $\frac{B}{0}$ by some other circumstances, and that the development of bloom on the upper surface alone has followed as protection to the pre-existing stomata; whereas, under other circumstances, we might imagine bloom to be developed for some other use, and then the distribution of stomata to be altered accordingly. In whatever way we look at the question, the contrast between Class $\frac{0}{B}$ and Class $\frac{B}{0}$ in the distribution of stomata is certainly striking.

Having been interested by the distribution of stomata in the Auricula, I thought it worth while to investigate a few other species of the genus *Primula*.

| | Stomata. | |
|---|---|---|
| Primula cortusoides ............ | $\frac{0}{8}$ | Or very rare on upper surface. \| Imperfect "greasiness" on both surfaces. |
| P. denticulata .................. | $\frac{3}{13}$ | Young leaves mealy on both sides; older ones mealy beneath. |
| P. purpurea?..................... | $\frac{0}{8}$ | "Greasy" above; good mealiness below. |
| P. luteola ........................ | $\frac{1 \cdot 8}{7 \cdot 3}$ | Good "greasiness" on both surfaces. |
| P. farinosa ....................... | $\frac{1 \cdot 3}{10 \cdot 3}$ | Lower side mealy. |
| P. sikkimensis ................. | $\frac{1}{17}$ | No mealiness on either side. |
| P. capitata ........................ | $\frac{0}{8}$ | Perfect mealiness on the under side; there appear to be traces of meal on the upper. |
| *P. marginata* * ................ | $\frac{11 \cdot 5}{0 \cdot 7}$ | Meal on both surfaces, but better on upper surface. |
| *P. integrifolia* *................ | $\frac{8}{0}$ | Imperfect mealiness on upper side only. |
| *P. Auricula* * ..................... | $\frac{8}{0}$ | Meal on upper side only. |

The meal or bloom on some Primulas is so easily washed off or injured that it is difficult to make certain of the distribution of the mealiness on plants growing in the open air. Nevertheless, I think the results are of some little interest:—(i) Where there is no mealiness, or where the lower surface is so protected, there is a tendency towards accumulation on the lower surface. When, as in the species printed in italics,* the meal is exclusively above or better developed above, we have the stomata exclusively or chiefly above.

The genus *Trifolium* appeared to be interesting in the matter of bloom; I therefore examined the species accessible to me. The genus (as far as I have examined the species) may be divided into two groups:—

(i) $\frac{B}{B}$. Those which have bloom on both surfaces.

(ii) $\frac{B}{0}$. Those which have bloom only above.

## Group i. $\frac{B}{B}$.

### Trifolium.

| | Stomata. | Taking the stomata on the lower surface = 100. |
|---|---|---|
| T. Aucheri | $\frac{0}{8}$ | $\frac{0}{100}$ |
| T. elegans | $\frac{77}{72}$ | $\frac{107}{100}$ |
| T. Lupinaster | $\frac{171}{162}$ | $\frac{106}{100}$ |
| T. medium | $\frac{0}{8}$ | $\frac{0}{100}$ |
| T. minus | $\frac{35}{32}$ | $\frac{109}{100}$ |
| T. pannonicum | $\frac{86}{90}$ | $\frac{96}{100}$ |
| T. pratense | $\frac{95}{97}$ | $\frac{98}{100}$ |
| T. striatum | $\frac{7}{5}$ | $\frac{140}{100}$ |

Two species have all the stomata below. Omitting these, the average stomatal formula is $\frac{109}{100}$.

## Group ii. $\frac{B}{0}$.

| | Stomata. | Taking the stomata on the lower surface = 100. |
|---|---|---|
| T. alpestre | $\frac{8}{0}$ | $\frac{8}{0}$ |
| T. cæspitosum | $\frac{72}{35}$ | $\frac{206}{100}$ |
| T. fragiferum | $\frac{100}{56}$ | $\frac{180}{100}$ |
| T. montanum | $\frac{68}{28}$ | $\frac{243}{100}$ |
| T. repens | $\frac{160}{98}$ | $\frac{163}{100}$ |
| T. uniflorum | $\frac{86}{25}$ | $\frac{344}{100}$ |

One species (*alpestre*) has all its stomata on the upper surface —the reverse of what holds good in Group i. $\frac{B}{B}$, where two species have all their stomata below. Omitting *T. alpestre*, the average is $\frac{227}{100}$.

Thus, when the bloom is on the upper surface only, the average number of stomata on the upper surface (as compared with the lower) is twice as great as in those cases where both surfaces are covered with bloom.

Expressed in symbols:

*Trifolium.*

$$\text{Group } \frac{B}{B}. \qquad \text{Group } \frac{B}{0}.$$

$$\text{Stomata} = \frac{109}{100}. \qquad \text{Stomata} = \frac{227}{100}.$$

This confirms my former result, viz. that when bloom is developed on the upper surface only, there is a strong tendency to accumulation of stomata on that surface.

Finally, it may be pointed out that the genus *Trifolium* confirms the generalization above made, that when bloom is on both surfaces a large proportion of the stomata appear on the upper surface; although some cases occur in which the stomata occur *exclusively* on the lower surface.

---

## On Dr. Fox's Collection of Orchids from Madagascar, along with some obtained by the Rev. R. Baron, F.L.S., from the same island. By Henry N. Ridley, M.A., F.L.S., Assistant Botanical Department, British Museum.

[Read 17th December, 1885.]

I have to thank the authorities at Kew for placing in my hands for description a collection of Orchids recently made by Dr. Fox in the neighbourhood of Imerina. There were in the collection about 50 numbers and almost as many species, the larger number of which were plants previously obtained by one or other of the botanists who have recently been exploring almost the identical locality. There is, however, on the whole, a very large proportion of novelties, and of these several are peculiarly interesting. The collection adds three new genera to the flora, viz. *Arnottia*, a Mauritian genus of perhaps two species, which it was to have been expected would occur also in Madagascar; the very curious genus *Brownleea*, hitherto only known from Southern Africa, where it is represented by 3 or 4 species; and *Holothrix*, an East- and South-African genus. The Madagascar species is a very remarkable one, differing at first sight from the rest of the genus in many striking particulars. Another interesting novelty is *Satyrium gigas*, probably much the largest species of the genus known.