which the entire heart was analyzed, it was possible to determine the total amount of radioactive norepinephrine formed. This value ranged from 0.110 to 0.161 μc per heart, and the fraction of the administered dopamine-C^{14} converted to norepinephrine ranged from 0.65 to 0.94 percent.

A radiochromatogram of the purified norepinephrine, shown in Fig. 1, demonstrates that the material is contaminated with only a small amount of radioactivity corresponding to the R_F of dopamine. To quantify the amount of this contamination more accurately, the specific activity of norepinephrine was determined before paper chromatography in one experiment and was found to be 0.24 μc/μmole. The area of the paper corresponding to the R_F of norepinephrine was then eluted, and the eluted radioactivity was adsorbed onto aluminum oxide. The specific activity of the aluminum oxide eluate was 0.22 μc/μmole. These results indicate that less than 10 percent of the radioactivity in the norepinephrine purified by the method employed in these experiments was due to contamination by dopamine.

The rate of synthesis of norepinephrine in these experiments may be estimated by relating the specific activity of the norepinephrine isolated to that of its precursor dopamine. If the neurotransmitter store were entirely replaced by norepinephrine newly formed from dopamine-C^{14}, its specific activity would be identical (100 percent) with that of the precursor. Actually, the specific activity of the isolated norepinephrine was found to range between 1.4 and 10.8 percent of the specific activity of the administered dopamine, indicating that between 1.4 and 10.8 percent of the norepinephrine in the heart after 1 hour's perfusion originated from the administered precursor. This fraction is a minimal estimate of the rate at which norepinephrine can be formed in the heart, being only a measure of the rate of formation from dopamine-C^{14}. The results of three experiments indicate that this fractional rate is substantially greater in the ventricles than in the atria (Table 1). The highest rate measured (10.8 percent per hour) may be sufficient for replacement of the entire norepinephrine store within a few hours. It is appreciated that these observations were made in isolated, perfused hearts and that the turnover is probably more rapid in intact animals, in which it may be conditioned by the rate of release of norepinephrine.

Our results show that dopamine is capable of acting as a precursor of norepinephrine in the heart. It remains to be determined whether synthesis of norepinephrine can be demonstrated from other potential precursors. Creveling *et al.* (*7*) have demonstrated that tyramine can serve as a precursor of norepinephrine in the whole rat, but three preliminary experiments with radioactive tyramine in the isolated canine heart preparation described herein have failed to demonstrate incorporation of its radioactivity into the norepinephrine isolated from the heart. It therefore appears unlikely that the whole rat has biosynthetic pathways for the formation of norepinephrine which are not present in the canine heart.

Our studies show that the heart can synthesize norepinephrine, and it need not be postulated that this organ is totally dependent upon extraction of norepinephrine from the blood to maintain its store. However, our observations do not provide evidence of the relative importance of synthesis and extraction in the maintenance of the neurotransmitter store in the intact animal.

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Stratigraphy of Beds I through IV, Olduvai Gorge, Tanganyika

Abstract. *Bed I at Olduvai Gorge is a conformable sequence of lava flows and varied sedimentary deposits that extend upward from a welded tuff overlying the Precambrian basement to the top of a widespread marker bed. Bed II is a sequence of lacustrine clays and laterally equivalent fluvial, eolian, and pyroclastic deposits. Bed III is made up of alluvial deposits and a laterally equivalent assemblage of fluvial, lacustrine, and eolian beds. Bed IV can be subdivided into a lower unit of fluvial clays, sandstones, and conglomerates, and an upper unit of eolian tuffs. The climate was relatively dry throughout much of the time that these beds were deposited, and semidesert or desert conditions may have prevailed at least twice. Tectonic movement seems to have taken place between the deposition of Beds III and IV.*

A stratigraphic and environmental framework more detailed than that of Reck (*1*) and Pickering (*2*) is presented here for the Pleistocene succession at Olduvai Gorge (Fig. 1), which contains hominid remains of great antiquity (*3*) and an unsurpassed sequence of Paleolithic culture levels (*4, 5*). The need for geological information about the succession at Olduvai became clear in recent controversies about K-Ar dates and the geologic histories of Beds I and II (*6, 7*). At least some of this argument would not have arisen if the geology had been properly understood. This paper summarizes the principal results of 8 weeks of geologic field work at Olduvai Gorge during the summer of 1962 (*8*). Field work has been supplemented by extensive microscopic and x-ray study of the rocks. The stratigraphic synthesis of Fig. 2 is based on approximately 50 measured sections and the lateral tracing of key horizons. This report is primarily intended to clarify the major stratigraphic relationships; the geology will be described more fully in a subsequent paper.

The succession in Olduvai Gorge was divided by Reck (*1*) into a basal series of basalt flows and mappable units termed Bed I, Bed II, Bed III, Bed IV, and Bed V. Bed V overlies the older beds with pronounced angular unconformity and will not be considered further. The subdivision and nomenclature of Reck are used here, with few modifications.

The basalts comprise a lower flow, 35 to 40 feet thick, which has a typical aa surface structure, and an overlying series of thinner, pahoehoe flows. The aa flow is a biotite-bearing olivine

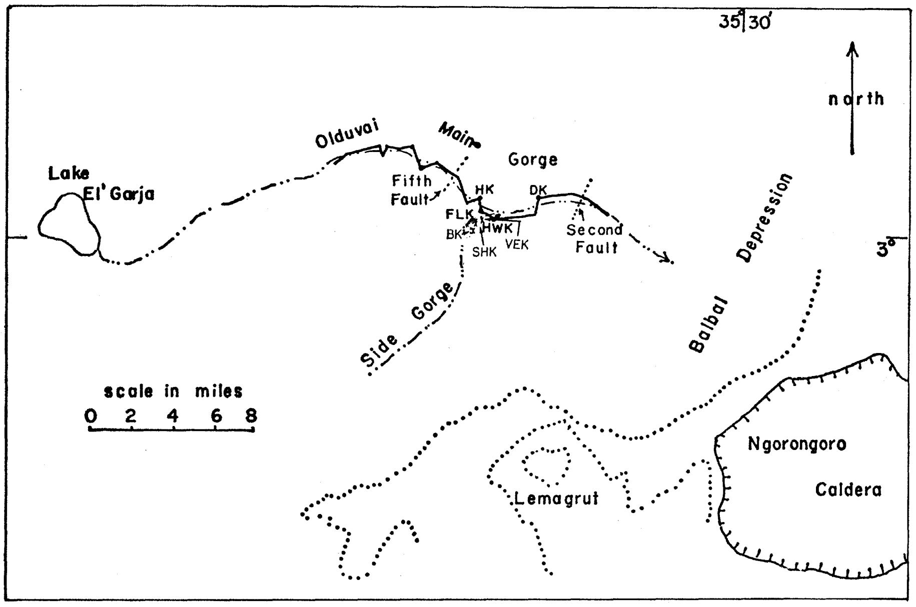

Fig. 1. Sketch map of Olduvai Gorge and its environs, after Leakey (*4*), showing the locations of the Second and Fifth faults and archeological sites DK, HWK, FLK, HK, VEK, SHK, and BK. Heavy line along the Olduvai Main Gorge is the line of section for Fig. 2.

basalt, and the pahoehoe flows are biotite-free olivine-rich basalt. The original ropy surface is widely preserved on the basalts, as Reck has noted (*1*), and the primary lava tumuli form a hummocky surface having a local relief of 5 to 20 feet. Five feet of trachyte tuff and claystone were exposed beneath the basalt flows near the Third Fault in the summer of 1962, and four more feet of tuff and claystone were exposed by excavating. These beds below the basalts resemble the tuffs and claystones of Bed I above. One tuff, 8 feet below the basalts, is rich in coarse anorthoclase crystals of two habits and compositions.

Bed I as defined by Reck is a series of tuffs, of which the lower limits are the basalt flows and the upper limits are the "lacustrine marls" of Bed II. This description seems to fit best the relationships at sites HWK and FLK, where Marker Bed B of Fig. 2 would be the uppermost stratum of Bed I, as Leakey has considered it (*9*). Marker Bed B varies in thickness and lithology, and pinches out locally in the area to the east, where it can easily be confused with a widespread reworked tuff 30 to 50 feet lower in the sequence (Marker Bed A of Fig. 2). Leakey, Curtis, and Evernden (*3*) gave a thickness of about 40 feet for Bed I at site MK, indicating that here they took Marker Bed A as the top of Bed I. The maximum thickness of 40 m for Bed I given by Reck suggests that he measured up to the top of Marker Bed B in the vicinity of the Second Fault (see Fig. 2). In the present report, Marker Bed B is taken as the top of Bed I.

A conformable series of rather uniform tuffs and clays 40 to 75 feet thick underlie Marker Bed B and overlie a trachyte welded tuff to the west of the Fifth Fault. These tuffs resemble those of Bed I to the east, except for a greater degree of weathering and the presence of conglomerates of welded tuff, gneiss, and quartzite debris supplied from the west or north. A coarse anorthoclase tuff near the middle of this sequence appears to be the same as that 8 feet below the basalt flows 12 miles to the east, suggesting that Bed I as defined by Reck is equivalent to only the upper part of this conformable sequence to the west of the Fifth Fault. In order to make Bed I a recognizable stratigraphic unit to the west of the Fifth Fault, it is redefined to include the entire sequence of tuffs between the welded tuff and the top of Marker Bed B. By this definition, the basalt flows constitute a member of Bed I in the area to the east.

In its easternmost exposures, Bed I consists largely of stream-worked trachyte tuffs, lapilli tuffs, and conglomerates. It also contains two unsorted trachyte lapilli tuffs, probably ignimbrites (that is, the deposits of Pelean eruptions), which can easily be traced within the eastern, fluvial facies of Bed I. Stream-channel alignments generally depart but little from S60°E, suggesting that the volcano Ngorongoro could have been the source of most or all of the trachytic materials. The stream-laid deposits interfinger westward with dominantly land-laid trachyte tuffs and tuffaceous clays that are extensively penetrated by root channels. A few diatoms, oolites, and thin-walled pelecypods in some of the tuff and clay suggest temporary floodings by a lake. Hominid remains (see Fig. 2) and artifacts within Bed I are largely or entirely confined to these subaerial and shallow-water deposits. Falls of volcanic ash and deposits of lacustrine clay have contributed to the preservation of artifacts and fossils.

A relatively small thickness of purely lacustrine clay underlies Marker Bed B near the Fifth Fault. Farther to the west, Bed I is mostly a weathered accumulation of ash deposited on the land surface. Caliche layers in the more weathered of these ash deposits suggest a climate that was not sufficiently humid for calcium carbonate to be leached from the soil. Rosettes of calcite after gypsum occur at a few horizons above the basalts in the area to the east. The gypsum, like the caliche, probably indicates a relatively dry climate.

Bed II conformably overlies Bed I, and the two are difficult to separate where Marker Bed B pinches out to the east of site DK and near the west end of the gorge. Purely lacustrine deposits as much as 90 feet thick occupy the axis of a small sedimentary basin transected by the Olduvai Main Gorge (Fig. 1). Unfossiliferous green clays form most of the lacustrine sequence which also includes trachyte tuff, dolomite, oolitic limestone, and chert nodules. The lack of fossils and the presence of dolomite beds and of authigenic potash feldspar in clays and tuffs suggest to me that the lake was moderately or strongly saline and alkaline for much of its history, and that it probably lacked a permanent outlet. In most years, evaporation must have exceeded inflow to the lake. Stream-worked tuffs form most of Bed II to the west of the lake, but there are substantial proportions of subaerial tuff and nonvolcanic sandstone and conglomerate.

Bed II to the east of site FLK is a diverse sequence of fluvial, eolian, and pyroclastic deposits 50 to 90 feet thick. Several horizons are moderately or deeply weathered, and channeling is visible in many places, particularly along the Side Gorge. Clays, sandstones, and conglomerates of fluvial origin form most of the eastern sequence, but some of the clays and sandstones appear to have been deposited by the lake when it spread eastward beyond its usual limits. Detritus of the sandstones and conglomerates is largely trachytic, and stream-channel trends suggest that most of it may have been supplied by Ngorongoro. Trachyte, nephelinite, and olivine basalt cobbles in conglomerates near sites HWK and VEK were derived from the direction of Lemagrut.

Trachyte tuffs of ash-fall origin and pyroxene-rich tuffs redeposited by wind constitute about a fifth of the eastern sequence. The eolian tuffs consist of mineral grains and rock fragments that were rounded and polished by wind action, and the thickness and extent of these eolian tuffs suggest a climate like that of the present time at Olduvai Gorge. At about the time these eolian tuffs were deposited, the lake to the west temporarily shrank. Lacustrine chert nodules were then eroded at its margin, and mud cracks formed over much of its floor.

Stone artifacts and well-preserved fossils are relatively abundant in beds deposited along the eastern and southern margin of the lake (for example, sites HWK, FLK, SHK, and BK). In the lower part of Bed II there are tools made from chert that was obtained from the margin of the lake during its brief period of desiccation. The "Chellean" skull reported by Leakey (*10*) was found 15 to 20 feet below the top of Bed II in land-laid tuffs deposited near the margin of the lake.

Bed III is separated by disconformities from Bed II and Bed IV. An eastern facies of Bed III consists largely of stream-laid conglomerates, clayey sandstones, and sandy claystones; it contains minor proportions of tuff and mudflow deposits. These beds were weathered as they accumulated, and most of them are reddish-brown, well consolidated, and penetrated by root channels. Irregular nodules and anastomosing twiglike structures of calcium carbonate are concentrated in horizontal layers at many places in the sandstones and claystones. These calcite bodies seem to have been formed at shallow depth as the beds were being deposited, for they are locally channeled by fluvial conglomerates. Volcanic debris forms most of the sandstones and conglomerates, and channel orientations suggest a southerly source —probably Lemagrut—for most of the detritus.

To the west, Bed III consists of yellowish-gray sandstones and smaller amounts of conglomerate, clay, and dolomite. Southeast of site HK these beds intergrade with the reddish-brown alluvial deposits, a fact evidently not recognized by Reck. Sandstones are dominantly of volcanic detritus, but many of them also contain a small to moderate proportion of gneissic debris and calcite oolites. The oolitic sandstones probably accumulated in and along the margin of a lake. Large-scale

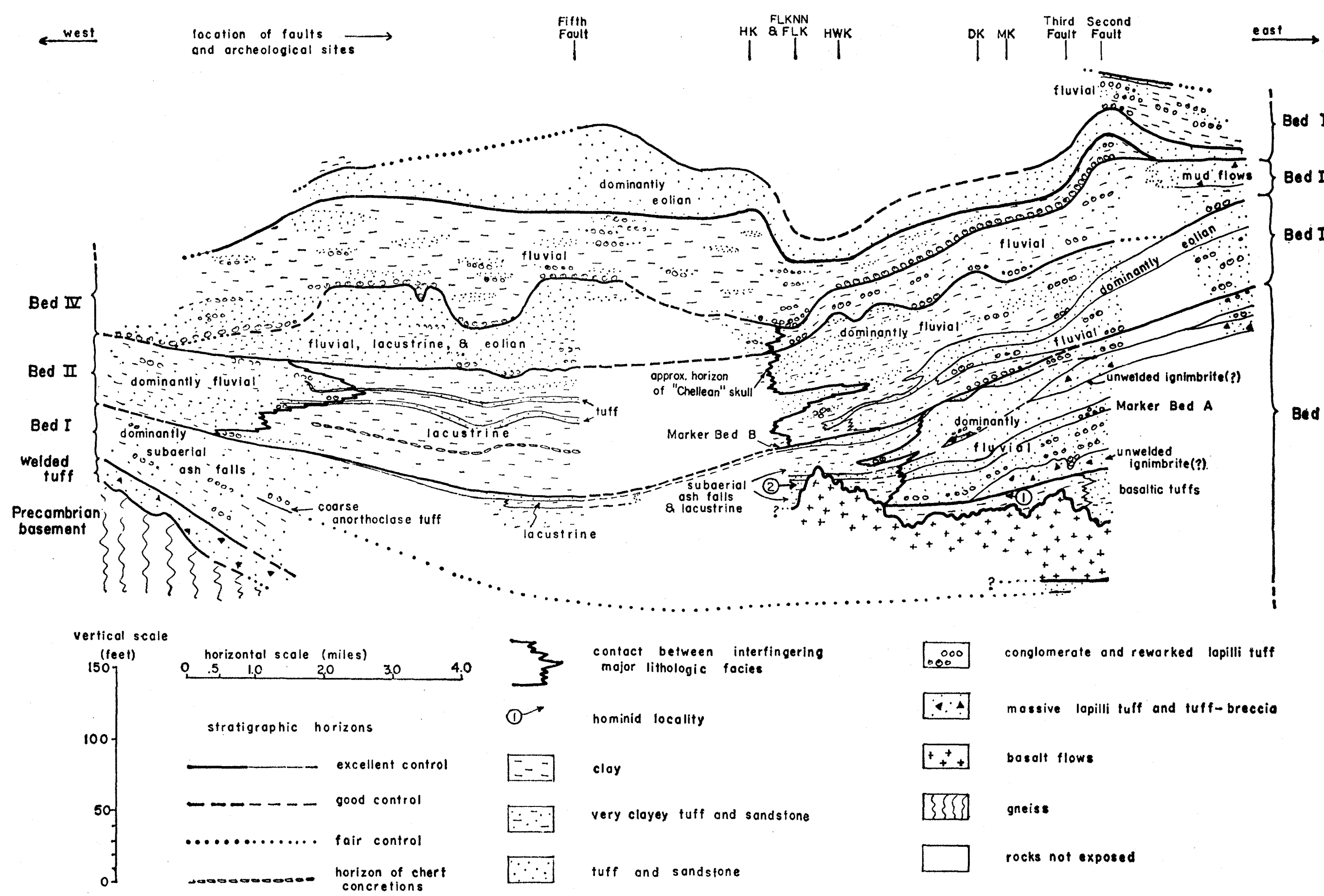

Fig. 2. Stratigraphy of Beds I–IV along Olduvai Main Gorge, based upon measurements along the line of section shown in Fig. 1. The sequence is reconstructed approximately as it would have appeared prior to faulting. Heavy lines separate major stratigraphic units, and light lines are used to delineate subdivisions of major units. Hominid locality 1 represents the hominid site at MK (*3*), which lies at approximately the same horizon as small stone tools and a structure built of basalt blocks at site DK (*5*). Locality 2 represents the *Zinjanthropus* site; the pre-*Zinjanthropus* child was found stratigraphically about 2 feet lower.

cross-bedding suggests that some of the oolitic sandstones are eolian dune deposits. Conglomerates and many of the sandstones are lenticular, and some of them fill steep-walled stream channels. The conglomerates are formed largely of quartzite, gneiss, and welded-tuff pebbles derived from the west or north. Dolomite is present both as lacustrine beds and as dolomitized caliche layers.

Dolomite and calcareous structures in the weathered alluvium suggest a climate in which evaporation exceeded precipitation, either seasonally or throughout the year. Climatic significance of the reddish-brown color in the weathered alluvium is controversial, as Pickering (*2*) has pointed out. More important is the dominance of montmorillonite and illite (clay mica) as the clay minerals in these beds, which indicates that leaching was mild by comparison with that on the rainy, upper slopes of Ngorongoro, where gibbsitic reddish-brown latosols have been formed. Stone artifacts occur in the reddish-brown alluvial deposits and in a few fluvial layers of the mixed lacustrine-fluvial-eolian assemblage.

Bed IV comprises a widespread lower unit of clays, sandstones, and conglomerates and an equally widespread upper unit of eolian tuffs. Near the mouth of the gorge the eolian tuffs are overlain by conglomerates, sandstones, and clays. The lower member of Bed IV, as much as 80 feet thick, consists almost exclusively of Precambrian debris which coarsens westward along the gorge. Lenticular shape of the sandstones and conglomerates, and root channels and evidence of subaerial weathering in the clays suggest to me that these beds were deposited in a stream-channel and floodplain environment, rather than in a lake, as Reck believed. Catfish bones and pelecypods (Unionidae) are common in the sandstones and conglomerates thought to have been deposited in stream channels, and stone artifacts are widespread in both stream-channel and floodplain deposits.

The eolian tuff member, as much as 60 feet thick, is formed of aegerine nephelinite ash particles that have been rounded, polished, and redeposited by wind. Cross-bedding characteristic of sand dunes can be seen in a few places. Dense, travertine-like layers of caliche, known in East Africa as *steppe limestone*, are interbedded with the tuffs. Neither stone artifacts nor fossils occur in these beds, as far as I am aware, and these eolian tuffs probably accumulated in a desert or semidesert environment, possibly even drier than that which prevails there today. The overlying beds are generally similar to the fluvial deposits underneath the eolian tuffs, and catfish bones were noted in a conglomerate. Reck does not mention the eolian tuffs of Bed IV, possibly because he confused them with the similar deposits of Bed V, which they often underlie.

The earth's crust here may have been slightly warped before Bed IV was deposited, for the direction of stream flow in the vicinity of Olduvai Gorge seems to have been reversed between Beds III and IV. Bed III received most of its debris from a volcanic source to the south and possibly southeast, whereas most debris at the base of Bed IV, nearly as far east as the Third Fault, was derived from exposures of welded tuff and Precambrian basement to the west and north. Crustal warping would also account for the channeling of Bed III by the base of Bed IV and the abrupt disappearance or displacement of the lake which had existed in approximately the same place for much of the time that Beds I, II, and III were deposited.

Only a few points concerning the geochronology of Olduvai Gorge will be mentioned here, for Curtis and Evernden will shortly publish many new dates. The 4.4 million-year date given by a basalt sample (*7*) implies a hiatus of 2.7 million years between the basalt and the overlying tuffs of Bed I, which have an average age of about 1.7 million years (*3*). Geologic evidence to the contrary suggests that the basalts were extruded and buried over a relatively short period of time. Evernden and Curtis have given me permission to state that their published figure of 4.4 million years on sample KA 927 is grossly erroneous because of procedural difficulties of which they were unaware at the time. Their statement is as follows:

"The argon extraction procedure used for the published date [(*7*)] involved the freezing out of CO_2 if it were present in the gas obtained from fusion of the sample. KA 933 had no such contaminant, but much disseminated carbonate in KA 927 resulted in large quantities of CO_2. Isotopic fractionation of the argon incorporated in the CO_2 (preferential selection of A_{36}) resulted in a residual argon sample enriched in A_{40}. High percentages of atmospheric argon in these samples magnified the effects as regards determination of the radiogenic argon content. Modification of procedure has resulted in ages on KA 927 of approximately 1.8 million years. As noted in our paper [(*7*)], the character of KA 933 was such as to suggest probable fractional loss of argon so that we feel that there is no disagreement between the ages of basalt samples KA 933 and KA 927 (1.7 and 1.8 $\times$ 10^6 years, respectively)."

The biotite sample giving an age of 1.0 to 1.1 million years (*3*) was probably obtained from Bed II rather than Bed I as reported, for only a few scattered flakes of biotite were noted in samples from Bed I, but biotite is locally common in and below the eolian tuff unit of Bed II. This change in stratigraphic assignment accords with the fact that the land-laid tuffs of Bed I which overlie the basalt flows are not weathered as severely as they should be if they had accumulated over a period of 700,000 years. Moreover, there appear to be no significant erosional gaps within this sequence of beds.

The sample from Bed II earlier dated as 360,000 years old (*3*) has been redone by an improved procedure, and Evernden and Curtis have allowed me to state that the present estimate of its age is 490,000 years. Thus, Bed II seems to span at least half a million years. This figure seems a reasonable minimum, in view of the fluvial channeling, horizons of moderate to deep weathering, and complex geologic history of Bed II.

This new information has several implications for anthropology.

1) The climate was relatively dry, at least seasonally, throughout most or all of the lengthy period of hominid occupation recorded by Beds I–IV. Hominid occupation may have been first interrupted by desert conditions which prevailed during the deposition of Bed IV.

2) For the period of Beds I and II, hominid occupation is recorded principally along the southern and eastern shore of a lake which was alkaline and rather strongly saline for most of its duration. Streams draining large active volcanoes to the east and south may have been the principal source of fresh water for this area.

3) Stone artifacts in the upper part of Bed I are only slightly older than those in the lower part of Bed II.

4) The Oldowan cultural sequence from Bed I probably represents a shorter period of time than stages 1 to 5 of the Chelles-Acheul culture, which span Bed II (*4*).

5) None of the stone artifacts or hominid fossils collected from Bed I are appreciably older than 1.7 million years.

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29 November 1962

Intrauterine Foreign Body: Effect on Pregnancy in the Rat

Abstract. *A silk suture placed in the lumen of one uterine horn of rats before mating prevented pregnancy in that horn although normal implantation occurred in the unoperated horn. The suture did not interfere with fertilization or the tubal transport of ova, nor did it induce a decidual reaction; it appeared to prevent pregnancy by causing failure of implantation.*

At a recent conference (*1*), on intrauterine contraceptive devices, there was no available experimental information on the mechanism of their action. Ishihama (*2*), reporting on a large series of women, discussed intrauterine devices for use in birth control. He presented no experimental data to identify the time, site, or mode of action. Our study was undertaken to determine at what stage of reproduction in the rat an intrauterine foreign body would interfere with pregnancy.

Mature, female rats (Long Evans strain) with normal estrous cycles and maintained on a standard diet were used for this study. They were anesthetized with ether, and the right ovary, oviduct, and uterine horn were exposed through a dorsolateral incision. An atraumatic needle, attached to a silk suture (5–0), was inserted through the antimesometrial wall of the horn, passed along its lumen, and brought out through the same wall, approximately 5 to 8 mm above the point of entry. The suture was pulled through the site of introduction until it lay within the uterine cavity. The upper end of the suture was cut, and a knot was tied adjacent to the uterine wall to fix the suture in position. The incision was closed, and a vaginal smear was taken. The female was then placed with a male. After the surgery, vaginal smears were taken each morning, and the day on which sperm were seen was designated as the first day of pregnancy.

An initial group of nine females (groups *A* and A_1, Table 1), autopsied or laparotomized between the 7th and 14th days of pregnancy, showed regular implantation in the control horns. In seven operated horns where the suture remained in place, neither sites of nidation nor deciduomata around the suture area could be found. In two animals (group A_1), the sutures were not in the uterus at necropsy, and implantation appeared normal bilaterally (Fig. 1). Nine operated animals (groups *B* and B_1, Table 2) were killed on the third and fourth days of pregnancy, at which time the reproductive tracts were dissected free, and the uterine horns and oviducts were flushed to recover ova. No demonstrable differences in the number of ova, position in the tract, morphology, or rate of cleavage could be found between control and operated sides. On the 5th day of pregnancy, only one of six animals (group *C*, Table 2) with retained sutures had ova in the operated horn, although all but one of the contralateral horns contained normal ova. In two animals (group C_1, Table 2), the suture had become displaced, and on the 5th normal ova were recovered from both horns.

Histological examination of uterine tissue from the sutured areas showed no decidual reaction or inflammation. In general, the only notable differences between sections from operated and control horns was a partial denudation of the epithelium lining the lumen and the presence of a few leukocytes within the lumen. This was possibly caused by passage of the suture. The lack of endometrial epithelium did not prevent implantation, since operated animals who had lost their sutures still implanted normally.

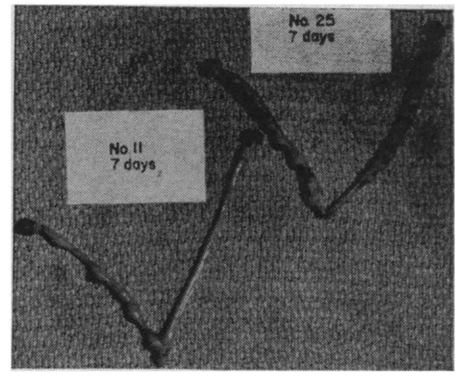

Fig. 1. Uteri from two animals, 7 days pregnant, showing normal bilateral implantation (No. 25, suture not present at autopsy) and unilateral implantation (No. 11, suture present at autopsy).

The results indicate that in rats an intrauterine foreign body prevents pregnancy by interfering with implantation rather than by interfering with fertilization or the tubal transport of ova. The cleavage rate and position in the reproductive tract of ova recovered from both horns on the 3rd and 4th days correlated well with those reported

Table 1. Effect of silk suture surgically placed in the right uterine horn before breeding.

Suture	No. of implantations of ova			
	Right side		Left side	
	Total	Average	Total	Average
Group A, nine animals, 7 to 14 days pregnant				
Retained	0	0	17*	4.3 ± 1.5
Group A_1, two animals, 7 to 14 days pregnant				
Displaced	13	6.5	14	7

* In three animals the implantations were confirmed by laparotomy but not counted.

Table 2. Effect on the number of ova recovered.

Suture	No. of ova			
	Right side		Left side	
	Total	Average	Total	Average
Group B, seven animals, 3 to 4 days pregnant				
Retained	22*	3.1 ± 1.9	31†	4.5 ± 1.1
Group B_1, two animals, 3 to 4 days pregnant				
Displaced	8	4	8	4
Group C, six animals, 5 days pregnant				
Retained	3	0.5	19	3.2 ± 2.1
Group C_1, three animals, 5 days pregnant				
Displaced	7	2.3	5	1.7

* Recovered from tube in all seven animals. † Recovery from tube in six animals and from uterus in three, including two animals in which ova were recovered in both tube and uterus.