Colanthium, limited to two Cape species, differs from Pharnaceum as Thylacospermum from Arenaria, by the union of the sepals at the base into a campanulate tube, round the edge of which are inserted the stamens, being thus much more decidedly perigynous than in the rest of the group.

The genera Psammotrophe, Eckl. & Zeyh., and Polpoda, Presl, with uniovulate cells to the ovary, enumerated by Fenzl among Molluginaceae, appear to have nothing to distinguish them from true Phytolaccaceae. Adenogramma, Presl, is also a Phytolaccaceeous plant allied to Giesekia, where the ovary and fruit are reduced to a single one-seeded carpel, not compounded of 2 or 3 carpels although one-seeded as in Paronychiaceae. Acrosanthes, on the other hand, both in habit and character, belongs to the apetalous Ficoideae.

IV. Paronychiaceae.

Without having sufficiently examined all the genera of this Order to ascertain their limits with respect to each other, or the order of their arrangement, we have, however, verified the ordinal characters in all the following (except Cardionema):


[Read Nov. 21, 1861.]

If a large number of Primroses or Cowslips (P. vulgaris and eris) be gathered, they will be found to consist, in about equal numbers, of two forms, obviously differing in the length of their pistils and stamens. Florists who cultivate the Polyanthus and Auricula are well aware of this difference, and call those which display the globular stigma at the mouth of the corolla "pin-headed" or "pin-eyed," and those which display the stamens "thumb-eyed." I
will designate the two forms as long-styled and short-styled. Those botanists with whom I have spoken on the subject have looked at the case as one of mere variability, which is far from the truth.

In the Cowslip, in the long-styled form, the stigma projects just above the tube of the corolla, and is externally visible; it stands high above the anthers, which are situated halfway down the tube, and cannot be easily seen. In the short-styled form the anthers are attached at the mouth of the tube, and therefore stand high above the stigma; for the pistil is short, not rising above halfway up the tubular corolla. The corolla itself is of a different shape in the two forms, the throat or expanded portion above the attachment of the anthers being much longer in the long-styled than in the short-styled form. Village children notice this difference, as they can best make necklaces by threading and slipping the corollas of the long-styled flowers into each other. But there are much more important differences. The stigma in the long-styled plants is globular, in the short-styled it is depressed on the summit, so that the longitudinal axis of the former is sometimes nearly double that of the latter. The shape, however, is in some degree variable; but one difference is persistent, namely, that the stigma of the long-styled is much rougher: in some specimens carefully compared, the papillae which render the stigmas rough were in the long-styled form from twice to thrice as long as in the short-styled. There is another and more remarkable difference, namely, in the size of the pollen-grains. I measured with the micrometer many
proof of the permanence of the two forms is seen in nursery gardens, where choice varieties of the Polyanthus are propagated by division; and I found whole beds of several varieties, each consisting exclusively of the one or the other form. The two forms exist in the wild state in about equal numbers: I collected from several different stations, taking every plant which grew on each spot, 522 umbels; 241 were long-styled, and 281 short-styled. No difference in tint or size could be perceived in the two great masses of flowers.

I examined many cultivated Cowslips (P. veris) or Polyanthuses, and Oxlips; and the two forms always presented the same differences, including the same relative difference in the size of the pollen-grains.

Primula Auricula presents the two forms; but amongst the improved fancy kinds the long-styled are rare, as these are less valued by florists, and seldom distributed. There is a much greater relative inequality in the length of the pistils and stamens than in the Cowslip, the pistil in the long-styled form being nearly four times as long as in the short-styled, in which it is barely longer than the ovarium; the stigma is nearly of the same shape in both forms, but it is rougher in the long-styled, though the difference is not so great as in the two forms of the Cowslip. In the long-styled plants the stamens are very short, rising but little above the ovarium. The pollen-grains of these short stamens from the long-styled plants, when distended with water, were barely $\frac{5}{6}$ of an inch in diameter, whereas those from the long stamens of the short-styled plants were barely $\frac{1}{6}$, showing a relative difference of five to seven. The smaller grains of the long-styled plants were much more transparent, and before distention with water more triangular in outline than those of the other form. In one anomalous specimen with a long pistil, the stamens almost surrounded the stigma, so that they occupied the position proper to the stamens of the short-styled form; but the small size of the pollen-grains showed that these stamens had been abnormally developed in length, and that the anthers ought to have stood at the base of the corolla.

In the two forms of Primula Sinensis, the pistil is about twice as long in the one as in the other. The stigma of the long-styled varies much in shape, but is considerably more elongated and rougher than that of the short-styled, the latter being nearly smooth and spherical, but depressed on the summit. The shape of the throat of the corolla in the two forms differs as in the Cow-
vations in detail, though I am far from supposing that all cases of
dimorphism are alike. The first idea which naturally occurred
was, that the species were tending towards a dioecious condition;
that the long-styled plants, with their rougher stigmas, were more
feminine in nature, and would produce more seed; that the short-
styled plants, with their long stamens and larger pollen-grains,
were more masculine in nature. Accordingly, in 1860, I marked
some Cowslips of both forms growing in my garden, and others
growing in an open field, and others in a shady wood, and gathered
and weighed the seed. In each of these little lots the short-styled
plants yielded, contrary to my expectation, most seed. Taking
the lots together, the following is the result:—

<table>
<thead>
<tr>
<th></th>
<th>No. of Plants</th>
<th>No. of Umbels produced</th>
<th>No. of Capsules produced</th>
<th>Weight of seed in grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-styled Cowslips</td>
<td>9</td>
<td>33</td>
<td>199</td>
<td>83</td>
</tr>
<tr>
<td>Long-styled Cowslips</td>
<td>13</td>
<td>51</td>
<td>261</td>
<td>91</td>
</tr>
</tbody>
</table>

If we reduce these elements for comparison to similar terms, we
have—

<table>
<thead>
<tr>
<th></th>
<th>No. of Plants</th>
<th>Weight of seed in grains</th>
<th>No. of Umbels</th>
<th>Weight of seed</th>
<th>No. of Capsules</th>
<th>Weight of seed in grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-styled Cowslips</td>
<td>10</td>
<td>92</td>
<td>100</td>
<td>251</td>
<td>100</td>
<td>41</td>
</tr>
<tr>
<td>Long-styled Cowslips</td>
<td>10</td>
<td>70</td>
<td>100</td>
<td>178</td>
<td>100</td>
<td>34</td>
</tr>
</tbody>
</table>

So that, by all the standards of comparison, the short-styled are
the most fertile; if we take the number of umbels (which is the
fairest standard, for large and small plants are thus equalized), the
short-styled plants produce more seed than the long-styled, in the
proportion of four to three.

In 1861 I tried the result in a fuller and fairer manner. I
transplanted in the previous autumn a number of wild plants
into a large bed in my garden, treating them all alike; the result
was—

<table>
<thead>
<tr>
<th></th>
<th>No. of Plants</th>
<th>No. of Umbels</th>
<th>Weight of seed in grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-styled Cowslips</td>
<td>47</td>
<td>173</td>
<td>745</td>
</tr>
<tr>
<td>Long-styled Cowslips</td>
<td>58</td>
<td>208</td>
<td>692</td>
</tr>
</tbody>
</table>
than the long-styled forms; consequently the anticipation that the plants having largely developed pistils with rougher stigmas, and having shorter stamens with smaller pollen-grains, would prove to be more feminine in their nature is exactly the reverse of the truth. If the species of Primula are tending to become dioecious, which possibly may be the case, the future hypothetical females would have short pistils, and the males would have short stamens; but this tendency is accompanied, as we shall presently see, by other conditions of the generative system of a much more singular nature. Anyhow, the possibility of a plant thus becoming dioecious by slow degrees is worthy of notice, as the fact would so easily escape observation.

In 1860 I found that a few umbels of both long-styled and short-styled Cowslips, which were covered by a net, did not produce seed, though other umbels on the same plants, artificially fertilized, produced an abundance of seed; and this fact shows that the mere covering in itself was not injurious. Accordingly, in 1861 I covered up under a similar net several plants just before they opened their flowers; these turned out as follows:

<table>
<thead>
<tr>
<th></th>
<th>No. of Plants</th>
<th>No. of Umbels produced</th>
<th>Product of Seed.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-styled</td>
<td>6</td>
<td>24</td>
<td>1-3 grains, or 50 seeds.</td>
</tr>
<tr>
<td>Long-styled</td>
<td>18</td>
<td>74</td>
<td>Not one seed.</td>
</tr>
</tbody>
</table>

Judging from the exposed plants which grew all round in the same bed, and had been treated in every way exactly the same, except that they were exposed to the visits of insects, the six short-styled plants ought to have produced 92 grains' weight of seed instead of only 1-3; and the eighteen long-styled plants, which produced not one seed, ought to have produced above 200 grains' weight. The production of the 1-3 grain of seed in the smaller lot was probably due to the action of Thrips or some minute insect. This evidence is sufficient, but I may add that ten pots of Polyanthuses and Cowslips of both forms, protected from insects in my greenhouse, did not set one pod, though artificially fertilized flowers in other pots produced an abundance. So we see that the visits of insects are absolutely necessary to the fertilization of Cowslips. As the exposed plants produced an abundance of seed, the tendency to a dioecious condition, previously remarked on, might have been safely carried on, as we see that there is an effect-
ive agency already at work which would have carried pollen from one sex to the other.

What insects habitually visit Cowslips, as is absolutely necessary for their regular fertility, I do not know. I have often watched them, but perhaps not long enough; and only four times I have seen Humble-bees visiting them. One of these bees was gathering pollen from short-styled flowers alone, another had bitten holes through the corolla; and neither of these would have been effective in the act of fertilization: two others were sucking long-styled plants. I have watched Primroses more attentively during several years, and have never seen an insect visit them; yet from their close similarity in all essential respects to Cowslips, there can hardly be a doubt that they require the visits of insects. Hence I am led to suppose that both Primroses and Cowslips are visited by moths. All the species which I have examined secrete plenty of nectar.

In Primula Sinensis, when protected from insects and not artificially fertilized, the case is somewhat, but not materially, different. Five short-styled plants produced up to a given period 116 flowers, which set only seven capsules, whereas twelve other flowers on the same plants artificially fertilized set ten capsules. Five long-styled plants produced 147 flowers, and set sixty-two capsules; so that this form, relatively to the other, sets a far greater number of capsules: yet the long-styled protected flowers do not set nearly so well as when artificially fertilized; for out of forty-four flowers thus treated, thirty-eight set. These remarks apply only to the early setting of the capsules, many of which did not continue swelling. With respect to the product of seed, seven protected short-styled plants, which bore about 160 flowers, produced only half a grain of seed; they ought to have produced 120 grains: so that the short-styled plants, when protected from insects, are nearly as sterile as Cowslips. Thirteen long-styled plants, which bore about 380 flowers, and which as we have seen set many more capsules, produced 25.9 grains of seed; they ought to have produced about 220 grains in weight: so that although far less fertile than the artificially fertilized flowers, yet the long-styled P. Sinensis, when protected from insects, is nearly twenty-four times as fertile as the short-styled when protected from insects. The cause of this difference is, that when the corolla of the long styled plants falls off, the short stamens near the bottom of the tube are necessarily dragged over the stigma and leave pollen on it, as I saw by hastening the fall of nearly withered flowers; whereas in the short-styled flowers, the stamens are seated at the mouth of the corolla,
and in falling off do not brush over the lowly seated stigma. In the Cowalip the corolla does not fall off; and both long-styled and short-styled plants are equally sterile when protected from insects. It is a rather curious case, that the falling of the corolla, or its remaining attached when withered, might have a considerable influence on the numbers of a plant, during a year unfavourable to the visits of the proper insects.

In three short-styled plants of *Primula auricula*, protected from insects, the flowers which I fertilized produced seed, but those which were not touched produced none.

In all the species of *Primula* the pollen readily coheres to any object. In all that I have observed, though the stamens and pistils differ in length relatively to each other in the different species, yet, in the two forms of the same species, the stigma of the one form stands at exactly the same height with respect to the corolla as the anthers of the other form. If the proboscis of a dead Humble-bee, or thick bristle, or rough needle be pushed down the corolla, first of one form, and then of the other, as an insect would do in visiting the two mingled forms, it will be found that pollen from the long-stamened form will adhere round the base of the proboscis, and will be left with certainty on the stigma of the long-styled form; pollen from the short stamens of the long-styled form will also adhere a little above the tip of the proboscis, and some will generally be left on the stigma of the other form. Thus pollen will be carried reciprocally from one form to the other. In withdrawing the proboscis from the long-styled form, with pollen adhering near the tip, there will be a good chance of some being left on the flower’s own stigma, in which case there will be self-fertilization; but this by no means always occurs. In the short-styled form, on the other hand (and it is important to remember this), in inserting the proboscis between the anthers situated at the mouth of the corolla, pollen, as I repeatedly found, is almost invariably carried down and left on the flower’s own stigma. Moreover minute insects, such as Thrips, numbers of which I have observed in Primrose flowers thickly dusted with pollen, could not fail often to cause self-fertilization. We positively know that the visits of large insects are necessary to the fertilization of the species of *Primula*; and we may infer from the facts just given that these visits would carry pollen reciprocally from one form to the other, and would likewise tend to cause self-fertilization, more especially in the short-styled (i.e. long-stamened) form.

These observations led me to test the potency of the two pol-
In the first part of the upper table, the number of flowers fertilized and the simple result is shown; and at the right hand, for the sake of comparison, the calculated product of the weight of seed from 100 good pods of each of the four unions is given; showing that in each case the heteromorphic union is more fertile than the homomorphic union. Beneath we have a simple summary of the two homomorphic and the two heteromorphic unions. And lastly, for the sake of comparison, a calculation has been made from this summary; first, assuming that 100 flowers of both kinds of unions were fertilized; and then to the right hand, assuming that 100 good pods were produced from both unions. If we compare the result, we see that the flowers of the two heteromorphic unions produced a greater number of good pods, and a greater weight of seed, than the flowers of the two homomorphic unions; and again (and this is the fairest element of comparison, for accidents are thus almost eliminated), that the good pods from the two heteromorphic unions yielded more seed, in about the proportion of three to two, than those from the two homomorphic unions. The difference in weight from 100 capsules of the two forms is 24 grains, and this is equal to at least 1200 seeds.

Beneath we have Table II. of *P. veris*, or the Cowslip. The upper part is exactly the same as in the Table of *P. Sinensis*, and we see in each case that the heteromorphic is more fertile than the homomorphic union. The calculated results from the summary of the two homomorphic and the two heteromorphic unions are more complex than with the last species, as I wished to show that, however we proceed, the general result is the same. We see that the assumed hundred flowers, heteromorphically fertilized by the pollen of the other forms, yielded more capsules, more good capsules, and a greater weight of seed; but I rely little on this, as some whole umbels perished after being fertilized. The fairest element of comparison is to take the good capsules alone; and we here see that the 100 from the two heteromorphic unions yielded seed which in weight was as 54 to 35 from the 100 good capsules.

<table>
<thead>
<tr>
<th></th>
<th>Number of flowers fertilized</th>
<th>Number of good pods</th>
<th>Weight of seed in grains</th>
<th>Number of good pods</th>
<th>Weight of seed in grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>The two homomorphic unions</td>
<td>100</td>
<td>63</td>
<td>25</td>
<td>100</td>
<td>40</td>
</tr>
<tr>
<td>The two heteromorphic unions</td>
<td>100</td>
<td>75</td>
<td>48</td>
<td>100</td>
<td>64</td>
</tr>
</tbody>
</table>
Primula auricula.—Table III.

<table>
<thead>
<tr>
<th></th>
<th>Total number of pods.</th>
<th>Number of good pods.</th>
<th>Weight of seeds in grains</th>
<th>Good Fods.</th>
<th>Weight of seed in grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-styled by own-form pollen (homomorphic union)</td>
<td>2</td>
<td>1</td>
<td>0.12</td>
<td>or as 100 to 12</td>
<td></td>
</tr>
<tr>
<td>Short styled by pollen of long-styled (heteromorphic union)</td>
<td>3</td>
<td>3</td>
<td>1.50</td>
<td>or as 100 to 50</td>
<td></td>
</tr>
</tbody>
</table>

Whoever will study these three tables, which give the result of 134 flowers carefully fertilized and protected, will, I think, be convinced that in these three species of Primula the so-called heteromorphic unions are more fertile than the homomorphic unions. For the sake of clearness, the general result is given in the following diagram, in which the dotted lines with arrows represent how in the four unions pollen has been applied.

We here have a case new, as far as I know, in the animal and vegetable kingdoms. We see the species of Primula divided into two sets or bodies, which cannot be called distinct sexes, for both are hermaphrodites; yet they are to a certain extent sexually distinct, for they require for perfect fertility reciprocal union. They might perhaps be called sub-dioecious hermaphrodites. As quadrupeds are divided into two nearly equal bodies of different sexes, so here we have two bodies, approximately equal in number,
forms in about equal numbers, with their pollen adapted for reciprocal union, is tolerably plain; namely, to favour the intercrossing of distinct individuals. With plants there are innumerable contrivances for this end; and no one will understand the final cause of the structure of many flowers without attending to this point. I have already shown that the relative heights of the anthers and stigmas in the two forms lead to insects leaving the pollen of the one form on the stigma of the other; but, at the same time, there will be a strong probability of the flower's own pollen being likewise placed on the stigma. It is perfectly well known that if the pollen of several closely allied species be placed on the stigma of a distinct species, and at the same time, or even subsequently, its own pollen be placed on the stigma, this will entirely destroy the simultaneous or previous action of the foreign pollen. So again if the pollen of several varieties, including the plant's own pollen, be placed on the stigma, one or more of the varieties will take the lead and obliterate the effect of the others: but I have not space here to give the facts on which this conclusion is grounded. Hence we may infer as highly probable that, in *Primula*, the heteromorphic pollen which we know to be so much the most effective would obliterate the action of the homomorphic pollen when left on the flower's own stigma by insects; and thus we see how potent the dimorphic condition of the pollen in *Primula* will be in favouring the intercrossing of distinct individuals. The two forms, though both sexes are present in each, are in fact dioecious or unisexual. Whatever advantage there may be in the separation of the sexes, towards which we see so frequent a tendency throughout nature, this advantage has been here so far gained, that the one form is fertilized by the other, and conversely; and this is effected by the pollen of each form having less potency than that of the other on its own stigma.

Bearing on this view of the final cause of the dimorphism of the *Primulas*, there is another curious point. If we look at the right-hand figures of the four first lines in the previous tables of *P. Sinensis* and *eris*, we shall see that one of the homomorphic unions, namely, the short-styled by its own-form pollen, is considerably more sterile than the other; and in *P. auricula*, though here there is no other homomorphic union as a standard of comparison, this union is likewise excessively sterile. That the fertility of this union is really less in a marked degree than in the other three unions, we have an independent proof in the seeds germinating less perfectly and much more slowly than those from the other unions.
lips, but further experiments are absolutely necessary. We may also suspect that the fact noticed by florists*, that the varieties of the Polyanthus never come true from seed, may be in part due to their habitually crossing with other varieties of the Polyanthus.

The simple fact of two individuals of the same undoubted species, when homomorphically united, being as sterile as are many distinct species when crossed, will surprise those who look at sterility as a special endowment to keep created species distinct. Hybridizers have shown† that individual plants of the same species vary in their sexual powers, so far that one individual will unite more readily than another individual of the same species with a distinct species. Seeing that we thus have a groundwork of variability in sexual power, and seeing that sterility of a peculiar kind has been acquired by the species of Primula to favour intercrossing, those who believe in the slow modification of specific forms will naturally ask themselves whether sterility may not have been slowly acquired for a distinct object, namely, to prevent two forms, whilst being fitted for distinct lines of life, becoming blended by marriage, and thus less well adapted for their new habits of life. But many great difficulties would remain, even if this view could be maintained.

Whether or not the dimorphic condition of the Primulae has any bearing on other points in natural history, it is valuable as showing how nature strives, if I may so express myself, to favour the sexual union of distinct individuals of the same species. The resources of nature are illimitable; and we know not why the species of Primula should have acquired this novel and curious aid for checking continued self-fertilization through the division of the individuals into two bodies of hermaphrodites with different sexual powers, instead of by the more common method of the separation of the sexes, or by the maturity of the male and female elements at different periods, or by other such contrivances. Nor do we know why nature should thus strive after the intercrossing of distinct individuals. We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis. When we look to the state in which young mammals and birds are born, we can at least see that the object gained is

* Mr. D. Beaton, in 'Journal of Horticulture,' May 28, 1861, pp. 154, 244.
† Gärtner, Bastarderzeugung, s. 165.
the Boragineae, Prof. Gray finds a new and inexplicable case,—
namely, some specimens with the stamens and pistil sub-exserted,
and other specimens with both organs seated low down the tube of
the corolla. Dr. Torrey and Prof. Gray have designated all such
plants as "dioeciously dimorphous." In the Labiatae, Mr. Bentham
informs me that several species of Ägiphyla, and some of Mentha,
are dimorphic like Primula. The case of Thymus is different, as I
know from my own observations; but I will not here enlarge on
this genus. Again, as I hear from Mr. Bentham, numerous species
of Oxalis are similarly dimorphic. I can add the genus Linum.
So that we already know of species (generally several in the same
genus) having distinct dimorphic individuals, as far as structure
is concerned, however it may prove in function, in no less than
eight natural orders.

With respect to Linum, I will not here enter on details, as I in-
tend to try further experiments next summer; but I may state,
that I observed many years ago two forms in Linum flavum, with
both the pistils and stamens differing in length. In Linum grandif-
orum there are likewise two forms which present no difference in
their male organs, but the pistil and stigmatic surfaces are much
longer in the one form than in the other. The short-styled form,
I have good reason to believe, is highly fertile with its own pollen;
whether it be more fertile with the pollen of the long-styled form,
I cannot at present say. The long-styled form, on the other hand,
is quite sterile with its own pollen: several plants grew in my
garden, remote from the short-styled plants; their stigmas were
coloured blue with their own pollen; but although they produced
a vast number of flowers, they did not produce a single seed-
capsule. It seemed a hopeless experiment; but I had so much
confidence from my trials on Primula, that I put a little pollen
from the short-styled plants on the stigmas (already blue with
their own pollen) of twelve flowers on two of the long-styled
plants. From these twelve flowers I got eight remarkably fine
seed-capsules; the other flowers not producing a single capsule.
The existence of plants in full health, and capable of bearing
seed, on which their own pollen produces no more effect than
the pollen of a plant of a different order, or than so much in-
organic dust, is one of the most surprising facts which I have ever
observed.