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Concluding remarks. *Mus domesticus* and *Sorex araneus* faced: two speciation models compared

BY

E. CAPANNA[1]

Summary.–CAPANNA E., 1991. Concluding remarks. *Mus domesticus* and *Sorex araneus* faced: two speciation models compared. *In*: J. HAUSSER, ed. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 141-151.
The speciation models of *Mus domesticus* and *Sorex araneus* were compared. Both models are founded on common evolutionary strategies, i.e. Rb fusions and meiotic depression in complex structural heterozygotes. Such depression is slight in *Sorex* while it is severe in *Mus*, so that chromosomal polymorphism and gene flow are allowed in *Sorex* whereas homozygote state is achieved rapidly in *Mus* chromosomal races with a block of gene flow. The comparison of demographic and behavioural characters of the two species also stresses the peculiar evolutionary forces acting in each process.

Résumé.–CAPANNA E., 1991. Remarques finales. *Mus domesticus* et *Sorex araneus* face à face: comparaison de deux modèles de spéciation. *In*: J. HAUSSER, dir. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 141-151.
Les modèles de spéciation de *Mus domesticus* et de *Sorex araneus* ont été comparés. Ils se fondent sur une statégie évolutive commune, soit des fusions robertsoniennes et une dépression meiotique chez les hétérozygotes. Cette dépression est légère chez *Sorex* alors qu'elle est sévère chez *Mus*. Par suite, le polymorphisme chromosomique et le flux génétique sont maintenus chez *Sorex* alors que l'état homozygote est atteint rapidement dans les races chromosomiques de *Mus*, accompagné d'un blocage du flux génétique. La comparaison des caractéristiquers démographiques et comportementales des deux espèces souligne également les particularités des forces évolutives agissant dans chacun des cas.

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When Jacques Hausser invited me to present the concluding remarks, he suggested that the title of my talk should be "The point of view of an outsider". I have no direct experience of *Sorex* chromosomes. However, because of my interest in chromosome variability and speciation, I have always been fascinated by this "first" case of chromosome polymorphism in mammals.

BAKER and BICKHAM (1986) presented a model of chromosomal speciation which was developed from one proposed by myself for *Mus domesticus* (CAPANNA 1982), but which, according to them, was of more general significance. This symposium on the cytogenetics of *Sorex araneus* offers an excellent opportunity to discuss wether the *Mus domesticus* model yet developed can, in fact, be of more general value for other taxa. While *Sorex araneus* shows similar cytogenetic features to *Mus domesticus*, the species displays very different ecological, ethological and demographic properties.

At first sight, *Mus domesticus* and *Sorex araneus* follow the same evolutionary strategy: Robertsonian (Rb) translocations, randomness of the fusion pattern, monobrachial homology of certain Rb metacentrics and consequent meiotic depression in complex structural heterozygotes, etc. Nevertheless, if one goes into details of these model species, several relevant differences appear.

The randomness of the fusion pattern is a common character in both species: no acrocentrics are preferentially involved in the fusions and a large proportion of the fusions that are theoretically possible are actually found (ZIMA *et al.* 1988) (Table 1). However, in *Sorex araneus*, there is not the dramatic diversity in karyotypes between adjacent populations as found, for example, in the populations of *Mus domesticus* from the Apennines (CAPANNA 1980, 1988). The sharing of Rb metacentrics –except, obviously, the three ancestral *cb, af* and *tu*– throughout the wide range of the species is the peculiar character of chromosomal variability in *Sorex araneus* (SEARLE 1988a, ZIMA *et al.* 1988). In this regard, the whole system of chromosomal variability in *Sorex araneus* is more similar to a single geographic system of *Mus domesticus*, like the one in the Rhaetian Alps, rather than the entire range of chromosomal variability in *Mus domesticus*.

Table 1.–Number of Robertsonian fusions compared in *Mus domesticus* and *Sorex araneus*.

	Mus domesticus	*Sorex araneus*
Rb metacentrics actually found / possible fusions	$\frac{116}{171} = 0.68$	$\frac{37}{66} = 0.56$

Ratio *Mus / Sorex* = 1.24

Jacques Hausser wrote on *Sorex araneus*: "... a basic question remains without answer: why such processes occur in some taxa while closely related ones remain karyologically stable ? " (HAUSSER *et al.* 1985). I posed the same distressful question for *Mus* (CAPANNA 1982, CAPANNA, CORTI and NASCETTI 1985). Why is *Mus domesticus* a prey of the 'Robertsonian craziness', while *musculus*, *spretus*, and *spicilegus* are 'judiciously conservative' ?

REDI *et al.* (1990) tried to give a molecular answer to this question for *Mus*. They suspected the satellite DNA homogeneity may have a role in promoting chromosomal changes; but some caution has to be used in transferring the molecular model to the pair *araneus* (a chromosome variable species) and *coronatus* (a stable one). *Sorex coronatus* had, in former times, a story of 'Robertsonian craziness' and, maybe, no differences could be found in the satellite DNA constitution of the two species. Really stable, all-acrocentric, karyotypes can be found in *Sorex granarius* or in *Sorex samniticus*.

Mentioning the all acrocentric karyotype of *granarius* and *samniticus*, another relevant difference between mice and shrews stands out: the ancestral all-acrocentric karyotype is still present within the polymorphic system of *Mus domesticus*, while, on the contrary, the all acrocentric karyotype can be found in well differenciated species of the genus *Sorex*.

Such a difference can be the consequence of the more recent chromosomal divergence in *Mus domesticus* compared with the genus *Sorex*. Nonetheless, this hypothesis may be inadequate to entirely explain the phenomenon. The peculiar structure of the populations of *Mus domesticus* has, per se, certain characters allowing the acceleration of the process of metacentric accumulation. We will discuss this point later.

Some indirect evidences may be used to date the beginning of chromosomal divergence both in *Mus* and *Sorex*. The start of the process in *Mus domesticus* may be supposed to have occured during the Neolithic Age, near 8000 years before present, at the time of the Agricultural Revolution in Italy (CAPANNA 1982). SEARLE (1984) dates the *Sorex araneus* spreading into Central Europe, and successively into Scandinavia and Great Britain, after the height of the Würm glaciation which was approxiamatively 20 000–15 000 years before present. Such recolonization of lands, again available after the ice sheet recession, could have triggered the karyotype variability of *Sorex* according to Bickham and Backer's theory of canalization of chromosomal evolution (BICKHAM and BACKER 1979). They suggest that the destabilization of the karyotype and the consequent start of the chromosome variability occurs when a population/species invades a new adaptive zone. SEARLE (1984) considers the divergence between *araneus* and *coronatus* even more remote, with *coronatus* isolated, during the Würm glaciation, to the West of Pyrenees. *Sorex granarius* and *S. samniticus* are not discussed by Searle in that paper. Such historical reconstruction agrees with the times of divergence evaluated by HAUSSER *et al.* (1985) by enzyme analysis. *S. araneus* and *S. coronatus* show a mean value of Nei's index equal to 0.071. *S. samniticus* seems to be a perfect outgroup: *samniticus-araneus* Nei's index is 0.35 and *samniticus-coronatus* 0.46.

However, this harmonious pattern is troubled by evidence arising from *granarius*. An all-acrocentric karyotype, like that characterizing *Sorex granarius*, has necessarily to be considered as a plesiomorphic character within a cytotaxonomic context where Robertsonian fusions operate (WÓJCIK and SEARLE 1988, VOLOBOUEV 1989). Accordingly, the divergence of the *granarius* line preceded the separation of the two clades *araneus* and *coronatus*. However, the electrophoretic evidence produced by HAUSSER *et al.* (1985) from analysis of *granarius* reveals a mean genetic distance between *araneus* and *granarius* equal to 0.022. Moreover, a genetic distance of this magnitude is only relevant if the *granarius* populations are compared with the southern Apennine populations of *araneus*. The gene pools of *granarius* are quite identical to those of the Swiss and north Italian populations of *araneus*. Such an amazing pattern has been confirmed during this meeting by the mtDNA analysis performed by TABERLET *et al.* (1991).

No rational answer exists for such a puzzling situation. It is possible that Nei's index, or other index desumed from allelic frequencies, or molecular genetics, is not reliable, in some cases, to evaluate the times of genetic divergence.

Coming back to the comparison of the speciation pattern of the mouse and the shrew, another relevant difference concerns the geographic size of the phenomenon, which is dramatically wide in the common shrew, from Pyrenees to Siberia. On the contrary, the chromosomally polymorphic system of *Mus domesticus* lies within a thin crescent the horns of which are placed in Scotland and Tunisia (Fig. 1). This crescent is really stuffed with a great number of isolated or semi-isolated Robertsonian chromosomal races.

Further differences between the species can be evidenced with a more detailed comparison of two restricted geographic areas of both systems: that is *Sorex araneus* in Great Britain and *Mus domesticus* in the Rhaetian Alps.

Great Britain is the site of the discovery of the *Sorex araneus* chromosomal polymorphism. 30 years of careful studies from those by SHARMAN (1956), FORD, HAMERTON and SHARMAN (1957), FORD and HAMERTON (1970), to those by SEARLE (1984a, 1984b, 1986, 1988a, 1988b), allowed a detailed knowledge of the polymorphism in *Sorex araneus* from this geographic area. The same occurs for the mice in the Rhaetian Alps. Val Poschiavo is the site of the first discovery of Rb fusions in the house mouse by Alfred Gropp twenty years ago (GROPP, TETTENBORN and VON LEHMAN 1970), and, through the joint effort of Gropp, myself and our coworkers (GROPP *et al.* 1982, CAPANNA and CORTI 1982, CAPANNA and RISCASSI 1978), this area of the *Mus domesticus* chromosomal polymorphism is well known.

In Great Britain, only three chromosomal races of shrews were found in a 240 000 square kilometers area. Nine chromosomal races of *Mus domesticus* –and maybe others will be discovered– crowd a 10 000 square kilometers mountain area in the Rhaetian Alps. Moreover, relevant differences exist in the karyological structure of the populations of the polymorphic system of the two species. The nine chromosomal races of *Mus domesticus* are fixed in the homozygous state for all Robertsonian metacentric pairs, and two or more metacentrics with monobrachial homology characterize the karyotypes of

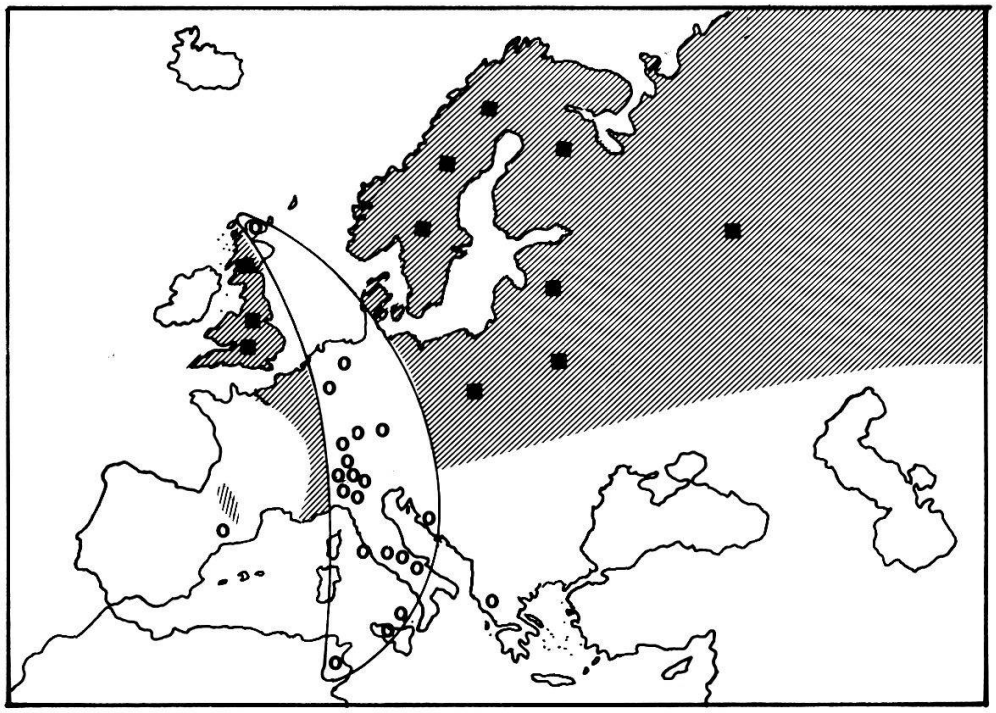

Figure 1.–The Robertsonian mouse crescent. Numerous house mouse populations (circles), each characterized by different homozygous karyotypes, crowd a thin crescent the horns of which are placed in Scotland and in Tunisia. Within its wide distribution area (sketched area) several *Sorex araneus* Robertsonian races were found (solid squares).

adjacent races. Consequently, no gene flow exists between races, as we clearly demonstrated by means of electrophoretic methods in two sympatric races, that is Poschiavo and Upper Valtellina (CAPANNA and CORTI 1982, CAPANNA *et al.* 1985a, 1985b). The situation is otherwise for the British *Sorex araneus* (see data reviewed in SEARLE 1988b). The Scottish Aberdeen race is karyotypically characterized: besides the ancestral metacentrics *cb*, *af*, and *tu*, five Rb metacentrics are homozygous, that is *gm*, *hi*, *ko*, *np* and *qr*. Only *jl* remains in a polymorphic state. According to the "Celtic fringe" hypothesis (SEARLE and WILKINSON 1987), successive invasions introduced new Rb metacentrics into the British Islands giving rise to the Oxford and Hermitage races. Only three Rb metacentrics with monobrachial homology differenciate the Oxford race from the Aberdeen one, that is *kq*, *no* and *pr*, but all these remain in a polymorphic state. Consequently, genes can easily flow between races via acrocentrics. The Hermitage race has no monobrachial homologous metacentrics if compared to the Aberdeen race: the difference lies only in the fact that the arms of the Aberdeen metacentrics are acrocentrics in the Hermitage karyotype, except *ko*. The Hermitage race is open to gene flow in connexion to the Oxford race too, because the Oxford Rb metacentrics, as well as *ko*, are in a polymorphic state.

Looking at such a cytogenetic scenario in *Sorex araneus*, from the point of view of an outsider who has studied *Mus domesticus*, I suggest that the British populations of *Sorex araneus* should not be considered to be real chromosome races, but instead different karyotypic local arrangements of the same great chromosomal pool where polymorphism is retained and a karyotypic divergence is in progress.

It is certainly of interest to underline that I speculated that such a situation (as a stage of chromosomal differentiation) occured in the house mouse during the phase of parapatric contact of newborn races or when they sympatrically merge (CAPANNA 1982, 1988, CAPANNA, CORTI and NASCETTI 1985a, CORTI, ESTABROOK and CAPANNA 1986).

Similar considerations could be suggested dealing with *Sorex araneus* in the Alps (MEYLAN 1964, MEYLAN and HAUSSER 1973, HAUSSER *et al.* 1985, 1991). The well differenciated Valais race occupied the Southern Alps, while the modern complex Vaud + Intermediate + acrocentric developped in the Northern Alps as a wave of introgression of the Vaud metacentrics in a primitive, acrocentric population, eventually splitted by *Sorex coronatus* which invaded the lowlands coming from France and Spain.

The situation of the polymorphism of *Sorex araneus* in Scandinavia (FREDGA 1973, 1982; FREDGA and NAWRIN 1977), in Finland (HALKKA *et al.* 1974, 1987) and in Central Europe (ZIMA and KRAL 1985, FEDYK 1980, 1986, FEDYK and LENIEC 1970, WÓJCIK 1986, WÓJCIK and FEDYK 1986) is certainly more intricate. Nonetheless, in these areas too there may be evidence of retained polymorphism and metacentric flow subsequent to hybridization.

The possibility to retain chromosomal polymorphism is, in fact, the major peculiarity of the *Sorex araneus* system. Such a peculiarity strongly contrasts with a situation of strictly homozygous populations as we found in mice. The comparison of these discordant characteristics enhances both the common and the peculiar evolutionary forces acting in each speciation process. To make a long story short, the general structure of the *Sorex araneus* polymorphic system is in arrears when compared to the speciation level reached by *Mus domesticus*. However, the process of chromosomal differentiation started in *Sorex araneus* 10 000 years before than in *Mus domesticus*. What, then, are the evolutionary forces speeding up the speciation of *Mus domesticus*, and what are, on the contrary, the causes delaying the process in *Sorex araneus* ?

Studies on meiosis and gametogenesis in *Sorex araneus* are at present in progress (SEARLE 1984b, 1986, 1988a, GARAGNA *et al.* 1989). Moreover, several talks during this meeting (See WALLACE *et al.* 1991, and MERCER *et al.* 1991) brought our knowledge up to date in this regard. It seems, then, that the frequency of malsegregation and the rate of production of unbalanced gametes is very much lower in *Sorex araneus* than in *Mus domesticus*. A slight meiotic trouble is caused by complex heterozygozity in hybrids consequent to monobrachial homology, but multivalent chains can be loosened and the gametogenesis well achieved. This is quite different from the dramatic consequence implying sterility observed in complex structural heterozygotes in *Mus domesticus* (see data reviewed in REDI and CAPANNA 1988). As a consequence of this fact, the selective advantage of the homozygotes is slight in *Sorex* and so is the drive toward the achievement of

the homozygosity. Consequently, the chromosomal polymorphism is easily retained, gene flow is allowed, and the genetic distance between races kept low (FRYKMAN *et al.* 1983, 1984, FEDYK 1986, HAUSSER *et al.* 1991). But all these are just the peculiar characters of *Sorex araneus* polymorphism.

A high inbreeding is a peculiarity of *Mus domesticus*, due to a small deme size. But, as Jacques Hausser stated "Neither small demes nor intensive inbreeding are very likely in the case of these shrews." (HAUSSER *et al.* 1985). Consequently inbreeding and negative heterosis of structural heterozygotes are the evolutionary forces cooperating in *Mus domesticus*, and they are responsible for the fast achievement of homozygozity and, on the whole, of the speciation pattern in mice.

Other demographic and behavioural characteristics operate in the case of *Mus* and are apparently irrelevant in *Sorex*, and *vice versa*. For example, although the vagility is not so high in *Sorex*, several ethological conditions, that is nomadism of adult males, autumnal dispersion of youngs (PUCEK 1960), etc., favour the spread of the chromosomal novelties; these, not controlled by meiotic constraints, can easily spread.

Well then, do mice and shrews run along the same evolutionary pathway ? We have to acknowledge that the major evolutionary forces and the general evolutionary strategy are the same. On this concern BACKER and BICKHAM (1986) are right. Nonetheless minor factors, consequences of the biological properties of each species, give peculiar features to each polymorphic system and singleness to each speciation pattern.

Finally, a brief consideration on *Sorex* and *Mus* mode of speciation referred to the stasipatric model of WHITE (1968, 1982). Recently I denied quite categorically such a model for *Mus domesticus* (CAPANNA 1982, 1988). The first step of my own model of speciation is the complete isolation of the deme where the chromosomal variant appears and the Rb metacentrics become fixed. This full isolation does not agree to the stasipatric mode. Such an isolation is assured in *Mus domesticus* just by those ethological and demographic "minor" factors which do not operate in *Sorex araneus*. Consequently, the mode of speciation of *Sorex araneus* could be considered more stasipatric than the *Mus domesticus* one.

Nonetheless, in agreement to the hypothesis of SEARLE (1984a), the *Sorex araneus* range expansion followed the ice sheet regression along a dramatically extended front (Fig. 2). Along this front of recolonization of new lands, several peripheral semi-isolated areas fitting the bioclimatic requirements for a rapid expansion of *Sorex araneus* could be localized. In these peripheral enclaves inhabited by 'ancestral' *Sorex araneus* populations –that is characterized by the 'ancestral' *af*, *cb*, and *tu* Rb metacentrics– new Rb metacentrics could have appeared, different in each isolate, like *gm*, *gi* or *gr*. Little by little the front was moving toward the North and North East, new peripheral areas, fitting the same conditions could become identified and new Rb fusions appeared. So, on this outline, the *Sorex araneus* pattern appears more like a 'peripatric' model, in the sense of MAYR (1982) rather than strictly stasipatric in the sense of WHITE (1968, 1982).

But these are the considerations of an outsider.

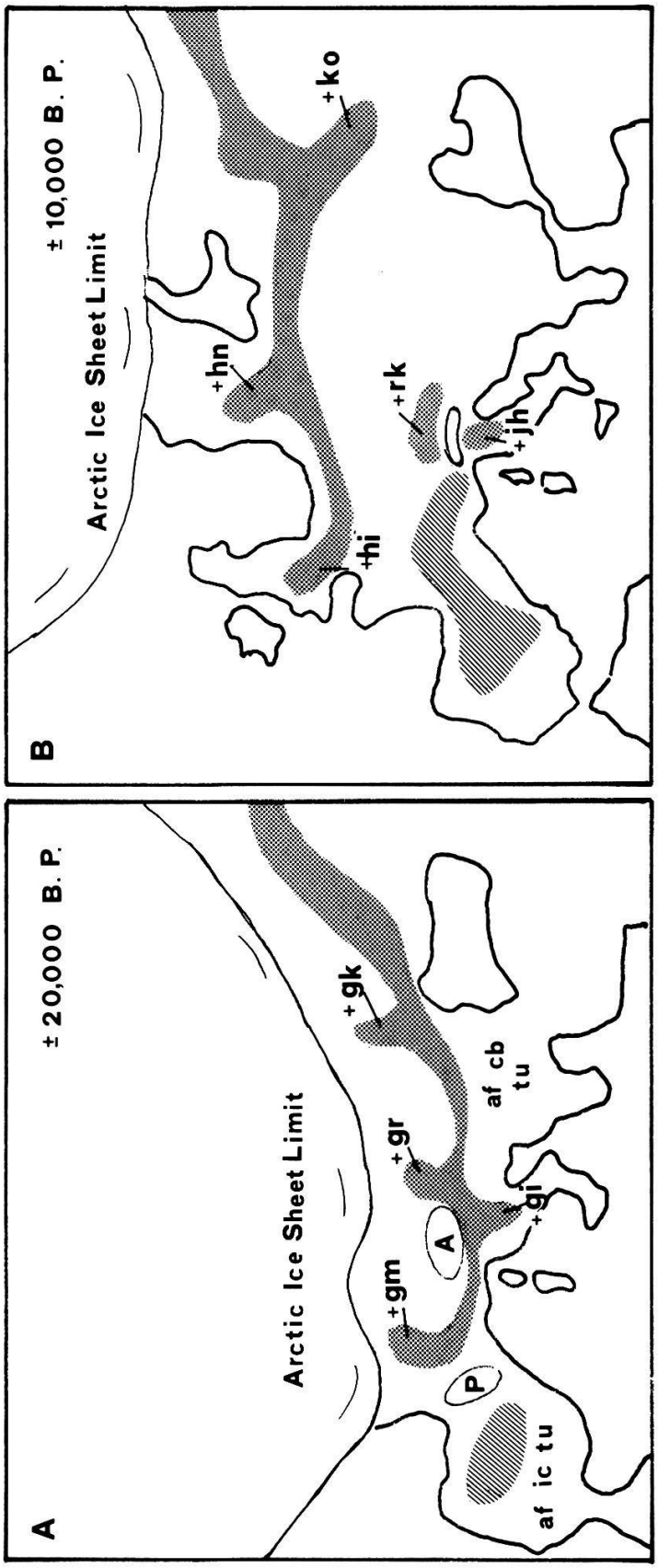

Figure 2.–A hypothesis of peripatric speciation model for *Sorex araneus*. Sketched area: front of expansion of *Sorex coronatus*; dotted area: front of expansion of *Sorex araneus*; af, ic, tu, cb = ancestral fusions; +gm (etc): chromosome novelties. P and A: Pyrenees and Alps Wurm glaciers.

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