Size variation of fossil rodent populations

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Pearson's coefficient of variation is in general not applicable in palaeontology, due to the heterogeneity of samples. The heterogeneity may be due to the mixing of two species, mixture of material from various biotopes, or from a relatively large time span. A new coefficient of variation is proposed, based on the range of the sample. This coefficient may be used to estimate the degree of variation of a sample, and to decide whether it is homogeneous. Its application is tested empirically on a large number of samples of cricetid molars from the European Tertiary.

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Introduction

In palaeontology a frequently used coefficient of variation is the one mentioned by Simpson et al., 1960, and which is known as Pearson's coefficient of variation:

$$V = \frac{100 s}{\overline{x}},$$

in which s is the standard deviation of a population of measurements, and \overline{x} is the arithmetic mean of that population. According to these authors, values of V fluctuate generally between 4 and 10, with a mean between 5 and 6, as far as the teeth of mammals are concerned.

Application of the above-mentioned formula to populations of molars of fossil Cricetidae (Rodentia, Mammalia) led the present authors to the view that the values found for V may easily pass beyond the limits stated; values between 3 and 4 turned out to be common, and we hardly ever found values over 5. Possibly each taxonomic group has its own specific values of V, and comparisons between populations may only be made within the limits of such a homogeneous group.

One of the practical applications of a coefficient of variation could be, that a high value for V might indicate that a sample is not homogeneous, but that it is composed of material of more than one species. Unfortunately, Pearson's (= Simpson's) coefficient of variation cannot be used in this way because: 1) calculation of V requires that the sample be taken from a normal distribution, and a sample containing more than one species is certainly not distributed normally; 2) if in a heterogeneous sample two species are represented by more or less equal numbers, Simpson's coefficient might still give a useful result. If, however, a sample is composed of a large number of specimens belonging to one species and only very few specimens belonging to a second species, the contribution of the latter to the value of the standard deviation will be negligible. As a result, the value of $100 \text{ s}/ \overline{x}$ will not deviate from the normal and the sample will be considered to be homogeneous.

Consequently, if one wishes to use V to decide whether a sample contains two species, the frequency of each of these species must be known in advance. But, if it were known in advance, there would be no need for further testing. This is particularly relevant, since hardly distinguishable species found together in the same locality usually do show a large difference in frequency.

This means that Pearson's coefficient of variation is not a good measure to decide whether a palaeontological sample contains one or two species. The quantity to be used for such a coefficient should be free from any preceding conditions. Mein & Freudenthal (1971) hinted that the range might be a quantity that fulfills this requirement.

The range gives much importance to the extreme measurements of the sample. Mathematically this is a disadvantage, because these values are much influenced by chance; a solution would be to leave out the upper and lower extremes, or the upper and lower quantiles, but this would reduce the palaeontological usefulness of the method. The best results were obtained by a new coefficient proposed here:

$$V' = \frac{100 R}{M},$$

in which R is the range (the difference between maximum and minimum), and M is the mid-point between maximum and minimum.

The mid-point is used instead of the arithmetic mean for several reasons: The mid-point requires little computation, as it is the sum of the minimum and maximum values divided by 2. This means that it may be calculated from every publication stating the minimum and the maximum value of a sample. For the calculation of the mean all measurements should be available. Secondly, the



Fig. 1. Relation between range and sample size. The unit of the vertical axis is the standard deviation. The horizontal scale is linear in the upper graph, logarithmic in the middle one, and in the lower graph the scale is $\sqrt{\log N}$.

range is - mathematically - such an inaccurate value, that using the mean would give a false idea of precision. Thirdly, in a sample containing many specimens of a large species, and only a few specimens of a smaller species, V' would be too small if the mean were used.

Evidently, the range, and so the value of V', is related to the number of specimens in the sample. The mean range, expressed in the standard deviation of the sample is a mathematical quantity known for samples taken from normal distributions. The relationship between the mean range and the sample size is given in Fig. 1. In the upper graph the scale of the horizontal axis (sample size) is linear. In the middle graph the scale is logarithmic, and in the lower graph the scale is the square root of the logarithm. In the latter case the relationship between the mean range and the sample size is practically linear, at least for values of N between 5 and 1000. In - palaeontological - practice values of N smaller than 5 are statistically not interesting, and values of N over 1000 are not found. It may be assumed that within the mentioned limits the relationship between V' and the square root of log N is linear too, provided that the samples be taken from normal distributions. Unfortunately, the latter condition is not necessarily fulfilled in palaeontological practice. Skew distributions appear not to be uncommon, and therefore results must be treated critically.

Variation in fossil Cricetidae

In order to get an idea of the distribution of V' for different values of N a number of about 140 populations were chosen, partly from the literature, partly from our own unpublished data, as specified in the following list. The figures preceding the items in the list refer to the publications cited in the chapter literature. Items without preceding figures are unpublished data, mainly from the research project 'Aragonian' which we are carrying out in collaboration with Dr R. Daams (Groningen University).

	Alcocer 2	Megacricetodon crusafonti
17	Anwil	Cricetodon hagni
17	Anwil	Democricetodon brevis
17	Anwil	Democricetodon freisingensis
17	Anwil	Eumyarion latior
17	Anwil	Megacricetodon gregarius
17	Anwil	Megacricetodon minor
17	Anwil	Megacricetodon similis
22	Armantes 1	Fahlbuschia koenigswaldi
22	Armantes 1	Megacricetodon collongensis
22,23	Armantes 7	Fahlbuschia larteti
22	Arroyo del Val 6	Fahlbuschia darocensis
22	Arroyo del Val 6	Megacricetodon crusafonti
2	Beaumont 3	Megacricetodon germanicus
13	Bezian	Megacricetodon bezianensis
29	Bolgenachtal	Eucricetodon praecursor
	Borjas	Megacricetodon crusafonti
	Borjas	Megacricetodon minor

15	Duñol	Demogricated on hispaniaus
15		Democricetoaon hispanicus
15		Eumyarion valencianus
15	Bunoi Con Lisheteree	Megacricetoaon primitivus
20	Can Liobateres	Cotimus ieemanni
20	Can Liobateres	Rotunaomys sabaaeiliensis
20,33	Can Liodateres	Ruscinomys inaleri
35	Caravaca	Ruscinomys lasallei
	Carrilanga I	Megacricetodon debruijni
	Carrilanga I	Megacricetodon ibericus
	Caseton I A	Fahlbuschia sp.
	Caseton 1 A	Megacricetodon collongensis
	Caseton 2 B	Fahlbuschia sp.
_	Caseton 2 B	Megacricetodon collongensis
7	Castell de Barbera	Democricetodon brevis
14	Cetina de Aragon	Eucricetodon gerandianus
27	Coderet	Eucricetodon thaleri
27	Coderet C.1	Adelomyarion vireti
27	Coderet C.2	Adelomyarion vireti
27	Coderet C.3	Eucricetodon collatus
2	Collet-Redon	Democricetodon mutilus
2	Collet-Redon	Megacricetodon bavaricus
35	Concud 3	Ruscinomys schaubi
12	Cournon-les-Soumeroux	Eucricetodon dubius
11	Dieupentale	Adelomvarion vireti
11	Dieupentale	Eucricetodon collatus
21	Dorn-Dürkheim	Democricetodon lavocati
16	Eichkogel	Kowalskia fahlbuschi
20	Erkertshofen	Democricetodon franconicus
33	Escobosa de Calatañazor	Cricetodon aguirrei
33	Escobosa de Calatañazor	Fahlbuschia larteti
33	Escobosa de Calatañazor	Megacricetodon crusafonti
19	Giggenhausen	Megacricetodon similis
9	Heimersheim	Eucricetodon moguntiacus
19	Hesselohe	Megacricetodon bavaricus
32	Hoogbutsel	Eucricetodon atavus
4	Hostalets de Pierola	Fahlbuschia crusafonti
6	Hostalets de Pierola	Hispanomus dispectus
5	Hostalete de Pierola	Magazziaatodon ibazicus
10	Lattingen	Megacricetodon megarius
17 27	Küttigen	Fueriestodon collatus
10	Langenmoosen	Democricetodon gracilis
19	Langenmoosen	Democricetodon gracilis
19	Langenmoosen	Democricetodon matilias
19	Langenmoosen	Megacricetodon bavaricus
22	Las Planas $A + A \mathbf{P}$	Engline days compine
22	Las Planas 4 A \pm 4 B	Fanibuschia darocensis
22	Las Planas 4 A + 4 B	Megacricetoaon collongensis
	Las rianas 4 U	megacricetoaon collongensis
	Las Flanas S B	megacricetoaon crusafonti
	Las Planas S B	megacricetodon minor
	Las Planas > H	Megacricetodon crusafonti
25	Las Planas > L	Megacricetodon crusafonti
33	Layna	Kuscinomys europaeus
2	La Grenatiere	ranibuschia larteti
2	La Grenatière	Megacricetodon gregarius

22	La Grive-St. Alban	Democricetodon affinis
22	La Grive-St. Alban	Megacricetodon gregarius
22	La Grive-St. Alban	Megacricetodon minor
22	La Romieu	Democricetodon romieviensis
22	La Romieu	Megacricetodon collongensis
23.35	Los Mansuetos	Ruscinomys schaubi
2	Luc-sur-Orbieu	Cricetodon sansaniensis
2	Luc-sur Orbieu	Democricetodon affinis
2	Luc-sur Orbieu	Megacricetodon crusafonti
22.23	Manchones	Cricetodon iotae
22	Manchones	Fahlbuschia darocensis
22	Manchones	Megacricetodon crusafonti
22	Manchones	Megacricetodon minor
35	Masada del Valle	Hispanomys freudenthali
23 35	Masia del Barbo 2 A	Hispanomy's preudentinan Hispanomy's peralensis
23, 35	Masia del Barbo 2 R	Hispanomys peralensis Hispanomys peralensis
23,55	Montredon	Hispanomys perdiensis Hispanomys mediterraneus
$\frac{2}{2}$, $\frac{3}{3}$	Montredon N Sun	Rotundomys meantisrotundi
2, 5	Navarrata del Rio	Fuericetodon aquitanicus
22 25	Nombrevilla	Hispanomys nombrevillae
25, 55	Nombreville	Meyacricetodon debruini
25	Nombreville	Megacricetodon ibericus
25	Olmo Redondo 1	Democricetodon sp
	Olmo Redondo 2	Democricatodon sp.
	Olmo Redondo 5	Magaariaatadan primitiwus
	Olmo Redondo 9	Megacricetodon primitivas
	Olmo Redondo O	Megacricetodon primitivus
25	Badromarca 2 A	Megacricetodon primitivas
23	Pedromiento 2 C	Democricetodon aebruijni
24	Pedregueras 2 C	DemocriceIoaon suicalus
25	Pedregueras 2 C	Hispanomys aragonensis Magamianta dau dahmiini
23	Pedregueras 2 C	Megacriceioaon aebruijni
24	Pedregueras 2 C	Kotunaomys nartenbergeri
33 25	Peralejos C Baralaias D	Hispanomys peralensis
33	Peralejos D	Hispanomys peralensis
2	Port-la-Nouvelle	Democricetodon mutilus
2	Port-la-Nouvelle	Megacricetodon collongensis
8	Povoa de Santarem	Fahlbuschia darocensis
8	Povoa de Santarem	Megacricetodon crusafonti
36 27	Puttenhausen	Democricetodon gracilis
36	Puttenhausen	Democricetodon mutilus
36	Puttenhausen	Eumyarion bifidus
36	Puttenhausen	Eumyarion weinfurteri
36	Puttenhausen	Megacricetodon germanicus
19	Rosshaupten	Megacricetodon gregarius
19	Sandelzhausen	Democricetodon gracilis
19	Sandelzhausen	Democricetodon mutilus
22	Sansan	Democricetodon brevis
22	Sansan	Democricetodon gaillardi
10	Sansan	Megacricetodon minor
	San Roque 1	Democricetodon sp.
	San Roque 2	Democricetodon sp.
28	Saulcet	Eucricetodon gerandianus
	Solera	Fahlbuschia sp.
	Solera	Megacricetodon crusafonti

6	St. Quirze	Cricetodon lavocati
4	St. Quirze	Fahlbuschia crusafonti
22	Suevres	Megacricetodon bourgeoisi
	Toril 1	Megacricetodon crusafonti
	Toril 1	Megacricetodon minor
22	Torralba de Ribota	Megacricetodon collongensis
35	Tortajada A	Hispanomys freudenthali
7	Trinchera Nord Autopista	Rotundomys bressanus
	Valalto 1	Megacricetodon crusafonti
	Valalto 2 B	Megacricetodon crusafonti
	Valalto 2 C	Megacricetodon crusafonti
22	Valdemoros 1 A	Fahlbuschia koenigswaldi
22	Valdemoros 1 A	Megacricetodon primitivus
22	Valdemoros 3 B	Fahlbuschia koenigswaldi
22	Valdemoros 3 B	Megacricetodon collongensis
	Valdemoros 3 D	Megacricetodon collongensis
	Valdemoros 3 E	Megacricetodon collongensis
22	Valtorres	Megacricetodon primitivus
	Vargas 1 A	Fahlbuschia sp.
	Vargas 1 A	Megacricetodon primitivus
18	Vermes 1	Democricetodon mutilus
31	Vieux-Collonges	Cricetodon meini
30	Vieux-Collonges	Cricetodon sansaniensis
	Vieux-Collonges	Democricetodon affinis
30	Vieux-Collonges	Democricetodon affinis brevis
	Vieux-Collonges	Fahlbuschia sp.
22	Vieux-Collonges	Megacricetodon collongensis
24	Villafeliche 2 A	Democricetodon hispanicus
22	Villafeliche 4	Megacricetodon collongensis
	Villafeliche 4 A	Fahlbuschia sp.
	Villafeliche 4 A	Megacricetodon collongensis
	Villafeliche 9	Megacricetodon crusafonti

Computation and the drawing of the graphs were carried out on the central computer of Leiden University, by means of a number of Fortran programs written by the first author. The full list of data and the computer programs are available upon request.

In the following M^1 stands for first upper molar, M_1 for first lower molar, and M1 for both upper and lower first molars. The same goes for M2 and M3.

V' was calculated for each of the six elements of the dentition separately, and also for length and width separately. So each species from each locality may give a maximum of twelve figures for V' (figures based on less than five measurements were not used). For each of these twelve categories (length M_1 , width M_1 , length M^1 , width M^1 , length M_2 , etc.) a diagram was drawn, and these diagrams are given in Figs. 2 through 13.

On the horizontal axis V' is in a linear scale, the vertical axis is the logarithm of N (number of specimens in a sample). Each circle represents a sample of specimens of one element (e.g. M_1) of one species from one locality. If two or more of these circles overlap, one larger circle has been drawn. The size of the circle grows with the amount of overlapping values.

Obviously, V' is smallest in M_1 and M^1 , and largest in M_3 and M^3 . Also, V' is smaller for the lengths than for the widths (except in M^3 , where generally the

absolute value of the length is smaller than that of the width). Furthermore, the circles are more concentrated in the diagrams of M1 and more scattered in M3, and also more concentrated for the lengths, and more dispersed for the widths.

Partly this is due to a technical problem: it is easier to measure the length of a molar of a cricetid, than the width. Also, large and small teeth are measured with the same equipment, so, the measurement error must be relatively greater in a small tooth. But, even taking this into account, it seems that M_1 and M^1 are the least variable teeth of cricetids, and that M_3 and M^3 vary most.

In all diagrams several points fall very much to the right, meaning that in these samples variation is extraordinarily high. These points were marked by the computer program that drew the diagrams, and represented by a letter or a cypher instead of a circle (in some cases these special characters are accompanied by an arrow, which means they actually should be farther to the right, outisde the limit of the diagram). If a sample was marked special in one of the diagrams, it is represented by the same letter or cypher in the other diagrams too. In these other diagrams, however, it may fall well within the normal distribution of the circles.

Remarks on samples with a high coefficient of variation

A) Eucricetodon moguntiacus from Heimersheim, published by Bahlo (1975). Bahlo states that it is difficult to separate this species from *E. atavus*, present in the same locality. Possibly his separation is not perfect.

B) Eucricetodon atavus from Hoogbutsel published by Misonne (1957). The high coefficient of variability found in the width of M^1 is probably due to the small amount of material and the quality of the measurements. In a larger sample of (unpublished) material from this locality variability is normal.

C) Eucricetodon gerandianus from Cetina de Aragon, published by Daams (1976). Variation in all elements but M_1 is normal. Inspection of an (unpublished) scatter diagram of the measurements of M_1 shows that possibly two different species are represented.

D) Eucricetodon gerandianus from Saulcet, published by Hugueney (1974). Several elements have a rather high variation coefficient. A possible explanation might be that the material from Saulcet is in part from old collections, and in part newly collected. May be it does not originate from one single bed.

E) Adelomyarion vireti from Coderet, published by Hugueney (1969), and from Dieupentale, published by Baudelot & Olivier (1978). In one of the populations from Coderet M^1 is rather variable in size. An explanation might be that Adelomyarion is not a cricetid, and that the so-called M^1 in reality is a mixture of P⁴ and DP⁴. This theory is supported by the fact that the number of specimens of M^1 is almost twice as high as the number of M_1 . This theory does not account for the very high variability of the width of M_2 . It agrees on the other hand with the highly variable morphology of M^1 .

F) Hispanomys freudenthali from Masada del Valle, published by van de Weerd (1976).

G) Hispanomys peralensis from Masia del Barbo, published by van de Weerd (1976).

H) Hispanomys peralensis from Peralejos C, published by van de Weerd (1976).
I) Hispanomys freudenthali from Tortajada A, published by van de Weerd (1976).

Several elements of these four populations show rather high variability figures, with exceptionally high values for M^3 from Masada del Valle and Masia del Barbo. Freudenthal (1966) noted a high variability for Masia del Barbo and expressed the opinion that two different species might be present, an opinion rejected by van de Weerd. The high values of variability found in *H. peralensis* and *H. freudenthali* may serve as an argument for a renewed study of this problem.

J) Cricetodon sansaniensis from Vieux-Collonges, published by Mein (1958). This is a mixture of two species. Mein & Freudenthal (1971) recognized two species, C. meini and C. aureus, both having a normal variability.

K) Democricetodon aff. brevis from Vieux-Collonges, published by Mein (1958). This small population shows high values for several elements. A much larger (unpublished) population (about 100 specimens per element) from the same locality has about the same range of measurements; due to the larger amount of specimens the variability coefficient is normal. Consequently, the high values found in Mein's population may be considered to be accidental.

L) Democricetodon mutilus from Port-la-Nouvelle.

- M) Democricetodon mutilus from Collet-Redon.
- N) Megacricetodon gregarius from La Grenatière.
- P) Megacricetodon germanicus from Beaumont 3.
- S) Democricetodon affinis from Luc-sur-Orbieu.

These five populations published by Aguilar (1980, 1981) show rather high variability values in some elements. A renewed study of this material might be worth-while.

T) Ruscinomys thaleri from Can Llobateres, published by Hartenberger (1965). Variability is rather high, possibly due to the presence of two species.

U) Eumyarion bifidus and Eumyarion cf. weinfurteri from Puttenhausen, published by Wu Wenyu (1982). The author states that variability in these species is very high. Our diagrams, however, show that this is not true.

V) Megacricetodon crusafonti from Valalto 2 C (unpublished). Variability is high to very high in M1 and M2, more normal in M3. Quite probably two unseparable species (crusafonti and minor?) are present. Like in many other cases (e.g. Megacricetodon from Armantes 7, Freudenthal, 1963, p. 92) the separation is first and best realized in M1, and the least in M3. Therefore, if a sample contains the first stage of separation of these two species, the M1 will give very high variability figures, whereas the values for M3 are quite normal. W) Megacricetodon crusafonti from Las Planas 5 H (unpublished). Variability is somewhat high in several cases, probably due to the fact that the material contains a few specimens of M. minor.

X) Megacricetodon collongensis from Las Planas 4 C. Variability is rather high in the widths of M_1 and M^1 and the length of M_2 . There is no obvious reason to explain this.

Y) Hispanomys nombrevillae from Nombrevilla, published by Freudenthal (1966) and van de Weerd (1976). Some elements show a high variability on the basis of van de Weerd's data, low on the basis of Freudenthal's data. The figures given by these two authors differ considerably. Maybe the measurements should be reviewed.

Z) Megacricetodon crusafonti from Alcocer 2 (unpublished). Variability is quite high in some cases, possibly due to the presence of a few specimens of M. minor.

1) Megacricetodon collongensis and Fahlbuschia darocensis from Las Planas 4 A and 4 B, published by Freudenthal (1963), plus some unpublished new material. Both when Las Planas 4 A and 4 B are treated seperately, and when they are taken together, variability in both mentioned species is quite high. The same goes for several other groups of rodents. A possible explanation is, that Las Planas 4 A and 4 B represent a stratigraphic level in which rather important faunal changes take place; that the fossiliferous bed represents a relatively large time span; that it contains - in part - reworked material; or that a considerable ecological change was taking place at the time of deposition (the locality is near the transition from one formation to another). In fact all these features may be causally related.

2) Megacricetodon crusafonti from Valalto 2 B (unpublished). The high variability in some elements may be due to the presence of a few specimens of M. minor.

3) Ruscinomys europaeus from Layna, published by van de Weerd (1976). M² shows a high variability. There is no obvious explanation.

4) Democricetodon gracilis from Puttenhausen, published by Wu Wenyu (1982). The variability of M_3 is very high, due to the presence of one extremely small specimen. Maybe this specimen belongs to a different species.

Table 1 lists the means and standard deviations of v'/ $\sqrt{\log N}$. For the computation those data have been left out, that presented severe doubt as to their homogeneity.

Element	Number of samples	Mean of V'/ Vlog N	standard deviation
length M ₁	126	13.48	3.22
width M ₁	126	15.30	3.90
length M ¹	118	13.38	3.38
width M ¹	118	15.18	3.62
length M ₂	124	13.03	3.60
width M ₂	124	14.55	3.77
length M ²	113	14.82	3.69
width M ²	113	15.15	3.66
length M ₃	96	16.24	4.12
width M ₃	99	15.77	4.76
length M ³	85	19.61	5.36
width M ³	85	16.51	5.12

Table 1. List of the means and standard deviations of v'/ $\sqrt{\log N}$.

Conclusions

The new coefficient of variation proposed in this paper appears to be a useful instrument to estimate variability of a sample. The value of V' appears to be dependent upon the type of material considered. It is not possible to give a general value for V'. For each group of related data the mean value of V' must be calculated separately, and conclusions may only be drawn if a sufficiently large number of comparable data is available. So far only for fossil cricetids such a number is available. We tried to apply the same method to glirids and sciurids, but for these groups the number of available data is not sufficient. Nevertheless we got the impression that for these groups the values differ considerably from those for cricetids.

Neither are the values we calculated for cricetids completely reliable. Our choice whether samples are homogeneous or heterogeneous is quite arbitrary. Future research may alter the results achieved in this paper.



Fig. 2. Relation of V' and sample size for length of M_1 . Vertical scale is logarithmic.

1000



Fig. 3. Relation of V' and sample size for width of M_1 . Vertical scale is logarithmic.



Fig. 4. Relation of V' and sample size for length of M¹. Vertical scale is logarithmic.







Fig. 6. Relation of V' and sample size for length of M₂. Vertical scale is logarithmic.



Fig. 7. Relation of V' and sample size for width of M_2 . Vertical scale is logarithmic.



Fig. 8. Relation of V' and sample size for length of M². Vertical scale is logarithmic.



Fig. 9. Relation of V' and sample size for width of M². Vertical scale is logarithmic.



Fig. 10. Relation of V' and sample size for length of M_3 . Vertical scale is logarithmic.



Fig. 11. Relation of V' and sample size for width of M_3 . Vertical scale is logarithmic.



Fig. 12. Relation of V' and sample size for length of M³. Vertical scale is logarithmic.





Fig. 13. Relation of V' and sample size for width of M³. Vertical scale is logarithmic.

VAR. WIDTH N3 SUP CRICETIDAE



Fig. 14. Histograms of V'/ $\sqrt{\log N}$ for the first molars of Cricetidae. The line under each histogram represents 2 standard deviations, the asterisk indicates the mean value.



Fig. 15. Histograms of V'/ $\sqrt{\log N}$ for the second molars of Cricetidae. The line under each histogram represents 2 standard deviations, the asterisk indicates the mean value.



Fig. 16. Histograms of V'/ $\sqrt{\log N}$ for the third molars of Cricetidae. The line under each histogram represents 2 standard deviations, the asterisk indicates the mean value.

Literature

The numbers preceding the titles refer to the list of material used.

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