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Follicular kinetics in the mare ovary

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Summary. Using histological techniques, 8 ovaries (1 per mare) of riding or pony mares were studied at different physiological states : 2 ovaries were collected during anœstrus, 4 during early pregnancy, 2 before (day 33) and 2 after (day 43) the onset of PMSG secretion, and 2 during the œstrous season. On each ovary all the follicles greater than 50 μ (one complete layer of round follicle cells) were counted, measured, checked for atresia and calculated for mitotic index. The mean total number of follicles larger than 50 μ in diameter was 48 $\pm$ 27 per mare, 23 $\pm$ 11 of which were antral ($>$ 300 μ in diameter). Atresia was rarely seen in follicles $<$ 350 μ in diameter, and the mean number of atretic follicles was 14 $\pm$ 10 per mare. *Thus, the follicular population in the mare was numerically much smaller than in the ewe or the cow.* To study the follicular population at different physiological states, the follicles were pooled and divided into four groups : preantral ($<$ 300 μ in diameter), small-antral ($<$ 1 500 μ), large-antral ($<$ 10 000 μ) and preovulatory ($>$ 10 000 μ). The first three size groups from ovaries collected during the anœstrous or œstrous season showed no difference in the mean number of follicles, incidence of atresia or mitotic index. The fourth group of follicles was different as there were no preovulatory follicles in anœstrous mares. *The ovaries of pregnant mares submitted to PMSG for 6 days contained significantly more follicles in the small-antrum group* than the control ovaries (day 33 of pregnancy). PMSG also seemed to modify antrum formation. In contrast, PMSG seemed to have no effect on follicle number or atresia in the large-follicle population. Follicular growth rates were estimated by two methods :

— follicles larger than 5 000 μ in diameter : cauterization of the preovulatory follicles during late œstrus showed that a follicle of less than 5 000 μ needed about a week to grow to ovulatory size ;

— follicles between 60 and 1 000 μ in diameter : measurement of the mitotic index indicated a follicle needed about 7 weeks to enlarge from 60 to 1 000 μ. *Thus, follicular growth in the mare seemed to be much faster than in the ewe.*

Introduction.

The management of mares is difficult owing to their physiological peculiarities : oestrus often occurs during the winter anovulatory season, which coincides with the beginning of the breeding season, and the length of the follicular phase, defined as the interval between luteolysis and ovulation, is highly variable both within the season

and between animals (Palmer, 1978). To control some of the reproductive processes in the mare, a factor is first needed to stimulate follicular growth ; PMSG seems to have less effect than in other animals (Squires *et al.*, 1974*a*, *b* ; Palmer, 1978). Next, we need more data about follicular populations. This information to date has been obtained by rectal palpation (Nishikawa, 1959), post-mortem macroscopic examination (Arthur, 1958 ; Warszawsky *et al.*, 1972), or by 17β-oestradiol (Oxender, *et al.*, 1977) or total oestrogen (Palmer and Terqui, 1977) assay. Data are still scarce since we do not know much about follicular number, size or atresia.

In this study, we wished to obtain information on follicular populations and growth rates in the mare using routine histological methods.

Material and methods.

The animals used were 3 to 6-year old Welsh ponies or riding mares fed a ration of dried lucerne, corn and oats to maintain body weight and submitted to natural photoperiod. Eight ovaries (1 per mare) were used : 2 collected during anoestrus, 2 on day 33 and 2 on day 43 of pregnancy (before and after the onset of PMSG secretion), and 2 during the breeding season.

Anoestrus was checked by the progesterone level (< 1 ng/ml ; Terqui and Thimonier, 1974), and the mares were ovariectomized in mid-Juanuary, which is normally the middle of the anoestrous season.

The preovulatory stage was said to occur when a follicle more than 3.5 cm in diameter and having a soft consistancy was detected by rectal palpation in an oestrous mare. The day of ovulation was detected by progesterone assay : ovulation was supposed to occur 36 h before plasma progesterone increased to more than 1 ng/ml (Palmer and Jousset, 1975).

Histological methods. — The ovaries were removed and fixed in Bouin-Holland's solution. They were then serially cut into sections 10 μ thick ; one out of 5 was mounted, stained with hematoxylin and examined. The nucleus was often not visible ; therefore the first and last sections where the follicle was seen were regarded as the extremities of the follicle and measurements were taken in consequence.

Follicular counts. — According to Mariana (1972), the follicular population can be divided in two : the pool of primordial follicles and the growing ones. We have studied the second category, i.e. those having at least one layer of cuboidal cells and thus growing. On each follicle we measured :

— The area of the follicle and of the antrum. The area of the follicle limited by the basement membrane was measured with an hyperbolic reticle. However, for very large follicles, we used an overhead projection microscope and planimeter. The area of the antrum was meaured using the latter two instruments.

— The number of granulosa cells. On follicles less than 200 μ in diameter, the number of granulosa cells was estimated from the linear portion of the regression line linking follicle size and granulosa cell number, which was previously determined using all the follicles of one ovary. The number of granulosa cells of the larger follicles was calculated from the area they occupied and from their cellular density measured

at ten different points on the follicle using a circular reticle. However, for follicles over 3 000 μ in diameter, the area occupied by the granulosa layer, and thus the cell number and mitotic index, could not be computed owing to technical difficulties (low magnification used in measuring follicles and thinness of the granulosa layer).

— The mitotic index. All cells undergoing mitosis were counted on the section studied in each follicle. The mitotic index was obtained by dividing the number of cells in mitosis by the total number of granulosa cells.

— Atresia. Each follicle was checked for atresia. A follicle was said to be atretic when more than five pyknotic nuclei were counted on the section studied.

To compare the different physiological states, we pooled the follicles and divided them into four groups : follicles smaller than 300 μ in diameter (mostly preantral), those between 300 and 1 500 μ in diameter (« small-antral »), between 1 500 and 10 000 μ in diameter (« large-antral »), and larger than 10 000 μ (« preovulatory »).

Follicular growth rates :

— Follicles between 60 and 1 000 μ in diameter. Follicular growth rate was calculated with doubling time. The computation of doubling times uses mitotic index values and an estimation of the mitotic time (Hoffman, 1949). No estimation of the mitotic time for mare follicles was available, and as there were large differences in the duration of mitotic time, we used two estimations : one of 30 min, agreeing with the data of Lushbaugh (1956) and Turnbull *et al.* (1977), and another of 90 min. agreeing with studies of Mazia (1961) and Cahill (1979*b*). Doubling and transit times were calculated for each mitotic index.

— Follicles larger than 5 000 μ in diameter. The preovulatory follicle during late œstrus was electrocauterized. During this physiological status, the largest non-atretic follicle after the preovulatory one was about 5 000 μ in diameter. It was thought that by destroying the preovulatory follicle during late œstrus, the time for a follicle of 5 000 μ in diameter to grow to ovulation could be estimated. To avoid between-ovary interaction, two hemicastrated mares were anesthetized with « Surital » so as not to disturb the gonadotropic secretion. They were then laparotomized, the preovulatory follicle was cauterized and the follicular fluid expelled. The next ovulation was detected by plasma progesterone levels of over 1 ng/ml.

Results.

Mensuration of normal follicles. — In order to study the pattern of follicular growth, we compared oocyte diameter, granulosa cell number, antrum percentage and follicular diameter. Ocoyte and follicular diameters were positively and linearly correlated ($r = 0.86$; $y = 1.76\ x - 13.4$ where x is the oocyte diameter and y the follicular diameter) until the oocyte mean diameter reached 70 μ and that of the follicle 110 μ (fig. 1*a*). Thereafter, oocyte growth slowed down whilst follicular growth continued by the multiplication of granulosa cells whose size remained unaltered. The relationship between follicular diameter and granulosa cell number (fig. 1*b*) in the widest cross-section of the follicle was curvilinear. For follicles less than 200 μ in diameter, follicular size and granulosa cell number were positively correlated ($r = 0.97$;

$y = 1.026\,x + 20.58$ where x is the number of granulosa cells and y follicle diameter). The dispersion on large follicles increased. Accumulation of follicular fluid rather than proliferation of granulosa cells appeared to determine follicle size. A noticeable antrum appeared in follicles 220 to 280 μ in diameter. For follicles less than 560 μ in diameter, the percentage of antrum and follicular size were correlated ($r = 0.60$) (fig. 1c). Thus, the percentage of antrum increased faster, and ultimately constituted about 95 p. 100 of the follicular size in preovulatory follicles.

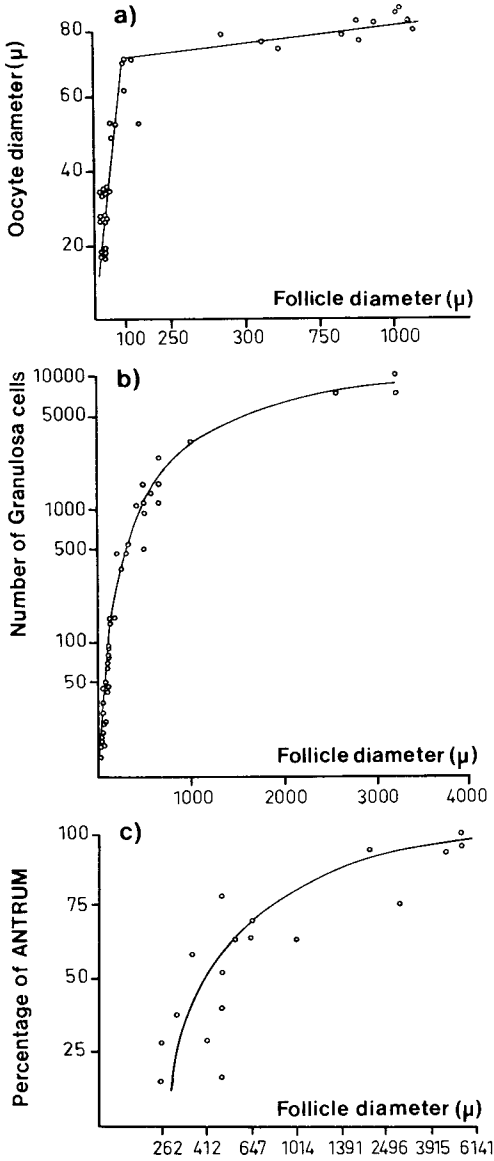

FIG. 1. — *Follicle characteristics* (a) *oocyte diameter* ((μm), (b) *number of granulosa cells per section and* (c) *proportion of follicule occupied by the antrum* (p. 100) *in relation to follicle diameter* (μm).

The mitotic index was heterogeneously distributed within a given follicle : the mitoses were more numerous in the cumulus than in the peripheral granulosa. This index also depended on follicle size (fig. 2) ; it was low in small follicles (0.35 p. 100), increased rapidly in follicles 150 μ in diameter, and reached maximum values in small-antrum follicles. The preovulatory values were low (0.3 p. 100).

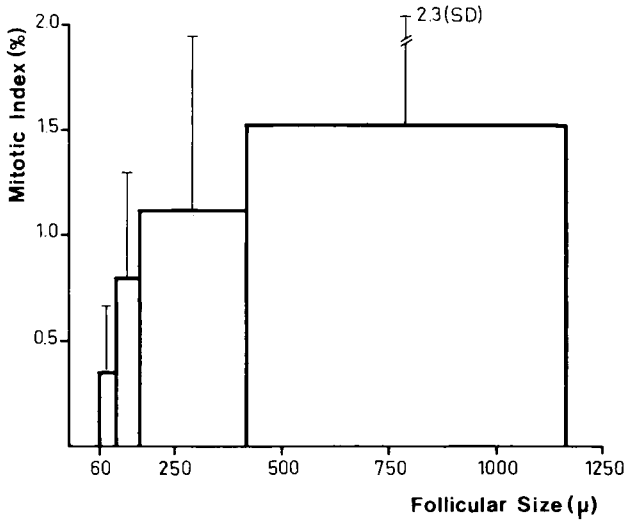

FIG. 2. — *Follicular mitotic index in relation to follicular size.*

Follicular population. — By pooling four non-stimulated animals (2 during oestrous season and 2 in early pregnancy before onset of PMSG secretion), we calculated the mean follicular population (fig. 3, 4). The total number of follicles larger than 50 μ

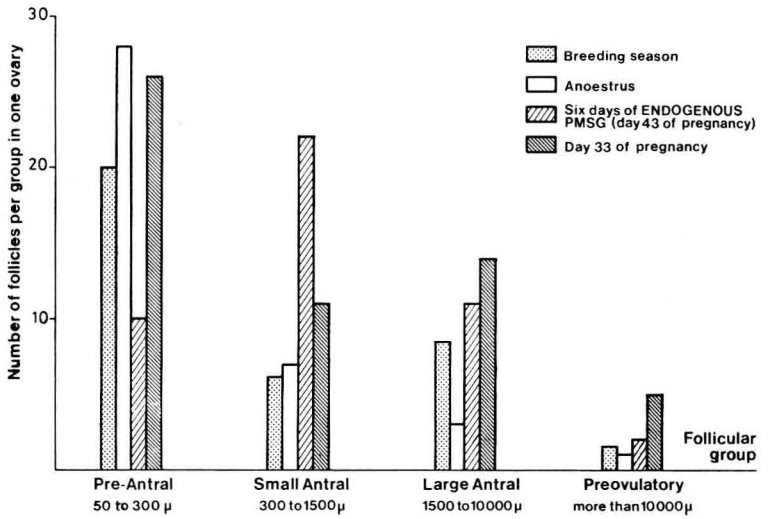

FIG. 3. — *Follicular number per class per group.*

in diameter was 48 ± 27 (SD) per mare, 23 ± 11 of which were larger than 300 μ in diameter (antral). Atresia was rarely seen in follicles < 350 μ in diameter, and the mean number of atretic follicles was 14 ± 10 per mare.

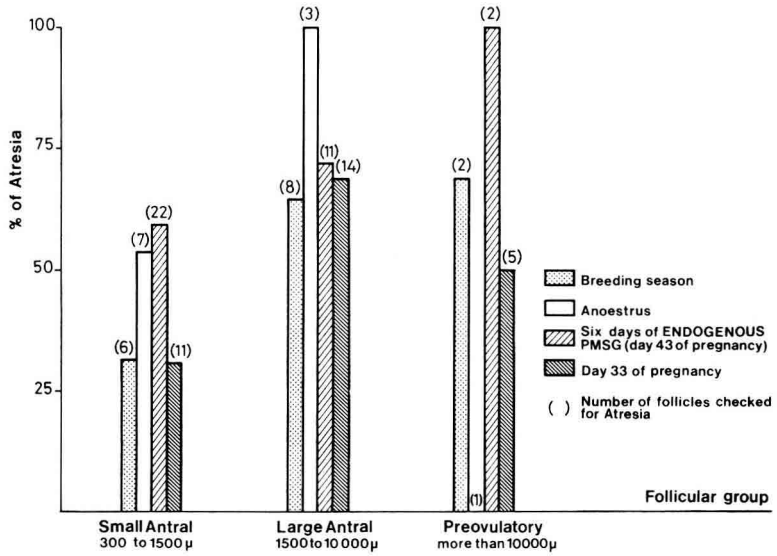

FIG. 4. — *Proportion of atretic follicles per class per group.*

The influence of seasonal anoestrus was then studied. The first three size groups of ovaries collected during anoestrus or the breeding season showed no difference in mean number of follicles, incidence of atresia or mitotic index ; normal or atretic follicles several mm in diameter were found in the ovary. In contrast, the fourth group of follicles was affected as there were no preovulatory follicles in the anoestrous mares.

Thus, the follicles grew continuously during anoestrus until they reached several mm in diameter, when they became atretic.

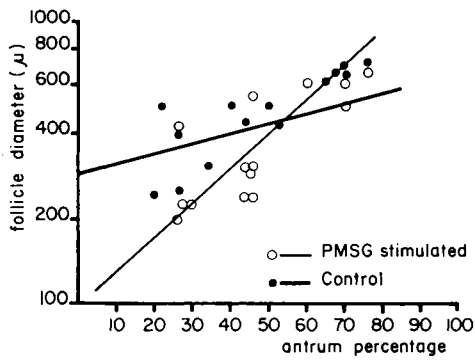

FIG. 5. — *Influence of* PMSG *on antral development.*

A comparison of the ovaries of pregnant mares collected before (day 33) or after (day 43) the onset of PMSG secretion (figs. 3, 4) showed that the ovaries submitted to PMSG for 6 days contained significantly more follicles ($P < 0.05$, Lord's test) of the small-antrum type than the control ovaries. PMSG also seemed to modify antrum formation (fig. 5) since regressions linking antrum percentage and follicle size differed significantly ($P < 0.01$) ($y = 2.99\,x + 291$; $r = 0.60$ for untreated and $y = 6.84\,x + 61.1$; $r = 0.60$ for « stimulated » follicles where y is follicle size and x the percentage of antrum). However, these stimulated follicles quickly became atretic. Owing to the low number of follicles per ovary, we were unable to find any modification of the mitotic index after PMSG treatment. On the other hand, the large-follicle population (more than 1 500 μ) appeared to be unaffected by PMSG, and no difference was found in follicle number and stage of atresia between untreated and stimulated follicles.

Estimation of follicle growth rate :

— Follicles between 60 and 1 000 μ in diameter. Using mitotic index values (fig. 2) and the two hypotheses of mitotic time (30 and 90 min), we found (table 1) that a follicle took between a fortnight and 50 days to grow from the smaller to the larger size ; between 11 and 37 days was required for the follicles to grow from 60 μ to antrum formation.

TABLE 1

Doubling times (TD) *and transit times* (θ) *of follicles*

Follicle diameter	60 μ	110 μ	170 μ	500 μ	1 000 μ
Number of cells in the largest cross-section	70	125	250	1 000	4 000
Total number of cells in the follicle	280	870	2 600	28 000	220 000
Mean mitotic index	0.35	0.79	1.21	1.52	
1st Hypothesis : Duration of mitosis : 30 min.					
TD_1	99 h	44 h	28 h	22 h	
θ_1	163 h	69 h	96 h	65 h	
	$\Sigma\,\theta_1 = 16$ days				
2nd Hypothesis : Duration of mitosis : 90 min.					
TD_2	297 h	132 h	86 h	68 h	
θ_2	490 h	207 h	295 h	204 h	
	$\Sigma\,\theta_2 = 50$ days				

— Follicles between 5 000 μ and ovulatory size. Cauterization showed that a 5 000 μ follicle needed about 5 days to grow to ovulatory size. After cauterization, there was only a slight increase in progesterone level (less than 1 ng/ml) which disappeared the next day.

Discussion.

This preliminary report presents some interesting peculiarities in the mare : the follicle number is low, follicular growth is rapid, and PMSG acts only on a small fraction of the follicular population. These results will be confirmed with a larger number of animals.

When the morphological characteristics of follicular growth in the mare are compared with those of other species (ewe : Cahill, 1979*b* ; woman : Lintern-Moore *et al.*, 1974), it is seen that the main phenomena occur when the oocytes are about the same size in the three species : oocytes stop rapid growth when they are about 80 μ in diameter, maximum ooxyte diameter is about 130 μ. Antrum formation occurs in similar-sized follicles, i.e. when they are between 250 and 300 μ in diameter. Preovulatory follicle size, however, is very different being about 6 mm in the ewe, 15 mm in the woman, and 40 mm in the mare.

Mares are also characterized by their mitotic index curve. The follicles start to grow earlier in the mare since the preantral follicles have a higher mitotic index than in the ewe (Cahill, 1979*b*). In the mare as in the cow, this index is low for preovulatory follicles (Mariana and Nguyen Huy, 1973). This is in contrast to the sow (Daguet, 1977), and shows that final follicular growth is rather due to an increase in antrum size than to granulosa cell multiplication. Since antrum formation appears in similar-sized follicles in the ewe, cow and mare, we compared the number of preantral follicles in these three species and found 22 follicles of this size group in the mare versus 102 in the Ile-de-France ewe (Cahill *et al.*, 1971*a*) and 56 in the cow (Mariana and Nguyen Huy, 1973), showing that the mare also differs from the other species by its low follicle population.

Seasonal anoestrus is more difficult to alter in the mare than in the ewe since ovulation cannot be induced by progestagen treatment (Palmer, 1978). Seasonal anoestrus in pony mares is more complete than in riding mares since in winter about 50 p. 100 of the latter cycle, while 100 p. 100 of Welsh pony mares are anoestrous (Palmer, 1978). Using the latter model, we found that the follicular population and the ovarian status are not strongly depressed. As in the ewe, preovulatory follicles are lacking (Cahill, 1979*b* ; Turnbull *et al.*, 1979), and the size of the largest follicle is highly variable (Sharp, 1975). With the exception of data from Freedman, Garcia and Ginther (1977) on FSH levels during late anoestrus, there is little information on the gonadotropin levels during anoestrus, especially as concerns the levels of FSH during deep anoestrus, pulsatile LH secretion, and follicle sensitivity to this gonadotropic stimulation. Since the ovarian status is identical in the ewe and in the mare, differences in the depth of anoestrus may be linked to different follicular sensitivity to gonadotropic stimulation, to a more profondly altered sensitivity of the HT-HP axis to gonadal steroids, or to a more depressed « spontaneous hypophyseal activity ».

As to PMSG action on the ovary, it is noteworthy that PMSG acts to stimulate the number of small-antral follicles and to hasten antrum formation as in other species (Mariana and Machado, 1976 ; Saumande, 1977), but most of these follicles quickly become atretic due to an unknown cause. This is the first time that a PMSG effect on the follicular population has been reported in the mare.

The lack of any stimulatory PMSG effect on the number of large follicles has already been noted either by rectal palpation or by post-mortem macroscopic examination (Squires *et al.*, 1974*a*), and by comparing follicular development in pregnant and hysterectomized mares (Squires *et al.*, 1974*b*). It is also supported by the data of Stewart and Allen (1978) who find that there is little large-follicle PMSG binding in the mare as compared to FSH and LH binding. The increase in total oestrogen secretion observed by Terqui and Palmer (1978) when PMSG appears might be explained by a stimulatory PMSG effect on steroid synthesis. In contrast to the data on rats (Peters *et al.*, 1975) or ewes either *in vivo* (Turnbull *et al.*, 1977) or *in vitro* (Hay and Moor, personal communication), PMSG does not seem to have any effect on atresia.

The classical methods of determining follicular growth by the use of thymidine labelling (Pedersen, 1969 ; Hartmann and Pedersen, 1970 ; Chiras and Greenwald, 1977 ; Hage *et al.*, 1978), acetylglucosamine labelling (Oakberg and Tyrrell, 1975) or colchicin treatment are unsuitable for the mare owing to its cost and to practical difficulties.

Thus to estimate the growth rate of follicles between 100 and 1 000 μ in diameter, we used two estimations of mitotic time (30 and 90 min) since the values obtained by different authors (Lushbauch, 1956 ; Mazia, 1961 ; Turnbull *et al.*, 1977 ; Cahill, 1979 mostly lie between these. The exact duration of follicular granulosa cell mitosis in the mare needs further investigation. Nevertheless, even assuming the longest mitotic time, follicular growth is much faster in this size group in the mare than in the ewe since it takes 2 months for the follicular diameter in the mare to increase from 100 to 1 000 μ while about 5 months is needed for the same growth to occur in the ewe. Only gross data were obtained by cauterization because we used hemicastrated mares, and hemicastration modifies the follicular kinetics (Dufour *et al.*, 1979) ; secondly, cauterization might have two effects : destruction of the largest preovulatory follicle, whose fluid contains a non-steroidal follicular inhibiting fraction (de Jong and Sharpe, 1976), might simply let the first non-atretic follicle grow further, and could also increase its growth rate : In immature animals having few large follicles, follicular growth is more rapid than in mature animals (Pedersen, 1969, 1970). Even if the 5-day value found for follicle growth between 5 000 μ and ovulation is an underestimation of the true growth, it none the less shows that follicular growth is very rapid in this size group.

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Résumé. L'analyse histologique de 2 ovaires de juments à chacun des stades physiologiques suivant : inactivité ovarienne, saison sexuelle, gestation avant (J 33) et après (J 43), l'apparition de PMSG a permis de dégager les conclusions suivantes :

— les effectifs folliculaires de la jument sont faibles comparés à ceux des autres espèces ;
— la croissance folliculaire paraît rapide chez la jument ;
— pendant la période d'« inactivité ovarienne », ni les effectifs, ni la vitesse de croissance des follicules ne sont sévèrement déprimés ;
— la PMSG endogène au début de gestation augmente le nombre des follicules à petit antrum et modifie les caractéristiques de formation de l'antrum. Par contre, elle paraît dépourvue d'action sur les plus gros follicules.

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