A1/*Wide ranging, common and much diffused species tend most to vary:*—The elder De Candolle, & several other Botanists[1] have insisted that it is the widely ranging, the common & vigorous plants which vary most./A1 v/Alph. De Candolle[2] gives a list of 117 species which range over at least a third of the terrestrial surface, & he states that the greater part of these offer varieties. I have attempted to test this proposition conversely; that is by taking the species which present varieties, & seeing whether a large proportion of them are common & widely diffused in their own country./A1/Ledebour divides the enormous territory, included in his Flora Rossica into 16 Provinces; & to each species he appends the number of Provinces which it inhabits. There are 999 phanerogamic species which present varieties, marked by Greek letters, & these on an average range over 4.94 Provinces; whereas there are 5347 species which have no varieties, & these range over only 2.43 provinces; so that the varying species range over rather more than twice as large an area as the other species. The rule holds very nearly the same when each of the four volumes is tried separately. But we shall presently see & have to discuss the many difficulties which arise in considering the value of the varieties appended by Botanists to their species/

A2/In the London Catalogue of British Plants the number of the 18 provinces, in which each species has been found, is added from Mr H. C. Watson's Cybele Britannica. The number of varieties given in this Catalogue is not great, but Mr Watson has added for me in M.S. some others; the principle on which he has acted in doing this, & the reasons for omitting some varieties & some few whole genera, are given in the Supplement to this Chapter; but I may add that all the varieties here included have been ranked as species by some one or more botanists. Now there are 1053 species which have no such varieties appended to them, & these on an average range over 10.76 of the Provinces; whereas there are 169 species which have such varieties, & these range over an average of 14.55 provinces. I have, also, tried these species in another way, not by taking an average, but by seeing how many species range over all 18 provinces; & I find that of the 1053 non-varying species, 216 occur in the whole 18 provinces, or in the proportion of 205/1000 whereas of the 169 species which present varieties, there are 70 which range over the 18 provinces, that is the proportion of 414/1000; so that proportionally twice as many of the varying species range throughout the eighteen provinces, as of the non-varying species./

[1] Boreau. Flore du Centre de la France. Tom. 1. p. 101.

[2] Geographie Botanique ‹1855› p. 586. [Actually 564-81.]

A3/With respect to '*commonness*', it is evident that a species might, as indeed is the case with many aquatic plants, range over an enormous territory, & yet not be common or individually numerous anywhere. In a small area, like Britain, where a plant is found in every province, diffusion & commonness almost blend together. Boreau in his Flora of the Central part of France (See supplement to this chapter, for particulars on this & other works quoted) has marked by C. C the very common species; & I find he has 1280 species not presenting ‹any marked› variety, of which 240 are very common,—that is in the proportion of 187/1000; there are other 193 species with varieties recorded, & of these 78 are very common, or in the proportion of 404/1000; so that proportionally more than twice as many of the varying species are very common in comparison with the non-varying. ‹I may here remark that Boreau draws a distinction between the polymorphic species, which vary almost indefinitely & are not included in the above number, & those species which present varieties sufficiently distinct to be marked by Greek letters.›/

A 4/ Miquel in his list of the plants of Holland, marks a very few species having varieties & marks all the very common species; but the recorded varieties are so few, & no particulars specified in regard to them, that the list is not satisfactory: there are 1133 non-varying species, of which 201 are common or in proportion of 177/1000; & on [the] other hand there are 46 varying species of which 27 are common, or in proportion of 586/1000; hence more than thrice as many of the varying species are common than of the non-varying species, but the proportion is probably here exaggerated.

Again Prof. Asa Gray in his Flora of the N. United States, appends the word common to many species, & I find that of the 1851 non-varying species, 439 are marked as common, 237/1000; whereas there are other 202 species which present varieties (either marked in small or large type, see supplement to this chapter), of which 82 are marked as common,—i.e.405/1000, here then, not far from proportionally twice as many varying species are common as of the non-varying.[1]

From the foregoing cases, we see, that such numerical evidence as can be obtained, subjected as it is [to] doubts on the value of

[1] In Mr Wollaston's Insecta Maderensia (Introduct. p. XIII) 12 Coleoptera are mentioned as the most abundant in individuals in this group of islets, to which may be added, as I am informed by Mr Wollaston, a Ptinus and Oxytelus. Hence out of the 482 species, about one in 34 of all the species is very common. But of the 61 species, which present varieties, six are very common, i.e. one tenth of the varying species are very common.

the recorded varieties, supports the opinion of those botanists, who believe that the much diffused & common/A 5/species are most liable to vary, or to present varieties, which have been thought sufficiently distinct to be recorded. We can understand why wide-ranging species, which live under various climates, & which come into contact with diverse groups of organic beings (a much more important consideration, as I think will be seen in a future chapter) should vary more than local species. Wide ranging species will also generally from/A 5A/the mere fact of their inhabiting many places, & from the vigour which they show in thus ranging far & coming into successful competition with many organic beings under different climates, will generally be common or individually numerous: indeed Dr. Asa Gray after examining this question says, "so true is it as a general rule that species of wide range in our country are species of frequent occurrence, that I have not noticed any strongly marked exceptions to it".[1] Even in regard to species strictly confined to a moderately sized & uniform locality, which are not exposed to very different conditions, we may, I think, see why such species, when common & much diffused in their own country, should present more varieties than when rare. If we suppose varieties to be mere fleeting productions, like monstrosities, then, if originating in exactly the same proportional numbers in common & rare species say one in a million individuals, they would, within the life-time of Botanists, be far oftener encountered amongst the common than the rare species; & so would be oftener /A6/recorded in botanical works. But of two species, if one were common & one rare during the whole or greater part of their existence on the earth, then a greater number of such fleeting varieties would, it is probable, actually originate in the common than in the rare species. Now I believe, though we are here forestalling what we shall have hereafter to discuss, that by far the most effective origin of well marked varieties and of species, is the natural selection or preservation of those successive, slight, & accidental (as we in our ignorance must call them) variations, which are in any way advantageous to the individuals thus characterized: hence there would be a better chance of varieties & species being thus formed amongst common than amongst rare. I may add, to illustrate what I mean, that a nurseryman who raises seedlings of a plant by the hundreds of thousand far oftener succeeds in his life-time in producing a new & valuable variety, than does a small amateur florist. So it would be with a common,

[1] Statistics of the Flora of the N. United States, in American Journal of Science, 2nd. Series, 1857, Vol. 23, p. 393.

in comparison with a rare species, raised by the hand of nature in millions on millions during the incomparably longer period of its existence on the earth.

But botanists do not actually wish (though unintentionally it is often done) to record, & define as varieties, mere fleeting variations or monstrosities./A7/Boreau, for instance, & others have expressly stated that they record only the more strongly defined varieties: more than one-third of the varieties marked by Asa Gray are considered by him as possibly deserving to be called species: in the London Catalogue, the greater number of the most trifling varieties have been removed for me by Mr. Watson & all those which are left (182 in number) have been ranked by some one botanist as species. Of the degree of permanence of varieties in plants we know hardly anything: but when a variety is the common form throughout any province or even quite small district, we must suppose that it is in some degree permanent. We have seen in the case of certain land-shells of Madeira that some of the varieties are of extremely high antiquity. Now when a variety is in some degree permanent, whether it has originated in a single accidental variation, or by the addition of several such successive variations through natural selection, or through the direct & gradual action of external conditions, as of climate, its first origin is even of less importance to it, than its preservation; for in order to become in any degree permanent, it has to struggle with all other organic beings in its own country; & this shows that it has/ A 8/at least nearly equal, or has perhaps acquired even some greater, constitutional advantages, in comparison with its parent-species. The mere fact of a species being very common or widely extended shows that it is advantageously situated in respect to the inorganic conditions of its life, & in respect to all the other organic beings, animal & vegetable, with which it has to come into competition; & the varieties produced from such common species, from differing little from them, will gradually partake of (or have in excess) their advantages, whatever they may be. Finally then, I suppose that common species present more varieties, when these are in some degree permanent, than do rare species, from partaking of the advantages which make the parent species common; and that varieties (not now considering those wholly due to the direct action of climate &c) originate more frequently amongst common species than amongst rare, owing to more accidental (as we must call them) variations arising during the whole existence of a species which abounds in individuals, than during the existence of a species which has presented much fewer individuals.

The law first enunciated by M. M. d'Archiac & Verneuil & since confirmed by several geologists, that the species which range over a very wide area, are those which have existed for the longest period, seems at first opposed to the/A 9/foregoing conclusion, taken in connexion with my view that closely allied species do not essentially differ from varieties; for it implies that the species which have ranged furthest have longest remained immutable. But if we reverse the proposition, which can be done with equal truth, it is not so discordant;—namely that species which have existed longest, have had, owing to geological & other changes, the best chance of spreading furthest. The majority of such species we may, without contradicting the law, suppose to have become modified either into varieties or into new species, but that a certain number having undergone no change (& it has never been pretended that wide ranging species universally vary) has given rise to the foregoing palaeontological law./

A10/*Geographical Range of Varieties themselves*:—I have met with scarcely any observations on this head. When two varieties inhabit two distinct countries, as is often the case & as is very generally the case with the higher animals, it is obvious that the two varieties separately have a much narrower range than the parent species. A variety, for instance, inhabiting N. America & another variety of the same species inhabiting Europe will both have a very much more confined range than the parent form; so on a much smaller scale, the many varieties of endemic species, confined to the separate islets of the same small archipelago (for instance in the case of the insects of the small Madeira group described by Mr Wollaston) follow the same rule.* So again the numerous alpine, maritime, shade or moisture-loving varieties of species, which commonly live in other and different habitats, have confined ranges compared with their parent-Types. These considerations alone make it probable that the far greater number of varieties have narrower ranges than the species whence they have sprung. I have looked to many local Floras, & as far as I could judge, the recorded varieties seem usually to have restricted ranges. In the London Catalogue (1857) the range within Britain is given by Mr Watson of some, namely 53 varieties, & I find that on an average they range over 7.7 Provinces; whereas the/A 11/46 species, to which these varieties belong, range over 14.3 of the provinces;—

* All this depends on the arbitrary assumption of which is var. & which species. [J.D.H.] Begin with stating that it is a truism Probably not worth giving so much of a *truism*. [CD.]

or over nearly twice as wide an area. At my request Mr Watson was so kind as to append remarks on the nature of the habitats & of the ranges of those varieties of British plants with which he was personally acquainted; but as he stated to me, it was not possible to arrive at any definite conclusions from the numerous sources of error; but I may add that from this list it seems that a large number are alpine, maritime, &c forms; sometimes confined to one or to a few localities, but often pretty widely diffused: a good many varieties are, as far as known, strictly local, & some of them have become extinct since having been first noticed: in several cases the varieties, when not strictly confined to any particular locality, or habitat, seem to be rarer than the type-forms :—

The only published observation which I have met with on the range of varieties is by Mr. C. B. Adams,—a competent judge in regard to the terrestrial mollusca on which he treats:[1] he states that the several/A 12/varieties of a species seldom have the same range with it or with' each other; 'each variety has its own limits of distribution;' one variety will often have an 'extent of distribution equal to that of two or more other varieties' of the same species. He believes that varieties follow the same laws of geographical distribution with species; and hence he concludes that they have been aboriginally created as varieties. But it follows from his remarks that varieties generally have more confined ranges than their type-species.*

In all cases, this latter remark, is to a large extent a mere truism; for when two forms are so closely similar, that one is called a species and the other a variety, the commoner of the two, is almost sure to be called the species, and the less common one, the variety: for we cannot tell which of the two has branched off from the other.[2]

As by our theory two closely allied species do not differ essentially from a species & its strongly defined variety, I was anxious to ascertain anything about the ranges of such closely allied species but I can advance only one single case, as follows: Mr Watson has marked for me in/A13/the London Catalogue (4th Edit:), which is a pretty well sifted list & does not include the most doubtful

* This is reasoning in a O [circle.] The idea of a var[iety] is founded on variety. [*J.D.H.*]

[1] Contributions to Conchology. No. 10. On the nature & origin of the species of Mollusca in Jamaica. p. 193.

[2] See an excellent discussion on this point in Dr. Hooker's Introductory Essay to the Flora of New Zealand. p. XVII & note.—Dr. Asa Gray, also has remarked to me that mere priority of description has in some cases determined which form has been called the species & which the variety.

species, the forms therein admitted as species, which he considers as most like varieties: he has marked 63, & adds that most of these have been of late years, as it were, cut out of other species: they have all been considered by some few botanists as mere varieties, but by the large majority of local authors have been ranked as good species. Now I find that these 63 species in the London Catalogue range on an average over 6.9 provinces; so that, they have very nearly the same extent of range, with that (7.7) of the 53 printed varieties in this same catalogue.*/

A14/*On the relation of the commonness and diffusion of species to the size of the orders and genera in which they are included:*—My object in looking at this question regards Variation:—As we have seen that a large proportion of the common and widely diffused species present varieties, if these common species occur most frequently in the numerically large groups, it would be some indication that a greater number of varying species would occur in them—& this latter subject is an important one which we shall presently have to discuss./A14 v/There is, as it seems to me, some a priori probability that the species in the large groups would be generally common & more widely diffused than in the small groups; for the simple fact of many closely allied species inhabiting any country shows that there is something in its condition, organic or inorganic favourable to them; & this by itself would tend to make the species numerous in individuals & widely diffused within that country beyond the common average.[1]/

A 14/Alph: De Candolle has shown[2] that there is some but very slight evidence that the Orders numerically large in a country, include more common or "vulgar" species than do the smaller Orders; but that the species of such large orders generally have

* Very good remark. [J.D.H.]

[1] Alph. De Candolle (Geograph. Bot. p. 562) takes a directly opposite view. ‹He supposes that when the conditions of life are most favourable to a group, many delicate species could live. "Or, les espèces les plus delicates doivent avoir l'aire la plus restrainte" But we have seen that there is generally a relation between the extent of range and commonness of a species: and how is a species known to be delicate except from being rare and having a narrow range? Is it not saying that certain species are delicate *because* they are rare & have a confined range, & *therefore* they are rare and have a confined range? The rarity and confined range of a species, depends, I believe, in the vast majority of cases, on its not being able to compete with or withstand other organic beings; and by no means on the conditions of its existence being favourable.› [Deleted in fair copy.] M. De Candolle throughout his admirable work seems to me very often to greatly underrate the predominant importance of the struggle for life on all organic beings,—a subject to be discussed in our next chapter.—

[2] Geograph. Bot. p. 465-470. p. 562.

more confined ranges; & he concludes with some doubt that where only a few species of an order exist, these will be the more robust & the widest rangers. It has appeared to me, from reasons not worth giving, that if any such rule did hold good, it would be more likely to appear in smaller groups or genera rather than in orders.[1] But whether in genera or orders/A 15/there are very many causes which would tend to conceal such a result. Namely, our best classifications are considered by many able botanists as still highly artificial. The species in large genera are as remarked to me by Mr H. C. Watson, more difficult to identify, & he believes that many species in such large genera, which are now ranked as, distinct in distant countries, would on close examination often be found to be identical; & consequently such species in the larger genera would really have wider ranges than they appear to have in books; moreover there would sometimes be the greatest difference in the range of a species, according to the value set on its specific characters; for instance a European species having a variety in N. America would have an enormous range, but if that variety were ranked as a species, the range of the European form would be immensely reduced. Aquatic & littoral plants generally have very wide ranges, quite independently of the question whether they form parts of large or small genera. Lowly organised plants as a general rule range further than the more highly organised, and lastly when two areas, separated by the sea or by other/A 16/ barriers, are considered, the capacity for dissemination in the species in common, would probably come into play.

(Some of these multiform causes of error may, I think, be in some degree eliminated by not considering the whole range of the species, but only the degree of diffusion & commonness of the species, described by a single botanist, within one continuous territory, more especially if not of vast size. And for my special object of finding out whether more varieties have originated in any country (or if originating elsewhere, are in this country enabled to subsist) amongst the larger or the smaller genera, it

[1] Dr. Asa Gray (in American Journal of Science, 2nd Series, Vol. 23 p. 391) has distributed under their orders 430 species which are the widest rangers in the northern U. States & at the same time the most common species. I have had these orders so arranged that all the species (977) included in the larger orders in the U. States are nearly equal in number to all the species (939) included in the smaller orders. And I find that the number of the wide-ranging & common species are more numerous in the smaller than in the larger orders, in the proportion of 233/1000 to 215/1000. If the species could have been arranged by *genera* instead of by *orders*, namely if all the larger genera had been put on one side & the smaller genera in the other: I hardly doubt from the following Table (Tab. A), that the larger *genera* would have included a larger proportion of these common & widely ranging species.

TABLE A[1]

The numerator gives the number of the much diffused or the common species in each country.

The denominator gives the number of species in the left column in the larger genera & in the right hand column in smaller genera—See Supplement to this chapter for titles of Works etc.

		Larger Genera	*Smaller Genera*
Britain:	London Catalogue (1857) H. C. Watson—Larger genera with 5 species and upwards, smaller with 4 species and downwards—The numerator expresses the number of species found in all the 18 Provinces, into which Britain is divided.	148 = 250 592 1000	138 = 219 629 1000
Russia:	Ledebour (Dicotyledonae alone). Larger Genera with 10 species and upwards, smaller genera with 9 species and downwards. The numerator expresses the number of species found in at least 8 of his 16 Provinces. The species inhabiting 8 Provinces have about thrice the average range of all the phanerogamic plants:—	239 = 70 3385 1000	131 = 67 1937 1000
Centre	France: Boreau—Larger genera with 5 species and upwards, smaller with 4 and downwards. The numerator expresses the species marked C.C. or very common.	163 = 222 732 1000	155 = 209 741 1000
Holland:	Miquel—Larger Genera with 4 species and upwards, smaller with 3 species and downwards. The numerator expresses the number of common species.	120 = 192 622 1000	108 = 193 557 1000
Ratisbon:	Furnrohr—Larger genera with 4 species and upwards, smaller with 3 species and downwards. The numerator expresses the number of species marked "sehr gemein".	102 = 191 533 1000	79 = 150 526 1000
N. United	States: Asa Gray—Larger genera with 5 species and upwards, smaller with 4 species and downwards. The numerator expresses the number of species marked as "common".	326 = 286 1136 1000	195 = 212 917 1000

[1] [Darwin's holograph draft of this table is ULC Darwin MSS. vol. 16.1, fol. 172.]

seems to me quite immaterial whether the same species in other countries have very wide or narrow ranges,—are very common or rare.)

(The following short table (Tab. A.) gives the proportions of the common & of the most widely diffused species, in the larger & in the smaller genera, in six countries.)

We here see a slight preponderance, in the larger genera in all the cases except in Holland, and Miquel's tables differ more or less, in every single respect, as far as I have tried them, from those of other Botanists. The slight preponderance would probably/ A17/be somewhat increased, more especially in such large territories as those included in the Flora Rossica, if some of the many above-specified causes of error could be removed: for instance the influence of peculiar stations on the range, which is independent of the size of the genera./A17 v/I may add, as supporting the table that Dr. Asa Gray finds that 75 per cent of the *widest ranging* species in N. America belong to genera having above the average number of species[1] and in regard to "commonness", we see in the table that a greater number of species marked as "common" are included in the larger genera; ‹& indeed as already remarked Dr Asa Gray has shown that the common & widely ranging species are almost invariably the same.) Dr. Hooker also finds a similar result by tabulating the species common to Europe & N. America, which have a vast range & these usually belong to large genera. Conversely, in regard to commonness, Dr. Hooker has remarked to me in a letter* that in a general Herbarium, genera with single species are represented by a single specimen far oftener than large† genera, showing that the genera with a single species are usually rarer in individuals./

A17/In regard to the extent of diffusion, the preponderance small as it is in Table A, quite or almost disappears, if an average of the ranges of all the species in the larger & smaller genera be taken, instead of, as in the Table, the proportional numbers of the species having unusually wide ranges. Thus in the Flora Rossica,

* I cannot now find your letter on this subject, but I hope I shall & I quote now only vaguely from memory. [C.D.]

† Or more local [J.D.H.]

[1] American Journal of Science, 2nd series. Vol. XXIII. 1857 p. 380, Dr. Gray remarks that the converse of the above proposition does not hold good for out of 33 species which have the narrowest range of all the species, 21 belong to large genera. But it is conformable with my views that many species in the large genera should like varieties be extremely local. The species with a wide but disjointed range (p. 387) seem to make a real exception: but with disjointed species, several interfering causes, as extinction, the action of the Glacial epoch, chance dissemination, may have come into play.

all the species (3955 in number) in the larger genera (for the size of the genera see the table) have an average range of 2.8 provinces: whereas the species (2407 in number) in the smaller genera have a slightly larger average range over 2.88 Provinces. Again in the London Catalogue of British plants (5th edit.), the species in the larger genera range on an average over 11.4 provinces, in the smaller over 11.2 provinces. Nor according to the views, which we are in this work discussing, is this surprising; for we here look at species as first branching off into varieties, & these then becoming modified (by means which it will hereafter be attempted to be explained) into closely allied, & ultimately into quite distinct species: now we have seen that varieties generally have narrow range, as have those closely allied forms which were marked for me by Mr Watson, &/A18/which are admitted in the London Catalogue as true species; & such forms, when a general average is struck, would greatly reduce the range of the widely diffused species,—including those species, of which the varieties had not as yet become converted into local species.

On our theory, however, another cause of doubt and difficulty here comes in. We have no reason to suppose that all forms, even within the same class, undergo modification at the same rate; indeed geology leads to the belief that the more highly organised forms,—as Vertebrata compared with most other animals—brachiopods in comparison with acephala, & these with gasteropoda —are replaced at a quicker rate than the more lowly organised. Hence of two sets of species, having originally exactly equal ranges, one set might become after a given period converted into a greater number of new specific forms having restricted ranges, whilst the other set remained unaltered with their original wide ranges. I suspect that, on our theory, this may be the explanation of the Compositae,/A19/for instance, which are considered by many botanists as very highly organised plants, having species on an average with very narrow ranges.[1] This view may perhaps, also,

[1] Mr Gould in his Introduction to the Birds of Australia (1848, p. 122) divides this country into five sections & adds one for a few outlying regions: he gives the range of each species in these six divisions. As Birds are very highly organised beings, & as Mr Gould admits extremely slight modifications of structure to be of specific value, I have thought it worth while to have the species (omitting the Natatores) tabulated in genera having four species & upwards & into genera with three species & downwards. The 300 species in the larger genera range over an average of 1.84 sections; whereas the 228 species in the smaller genera range over an average of 2.24 sections. Here we see that the closely allied species in Mr Gould's larger genera have narrower ranges than those species which have not according to my view, been converted into representative races & species in the several sections of the country.

throw light on the general rule[1] of lowly organised plants having wider ranges than the more highly organised: though probably the greater facility of dissemination in most of the lowest plants has largely influenced the result. On this view, it is not that the more highly organised productions of nature have originally had narrower ranges, but that they soonest become changed into local & distinct species.*/

A19 A/The undoubted fact that not rarely species in the smallest genera in a country are extremely common & range very widely is not opposed to our view; for a species, before it can have become modified into several distinct species inhabiting distant localities, must have ranged, according to our theory, over the whole area, inhabited by the forms derived from it, either in its original unaltered specific state, or during its successively modified states. On the other hand, some cases are on record of groups, possessing numerous species, all of which are individually very rare & have very confined ranges, & yet with nothing special in the stations inhabited by them to account for this. Dr Hooker has given[2] a most striking instance of this fact in the Coniferae of New Zealand & Tasmania; & whilst examining the fossil Lepadidae of the Chalk period, I was much struck with the number of the species of certain genera in comparison with those now living; & yet all were very scarce in individual specimens. We may, perhaps, hypothetically account for such cases, by supposing that such genera are on the road towards extinction: for E.Forbes & others have remarked that the first step in this road is marked by a reduction of the individuals of the species.†/

A 20 /*On species with recorded varieties being more frequent in large than in small genera*:—/[3]

/Fair copy 15 A/From looking at species as only strongly marked & well defined varieties, I was led to anticipate that the species of the larger genera in each country would oftener tend to present varieties, than the species of the smaller genera; for on this view wherever many closely related species, (i.e. species of the same genus)/A20/have been formed [,] many varieties, or as I look at them incipient species ought, as a general rule, to be now forming.

* Good [J.D.H.]

† how can it be otherwise? [J.D.H.]
by catastrophe it would be otherwise [C.D.]

[1] Alph. De Candolle. Géographie Botanique. p. 499, 519.

[2] Dr. Hooker in [*Flora Novae-Zelandiae*, I, xxix.]

[3] [See Appendix for Darwin's earlier version of the opening for this section.]

Where many large trees grow, we expect to find saplings. But if we look at each species as a special act of creation, there is no apparent reason why more varieties should occur in a group having many species, than in one having few. On the other hand, where many species of a genus have been formed through variation, circumstances have been favourable for variation; & hence we might expect that the circumstances should generally be still favourable to variation & that varieties should occur there at the present day in larger numbers than elsewhere./

A21/To explain my meaning further by a loose simile,—if a nation consisted of clans of very unequal sizes, & if we ‹knew that these clans in ancient times had been very different in size, some much larger, some much smaller & some not then existing, & yet imagine ourselves quite ignorant of the cause of the difference of size, whether due to immigration or some other influence; then› if we divided the population into two nearly equal halves, all the large clans on one side, & the many small clans on the other side; we should expect to find, on taking a census at a moderately long interval that the rate of births over deaths was greater in the larger clans than in the smaller; and we should expect to find it so, notwithstanding that we knew that some of the small clans were now rapidly increasing in size & some of the larger clans declining./A 21 v/If we found this to be the case in several nations composed of clans, we should conclude that the greater rate of births over deaths was the cause of the size of the larger clans: & not, for instance, the recent immigration of the large clans./A21/ What the rate of births over deaths is to our clans, I suppose the production of varieties to be to the number of species in a genus; but unfortunately in looking to the varieties existing at any one time, we are acting as if we took a census of the clans at excessively short intervals. Each child does not grow up to man's estate, nor by any means do I suppose that each variety becomes converted into a species. What death is to the individual & ultimately to the clan, I suppose extinction to be to the varieties, to the species, & ultimately to the genus. I may add that if we found any trace of the breaking up of the larger clans into smaller clans, we should infer that this was the origin of any new clans, which, had arisen since ancient historical times./

A 22/I was strengthened in my expectation of finding more varieties in the larger genera by a remark of Fries,[1] that, "in genera containing many species, the individual species stand much closer together than in poor genera: hence it is well in the former case to collect them around certain types or principal species,

[1] Quoted in Henfrey's Bot. Gazette. Vol. I [actually vol. II], p. 188.

about which, as around a centre, the others arrange themselves as satellites." And according to our theory the closer two or more species stand together, the more nearly do they in so far approach the character of varieties; we should also bear in mind, as has been shown in the earlier parts of this chapter, with how much difficulty naturalists distinguish species from varieties, even in the best known countries, How many debateable forms there are amongst the plants of Great Britain, of France and of the United States, ranked confidently by one eminent botanist as a species, by another as only a variety. In regard to insects, Mr. Westwood has made[1] nearly the same remark with Fries: he says 'in very extensive genera, the distinctions of the species are so minute, that it requires the most practised eye to separate them'. I consulted Dr. Hooker on Fries' remark, & though he at first dissented* he subsequently quite concurred in its substance; & indeed this I find is an extremely general impression with all good observers. I likewise consulted Mr. H. C. Watson, of whose caution & judgment I have the highest opinion: after some deliberation he wrote to me, that although the difficulty/A 23/in distinguishing in a genus of 50 species, each species from 49 others, is obviously much greater than in distinguishing one species from two others in a genus of three species; yet he believes that generally the extremes are more remote in the larger genera than in the smaller, & moreover that the species in the smaller genera are more distinct from each other.

He represented the difference in the following diagram. Larger genus with ten species.—1, 2, 3, 4, 5, 6, 7, 8, 9, 10 Smaller genus with four species, 2, 4, 6, 8.

No one will pretend that the rule is universal; some small genera having very closely related species; & some few large genera having very distinct species. Further, I feel sure that all these naturalists would allow that in very many genera, some few species stand out much more distinctly than the others; & that the remaining closely allied species are not all equally related to each other: this might have been represented by the figures in the above two rows being placed at unequal distances from each other; some being crowded, like satellites, as Fries would have called them, around certain figures.—

I have tried to test numerically this doctrine of large genera including many very closely related species. But numerous dif-

* Because Fries does not observe that all? [sic] large genera are made up of two sets of species, one set as distinct inter se as those of small genera—the other all inosculate. [J.D.H.]

[1] Quoted in the Boston Journal of Nat. Hist. Vol. 4, p. 474. [In article by Haldeman.]

faculties interfere: thus all the genera with a single species have to be entirely removed, as such genera/A 24/could not include two closely related species; but one species is sometimes equally related closely to two or even three other species, & then one does not know what to do for a standard of comparison. Moreover in these very closely related forms, the difference of opinion between botanists, whether or not they have been rightly classed as species, is carried to an extreme. However, I may briefly state that Mr Watson marked for me in the London Catalogue 71 forms therein admitted as true species, but which are very closely related to other species, & have indeed all been ranked by at least some one botanist as only varieties: of these, 57 occur in genera having five species and upwards, & only 14 in genera having 4, 3 or 2 species; so that in proportion to the number of species in these two great bodies of genera, the very closely related species stand as .90 in the larger genera to .35 in the smaller. Dr. Asa Gray has kindly gone through his Flora of the N. United States & has marked for me all the closest-allied forms, which he has classed as & believes to be nearly all, true species, but which he considers as the most likely hereafter to be ranked as varieties: he has marked these in couplets & sometimes in triplets: in the 996 species included in genera having six species & upwards, there are 296 close species: in the 696 species included in genera, having 5, 4, 3 & 2 species, there are 192 close species: so that the close species in the larger genera are as .297 to .275 in the smaller genera. Dr. Hooker also marked for me the closest allied species in his Flora of New Zealand (see supplement for certain omissions & for manner in which the genera are divided) & they occurred in the larger genera, in the proportion of .175 to .166 in the smaller genera./

A25/To return to our question whether a greater number of varieties occur in the larger genera, which, as we have just seen, appear to include a larger proportion of closely allied forms, distinguishable with difficulty, or indistinguishable with any approach to certainty, from varieties. At first, I thought it would be a simple affair to discover this by dividing all the species in a Flora into two nearly equal masses,—all those in the larger genera on one side, & all those in the smaller on the other side, & *then count the number of species presenting varieties./*A 25 v/ I chose Floras, because these are much better known than any considerable Faunas, & plants are highly variable. But I have taken two well-worked out insect faunas./A 25/I soon found, however, owing to the kind suggestions of Mr Watson & Dr Hooker

TABLE II

For particulars on the works here tabulated and on the few corrections made, see the Supplement to this Chapter.	The numerators in the columns give the number of species presenting varieties; the denominators the number of species in the larger and smaller genera: these fractions are all reduced to common denominators of a thousand for comparison, and are printed in larger type to catch the eye. The right hand rows of figures in the three columns, with decimals, show the average number of varieties which each varying species has,—thus the number 1.50 shows that each two varying species have on average between them three varieties.		
	Larger Genera	*Smaller Genera* (including those with single species)	*Genera with a single species*
Great Britain. Bentham			
Great Britain: Babington —Larger Genera with 5 species and upwards, smaller with 4 species and downwards [Pencilnote by C.D.: Write this column larger'.]	101 = 152 1.40 663 1000	89 = 119 1.30 745 1000 [Pencil note by CD.: 'Write this larger'.]	24 = 94 1.50 255 1000
Great Britain, Henslow— Larger Genera with 5 species and upwards, smaller with 4 species and downwards.			
The Varieties are divided into two groups, the less strongly marked, and those which have been ranked by some eminent Botanists as species. Lesser Vars:	69 = 123 1.55 560 1000	67 = 96 1.40 692 1000	
Stronger Vars:	33 = 58 1.33 560 1000	29 = 41 1.20 692 1000	
Great Britain—London Catalogue (1853) (see Supplement for nature of Varieties)—Larger Genera with 5 species and upwards, smaller with 4 species and downwards	97 = 157 1.35 616 1000	85 = 132 1.27 642 1000	
Great Britain—London Catalogue—forms ranked as species in this catalogue but which have been thought by some authors to be varieties. In this second line, larger genera with 5 species and upwards, smaller with 4, 3, and 2 species	57 = 101 559 1000	14 = 37 377 1000	

[1] [Darwin's holograph draft for this table is in ULC vol. 16.1, fol. 167.]

Table 1 cont.

	Larger Genera	*Smaller Genera* (including those with single species)	*Genera with a single species*
Centre France: Boreau—Larger Genera with 5 species and upwards, smaller with 4 species and downwards.	113/732 = 154/1000 1.38	84/741 = 107/1000 1.47	19/267 = 721/1000 1.47
Holland: Miquel—Larger Genera with 4 species and upwards, smaller with 3 species and downwards.	22/622 = 35/1000	25/557 = 44/1000	
Germany & Switzerland: Koch—Larger Genera with 7 species, and upwards, smaller with 6 species and downwards	390/2093 = 186/1000 1.72	162/1365 = 118/1000 1.79	32/345 = 92/1000 1.50
Dalmatia: Visiani—Larger Genera with 5 species and upwards, smaller with 4 species and downwards.	164/1007 = 162/1000 1.37	130/899 = 144/1000 1.31	46/290 = 158/1000 1.26
Rumelia: Grisebach—Larger Genera with 6 species and upwards, smaller with 5 species and downwards.	98/1136 = 86/1000 1.45	54/1083 = 49/1000 1.14	12/326 = 36/1000 1.16
Russia, Ledebour (All 4 vols together) Larger Genera with 10 species and upwards, smaller with 9 species and downwards	692/3955 = 174/1000 1.48	307/2407 = 127/1000 1.39	45/475 = 94/1000 1.26
Ledebour—Vol: I separately.	207/1237 = 167/1000 1.42	62/576 = 107/1000 1.32	
——Vol: II——	192/1243 = 154/1000 1.56	94/767 = 122/1000 1.35	
——Vol: III——	171/905 = 188/1000 1.49	94/595 = 157/1000 1.50	
——Vol: IV——	122/570 = 214/1000 1.45	57/470 = 121/1000 1.36	
N. United States. A. Gray-Larger Genera with 5 species and upwards, smaller with 4 sp. and downwards. The two kinds of vars. marked in this work are here classed together.	112/1136 = 98/1000 1.40	65/917 = 70/1000 1.36	32/361 = 88/1000 1.37

Table I cont.

	Larger Genera		*Smaller Genera* (including those with single species)		*Genera with a single species*	
Canary Islands, Webb & Berthelot—Larger Genera with 4 species and upwards, smaller with 3 and downwards.	49/421 = 116/1000		42/551 = 76/1000			
India (part of Flora) Hooker & Thomson—Larger Genera with 7 species and upwards, smaller with 6 species and downwards.	21/258 = 81/1000	1.01	13/165 = 78/1000	1.53		
Tierra del Fuego: Hooker—Larger Genera with 3 species and upwards, smaller with 2 species and downwards	19/177 = 107/1000	1.57	16/163 = 98/1000	1.37		
New Zealand: Hooker—Larger Genera with 4 species and upwards, smaller with 3 species and downwards	52/361 = 149/1000	1.82	37/323 = 114/1000	2.05	15/159 = 94/1000	2.00
Insecta: Coleoptera Madeira: Wollaston—Larger Genera with 4 species and upwards, smaller with 3 species and downwards	35/225 = 155/1000	1.71	26/257 = 101/1000	1.34		
Sweden- Gyllenhal—Larger Genera with 11 species and upwards, smaller with 10 species and downwards	512/1344 = 380/1000	1.85	151/485 = 311/1000	1.43	11/43 = 255/1000	1.54

that there were many great difficulties in the way. The subject is so highly important to us, as we shall see in a future chapter, that these difficulties must be discussed at tedious length; but it will be convenient first to give the tables./

A26/In Table 1, we have several of the best known local Floras, (some of which were selected for me by Dr. Hooker) with the species divided into two great groups, those in the larger & those in the smaller genera. On the extreme right hand we have the genera with only a single species, but these are likewise included amongst the smaller genera. Some of the smaller Floras have been selected simply from giving remote countries under different climates. I may premise that I have given every single Flora (&

TABLE II[1]

	Larger Genera			*Smaller Genera* (with the smallest wholly removed)		
Great Britain: Bentham Great Britain: Babington— Larger Genera with 8 species and upwards, smaller with 7-4 species both included.—	79 / 55	= 173 / 1000	1.41	53 / 360	= 147 / 1000	1.24
Centre of France: Boreau— Larger Genera with 8 species and upwards, smaller with 7-4 species both included	86 / 505	= 170 / 1000	1.40	41 / 343	= 119 / 1000	1.31
Germany & Switzerland: Koch — Larger Genera with 11 species and upwards, smaller with 10-5 species both included	257 / 1216	= 211 / 1000	1.99	114 / 683	= 166 / 1000	1.95
Dalmatia: Visiani—Larger Genera with 8 species and upwards, smaller with 7-4 species both included	120 / 707	= 169 / 1000	1.39	71 / 492	= 144 / 1000	1.36
Rumelia: Grisebach—Larger Genera with 8 species and upwards, smaller with 7-4 species both included	78 / 917	= 85 / 1000	1.44	33 / 513	= 64 / 1000	1.33
Russia: Ledebour—Larger Genera with 16 species and upwards, smaller with 15-6 species both included	573 / 3285	= 174 / 1000	1.48	234 / 1437	= 162 / 1000	1.42
N. United States: A Gray-Larger Genera with 9 species and upwards, smaller with 8-5 species both included. (The two kinds of varieties classed together.)	76 / 710	= 107 / 1000	1.36	34 / 426	= 79 / 1000	1.26

two Entomological Faunas) which I have had tabulated, & have not picked out those which favoured my views. Nor have I divided the genera first in one way & then in another; but before knowing what the result would be, I determined to divide the smaller Floras nearly equally, but in the larger floras to have a greater number of species on the side of the larger genera, & then reduce

[1] [The holograph draft for this table is in ULC vol. 16.1, fol. 170.]

TABLE III.[1] *Decandolle Prodromus, Vols. 2, 10, 11, 12, 13, 14*

Name of Orders The Numerator and Denominator as in the foregoing Tables.	*Genera with 11 species* and upwards			*Genera with 10 species* and downwards		
Leguminosae	223/2937	= 75/1000	1.34	38/619	= 61/1000	1.39
Rosaceae	103/562	= 183/1000	3.09	24/144	= 166/1000	2.20
Borragineae	59/480	= 122/1000	1.38	10/111	= 90/1000	1.40
Scrophulariaceae	118/1413	= 83/1000	1.15	24/347	= 68/1000	1.29
Acanthaceae	232/1088	= 213/1000	1.43	65/335	= 194/1000	1.35
Verbenaceae	21/500	= 41/1000	1.00	5/82	= 60/1000	1.00
Labiatae	207/1999	= 103/1000	1.34	32/278	= 115/1000	1.62
Solanaceae	258/1419	= 181/1000	1.45	11/139	= 79/1000	1.72
Proteaceae	153/912	= 167/1000	1.41	6/72	= 83/1000	1.16
Polygonaceae	130/614	= 211/1000	1.63	8/62	= 129/1000	1.37
Nineteen Small Orders	112/1120	= 100/1000	1.50	48/406	= 118/1000	1.14
All the species in the 6 Vols.	1616/13050	= 123/1000	1.51	271/2595	= 104/1000	1.43
Urticaceae—Weddell—Tabulated by Dr. Hooker	65/334	= 194/1000	1.89	26/100	= 260/1000	1.57*
All six volumes together	Genera with 17 species and upwards			Genera with 16-8 species both included		
	1510/12103	= 124/1000	1.52	188/1472	= 127/1000	1.48

* Is Weddell's Urticaceae part of Deeandolle or a separate work? [C.D.]

[1] [Darwin's draft of this table is in ULC vol. 16.1, fol. 169.]

Table III cont.

All six volumes	Largest Genera (76 in number) including half the species		Smaller Genera (1088 in number) including the other half of the species	
	$\frac{959}{7815} = \frac{122}{1000}$	1.59	$\frac{929}{7830} = \frac{118}{1000}$	1.40
28 Largest Genera, each including on average 134 species, taken out of all the Orders in the Six Vols.	$\frac{455}{3772} = \frac{120}{1000}$	1.74		

all to a common denominator: for if the larger Floras had been divided equally, from the great size of many of the genera, but comparatively few would have been included amongst the "Larger Genera": & as we cannot suppose that the larger genera go on varying or increasing in species for ever, it requires a considerable number of genera, as will presently be more fully explained, to strike a fair average. In the very large Flora Rossica, I have given in the table, the result for each volume separately, just to show that the excess of varieties in the larger genera is common to the whole/A 27/Flora: I did the same in some other cases with the same results. I have given Great Britain as worked out by several Botanists,/A27 v/not as being particularly well-known, but in order to show that personal differences in estimating the value of species & varieties, makes no essential difference in the general result. /

A27/Now if we look to the two columns, under the larger & smaller genera, printed in larger type, in which the number of species, presenting varieties, are reduced to a common denominator, we see that with one single exception, the species in the large genera present decidedly more species having varieties, than do the species in the smaller genera. Moreover the average number of varieties to the varying species, with few exceptions, is larger in the larger than in the smaller genera: this is seen in the right hand columns of decimals,—the figures 1.50 for instance, showing that each two varying species have an average of three varieties. The one exception in the table, just alluded to, is Miquel's list of the plants of Holland: but so extremely few varieties are here marked, & as the results deduced from his list differ in several other respects from those obtained by other botanists, it may, I think, be disregarded.

In Table II, I have selected a few (& given all which I have selected) of the larger local Floras, & have entirely removed the smallest genera: & by looking at the columns printed in the larger type, & at the column with decimals we see the same rule throughout, namely of a greater number of varying species, & a greater average number of varieties, in the larger than in the smaller genera.—

If, then, local floras are to be trusted, & if the varieties recorded by various botanists (& two celebrated Entomologists) are worth anything, & if the varieties have been recorded fairly or nearly equally in the larger & smaller genera.—/A 28/all subjects presently to be discussed—we must conclude that there is a decided preponderance of varieties in the larger in comparison with the smaller genera.—

Table III gives the results of the tabulation of all the species (15,645 in number) in six volumes of De Candolle's Prodromus: selected for me by Dr. Hooker, & done at his suggestion. We here see a very different result from that deduced from the local Floras. In the genera having only 11 species & upwards there are more recorded varieties than in the genera with 10 species, & downwards; this holds good for the summary of the six volumes, & for most of the separate orders, but fails in some orders, especially in the great, natural & most carefully worked out (by Bentham) order of the Labiatae. The rule, however, does not hold good, (see Table) if all the genera with seven species & downwards be wholly excluded; so that all that can be said, is that the smallest genera usually present fewer recorded varieties. It deserves remark, how closely similar the result is when all the genera with 10 [11] species & upwards, with 17 species & upwards, when the 76 largest genera which include half the species, & when the 28 very largest genera are taken:—the proportion of the species having varieties in these several cases varying only from120/1000 to 124/1000. The larger the genera are, however, the average number of varieties to the varying species seems to increase being in the 28 gigantic genera, as much as 1.74: so that each two varying species has on an average more than three varieties./

A 29/Now what is the evidence from these three Tables worth? The first question to consider is, whether it is best to take local Floras, or parts of the whole vegetable kingdom. The latter though having some advantages, has, for my special purpose several most serious sources of error. Geology tells us that in the long course of time, small groups have increased, come to a maximum, then declined, & ultimately disappeared. Hence we may feel pretty sure that some groups of plants, now numerically large, have nearly or quite arrived at their maximum, or are now declining; & that

other small groups are now increasing more or less rapidly in numbers./A29 v/Greatly as genera differ in size, yet there is a limit ‹in number of species› beyond which they rarely pass; & therefore, on my view of varieties being incipient species, there must always come a period when the largest genera will cease to increase at least as a single genus; though it does not by any means follow that sections or portions of such genera may not go on increasing, & other sections decline & be lost./A29/It is idle to speculate what would be the precise effect on varieties of the declination, from less favourable conditions of life, of a group of species; but as the individual numbers of most of the species would probably decrease, from the relations lately pointed out, the amount of variation at any one time would probably be less: we do not even at all know, whether commencing extinction would generally first act on the species in the larger or smaller genera: though one may surmise on the latter: the ultimate result, we shall in a future chapter see, would probably be to leave in any group, those forms which are most distinct from each other. Now in a local Flora any genera, still large, which had come to/A30/vary in a less degree, or a small genus which was varying largely, would, supposing for the moment our rule to be true of the species in large genera varying more than those in small genera, be on an average compensated by the other genera of the same country: so it should be in a Prodromus of the whole vegetable kingdom, if such existed, & there were no other causes of error: but looking to each separate order we might expect, if there be any truth in my view, to find some orders in which the large genera varied little,[1] & some in which the small genera varied greatly.

Secondly it is known[2] that the same order or genus often has

[1] I suspect that the Labiatae, viewed as a whole are now undergoing some great change in development. When divided in the three different ways shown in Tab III the smaller genera have a preponderance of varying species: yet there are two gigantic genera containing together no less than 653 species, & these contain fewer varying species (viz. 90/1000 & only 1.20 varieties to each varying species)
than the smaller genera however divided. If the sub-order Satureieae, (including only between 1/5 and 1/6 of the Labiatae) be removed, the larger genera have
a preponderance of varying species. In the smaller genera of Labiatae the average number of varieties to the varying species is unusually large. Lastly looking to some of the local Floras, I find that in Boreau, Koch & Visiani the smaller genera in this order have more varying species than the larger: on the other hand in Babington & Ledebour, the large genera in this order, as generally throughout all these several Floras, have a preponderance of varieties.

[2] Alph: De Candolle, Geographic Bot. p. 1237-1245. In Hooker's Hot. Miscell: (Vol. 2 p. 257) there is given from Ledebour several curious cases of the great predominance of certain genera in the Altai: for instance there are 62 species of Personatae, & one-third of these belong to the genus Pedicularis: of the 130 Leguminosae, three-fourths belong to Astragalus, Oxytropis & Phaca.—

many more species in one country, than in another, either owing to differences of climate or other unknown conditions. Where many species of a genus exist, relatively to the other inhabitants of the country, we have seen that there is some evidence that, on an average, a large number of them are common & widely diffused; and that of such common & diffused species a large number present varieties. This at least is possible, but it could be hardly detected except in a local Flora; for when all the species of the genus were collected in a general Prodromus, the supposed greater amount of variation where the species were numerous, & the less amount, where thinly scattered & where the genus did not seem to flourish, would tend to counterbalance each other, & conceal the result. Again there are many moderately-sized genera with all their species confined to one country, & which in that country would be a large or rich genus, & which, according to my general theory ought to be largely varying, as they have in that/A 31/ country become modified into many species; but the greater number of such moderately-sized endemic genera would in a general Prodromus have to be tabulated amongst the smaller genera, & would vitiate the result. In fact such genera with absolutely few species in comparison with genera in the whole vegetable kingdom, but rich in species in their own country, are exactly those genera which we might expect would yield the best evidence on our view. Gigantic genera are often widely distributed over a large portion of the world; & we must believe (as Sir C. Lyell has remarked in his Principles in regard to the wide range of the *same* species) that owing to the slowness of geological changes, of climate, &c., this spreading of the species of the same genus (descendants from common parents according to our theory) must have taken an enormous length of time: hence, although in a very large widely-spread genus there must have been, on our view, a great amount of modification, this modification may have been slow. On the other hand in local genera, we may believe from the very fact of their not having ranged widely, that they often are not of such ancient origin as the widely spread genera; & in taking a census of such comparatively fleeting objects as varieties, we ought to look as much as possible to those groups of species, which are undergoing the most rapid change; & it is just these very endemic genera/A32/rich in the species in their own country, which would be lost, or rather would give a directly false answer when tabulated in a general prodromus.

To take as a final illustration, the case alluded to in a previous note of the genera Pedicularis and Astragalus, so extraordinarily

rich in species in the region of the Altai. As so many species have been formed there, we ought to look to these two genera/A 32 v/in that quarter, in order to see the manufactory of species at work: that is, according to my view, we ought there to find in these two genera, a greater than average number of varieties. And if this rule were found generally to hold good in local Floras, namely that the genera which had many species had many varieties, it would throw much light on the origin of species. But what can it signify under this special point of view, whether or not other species of Pedicularis and Astragalus are varying in other quarters of the world?*[1]

A32/Hence I conclude from the several reasons just assigned, namely that some large genera must have arrived at their maxima and be now declining, & some small genera be rapidly increasing in number of species,—that some genera have been largely developed in certain countries, and elsewhere much more feebly,—that endemic genera probably have in many cases increased at a quicker rate than mundane genera, & yet would be ranked as small genera in a general Prodromus,—from these several reasons, I conclude/A 33/that a fragment of a Prodromus would be of little service, and an entire Prodromus of far less service for our special purpose than local floras. Nor should I have tabulated the six volumes of De Candolle, had it not been for Dr. Hooker's advice, nor should I have published the results, had not honesty compelled me, as they are on the whole unfavourable. Nevertheless I am bound to confess that from the wide diffusion of plants, and from genera largely dominant being generally everwhere numerous, I had expected more favourable results.

The best territories for my special object, would be those with all the species endemic, for all the species will probably have originated in such areas and where many species of the same genus have been formed, there as a general rule we ought now to find most variation in progress. Under this point of view, New Zealand & Madeira are the best areas in Tab. 1, but they would have been better, had they included a greater number of species. I can, however, see no valid objection to taking, as a representative of the whole, fragments of one natural area, as (in Tab. 1) the several kingdoms of Europe. Another advantage in local floras over a Prodromus, in which latter the orders are worked out by different men, is that there would be generally more uniformity

* Hence the smaller the area the better the result? [J.D.H.]

[1] [From here until the middle of fol. A 41, the text of the draft is not in Darwin's handwriting.]

in the value attached to varieties & species; there must be a prodigious difference in the value of the species as given by Dunal in the Solanaceae and by Bentham in the Scrophulariaceae, & though it is quite immaterial for us whether a greater or less amount of difference causes two forms to be called species or varieties, it is of some consequence that there should/A 34/be some approach to uniformity in the relative value of the species & varieties when all are tabulated together.

Now comes the question, what is the value of the varieties recorded in Botanical works? Am I justified in hypothetically looking at them as incipient species? do they differ in the same manner, only less in degree, from their types, as one closely allied species differs from another? I do not doubt that mere monstrosities have been recorded sometimes as varieties, though I do not suppose that any botanist would intentionally do so, & some authors have expressly stated that they have endeavoured to avoid this. Some also have stated, for instance Boreau, Visiani & Wollaston, that they have endeavoured to record as varieties not mere fleeting differences, but those alone with some degree of permanence. So again I do not doubt that a good many varieties are merely nominal, & owe their origin to doubts & confusion; & as such would be more likely to arise in large genera, than in small, this would directly vitiate our tables. That varieties even in the most carefully worked out floras are of very unequal values must be admitted; but it would have been a serious objection to my view of varieties being incipient species in various stages of modification, had they been all equally like or unlike each other and their parental types. I may here repeat that I am far from supposing that all varieties become converted into what are called species; extinction may equally well annihilate varieties, as it has so infinitely many species. That many varieties have in some degree the character of species I cannot doubt, for so many have been ranked as species by one botanist or another. Thus in the small British Flora, we have in Mr. Watson's list (Tab 1) 182 varieties, so ranked by the greater number of sound botanists, /A35/but which have all been considered as species by some one botanical author; & we have in addition 71 other forms called species in the well sifted London Catalogue, but which have been ranked as varieties by some one botanist. So again in Professor Henslow's list there are 62 forms considered by him as varieties, but which have been ranked by such eminent men as the elder De Candolle, Sir J. Smith, Sir W. Hooker & Lindly as true species.

Dr. Hooker objects to my whole manner of treating the present

subject because varieties are so ill defined; had he added that species were likewise ill defined, I should have entirely agreed with him; for my belief is that both are liable to this imputation; varieties more than closely allied species, & these more than strongly marked species.

Mr. Watson & Dr. Hooker have also objected that there are many species so highly variable, & with the varieties running so closely into each other, that botanists do not attempt to mark them as distinct; hence in my tables, some of the most variable species do not appear to have any varieties. Boreau & Mr Wollaston also state that such polymorphic forms are not included amongst their recorded varieties. In the former part of this chapter we have seen how difficult it is to decide whether Polymorphism is of the same nature with more defined variation,/A 36/so that I am inclined to think that it is an advantage that such polymorphic species are partly excluded from my tables. That they are not by any means wholly excluded I am aware; for botanists occasionally mark by Greek letters ideal types which cannot really be defined from an inextricable mass of varying forms. So again when only a few specimens have been collected of some *rare* polymorphic species, the varieties would necessarily appear far more defined than they really are, & so would be liable to be recorded as distinct. I do not suppose that polymorphism which is partly excluded from our tables is much commoner in small than in large genera, or conversely; if it were so, it would have seriously vitiated our tables,—that is, if we suppose Polymorphism to be essentially of the same nature with more definite variation. In some of the floras I have excluded the most notorious polymorphic genera, which abound with doubtful species & doubtful varieties; but this has *never* been done except with the larger genera; & the result has invariably been to make the preponderance of varieties in the larger genera, *less* than it would have been, had these genera been admitted.

Mr Watson & Dr Hooker likewise object that* our best classifications are very far from natural; but any great perfection on this head is not material for my purpose: I divide all the species in a country /A 37/in to two great bodies; all those in the larger genera on one side, all those in the smaller on the other side; & I presume it will not be disputed that the species in the larger genera taken together present a greater number of forms more closely allied together in little groups, than do the species in the smaller genera. I have however, found in tabulating the British

* remind me [J.D.H.]

Flora that the species of some few genera when split up into smaller genera, had to be placed among the smaller genera, whereas in other British floras they stood on the other side. But the several British floras in Tab. I show that this has not materially affected the result.

I cannot look at any of these causes of error as very important; they would, I think, to a large extent disappear when averages are taken; & the uniform result in Tab I & II bears out this conclusion. But now comes a far more serious cause of doubt, suggested to me by Dr. Hooker after seeking some of my tables; namely that botanists have recorded varieties more fully in the large than in the smaller genera. He believes this to have been the case from several reasons, but more-especially from floras serving in part as mere dictionaries; & as it is obviously more difficult to name a species in a large than in a small genus, he thinks botanists have guarded against error by more carefully recording the varieties in the larger genera. I have consulted several other botanists, & though it does not appear that they had previously thought on this point, they generally/A 38/concur in this view. One botanist, however, Dr. A. Gray, whose opinion will be considered by all as of the greatest weight, after deliberation does not believe that he has himself so acted: he at first thought that he might have unfairly recorded a greater number of varieties in the smaller genera, which, from what little systematic work I have myself done, was my impression owing to the greater interest of monotypic genera. Now if Dr. Hooker & the others who concur with him be right, all the foregoing tables are utterly worthless;* for they do not show nature's work only the imperfect handiwork of botanists. It is presumptious in me to believe that botanists have worked more philosophically than they themselves think they have; but I can hardly avoid this conclusion.

For in the first place it is somewhat remarkable that so many botanists & two Entomologists should all unconsciously & unintentionally have produced so uniform a result, as may be seen in the first two tables: more especially as the varieties recorded by different authors are of such different values. To test Dr. Hooker's capital objection, I selected some of the principal local floras, & entirely removed the genera of least size; these are all given in Tab. II; here the larger genera (larger than in Tab. I) still show a marked preponderance in the proportional number of varying species over the smaller genera,† here not so small as in

* vitiated though perhaps not overturned [J.D.H.]

† give the case of Rubus [J.D.H.]

Tab. I. Dr. Hooker/A 39/would probably account for this fact by saying that the larger the genera & the more difficult the species were to identify, the greater the number of the recorded varieties would be; but as the difficulty goes on regularly increasing with the size of the genus the excess is not so great or so uniform as might have been expected on this view. The excess in the number of the varieties in the larger genera not regularly increasing with the size of the genera, may be explained on my hypothesis by some of the largest genera having reached their maxima. If we now look to the genera with a single species (right hand column in Tab. I) the difficulty in identifying the species is reduced to a minimum, yet we find that the number of species in these monotypic genera[1] which have varieties, though proportionally less than in the next group of larger genera, is by no means diminished in an extreme degree, as might have been confidently expected on Dr. Hooker's view: in two instances, namely in the U. States & Dalmatia, the number is actually greater than in the next group of larger genera. All this may be seen by comparing the right hand & middle columns in Tab. I.

If we look to the rows of figures with decimals in Tab. I & II, which give the average numbers of varieties which the varying species include, we find a degree of uniformity, especially in Tab. II very remarkable as it seems to me on Dr. Hooker's view. For my own part I look at these rows of figures as shewing, that not only/A40/more species present varieties, but that the varying species generally present more varieties in the larger than in the smaller genera.

In the monotypic genera (right hand column in Tab. I) where the difficulty in naming species is reduced, as already remarked, to a minimum, we find the average number of varieties to the varying species, in five cases, either equal to, or actually greater, than in the next group of larger genera. ‹This fact, I think, if the average from the small number of species in the monotypic genera can be trusted, might be explained on my view, but the explanation is not worth giving.*› On Dr. Hooker's view that the species in the larger & smaller genera really have on an average an equal number of varieties; but that the varieties have not been fully

* Small genera being few in individuals do not present so many Herbarium varieties. *[J.D.H.]*

[1] [ ] says p. 574 that some have thought that monotypic species do not vary. He does not give any authority except [Puvis] (De la Dégéneration p. 37) who refers only to varieties raised under [cultivation], and adduces the supposed fact in regard to all variations being due to intercrossing.

recorded by botanists in the smaller genera, we are driven to conclude (as may be seen by comparing the middle & left hand columns in Tab. I) that although Boreau in France, Koch in Germany, & Hooker in New Zealand, did not fully & fairly record all the species having varieties in the small genera: yet that in these very genera/A 41/they have recorded a greater than average number of the varieties themselves. This strikes me as improbable, & on the whole it seems to me far more probable that the tables make some approach to a fair representation of the manner in which species vary in nature. Any how I have endeavoured to give an abstract of the more important facts & arguments on both sides, & those few naturalists who are interested in the subject, can form their own judgement.

Finally, then, if we review our whole discussion on local Floras, which alone are well adapted for our purpose, it may I think be concluded, that on an average, a greater number of species in the large genera are common & widely diffused in their own country, than in the smaller genera; but that this greater number is (according to our theory) being slowly & steadily diminished by these species tending to vary, & thus being converted first into local varieties & then into local species. We can understand why a species which ranges widely & thus becomes exposed to somewhat different conditions of life is the most likely to vary; and a species numerous in individuals has a better chance, within any given/A 42/period, of breaking into varieties, which from possessing some advantage might be preserved & so become more or less permanent. Moreover common & widely diffused species must generally be better adapted to the conditions of life, to which they are exposed than the rarer & more local species, as will be more fully discussed in the next chapter when we treat of the severe competition to which every being is exposed; hence varieties from such favoured species will have the best chance of enduring for a long period & of increasing in numbers. It may be added that if a variety has ever increased so largely in individual numbers that it has come to exceed those of its parental type; it assuredly will have been called the species, & the original species the variety.

From these relations, & more especially from the actual facts given in the tables of the local Floras, I believe that the species in the larger genera, which as a general rule are very closely related to each other & in so far themselves approach in character to varieties, oftener present varieties (& a greater number of

† had [not] the means [J.D.H.]

varieties) than do the species in the smaller genera./A 42 v/It is not that the species of very small genera never vary, or that the species of large genera invariably present a great number of varieties; for if it were so, it would be fatal to my theory, as genera of all sizes have to increase & decline. Nor by any means is it, that all the species of a genus present varieties; for this is a very rare case;—it is only that more species have varieties clustered round them in the larger than in the smaller genera. And in regard to the close affinity of the species to each other in the large genera, it is not that all are equally related to each other; but, that some species are closely clustered round other species; causing the genus to consist of smaller & unequal sub-groups. These/A 43/conclusions as far as they can be trusted, strengthen our general theory, that species do not essentially differ from varieties, & that varieties by further modification may be converted into species. But our tables more especially throw light on the origin of the species of a genus, where very many are endemic in a moderately sized territory, & where we may suspect that they have been formed within comparatively recent times; for it is in local floras alone, that we invariably find more recorded varieties in the large genera, than in the small; & I have given my reasons for putting some faith in the records of so many Botanists, whose works agree in this respect. Furthermore, I believe, that the rule of the species in the larger genera on an average varying more, & therefore as I look at it, increasing in the number of their species at a quicker rate, than the species in the smaller genera, when taken in connexion with a large amount of extinction & with a principle, hereafter to be explained, which may be called that of divergence—taken together throw a clear light on the affinities of all organic beings within the same great classes; for we invariably see organic beings related to each other in groups within groups—or somewhat like the branches of a tree sub-dividing from a central trunk.

Conclusion. From the various facts now given in this chapter, & innumerable others might have been added, I cannot doubt that there is much variability in organic beings in a state of nature/80 v/ The widely-ranging, the much diffused & common, in short the vigorous species are those which are the most apt to vary./80/The variation differs greatly in degree; in some it is scarcely perceptible, in others strongly marked; so that we have a graduated series from the finest shades of individual differences, to well defined races, distinguishable with great difficulty, if really distinguishable

at all, from sub-species & closely allied species. In certain protean genera, the variability may in part be of a different nature; but on this point it seems difficult to arrive at any definite conclusion. From what we have seen of the effects of domestication or changed conditions on organisms of all kinds, & which beings, it has been shown in the second chapter, could not have been originally selected from the plasticity of their organisation, & knowing well that the history of the world is emphatically that/81/of Change, it would have been a discordant result if there had been no variability in a state of nature. Judging from the effects of domestication it is indeed surprising that we do not clearly see in nature more organic change, but if such greatly changed organisms do exist, they would be universally called species & not varieties.

According to the views discussed in this work, species do not differ essentially from varieties;—two closely allied species usually differing more from each other than two varieties, & being much more constant in all their characters. This greater constancy may be looked at as partly due to the several causes of variability having acted less energetically on the two species under comparison than on the one species yielding the two or more varieties; and partly to the characters of the two species having been long inherited, & by this very cause having become more/82/fixed. The greater amount of difference between the two species than between the two varieties, may be looked at as simply the result of a greater amount of variation; the intermediate varieties between the two species or between them & a common parent having become extinct. Hence as a general rule, species may be looked at as the result of variation at a former period; & varieties, as the result of contemporaneous variation.

But the forms generally considered as varieties & those considered as species differ in one other most important respect; namely in the perfect fertility of varieties together & the lessened fertility of the offspring of two species. This subject will be discussed in a separate chapter; & I will here only repeat that the infertility of species when crossed graduates away so insensibly/83/that the two most experienced observers who ever lived have come to diametrically opposite results when experimentising on the same forms;—that the infertility does not closely go with the general amount of difference between the two forms, but follows laws of its own;—that it is most powerfully affected by the sex in reciprocal or reversed crosses of the very same two species;—and finally that, as we have seen in the last chapter, the reproductive system is eminently subject to disturbance & that infertility of an analogous

kind to that resulting from hybridism supervenes from other & totally distinct causes. Hence, as it will be attempted to be shown in the chapter devoted to this subject, there is no valid reason, why the different "sexual affinity" (to use Gaertner's expression) of different species to each other should be thought a character of overpowering weight, in comparison with the other differences between species when contrasted with the difference between varieties. ‹with each other; as, for example, in the tendency to adhere when grafted together.› /

84/It seems to me that the term species is one arbit[r]arily given for convenience sake to a set of individuals closely like each other; &, that it is not essentially different from the term variety, which is given to less distinct & more fluctuating forms. The term variety, in comparison with mere individual differences, is applied, also, arbit[r]arily & for convenience. Practically if two forms are tolerably constant in their characters & are not known to be connected by a nearly perfect series of intermediate forms they are called species; & according to the views here given, even should the two distinct forms be thus connected, if the intermediate forms are comparatively rare, so as seldom to cause much difficulty in naming an individual specimen, there seems no good reason why they should not be called species; & in that case science & common language would accord in giving names of equal value, to the primrose & cowslip,—/85/to the deodar & cedar of Lebanon, —to the Durmast and common oak,—as well as to the many fine species distinguished by the naturalists on characters of little physiological importance.

As the only known cause of close similarity in two organic beings, is descent from a common parent, it is natural that the idea of descent should have entered into almost every definition of the term species. A monster may be abnormal in any degree, but the instant we know its parentage, we do not doubt about referring it to its species.—On the views here discussed, the idea of the common descent of all the individuals of the same species equally comes into play; but it is not confined, as in the ordinary definition, to the individuals of the same species, but is extended to the species themselves belonging to the same genus & family, or to whatever higher group our facts will lead us.—/

86/According to these views it is not surprising that naturalists should have found such extreme difficulty in defining to each other's satisfaction the term species ‹as distinct from variety.) It ceases to be surprising, indeed it is what might have been

expected, that there should exist the finest gradation in the differences between organic beings, from individual differences to quite distinct species;—that there should be often the gravest difficulty in knowing what to call species & what varieties in the best known countries, & amongst the most conspicuous & best known organic beings if ranging over a wide territory; & that the difficulty should be hopelessly great in two adjoining but now perfectly, or almost perfectly separated regions./86 v/We can understand why it is that the species in large genera are generally more closely related to each other & related in little clusters like satellites around certain other species, why they are apparently often confined in their distribution, & lastly why they oftener present varieties & a greater number of varieties, than do the species in small genera: for, on our views, where, in any country, many species of a genus have been formed there has been in such genus a greater than average amount of modification within the existing geological period; & hence we might expect that the resultant forms would tend to resemble varieties in closely resembling each other & in being grouped around certain species, like varieties around their parents & in being local. We might moreover, expect, on these views that where there has been lately much specific modification, there generally would be now most variation in progress.

The conclusion that there is no/86/essential difference, only one of degree & often in the period of variation, between Species & Varieties, seems to me at least as simple an explanation of the many/87/difficulties by which naturalists are beset, as that each species should have been, independently created with its own system of variability,—the varieties imitating the characters of other species, supposed to have also been independently created, so closely as to defy in many cases the labours of the most experienced Naturalists.

CHAPTER IV, SUPPLEMENT

a/Phanerogamic plants alone have been tabulated out of the following works./av/In the counting the number of varieties themselves, I have not except in a very few cases which are specified counted those marked a: for these seem generally to be the type-forms more fully described: or the type forms in an exaggerated degree. I would, however, here make no important difference for our object whether counted or not, as they would have been counted both for the large & small genera.—/