

## Analysis of genetic variability in six local pig breeds

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*This analysis of genetic variability of six local pig breeds, based on available pedigree data, has been studied via two approaches: coefficients of inbreeding and probabilities of gene origin. In these closed populations, increasing inbreeding is inevitable. Average rate of inbreeding in these local breed populations ranged from 10.2% for Blanc de l'Ouest to 21.8% for Bayeux. The coefficients of inbreeding measured here highlight that mating policy has proved efficient over the last ten years. Analysis of the probabilities of gene origin shows that genetic variability in the Basque, Bayeux and Limousin breeds stayed relatively stable between 2000 and 2013. The Gascon breed lost some genetic diversity between 2000 and 2010 but has since stabilized. The 2013 figures for the Blanc de l'Ouest breed are alarming—the decline in size of the reference population paired with low litter numbers could explain this result, but a recount with 2015 figures looks imperative. The results for the Nustrale breed are to be taken with caution, as a significant percentage of Nustrale breed births do not get registered in the database. Regular recounts like this can help contain genetic drift.*

### Analyse de la variabilité génétique des six races locales porcines

*L'analyse de la variabilité génétique des six races locales de porcs, réalisée à partir des informations généalogiques disponibles, a été étudiée selon deux approches : estimation de la consanguinité et des probabilités d'origine des gènes. Pour ces populations fermées, l'augmentation de la consanguinité est inéluctable. La consanguinité moyenne des races locales est comprise entre 10,2 % pour le Blanc de l'Ouest et 21,8 % pour le Bayeux. Les coefficients de consanguinité observés mettent en avant une gestion efficace des accouplements sur les 10 dernières années. L'analyse des probabilités d'origine des gènes montre une relative stabilité de la variabilité génétique des races Basque, Bayeux et Limousin entre 2000 et 2013. Le porc Gascon a perdu un peu de diversité génétique entre 2000 et 2010 mais s'est stabilisé depuis. Pour le Blanc de l'Ouest, les chiffres de 2013 sont inquiétants, cependant la diminution de la taille de la population de référence et le faible nombre de portées peuvent expliquer ces résultats ; un nouveau bilan en 2015 s'impose. Les résultats pour la race Nustrale sont à considérer avec précaution car, dans cette race, une large partie des naissances n'est pas enregistrée dans la base de données. La réalisation régulière de ce type de bilan permet de limiter les dérives.*

**Keywords:** local pig breeds, inbreeding, probabilities of gene origin

**Mots clés :** races locales porcines, consanguinité, probabilités d'origine des gènes

## Introduction

The French local pig breeds studied have been under a rare breed preservation programme run since 1981 for the Basque, Gascon, Cul Noir Limousin and Blanc de l'Ouest breeds, and opening out to register the Bayeux breed in the late 1980s and the Nustrale breed in the early 2000s. The breed organizations managing each of these six local breeds are federated together as the *Ligéral* [association for pooled-population herdbooks on regional-heritage pig breeds] and all follow the rules on compiling herdbooks. These six breeds are not enrolled in official breed selection programmes—breedstock selected on the basis of phenotypic traits is the only bloodline preservation practice employed. In these closed populations, controlled management of genetic diversity is vital to keep the inevitable increase in co-ancestry between breeding animals in check. Inbreeding is regularly monitored. Regular re-analysis of the probabilities of identity-by-descent can also be used to gauge genetic diversity trends in whole populations.

Here we analyze genetic variability trends between 2000 and 2013 in six local pig breeds studied using the available pedigree data.

## Material & Methods

### Data

Genetic diversity was analyzed using the software PEDIG (Boichard, 2002) on a set of herdbook data extracted from the local pig breeds database. This database is managed and hosted by the Ifip and populated with data forwarded to the Ifip from both independent and local organizations pig farmers.

Table 1 reports the key characteristics of the pedigree files studied for each breed.

The pedigree files vary wildly in size, from just 2,563 individuals registered in the Nustrale breed up to 106,123 individuals registered in the Gascon breed. However, looking at the Nustrale breed figures, the low effective population size is explained by the fact that breeders have only been

registering pedigrees since the late 1990s. Furthermore, again for the Nustrale breed, as the 2013 data was incomplete when the calculations were put together, all the results reported here are for the year 2012.

Maximum number of known generations swings from 8 (Nustrale) to 39 (Blanc de l'Ouest). The Blanc de l'Ouest breed was under a selection scheme up until the late 1970s, and so it logically has a bigger and broader pedigree dataset available (the oldest recorded date of birth goes back to 1950).

Number of generation-equivalents captures population-mean pedigree completeness (Boichard et al., 1996). It is calculated, for each animal, by summing the  $(1/2)^n$  coefficient on all known ancestors, where n is level of descent from the ancestor. This means that each known parent counts for 0.5, each known grandparent for 0.25, and so on. To illustrate, if all the parents, grandparents and great-grandparents of a given animal are known, then the number of generation-equivalents will be 3.

## Demographic trends

Figure 1 charts realized effective female breeding population size for each of the six breeds studied since the year 2000. The differences in effective population sizes are explained by breed history and particularly breed promotion efforts

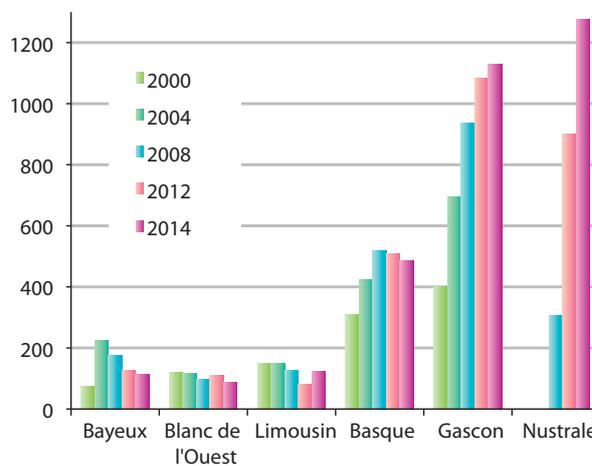


Figure 1: Trends in sow numbers per breed

Tableau 1 : Summary of the pedigree files

Breed	Effective population size	Max. number of known generations	Number of known generation-equivalents*
Basque	42,591	25	14.3
Bayeux	6,409	22	13
Blanc de l'Ouest	5,398	39	13.3
Cul Noir Limousin	8,822	26	14
Gascon	106,123	23	13.2
Nustrale	2,563	8	5.3

\*females born in 2012 for the Nustrale breed

(Lenoir, 2014a). Two clear subgroups emerge: —the Gascon, Nustrale and Basque breeds count higher effective population sizes on an upward curve, driven by their respective active breed promotion efforts, with Gascon and Nustrale passing the 1,000 sow-count mark; —the Bayeux, Blanc de l'Ouest and Cul Noir Limousin breeds have stabilized at around the 100 sow-count mark, with only Cul-Noir Limousin expected to see its gamodemes grow mid-term with the freshly-created collective marketing strategy (Lenoir, 2014b).

## Inbreeding

The coefficient of inbreeding of an animal is defined as the probability that the pair of alleles (two versions of the same gene—one inherited from the father, the other from the mother) at a randomly-chosen locus will be identical by descent, or in other words, they come from a same allele present in a same common ancestor to both father and mother. A non-zero coefficient of inbreeding highlights the presence of at least one common ancestor shared somewhere in both parents' ancestry. By definition, the coefficient of inbreeding of an individual animal is equal to the coefficient of relationship between its two parents. In closed populations like those studied here, the increase in inbreeding is inevitable. This translates as a decrease in mean heterozygosity ultimately leading to random loss of alleles (genetic drift) and, consequently, less genetic diversity.

## Analysis of probabilities of gene origin

This approach revolves around studying genetic contributions of ancestors to a given population. The method works from the premise that the probability of any given autosomal gene being transmitted from parent to offspring is 0.5. This same gene can therefore be passed down from each of all four grandparents with a same probability of 0.25, and from each of all eight great-grandparents with a same probability of 0.125. Continuing in this calculation scheme makes it possible to back-track all the way up an animal' ancestry to the founder ancestors, i.e. the first ancestors to have unknown parents. Leaving aside potential mutation events, these founder ancestors basically constitute the gene pool encountered in the current population.

The founders reflect the startpoint stock of each population. However, not all founders will have contributed equally to the current population—some will have had more descendants than others. We therefore compute the effective number of founders ( $F_e$ ) which accounts for the inequity in founder contributions.  $F_e$  is the virtual number of founders needed, assuming equity in all founder contributions, to explain the genetic diversity found in the pedigree population studied. If number of founders equals

effective number of founders, then the genetic contributions are well-balanced between and across all founders.

$F_e$  does not account for population bottlenecks, i.e. non-founder animals siring large numbers of breedstock descendants. We therefore compute the effective number of ancestors ( $F_a$ ), i.e. the number of ancestors needed, assuming all ancestors contributed equally to each generation of descendants, to explain the genetic diversity found in the pedigree population studied. Comparing  $F_a$  against  $F_e$  makes it possible to capture inequity in genetic contributions between ancestors where  $F_a < F_e$ .

$F_a$  does not fully translate the process of genetic drift, i.e. the random loss of original alleles over the course of successive generations due to certain allele-carrying animals being removed. To integrate this factor, we use computer simulation to calculate the number of founder genome-equivalents ( $N_g$ ) as the number of totally-independent genomes capable of being recomposed based on genetic print still identifiable in the pedigree population. Regular recounts are performed and the figures are presented to the breed preservation organizations. Here we took the year 2000 as basis for comparison in order to establish a transition to the latest recount published (Maignel, 2001). For each breed, there is a reference population defined as all in-breed female stock born in a given year. The analyses conducted in this study span three different reference populations (2000, 2010 and 2013) in order to gauge the pace of change in genetic diversity trends within each of the six populations.

## Results & Discussion

### Pedigree completeness

Table 1 shows that the number of complete generation-equivalents, calculated for all female stock born in 2013, is in the range 13–14.3 for the five breeds registered in the 1990s. The pedigree completeness of these five populations is very good. For the Nustrale breed registered late in 2006, the number of generation-equivalents calculated for all female stock born in 2012 is 5.3.

Figure 2 charts the trend in percentage of known ancestors per step in the line of descent for all female stock born in 2013 (born in 2012 for the Nustrale breed). For all these populations, 100% of ancestors are known at assigned generation number 1, i.e. the parent-sires generation. Excluding the Nustrale breed, percentage of known ancestors is over 90% up to direct-line generation number 8, after which the rates tail off at different speeds for different breeds, reaching zero at generation number 21 for Gascon and 32 for Blanc de l'Ouest. Nustrale logically hits zero known ancestry early at generation number 11, as population records were started only recently.

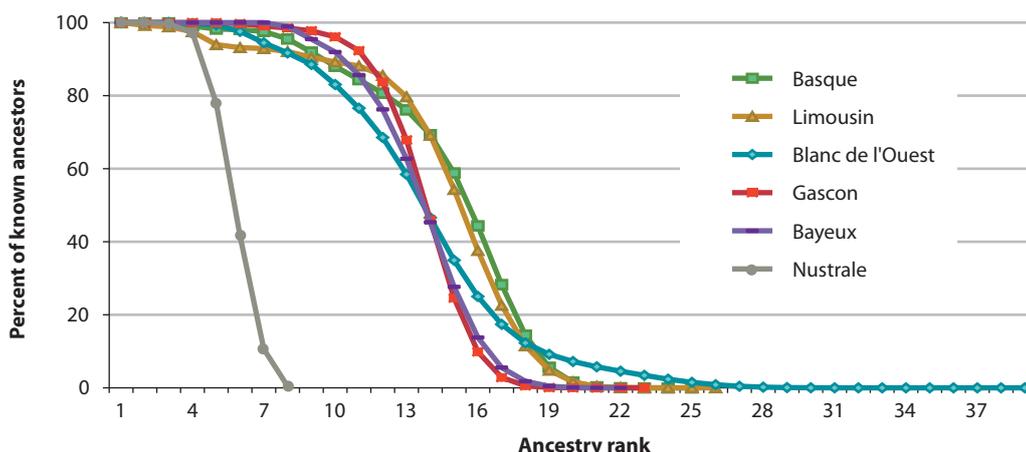


Figure 2: Pedigree completeness of the female stock born in 2013 (or 2012 for the Nustrale breed)

The good level of pedigree completeness should enable a sharp estimate of genetic diversity trends with the six populations studied. For the Nustrale breed, however, the lower level of pedigree completeness rules out any reliable comparison of genetic diversity statistics with the other pedigreed populations.

### Inbreeding

Figure 3 charts the trend in mean rate of inbreeding per birth-year of female stock (breedstock or otherwise) in the six populations since 1980. The early jump in coefficients of inbreeding is explained in part by the steady accumulation of pedigree data over these years. The coefficients of inbreeding followed different patterns in different breeds.

Mean coefficients of inbreeding of female stock born in 2013 ranged from 10.2% for Blanc de l'Ouest to 21.8% for Bayeux. For the Bayeux breed, inbreeding increased at a rate of 0.5% per year since 2000, which stands out as the highest rate found in the five populations. For the four

other breeds, inbreeding increased at a rate of around 0.2% per year since 2000.

The populations collapse into three subgroups.

- The Gascon and Blanc de l'Ouest breeds are on a similar curve marked by lower coefficients of inbreeding than the other breeds, with Blanc de l'Ouest presenting the lowest coefficient of inbreeding of all six breeds. The trend is not unsteady, probably due to the low litter numbers born each year. The slight dip observed in 2007 is explained by an ex-situ AI programme engaged by the French national cryobank [*Cryobanque Nationale*] (Mercat et al. 2008) using semen collected from boars that injected diversity. For the Gascon breed, the constant yet containable increase in inbreeding is explained by a regular boar replacement policy and closely-managed mating schemes.
- The Basque and Cul-Noir Limousin breeds share coefficients of inbreeding that are comparably similar, although more volatile in the Limousin breed which experienced two dips, one in 2006 and another 2010, due to a number

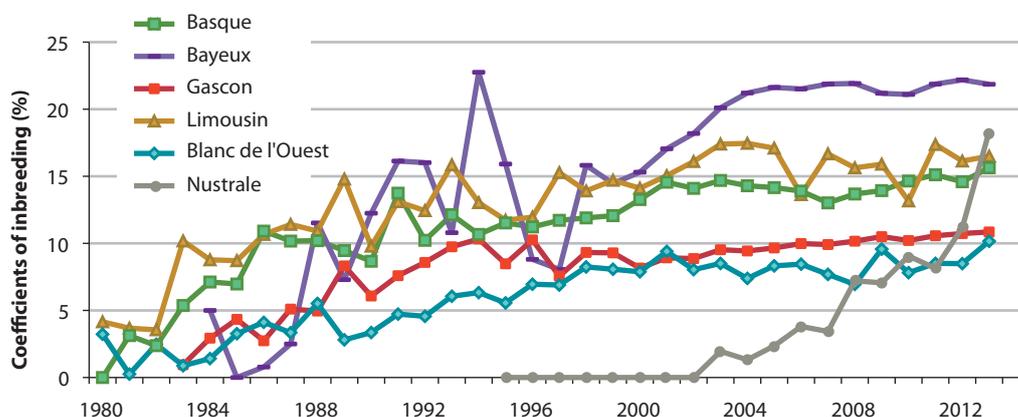


Figure 3: Trends in average rate of inbreeding per birth-year of female stock

of females entered into the supplementary section of the herdbook. Furthermore, given the low herd-population sizes, a handful of highly-inbred individuals can skew the mean. Inbreeding increased at a faster rate in these two breeds than in the Gascon breed, despite similar founder numbers between the three breeds (Table 2). This can be explained by less-controlled mating and, primarily, under-renewal of stud boar stock.

- The Bayeux breed has the highest coefficient of inbreeding yet managed to curb its rate of increase from 2004 on (+0.07% per year). This high level of inbreeding is explained by the low number of breed founders (Table 2) and the programme to eradicate the stress susceptibility gene which excluded a number of halothane-sensitive animals from further breeding. The 2007 withdrawal of the Longué strain (counting around 30 sows) from the pedigree herdbook had no marked impact on inbreeding-rate trends.

The pace of change in inbreeding rates appears to be under control for these five populations. These breeds are currently managed under planned mating schemes devised and distributed by the Ifip. Computing coefficients of relationship makes it possible to plan mating policies and keep the increase in inbreeding from snowballing.

The CRB-Anim (functional network connecting French Biological Resource Centers for domestic animals) programme financed by the French national research funding agency [ANR] includes plans to thaw and refreeze French national cryobank stocks of stored semen. This programme will open opportunities for using boars that share little relatedness with the current populations (in all

these local but Nustrale) and help curb the rate of increasing inbreeding.

The Nustrale breed registered a fairly strong jump (+3.8%) in rate of inbreeding between 2007 and 2008. This jump is tied to the better level of pedigree completeness. Since late 2006 (when the breed became officially recognized), the herdbook rules state that only fully-pedigreed boars are eligible to be registered. A second jump in inbreeding rate occurred between 2011 and 2013 and is almost certainly due to under-controlled mating. The problem here is that pedigree data gets reported back too slowly to enable coefficients of relatedness between breeding animals to be calculated in time to establish the mating plans of each farm and guide breeding programme selection decisions for future breeding stock. A strong pedigree data collection campaign was deployed in 2014 that should lend the population figures a brighter outlook in the near future.

## Probabilities of gene origin

### Founder numbers

Table 2 gives a breed-by-breed breakdown of number of founders, number of effective founders ( $F_e$ ), number of effective ancestors ( $F_a$ ) and number of founder genome-equivalents ( $N_g$ ) for the reference populations composed of females born to known parent-sires in 2000, 2010 and 2013 (2012 for the Nustrale breed). Reference population sizes are over 1,000 individuals for the Basque and Gascon breeds, which are now organized into streamed production sectors, whereas the Bayeux and Blanc de l'Ouest breeds count less

Table 2: Probabilities of gene origin

	Years	Size of the reference population	Number of founders	$F_e$	$F_a$	$N_g$
Basque	2000	968	43	10.4	9.3	3.9
	2010	1,267	33	10.4	9.2	3.6
	2013	1,091	33	10.7	9.4	3.6
Bayeux	2000	126	17	9.3	7.7	2.5
	2010	159	17	9.1	7.3	2.2
	2013	82	17	9	7.3	2.1
Gascon	2000	1,546	47	18.7	13	5.6
	2010	3,673	41	17.9	12.3	4.9
	2013	4,869	41	17.8	12.3	4.7
Limousin	2000	304	35	15.5	9	3.5
	2010	158	42	17.3	10.3	3.3
	2013	163	43	16.8	10	3
Blanc de l'Ouest	2000	125	151	23.4	13	4.6
	2010	146	151	25.1	16.4	4.4
	2013	72	151	23.6	8.7	3.3
Nustrale	2000	20	17	12.5	12.5	9.6
	2010	238	60	23.4	18	9.7
	2012	154	58	21.8	15.9	7.4

than 100 individuals in the 2013 reference population as they farrow few new litters per year (the Bayeux population is ageing and the Blanc de l'Ouest finds few marketable perspectives). The sizes of the Cul-Noir Limousin and Nustrale reference populations are similar, at 163 and 154, respectively. Note that the Nustrale breed reference population is very small compared to the Nustrale brood sow population (which counts > 1,000 sows). This is explained by the fact data records are registered on litters in which breeding animals are kept. For the other breeds, all births are registered and so both breeding animals and slaughter pigs get counted. Number of founders, which reflects the startpoint stock situation when pedigree records started, is higher in the Blanc de l'Ouest breed (n=151) due to its high popularity in the 1960s. Founder count in the other breeds ranges from 17 (Bayeux) to 58 (Nustrale). For the Basque and Gascon breeds, number of founders declined between 2000 and 2010, which is explained by the exclusion of piggeries located outside the breed production, and consequently the loss of bloodlines. In contrast, for the Cul-Noir Limousin breed, number of founders actually increased over this same period due to a females entered into the herdbook's supplementary section. The three criteria  $F_e$ ,  $F_a$  and  $N_g$  are all dependent on conservancy efforts and reflect how efficient the conservancy work has been.

For the populations studied here, number of founders is greater than effective number of founders. The gap between these two criteria highlights inequity in genetic contributions between founders. In 2013, the gap between number of founders and effective number of founders ranged from 47% in the Bayeux breed to 84% in the Blanc de l'Ouest breed which started out with the highest number of founders. The Bayeux breed conservation community has made a very conscious effort to maintain equity in genetic contributions between founders.

Effective number of ancestors, which accounts for population bottlenecks, has been relatively stable over time, which points to balanced use of breeding animals. This kind of

stability is not found in the Blanc de l'Ouest breed, where  $F_a$  increased in 2010 and then fell strongly in 2013. In parallel, the reference population size was slightly higher in 2010 than 2000 and yet very low in 2013 (only 72 breeding gilts born that year). The increase observed in 2010 is almost certainly explained by the birth of progeny from the ex-situ AI breeding programme led in 2007. However, the drop observed in 2013 (effective ancestor number down -7.7) is a big wake-up call, as the figures for 2011 and 2012 were 13.2 and 14.3, respectively. A fresh count is needed with the 2014 data to see whether the drop is just a transient dip due a number of sows temporarily failing to farrow. If the drop in  $F_a$  observed in 2013 was linked to a significant cull of brood sows going unreplaced, then it would translate a loss of effective genetic diversity.

Number of founder genome-equivalents, which factors in genetic drift, is fairly low across all five populations, which are small-sized and posses little genetic diversity. The decreases in number of founder genome-equivalents remain only minor.

The Nustrale is a special case. All three criteria computed,  $F_e$ ,  $F_a$  and  $N_g$ , were increased between 2000 and 2010 with the recording of pedigree data, but it remains difficult to gauge how the trend in genetic diversity developed between 2010 and 2013 and get a reliably picture due to incomplete reporting of pedigree data.

### Genetic contributions of ancestors

Figure 4 charts the cumulative contribution of the 30 main ancestors of the gilts born in 2013 (or 2012 for the Nustrale breed). For the six local pig breeds studied, a very tight number of ancestors explain the vast majority of the current population's gene pool. The Bayeux breed is most extreme case, with just 8 ancestors that contribute 90% of the whole-population genetics. In the Nustrale breed, 25 ancestors explain 90% of the whole-population genetics. The other breeds are positioned mid-way (12 to 15 ancestors sharing 90% of the gene pool contributed).

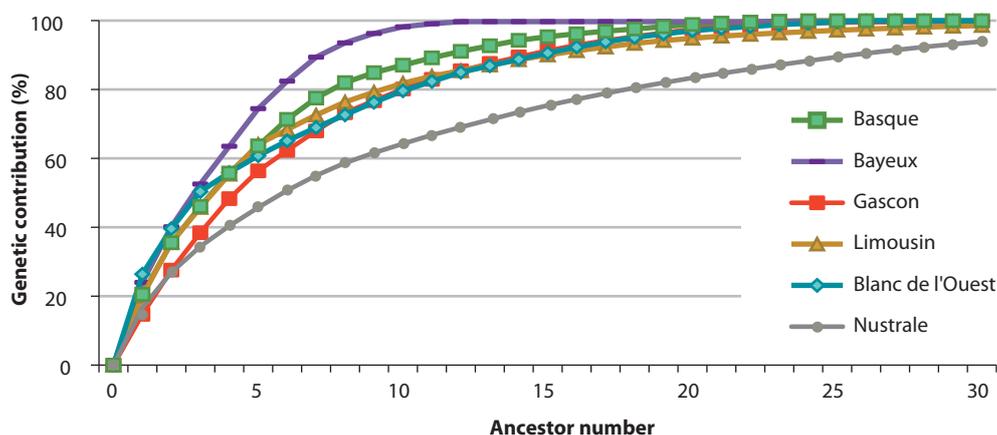


Figure 4: Cumulative genetic contribution of the main 30 ancestors to the females born in 2013 (2012 for the Nustrale breed)

## Conclusion

This study highlights a good level of pedigree completeness in these small-breeding-population rare-breed pigs. The two approaches used here to describe in-population genetic diversity and its pace of change (inbreeding and probabilities of gene origin) are complementary methods that produced convergent net results. Tracking patterns of change in coefficient of inbreeding can emerge the long-term trends whereas probabilities of gene origin are more a reflection of recent shifts in population structure. The net slide in probabilities of gene origin figures observed in the Blanc de l'Ouest breed is not yet visible in the inbreeding criteria.

Controlled conservancy of genetic diversity in these rare-breed pig populations hinges on renewal of the boar stock and tightly-controlled mating schemes. In this perspective, the optimal contribution selection method (Meuwissen, 1997) could be relevant for identifying the breeding animals carrying the freshest gene pool and the right degree of controlled use in the populations so as to curb the inexorable increase in inbreeding.

For the Blanc de l'Ouest breed, the recent net slide in probabilities-of-gene-origin figures is cause for concern and warrants special focus.

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