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THE GENERIC RELATIONS OF SPECIES IN SMALL ECOLOGICAL COMMUNITIES

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1. INTRODUCTION

The problem of the importance of competition between two or more species in the same genus, in determining whether they can survive side by side in the same community, is of great ecological interest. The following is a statistical approach to the problem based largely on the fact that in most animal and plant communities the numbers of genera with one, two, three, etc., species appear to form a mathematical series very close to the 'logarithmic series'.

The species in any group of animals and plants that are found living side by side in any relatively small community have presumably been selected in the course of time from all the species in the surrounding areas which have been able to reach the smaller area in question. Those that survive are those which are capable of existing in the physical environment of the area and also in association with, or in competition with, the other members of the community.

Such a natural selection could conceivably be brought about under three different conditions: (1) without reference to the generic relations of the species, (2) more or less *against* species in the same genus, (3) more or less *in favour of* species in the same genus. Extremes of either (2) or (3) would result in only one species to each genus on the one hand, or in all the species in each genus on the other hand being represented. We know, however, that biologically, neither of these extremes is correct.

It is, however, most important to consider in detail what exactly happens when a selection of a relatively small number of species is made from a larger fauna or flora, without reference to their generic relations (no. (1) above), as a true interpretation can only be made by comparing the observed data with the results of a selection of the same size made at random. If the average number of species per genus in a small community is smaller than that expected by random sampling, then there is evidence of a selection against generically related species; if the number of species per genus is larger than would be expected by random sampling, then there is evidence of selection in favour of species in the same genus.

Before we can discuss the problem of sampling, it is, however, necessary to consider what is the general structure of the relative numbers of genera with 1, 2, 3, etc., species in any group of animals or plants.

2. GENERIC CLASSIFICATION AND THE LOGARITHMIC SERIES

I have shown recently (Williams, 1944) that in a number of classifications of particular families or orders of plants, insects and other animals, the number of genera with 1, with 2, with 3, etc., species forms a series which can be represented very closely by the logarithmic series.

This will be discussed more fully below, but for the moment it should be noted that if we know the number of species and the number of genera in any group, a logarithmic series of the genera with 1, 2, 3 species (which we will call n_1, n_2, n_3, etc.) can be calculated and this can be checked against the observed frequencies. If a close fit is found, it is evidence of the likelihood that the logarithmic series is a correct interpretation, and we can then use for further argument known properties of the logarithmic series.

I have shown, as stated above, that the logarithmic series gives a very close fit to published classifications of large groups, such as the flowering plants of Britain, the Mantidae of the world, the birds of Great Britain, and many other systematic and geographical groups. It is, however, important to know if the same principle is found in the classification of small communities. For this purpose some evidence brought forward recently by Elton (1946) is of great value.

Table 1 shows particulars of ten of his animal communities and three of his plant communities, together with the total (reduced to an average) of his 49 animal and of his 27 plant communities; with the number of genera with 1, 2 and 3 species in each case as given by Elton and as calculated by the logarithmic series.

The communities analysed here are all comparatively simple ones, because reliable surveys of more complex communities such as woodland do not yet exist; some of them, however, are quite large in area.

No one can deny the extremely close approximation of the observed and calculated figures in nearly all the examples and particularly in the averages. Thus in the average figure for 49 animal communities the calculated number of genera with one species is 38·1—the observed 39; in the average of 27 plant communities the calculated number of genera with one species is 30·7 and the observed 31·1. The fit for n_2 and n_3 is almost equally good.

Thus we have very strong evidence that the number of genera with 1, with 2 and with 3, etc., species is arranged in a logarithmic series in quite small or simple ecological communities as well as in large systematic groups and in large areas.

where the successive terms are the numbers of groups (in this case genera) with 1, with 2, with 3, etc., units (in this case species).

n_1 (which $= \alpha x$) is the number of genera with one species; x is a constant less than unity, α is a constant which we have called the Index of Diversity. If we know the number of species (N) and the number of genera (S) in a population which is arranged in a log series, we can calculate both n_1 and x, and hence the whole series, and also the Index of Diversity.

Table 1

	Elton's community	No. of genera	No. of species	No. of genera with 1 species	No. of genera with 2 species	No. of genera with 3 species	Index of diversity
	Animal	S	N	n_1	n_2	n_3	α
9	Temperate woodland (logs)	126	136	118	6	2	
				116	*8·7*	*0·9*	773
10	Subarctic bog	19	21	17	2	0	
				19·1	*1·6*	*0·2*	94
11	Subarctic bog	29	32	26	3	0	
				26·3	*2·2*	*0·25*	155
12	Temperate fresh-water pond	26	32	21	4	1	
				21·4	*3·5*	*0·8*	65
13	Temperate fresh-water pond	72	90	61	8	1	
				59	*11*	*2·2*	171
14	Temperate lake benthos	46	59	38	6	0	
				36·8	*6·9*	*1·7*	98·1
15	Temperate lake benthos	8	13	6	1	0	
				5	*1·8*	*0·7*	8·3
16	Temperate lake benthos	58	86	44	8	1	
				40	*10·8*	*3·9*	74
20	Temperate river	99	131	82	7	6	
				79·6	*15·6*	*4·1*	203
22	Temperate river	59	87	47	6	3	
				42	*10·8*	*3·7*	81·5
	Average of 49 animal communities	45·3	54·41	39·0	4·6	1·12	
				38·1	*5·7*	*1·14*	127
	Plant						
1	Arctic rocky soil	22	31	16	4	1	
				16·4	*3·9*	*1·2*	35
3	Arctic heath	37	51	28	7	0	
				27·8	*6·3*	*1·9*	62
4	Subarctic heath	32	42	26	3	0	
				26	*4·9*	*1·35*	68
	Average of 27 plant communities	37·0	95·1	31·1	4·4	1	
				30·7	*4·9*	*1·05*	96

Data from Elton (1946). Numbers in col. 1 are those of communities given in his Tables 1 and 4.

In the figures for n_1, n_2 and n_3 the upper line is the observed number, the lower line (in italics) that calculated on the basis of the log series.

3. THE PROPERTIES OF THE LOGARITHMIC SERIES

The logarithmic series will be found fully discussed in Fisher, Corbet & Williams (1943), Williams (1944) and Williams (1947).

The series can be represented in two ways, either

$$n_1, \quad \frac{n_1 x}{2}, \quad \frac{n_1 x^2}{3}, \quad \frac{n_1 x^3}{4},$$

or

$$\alpha x, \quad \alpha\frac{x^2}{2}, \quad \alpha\frac{x^3}{3}, \quad \alpha\frac{x^4}{4},$$

If a random sample is taken from a population which is arranged in a logarithmic series, a new logarithmic series is found in the sample, with a new n_1 and a new x. But for all samples of whatever size from one population the ratio of n_1 to x, which we have called 'α', is constant. In other words, this is a property of the population and not of one particular sample. It is a measure of the extent to which the species are grouped into genera, or the genera divided into species. It is high when there are a large number of genera in relation to the number of species, and low when there are a small number of genera relative to the number of species, and it is independent of the size of the sample. It is thus a measure of the generic diversification of the species population, and for this reason we have called it the 'Index of Diversity'. It is, indeed, an index of exactly the property which is at present at issue. If a small sample of a larger population has the same Index of Diversity as the larger population, then it has been selected without reference to the generic relationships of the species. If the smaller sample has a larger Index of Diversity, it is evidence that there has been selection against species in the same genus. If it has a smaller Index of Diversity, it is error is particularly high when the average number of species per genus is very low, which is usually the case in small communities.

An example of the application of the logarithmic series is as follows: In Bentham & Hooker's *British Flora*, 1906 edition there are 1251 species of plants classified into 479 genera. These are arranged reasonably closely to a logarithmic series and give an Index of Diversity = 284 (Williams, 1944, p. 30).

If samples of different numbers of species are taken from the above flora, *without any reference to generic relationships*, they must each have the same index of diversity; and from this and the number of species we can calculate that the expected number of genera would be, as shown in Table 2.

Table 2. *Calculated properties of samples of different numbers of species taken from Bentham & Hooker's 'British Flora' (1906 ed.), without any bias with respect to generic relations. All samples have an Index of Diversity of 284.*

No. of species	Expected no. of genera	Average no. of species per genus	Expected no. of genera with 1 species	% of genera with 1 species
N	S	N/S	n_1	$100\ n_1/S$
		Original population		
1251	479	2·61	231	48
		Samples		
1000	428	2·34	222	52
500	288	1·74	181	63
200	151	1·32	117	78
100	86	1·16	74	86
50	46	1·09	42·5	92
30	28·5	1·05	—	—
20	19·3	1·04	18·7	95
10	9·8	1·02	—	—

evidence that there has been selection in favour of species in the same genus.

The average number of species per genus (N/S), the proportion of genera with one species (n_1/S), and the proportion of species in genera with one species (n_1/N) are all dependent on the size of the sample (see Table 2); but the Index of Diversity is the same for all samples from the same population provided that they have been randomized for generic relationships.

It is, however, important to note for the present study that the error of estimation of the Index of Diversity increases rapidly as the sample gets smaller (see Fisher *et al.* 1943, pp. 53 and 56). Thus for populations with 1000 species in 100 genera the error (standard deviation) of α is about 6%; but with 100 species in 70 genera it is 20%, and with 10 species in 9 genera it is just under 100%. The

It will be seen that the average number of species per genus steadily falls, and the percentage of genera with one species each steadily rises as the sample gets smaller. In a random sample of only 20 species of British flowering plants less than one genus with more than one species would be expected to be present.

It should be noted that if our biologically selected community contains as few as 30 species, the only possible high values for n_1 (since fractions do not exist in nature), are 30; 29; 28; 27; 26; 25. These give respectively Indexes equal to infinity; 420; 270; 195; and 150, etc. so that no community as small as this will give statistical data sufficient to distinguish between small changes in α, or small biases in favour of, or against, species in the same genus.

The data brought forward by Elton are not suitable for further inquiry along these lines as firstly the numbers of species are in general too small, and secondly we have no available lists of the number of species and genera (and that is to say of the Index of Diversity) in the larger groups, floras or faunas, from which these communities have been selected by nature. What we require is a series of natural groups of different sizes selected by nature from one much larger group; all the species and genera in each series being of course in exactly the same classification.

For example, if we could take the butterflies of the world, the butterflies of England, the butterflies of an English county, the butterflies of a small area in this county, and the butterflies of a single ecological community in the small area (all in the same classification), then we would have a series of observed facts which could be analysed to see if the Index of Diversity in each sample indicated greater or less generic diversification as the samples got smaller.

It has not been possible to get such a perfect series of data, but in what follows I give the evidence I have been able to find that appears to be suitable for study.

4. COMPARISONS OF SMALL WITH LARGE SERIES

(*a*) *Plants on Broadbalk Wilderness, Rothamsted Experimental Station, Hertfordshire*

Brenchley and Adam (1915) have published a list of the species of flowering plants that have been found on this piece of abandoned wheat field which covers an area of about half an acre. In their table on p. 198 (emended to agree with the nomenclature of Bentham & Hooker's *British Flora*, 1906 ed.), they mention 73 species which were found in four surveys carried out between 1867 and 1913. These are classified into 59 genera. Of these, 50 genera have one species; six have two species; one has three and one has four. This gives an average number of species per genus of 1·24; and an Index of Diversity of 147.

If only the plants observed in 1913 are considered, the numbers are 65 species in 52 genera (41 with one species, ten with two, one with three). The average number of species per genus is 1·25 and the Index of Diversity 134.

I have already published (Williams, 1944, p. 30) data on the whole classification of Bentham & Hooker's 1906 edition which gives an average number of species per genus of 2·61 and an Index of Diversity = 284.

The two Broadbalk Communities thus have—as would be expected from the small size of the sample—a lower average number of species per genus; but the Index of Diversity is in each case lower than the whole British flora, and the smaller sample has a lower value than the larger. Thus the evidence is that there is less generic diversification in the Broadbalk Wilderness flora, or a smaller number of genera than would be expected by a random sample including the same number of species.

In fact a random sample of 73 species from the British flora, as classified by Bentham & Hooker, would have about 65 genera instead of the 59 observed.

(*b*) *Flowering plants of Scolthead Island, Norfolk*

Chapman (1934) gives a list of the flowering plants of Scolthead Island, an island of sand-dunes which covers an area of about one and a half square miles.

His list, when altered to the nomenclature of Bentham & Hooker's *British Flora* (1906 ed.), gives the following results (Table 3).

Table 3

Species N	Genera S	Species per genus N/S		No. of genera with: 1 species n_1	2 species n_2	3 species n_3	4 species n_4	5 species n_5	Index of Diversity
161	114	1·41	Obs.	82	22	7	1	2	
			Cal.	85·3	20·1	6·3	2·26	0·8	182

It will be seen that the observed numbers conform very closely to a logarithmic series as checked by the calculated values of n_1, n_2, and n_3; and that the Index of Diversity is 182, as compared with 284 for the whole British flora.

In a purely random sample of 161 species from the British flora, irrespective of generic relations, we would have expected to find representatives of approximately 126 genera. Thus the observed number is smaller than the calculated, indicating a selection in favour of generically related species rather than against them.

(*c*) *Flora of Park Grass Plots, Rothamstead Experimental Station, Hertfordshire*

At Rothamsted there are a series of plots of grass, of areas varying from $\frac{1}{2}$ to $\frac{1}{8}$ acre, which have been manured in special ways for many years, but in which no further interference has been made in the natural flora which develops under such conditions of manuring and soil.

Brenchley (1924) has given a series of tables from which Table 4 is extracted; the classification has been altered slightly to agree with Bentham & Hooker's *British Flora* (1906 ed.).

Table 4

	No. of species N	No. of genera S	Average species per genus N/S	Index of Diversity
All plots all years	59	53	1·11	263
	1919 Survey only			
Plot 3. Unmanured:				
Without lime	30	27	1·11	134
With lime	30	27	1·11	134
Plot 13. Farmyard manure:				
Without lime	20	18	1·11	89
With lime	23	21	1·10	111

The original Index of Diversity for the whole of Bentham & Hooker was 284 so that all the smaller floras have a smaller Index of Diversity. The error of estimation of α is however very high.

Plots 9 and 10, with sulphate of ammonia for many years, gave (with and without potash) from 9 to 14 species each in its own genus. It is not possible to calculate a finite value of α from such data. It is, however, interesting to note that in a random sample of ten species from Bentham & Hooker's *British Flora* ($\alpha = 284$) one would expect 9·8 genera! So the observed figure of 10 cannot be taken as evidence of any extreme departure from randomization.

(*d*) *Lepidoptera of Wicken Fen, Cambridgeshire*

Farren (1936) gives a list of the Macrolepidoptera of Wicken Fen according to the classification of Meyrick's *Handbook of the British Lepidoptera* (1895). In the whole group 368 species are listed in 135 genera. This gives an average of 2·73 species per genus and an Index of Diversity of 76·4. The number of species in the same families for the whole of Great Britain, as listed in Meyrick's handbook, is 788 in 212 genera, which gives an average of 3·72 species per genus and an Index of Diversity of 96·5.

For the family Caradrinidae (Agrotidae) alone, there are 146 species in 29 genera for Wicken Fen (average per genus 5·04; Index of Diversity 10·8); and 273 species in 39 genera for the whole of Great Britain (average per genus 7·00; Index of Diversity 12·7). In the family Plusiidae there are 24 species in 12 genera for Wicken Fen (average 2·00; $\alpha = 9·3$) and 54 species in 22 genera for the British Isles (average 2·45, $\alpha = 14·0$).

So we see that for the whole Macrolepidoptera and also for two separate families, one large and one small, the Index of Diversity of the local fauna is smaller than that of the larger area. In other words, there are fewer genera in the local fauna than would be expected by a random selection, thus giving evidence of a selection in favour of generically related species.

(*e*) *Coleoptera of Windsor Forest, Berkshire*

Donisthorpe (1939) gives a list of 1825 species of Coleoptera found in Windsor Forest. They are grouped into 553 genera, according to the classification of Beare & Donisthorpe (1904). The list gives a good approximation to a logarithmic series. There is an average of 3·30 species per genus and an Index of Diversity of 278. The original classification of the Coleoptera of the British Isles gave 3268 species in 804 genera, with an average of 4·60 species per genus and an Index of Diversity of 341 (see Williams, 1944, p. 24). Thus the Coleoptera of Windsor Forest have, as expected from the smaller number of species, a lower average number of species per genus; but have also a smaller Index of Diversity, indicating a selection in favour of species of the same genus rather than against.

(*f*) *Capsidae* (= *Miridae*) (*Heteroptera*) *of Hertfordshire*

China (1943) gives a list of the Heteroptera of the British Isles. The family Capsidae (= Miridae) in this includes 186 species in 76 genera as shown in Table 5. The Index of Diversity is 48.

Table 5

No. of species N	No. of genera S	Average sp. per gen. N/S		No. of genera with: 1 species n_1	2 species n_2	3 species n_3	4 species n_4	5 species n_5	Index of Diversity
				British					
186	76	2·45	Obs.	40	16	11	3	1	
			Cal.	38·1	15·2	8	4·8	—	48
				Hertfordshire					
127	60	2·12	Obs.	39	12	3	1	0	
			Cal.	32·5	12·1	6	—	—	43·7

Bedwell (1945) has given a list of the Hemiptera of Hertfordshire; the particulars of the Capsidae from this are given in the second half of Table 5. It will be seen that the Index of Diversity is slightly below that of the British fauna, but probably not outside the limits of error.

It shows, however, no evidence of selection against species of the same genus.

Table 6

Plants	No. of species observed	No. of genera		Av. no. of species per genus		Index of Diversity	
		obs.	calc.	obs.	calc.	orig.	sample
Broadbalk: 4 surveys	73	59	65·0	1·24	1·12	284	147
1913 survey	65	52	58·5	1·25	1·11	284	1·34
Scolthead Island	161	114	126	141	1·28	284	182
Park Grass, all plots	59	53	55·9	1·11	1·055	284	263
Plot 3 (1919)	30	27	28·5	1·11	1·05	284	134
Plot 13 (1919)	20	18	19·3	1·11	1·04	284	89
Plot 13 (1919)	23	21	22·2	1·10	1·04	284	111
Insects							
Wicken Fen:							
Macrolepidoptera	368	135	151·6	2·73	2·43	96·5	76·4
Caradrinidae	146	29	32·1	5·04	4·55	12·7	10·8
Plusiidae	24	12	14·0	2·00	1·71	14·0	9·3
Windsor Forest:							
Coleoptera	1825	553	630·0	3·30	2·90	341·0	278
Hertfordshire:							
Miridae	127	60	62·1	2·12	2·05	48	43·7
Macrolepidoptera	561	186	188·4	3·02	2·98	99·6	99
Caradrinidae	180	33	38·31	5·15	4·70	14·9	13·2

Table 7

No. of species in sample	No. of genera in sample			Av. no. of genera in sample	Observed no. in natural samples of same
	1	2	3		
20	20	19	20	19·7	18
23	23	22	22	22·3	21
30	29	28	29	28·7	27
59	56	50	54	53·3	53
65	60	54	59	59·7	52
73	67	60	66	64·3	59
161	128	117	126	123·7	114

(g) *Lepidoptera of Hertfordshire*

Foster (1937) gives a list of the Lepidoptera recorded for Hertfordshire. The classification used is that of Meyrick's, *Revised handbook of British Lepidoptera* (1927). He enumerates 561 species in 186 genera. This gives an average of 3·02 species per genus and an Index of Diversity of about 99. In Meyrick's *Revised handbook* the figures for the same families for the whole British Isles are 806 species in 218 genera. This is an average of 3·7 species per genus and an Index of Diversity of 99·6. In the Family Caradrinidae (Agrotidae) alone, there are 180 species in 33 genera in Hertfordshire (average 5·15, $\alpha = 13{\cdot}2$), and 290 species in 45 genera for the British Isles (average 6·44; $\alpha = 14{\cdot}9$). Thus the differences indicated that the smaller faunas have an Index of Diversity just equal to or smaller than the larger areas.

It is interesting to note that Meyrick wrote his first *Handbook* in 1895, and his 'Revised' edition in 1927. The first gives an Index of Diversity of 96·5, the second of 99·6; which shows how little his ideas on the scope of genera had changed in the 32 years between the two editions.

5. DISCUSSION

In Table 6 is a summary of the evidence brought forward in seven plant communities and seven animal communities. None of them is very small, as we have already explained that in the very small communities the chance of getting two species in one genus is too low to be the basis of discussion.

The table shows the number of genera observed in each natural sample and also the number of genera calculated on the assumption that it is a random sample from a larger flora or fauna which is arranged in a logarithmic series. It will be seen that in practically every case the observed number of genera is smaller than the calculated. It follows that the observed average number of species per genus is larger than that calculated on the assumption of a random selection from a logarithmic series, although much smaller than that in the larger area used for comparison.

These figures are calculated on the acceptance of the logarithmic series. If this is not accepted, it is still possible to make a practical demonstration that the same difference still exists between observed figures and a random sample. Bentham & Hooker's *British Flora* contains 1251 species. A series of numbers up to 1251 was typed on small cards and extremely well mixed. Three complete sets of random samples were then drawn from the complete set, each set being returned before the next set was selected. At intervals during the draw the number of genera represented in the species already selected was checked up. The results were as shown in Table 7. It will be seen again that in every case except one the observed natural number of genera is smaller than any of the three sets of mechanically randomized samples taken from the original flora. The amount of data at present available is insufficient for an overwhelming proof that the number of genera is really smaller, but at least it contains no evidence whatever that the number of genera is larger in a natural sample than in one selected absolutely independent of generic relationship, which would be expected if competition between species of the same genus was a major factor in determining survival.

From all this evidence it will be seen that a statistical treatment of the number of genera and species of different groups of animals or plants, in small and in large communities, indicates that the 'diversification' of species into genera is smaller in the small samples than in the larger. In other words, the smaller samples have fewer genera than would be expected in a random sample of the same number of species taken from the larger fauna or flora. This can only be interpreted as a natural selection—in the course of time—in favour of species in the same genus rather than against them.

It is possible to suggest reasons for this—for example, if one species in a genus is capable of survival in a given physical environment, it seems likely that other species in the same genus might be more likely to have a similar genetic make-up than species in another genus, and so might also have a good chance of survival.

If two or more species in the same genus are each capable of surviving in a particular ecological niche, the problem of their joint survival seems to be a question of the balance between the advantages of suitability to the physical environment and the disadvantages of the increased number of competitors with very similar habits—not only individuals of the same species, but of other species very closely related.

There are undoubtedly increasing difficulties to a species when the numbers increase beyond a certain level and in some cases the individuals of two closely related species might act almost as individuals of the same species, and so bring all the difficulties of increased numbers (e.g. competition for available food) without any compensating advantages.

The evidence at our disposal, however, seems to indicate that on an average, the advantages of increased suitability to the environment outweighs the disadvantages of any possible intensification of competition due to close relationship. Such increased competition possibly, or even probably, exists, but its effect cannot be estimated by study of the present type, as it is undoubtedly overshadowed by other factors acting in a reverse direction.

6. SUMMARY

1. Evidence of conditions being more favourable or less favourable to species of the same genus, as compared with species on different genera (intra-generic versus inter-generic competition), can be found in the relative number of species and genera in small and in large natural communities of animals or plants.

2. It is, however, insufficient to show that the average number of species per genus is smaller in the smaller communities than in the larger as this is a mathematical result of taking a smaller sample from a larger group. It is necessary to show that the proportion of genera to species in the smaller communities is *smaller* or *larger* than would have been expected in a randomized sample of the same number of species, selected without reference to generic relationships from the larger fauna or flora.

3. Evidence had previously been brought forward to show that in large groups of animals or plants the number of genera with 1, 2, and with 3 and more species are closely represented by the mathematical 'logarithmic series'. New evidence is here given to show that the same order exists in the genera and species of quite small ecological communities.

4. The logarithmic series has several mathematical properties of biological interest, including the possibility of calculating, for any population or sample, a factor known as the 'Index of Diversity' which is common to all random samples from a single population. It is a measure of the extent to which the species are grouped into genera, and it is inde-

pendent of the size of the sample. If the Index of Diversity is high, there are many genera in relation to the number of species; if the Index is low, there are fewer genera in relation to the number of species.

5. It thus becomes possible to compare the Index of Diversity in natural small or simple ecological communities, with that of the larger population from which these have been selected by nature. This has been done for a number of cases, including both animal and plant communities, and in every case from which significant results can be obtained the Index of Diversity in the small community is smaller than that of the larger fauna or flora.

6. The result therefore indicates that there are fewer genera in a small or simple community than would be expected in a sample of the same number of species selected at random—that is, independent of genera relationships—from the larger series. In other words, the evidence brought forward by this method indicates a selection by nature in favour of more than one species in the same genus rather than in favour of single species in different genera.

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