Quantitative Evolution XIX The numerical composition of COPELANDS Filicales

by

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With 1 Figure in the Text

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The interesting picture presented by Copeland 1947, of existing Filicales as mainly a late Tertiary development from some genera which were differentiated before the Antarctic concentration of ferns was finally obliterated in Miocene, acquires an added interest when its numerical composition is compared with the rules-within-limits which have been found to govern other existing groups with mainly Tertiary histories.

For example, one of the rules-within-limits for groups counted by the writer is that about one third, or 33 per cent, of the genera are monotypic (SMALL 1945, 1946, 1947, 1948, 1949, 1951, 1952). This is rather less than the 38 per cent given by WILLIS 1940: 42 for flowering plants. But the Filicales have 102 monotypic genera out of 300, and in 15 of COPELANDS 19 families the divergence from a nearest approach to 33 per cent with available numbers of genera does not exceed more than one or two monotypes in totals of 3 to 67 genera in the various families (see Table I). Three of the other four families have only one genus each, and the fourth family has only two genera, so that agreement with the ,one-third monotypic rule is very close and is followed in every available family in this modern classification of the Filicales 1). Therefore, it seems desirable to put on record some of the details.

Copelands Genera Filicum (1947) contains descriptions of all the living genera of ferns, including for almost every genus either a definite number for recognised species or an estimate preceded by the qualifying term ,about'. Since these estimates rarely cut across the size-classes used for comparisons with other groups, the numerical data have been sufficient for the analysis which yielded the above mentioned results.

In his ,Introduction' COPELAND details and discusses the evidence which has led him to the conclusion that about 90 per cent of living fern

 $^{^{1}}$) Although the closeness of this fitting may be coincidental, its occurrence here stimulated the further work which has been presented in the 1951-52 papers (Q E. XX and XXI) and the beginnings of which are explained below.

species and genera are of Antarctic ancestry. "It is certainly the case with ferns that the most primitive, even archaic, representatives of many groups are to be found as near as is now possible to their Antarctic source". This Antarctic source was closed about 20 million years ago, and genera

 $\begin{table} Table\ I\\ Frequency\ Distributions\ of\ Generic\ Sizes\ in\ the\ Families\ of\ Copelands\ \it{Filicales} \end{table}$

		Num-						
	Num-	ber of	Numbers of Genera in each of the					
Families	ber of	Mono-	Size Classes					
	Genera	types	2 - 3	4 - 8	9 - 20	21 - 40	41 - 50	over
								50
1. Osmundaceae	3	1	-	1	1	_	-	_
2. Schizaeaceae	4	1	_	-	_	2	-	1
3. Gleicheniaceae	6	2	-	-	3	_	_	1
4. Loxsomaceae	2	1	1	_	_	_	_	_
5. Hymenophyllacea	e 34	11	3	7	5	4	2	2
6. Pteridaceae	64	23	6	12	11	4	2	6
7. Parkeriaceae	1			1	-	_	_	
8. Hymenophyllop-					· o			
sidaceae	1	-	1	_	-	_	_	_
9. Davalliaceae	12	3	1	1	3	3	1	_
10. Plagiogyriaceae	1	-	-		-	1		-
11. Cyatheaceae	7	3	_	1	-	2	_	1
12. Aspidiaceae	67	24	16	6	6	4	-	11
13. Blechnaceae	8	3	-	2	2	_	_	1
14. Aspleniaceae	9	2	4	1	1	_	_	1
15. Matoniaceae	2	1	1	_	_	_	_	_
16. Polypodiaceae	65	22	9	15	8	6	2	4
17. Vittariaceae	9	4	1	1	1	_	1	1
18. Marsileaceae	3	1	_	1	_	-	_	1
19. Salviniaceae	2	_	0 (1	1	_	_	_
Totals	300	102	43	49	42	26	8	30
%	100	34	14.3	16.3	14	8.7	2.7	10

which were differentiated at that time are indicated in the numerical lists and Tables of the present analysis by "A" after the number of their species.

There have been various other accounts of the genera of ferns, from the 14 genera and 182 species given by Linnaeus 1753, and Hooker 1868 with about 2350 species in 68 genera of the order *Filices*, to more modern works which vary considerably in the numbers of genera and species recognised as valid. Since Ching 1940 divides Christensens *Polypodiaceae* into 33 families, while the number of genera recognised by Christensen 1934, is not quite clear", it has not been possible to find a modern nume-

rical basis for a quantitative analysis of Filicales until Copelands ,,Genera Filicum" (1947) was available.

Like Hooker, he includes Ophioglossales and Marattiales as well as Filicales, but only the last group is now large enough for numerical analysis. Copeland emphasises the fact that monographic studies of large genera or families, such as Grammitis and Hymenophyllaceae, show that the whole group of species is mainly southern, with isolated genera austral and along lines of migration, and that the larger, presumably more primitive genera are discontinuous in present range. He regards the Antarctic continent as the "fern centre" at various periods, with its last possible activity ending during Miocene, about 20 million years ago.

This point of view makes it possible to re-write his list of fern genera, as given in the "Contents" of "Genera Filicum", using size-classes as a grading which, on the whole, brings the older Antarctic genera (A) to the beginning of the list for each family with the, usually recent and local, monotypic genera making up a "tail" which is about one third of the total length of each family list. The story of the Tertiary development of each family of Filicales is more or less summarised by this plain statement of generic sizes, with "A" indicating Antarctic origin, but there are several features which require comment, after the following list has been inspected.

COPELANDS Filicales

In his "Genera Filicum" COPELAND 1947 includes the Ophioglossales, Marattiales, and Filicales.

The Ophioglossales consist of the genera Ophioglossum with 28 to 56 species, Botrychium with 23 to 36 species, and two monotypic genera Helminthostachys and Rhizoglossum.

The Marrattiales consist of the genera Marattia with about 60 species and with an "Antarctic" centre, Danaea with 32 species, Angiopteris with from one to 111 species according to the authority followed, Christensenia with 1 to possibly 5 species, Archangiopteris with 1—4, and Macroglossum with 1 or possibly 2 species.

The Filicales consist of 19 families, distributed into 300 genera. The number of species in each genus is given either precisely or as an estimate qualified by the term "about". These counted or estimated numbers are sufficient for grouping in the generic size-classes used in the determination of frequency distributions into the size-classes used, namely monotypes, 2-3, 4-8, 9-20, 21-40, 41-50, and above 50. The number of species in Filicales is about 8800. As a basis for reference, the families and their genera are given below, with a number of species for each genus. In all cases where the last digit is "0" the term "about" can be added before the number given, but this seldom means any dubiety about the size-class of the genus. "A" after a number indicates that COPELAND

suggests an Antarctic, Miocene at latest, centre for the Tertiary distribution of the genus, as described above.

Filicales - as classified by COPELAND

- 1. Osmundaceae: 3 genera, 21 species. Osmunda 14 (Jurassic to Recent); Leptopteris 6; Todea 1.
- 2. Schizaeaceae: 4 genera, about 160 species. Aneimia 90 (recent speciation); Lygodium 39 A (Cretaceous), Schizaea 30 A; Mohria 1.
- 3. Gleicheniaceae: 6 genera, about 140 species. Sticherus 100; Dicranopteris (10 or more = 9-20 size-class); Hicriopteris 11, Gleichenia 10; and 2 monotypes: Platyzoma, Stromatopteris.
 - 4. Loxsomaceae: 2 genera, 4 species. Loxsomopsis 3; Loxsoma 1.
- 5. Hymenophyllaceae: 34 genera, about 150 species. Mecodium (= Hymenophyllum in part) 100, Meringium 60 A; Sphaerocionium 50, Trichomanes (over 40); Hymenophyllum 25, Vandenboschia (25 or 20—40), Didymoglossum (over 20 or 20—40), Microgonium (no definite estimate given, taken as (20—40); Crepidomanes 12, Macroglena 12, Cephalomanes 10, Microtrichomanes 10, Selenodesmium 10; Gonocormus 7, Amphipterum 5, Buesia 5, Callistopteris 5, Crepidopteris 5, Feea 5, Nesopteris 4; Pleuromanes 3, Craspedophyllum 2, Hemicyatheon 2; and 11 monotypes: Abrodictyum, Apteropteris, Cardiomanes, Davalliopsis, Hymenoglossum, Lecanium, Leptocionium, Myriodon, Polyphlebium, Rosenstockia, Serpyllopsis.
- 6. Pteridaceae: 64 genera, about 1500 species. Pteris 280 (old), Adiantum over 200 A, Lindsaea 200 A, Cheilanthes 180 A, Pellaea 80, Dennstaedtia 70 U. C.; Microlepia 46, Hypolepsis 45; Pityrogramma 40, Doryopteris 35, Eriosorus 35, Dicksonia 25 A; Coniogramme 20, Syngramma 20, Jamesonia 18, Sphenomeris 18, Aleuritopteris 15, Tapeinidium 14, Paesia 12 ? A, Odontosoria 11, Orthiopteris 10 A, Cibotium (8—11), Culcita (8—9); Histiopteris 8 A, Isoloma 8, Anogramma 7 A, Hemionitis 7, Craspedodictyum 6, Gymnopteris 6, Onychium (3—6), Monachosorum 5, Bommeria 4, Cryptogramma 4, Oenotrichia 4, Pterozonium ? 4; Schizostege 3, Aspidotis 2, Ormoloma 2, Pareceterach 2, Taenitis 2, Trachypteris 2; and 23 monotypes: Acrostichum 1 ?, Actinopteris, Anopteris, Aspleniopsis, Cerosora, Cheiloplecton, Cystodium, Hemipteris, Lepidocaulon, Leptolepia (relic), Llavea (old), Mildella, Neurocallis, Neurosoria, Ochropteris, Ormopteris, Pleurosoriopsis, Pteridium (1—? 6), Saccoloma, Saffordia A, Schizoloma, Thyrsopteris A, Trismeria.
 - 7. Parkeriaceae: 1 genus, 5-6 species. Ceratopteris 5-6.
 - 8. Hymenophyllopsidaceae: 1 genus, 2 species. Hymenophyllopsis 2.
- 9. Davalliaceae: 12 genera, about 230 species. Humata 50; Oleandra 40 (old), Davallia 40, Nephrolepis 30 (old); Arthopteris 20 A, Araiostegia 12, Davallodes 12; Scyphularia 8; Leucostegia 2; and 3 monotypes: Parasorus, Psammiosorus, Trogostolon.

10. Plagiogyriaceae: 1 genus, 34 species. — Plagiogyria 34.

11. Cyatheaceae: 7 genera, about 850 species. — Cyathea 800 A; Cnemidaria 24, Gymnosphaera over 20; Schizocaena 7; and 3 monotypes: Amphidesmium, Lophosoria, Trichopteris.

- 12. Aspidiaceae: 67 genera, about 3000 species. Athyrium 600 A, Lastrea 500 A, Elaphoglossum 400 (old), Cyclosorus 300 A, Tectaria (Aspidium) 212 A, Polystichum 175 A, Ctenitis 150 A, Dryopteris 150 A, Bolbitis 85 (old), Rumohra over 70 A, Geniopteris 70; Woodsia 40, Lomariopsis (over 20, up to 40), Stigmatopteris 26, Polybotrya 25; Phanerophlebia 20, Cystopteris 18, Lomagramma 15, Meniscium 12 or more, Cyclopeltis over 10, Egenolfia 10; Pteridrys 8, Teratophyllum 8, Hemigramma 6, Sphaerostephanos 6, Rhipidopteris 4, Stegnogramma 4; Atalopteris 3, Microstaphyla 3, Stenosemia 3, Arthrobotrya (2-3) Callipteris (2-3), Cyclodium (2-3); 10 ditypes: Adenoderris, Ampelopteris, Anisocampium, Currania, Dictyocline, Diplaziopsis, Haplodictyum, Matteucia, Peranema, Tectaridium; and 24 monotypes: Acrophorus, Amphiblestra, Camptodium, Cheilanthopsis, Cionidium, Diacalpe, Dictyoxiphium, Didymochlaena (old), Dryopolystichum, Fadyenia, Hemidictyum, Heterogonium (1-2), Hypodematium, Hypoderris, Lithostegia, Luerrsenia, Maxonia, Onoclea (Miocene, U.S.A.), Onocleopsis, Pleuroderris, Psomiocarpa, Quercifilix, Stenolepia, Thysanosoria.
- 13. Blechnaceae: 8 genera, about 240 species. Blechnum over 200 (old); Woodwardia 12 or more, Doodia 11, Sadleria (6-7), Stenochlaena ? 6 (no number given); and 3 monotypes: Brainea, Lorinseria, Salpichlaena.
- 14. Aspleniaceae: 9 genera, about 730 species. Asplenium 700 A; Diellia 9 or more; Loxoscaphe 7 ? A; Cetarach 3, Pleurosorus ? 3, Antigramma 2, Camptosorus 2; and 2 monotypes: Holodictyum (1 or ? 2), Schaffneria.
- 15. Matoniaceae: 2 genera, 3 species. Phanerosorus 2; Matonia 1 (both genera known in Cretaceous).
- 16. Polypodiaceae: 65 genera, about 1060 species. Ctenopteris 200 A, Grammitis 150 A, Pyrrosia 100, Polypodium 75, Xiphopteris 50 A, Crypsinus 40 or more; Pleopeltis 40? A, Loxogrammitis 40, Microsorium (20—? 40), Colysis 30, Calymmodon 25, Campyloneurum 25; Drynaria 20, Goniophlebium 20, Microgramma 20, Prosaptia 20, Platycerium 17, Belvisia 15, Lecanopteris 15, Arthromeris 9; Dipteris 8, Cochlidium 7, Amphoradenium 6, Pteropsis 6, Scleroglossum 6, Neocheiropteris (5—6), Acrosorus 5, Eschatogramme 5, Aglaomorpha 4, Christiopteris 4, Dendroglossa 4, Glyphotaenium 4, Lemmaphyllum 4, Selliguea ("a small genus", ? 4—8); Dictymia (2—? 4), Paraleptochilus 3, Polypodiopsis 3, Pycnoloma 3; 5 ditypes Grammatopteridium, Holcosorus, Paragramma, Thayeria, Weatherbya; and 22 monotypes: Anarthropteris, Cheiropleuria, Dendroconche (1 or ? 2), Diblemma, Drymotaenium (1 or ? 2), Drynariopsis, Holostachyum, Holttumiella, Leptochilus, Marginariopsis, Merinthosorus, Nematopteris, Niphi-

dium, Oleandropsis, Oreogrammitis, Paltonium, Pessopteris, Phlebodium (1 or more), Photinopteris, Pseudodrynaria, Synammia, Thylacopteris.

17. Vittariaceae: 9 genera, about 150 species. — Vittaria 80 or more; Antrophyum 40 or more, Polytaenium 10; Vaginularia 6; Monogramma 2; and 4 monotypes: Ananthocorus, Hecistopteris, Pteridanetium, Scoliosorus.

18. Marsileaceae: 3 genera, about 80 species. — Marsilea 70; Pilu-

laria 6; Regnellidium 1.

19. Salviniaceae: 2 genera, 16 species. — Salvinia 10; Azolla 6 (U. C.); and no monotype.

In a few cases the monotypic condition of a genus is questioned by a record for a second species, and where COPELAND expresses doubt about this addition the genus has been classed with other monotypes about which there is no difference of opinion. These cases of 1 or ? 2 are sunk in the 1-3 size-class for comparisons with the frequency distributions of present generic sizes in other groups. The one exception to this sinking is Pteridium where COPELAND 1947: 60 differs on the side of more than one species in these words "As usually construed, a single variable species, in all tropical and temperate lands, better treated as six or more species even though they blend in some places". The ,usual construing has been followed here with the result that out of 64 genera there are 23 monotypes. instead of the "expected" 21 or 22 as nearest approaches to the one third of 64. Angiopteris in Marattiales with from one to 111 species spreads over all the size-classes used, according to the authority followed, but there is no genus in this condition within the Filicales. Among the medium and larger genera, a few odd genera have estimated sizes which include two size-classes, such as Cibotium (8-11) and Culcita (8-9) in Pteridaceae both included provisionally as genera on the lower edge of the higher size-class (9-20).

The percentage totals for the numbers of genera of Filicales in the various size-classes approximate closely to those found for other large groups which have been analysed in the same way (fig. 1). These are all cases which follow the Hollow Curve discovered by Willis 1922 and developed by Yule 1924. The origin of this curve was briefly summarised by Longley 1929 (see Willis 1940: 174) as the result of "some sort of compounding of a series of geometric series of different common ratio, but all lying between the limits of $^{1}/_{3}$ and 1". The limits $^{1}/_{3}$ to 1 do not seem to be compatible with the now known histories of the two main groups of diatoms (Small 1945—1950). And Yules 1924 mathematical treatment involved the assumption that neither genera nor species became extinct in proportions sufficiently large to effect the basic theoretical considerations, although Yule in his Appendix gave some data on the effects of cataclysmic killings of various proportions of hypothetical floras.

It has been found empirically that the end-products of the two pairs of geometric series for increase of species and of genera in diatoms, are different in that the pair for allogamous pennate diatoms gives a percentage frequency distribution of present generic sizes (Pn in Fig. 1) that is

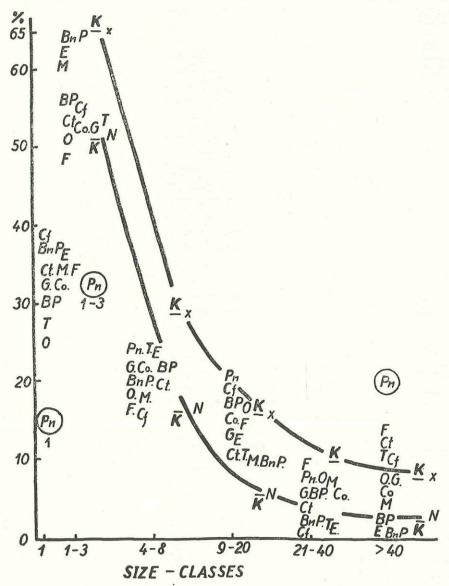


Fig. 1. Frequency Distributions as percentages of genera in various size-classes. K = fossil key from Centrales known history; F = Filicales; Ct = centric diatoms; Co = Compositae; Cf = Coniferae; E = earwigs etc.; G = Gramineae; E = earwigs etc.; E = earwigs; E =

anomalous for the size-classes 1, 1—3, and over 40, while the corresponding frequency distribution of generic sizes (F. D. G. S.) for centric diatoms (Ct in Fig. 1) is within the range shown by other groups of plants and animals, including in fig. 1 the *Compositae*, *Gramineae*, *Coniferae*, *Filicales*, also termites, rats, earthworms, earwigs, birds — passerine and nonpasserine.

Therefore, the relation between the geometric progression for increase of species and that for increase of genera is a subject for more than either vague generalisation or precise but purely theoretical consideration. This relation has now been measured, as rS/rG = rM where rS is the common ratio or rate of geometric progression in numbers of species, rG is the corresponding constant for genera, and rM is the consequential constant as measured and compared in some groups, particularly diatoms. They have been correlated one with the other in time. Now it has been found that all the complexities are centred around the expansion in time of numbers of genera and species with quite a simple correlation. The species have increased in number by doubling (x 2.0) in similar successive intervals of time, as in the pennate diatoms (and also in the centric diatoms with longer intervals of time). The genera have increased in number according to the summation of additions of new (and therefore monotypic) genera in the proportion of 50 per cent more (x 1.5) in each successive doublingperiod for species. The numerical correlation is therefore very simple, x 2.0 for numbers of species in each genus (generic sizes), and x 1.5 for numbers of new monotypic genera. Since these are exponential increases or geometric progressions, the calculations are done by adding logarithmic values and taking the nearest whole numbers as corresponding numerical values.

The basic logarithmic values as measured empirically in diatom history have been published (SMALL 1948 a: 315, 318, Figs. 1 and 2) with . 300 as an approximation to the log. of 2.0, and .173 as an empirically observed value which approximates to .176 as the log. of 1.5.

It has been suggested repeatedly that the one-third monotypic rule is a matter of psychology of systematists, so it is interesting to find that COPELAND as well as many other botanical and zoological taxonomists have followed a rule which has controlled the numbers of species and genera in accordance with the following correlated formulae: — log. number of monotypes = .125 + .176 t. n., therefore log. total number of genera = Σ (.125 + .176 t. n.) and log. generic sizes in means of numbers of species = .150 + .301. t. n.; where t = a unit of time on a scale which is uniform for any one family of genera, and n = the number of such units from the time of origin either of the group as one monotypic genus or of any one genus considered separately.

The extent to which this control has acted upon the Tertiary expansion of the *Filicales* can be seen when corresponding numbers are compared as follows: — Monotypes in Families, (n = 1 to 9) —

As will be seen, the *Filicales* numbers for monotypes correspond to the calculated numbers for monotypes in all groups of family sizes, except for the (1), (2) and (3) in brackets, and the four zeros. These four, (0, 0, 0) for monogeneric families, and (0) for one family out of the three with two genera each (see Table I), are part of the peculiar history of *Filicales* as a group of genera which, instead of dying out into a few relics like the rest of the Pteriodophytes, have undergone a remarkable expansion during Tertiary time. The four families with no monotypic genera (see Table I) are the monogeneric *Hymenophyllopsidaceae* with 2 species, *Parkeriaceae* with 5—6 species, *Plagiogyriaceae* with 34 species, and *Salviniaceae* with 10 species of *Salvinia* and 6 species of *Azolla* (see list pp. 214—216).

The other families have clearly been controlled by the normal rules of expansion, possible with t varying in its year-value and certainly with n varying, to yield various total numbers as different stages of expansion. It should be noted that the calculated proportion of monotypes moves from 50 per cent for the earliest stage of 2-total with 1 monotype, through 7-total with 3 monotypes, nearer to 33 per cent for later stages such as 43-total with 15 monotypes, and 66-total with 23 monotypes. According to the formulated smooth logarithmic calculations an accurate 34.0 per cent is not reached until n=10 and the total genera are at least 100; with 66-total the calculated percentage is still 34.8 per cent or 23 not 22 as suggested in the preamble of this numerical analysis.

From the basic values of x 2.0 for generic sizes and x 1.5 for the number of new monotypic genera the mean size of genus can be calculated as increasing from the initial value of 1 by a geometric progression with an average common r of 1.33, but even the calculated values show wide ranges with larger numbers, and the total mean for *Filicales*, at 29.3 species per genus, is outside the usual range of M=6.2 to 18.7 for many large groups (see fig. 1) which show closely similar frequency distributions of generic sizes, in accordance with the expansion of x 1.5 for x 2.0 as the relation of the rates for new genera and total species respectively.

The peculiar history of Filicales, as given by COPELAND, of a large Tertiary development from a group of Mesozoic Antarctic genera should include a larger initial Tertiary M value than 1.0 for the group of about 30 old genera, which spread later from Antarctica. About 4 or 5 species per genus would appear to be quite a reasonable estimate for this part of the numerical composition of Filicales at the beginning of the Tertiary, so that the divergence of the M value for this group can be regarded

as being due to its peculiar arithmetical beginnings in early Tertiary rather than as anomalous during its subsequent Tertiary development.

Note

All the above was communicated to the Symposium on Ferns, Bot. Soc. America, in 1950, and had no connection with Professor Mantons "Problems of Cytology and Evolution in the *Pteridophyta*" which valuable book appeared in the same year. Professor Mantons numbers refer to chromosomes, many in one nucleus as polyploid complexes, and she comes to conclusions concerning their history, rise and decay, "as the inevitable consequence of the working of their evolutionary machinery", "a highly mechanistic conception" which "disregards the actual morphology of the plants themselves and also their degree of structural" adaptation "to their mode of life", merely "by the force of logic in the facts before us": in much the same way as the enumeration of the numerical structure of Copelands *Filicales*, and of other groups, forces upon any open-minded student certain obvious conclusions.

Summary

- 1. The numerical composition of the *Filicales* as classified by Copeland in his Genera Filicum (1947) is analysed for the distribution of about 8800 species in 300 genera of 19 families.
- 2. All the 14 families with more than 2 genera follow the rule of having about one third of their genera monotypic, within one monotype more or less in any one of the families, such as 1/3, 2/6, 22/65, 23/64, etc.
- 3. The frequency distribution of present generic sizes fits the normal FDGS for other groups (fig. 1), much better than does that for the pennate diatoms, although the *Filicales* are ,marginal in the 1-3 and over 40 size-classes.
- 4. It is suggested that the peculiar history of about 30 now large genera, having spread from Antarctica before Miocene at latest and having developed during Tertiary, accounts for this marginal position, and for other divergences from a standard pattern of A^x increases in numbers of species and genera.

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