with pregnenolone- $7\alpha$ -<sup>3</sup>H formed larger amounts of testosterone-3H than did control ovaries. Thus the activity of enzymes involved in the synthesis of steroid hormones in the ovary and adrenal of the adult rat was influenced by previous exposure of these tissues in organ culture to homologous RNA extracted from the adrenal or testis.

Similar effects of RNA on the pattern of steroid synthesis could be demonstrated by the second method of enzyme assay. Mouse adrenals previously. exposed to RNA from mouse testis, and subsequently incubated in a cell-free system in the presence of excess pregnenolone- $7\alpha$ -<sup>3</sup>H, NAD, NADP, and glucose-6-phosphate, formed more testosterone-<sup>3</sup>H and less corticosterone-<sup>3</sup>H than control adrenals did (Table 3). In a similar experiment, rat adrenals previously exposed to RNA from rat testis formed more testosterone-3H than adrenals exposed to RNA from rat adrenal did. These results are in complete agreement with those in which the enzymes were assayed in organ culture (Table 1). Rat ovaries previously exposed to RNA from human fetal adrenals formed more progesterone-3H, deoxycorticosterone-3H, and corticosterone-<sup>3</sup>H than control ovaries (Table 3) did. In this instance, heterologous RNA

showed an effect on the pattern of steroid synthesis in rat ovary in organ culture. These results are similar to the effects of homologous RNA from the adrenal noted in Table 2. Under both assay conditions, rat ovaries previously exposed to adrenal RNA formed more progesterone and corticosterone than control ovaries did.

Because of the extensive purification procedures necessary for isolation and identification of the radioactive steroid products, it was not feasible to do a large number of duplicate experiments and apply the usual criteria of statistical significance. However, many experiments have been completed in which the material added to the organ culture was RNA from the same gland or an inactive fraction of RNA isolated from a methylated-albumin column. In such experiments, in which no effect was expected, the agreement between the steroid products isolated from control and experimental incubations was quite striking (Table 4).

The evidence from these experiments supports the concept that RNA from one steroid-producing gland can alter the enzyme activity of another steroidproducing gland and that the pattern of steroid hormone synthesis reflects the origin of the RNA. There are several

Table 2. Radioactive steroid products, expressed as counts per minute per milligram of ovary, isolated from organ cultures of rat ovaries previously exposed to RNA from either rat adrenal or rat testis. The substrate was pregnenolone- $7\alpha$ -<sup>3</sup>H (0.25  $\mu$ c per milligram of ovary).

	Amounts (count min <sup>-1</sup> mg <sup>-1</sup> )							
Product	Ovai	ries from pregnan	Ovaries from nonpregnant rat					
	Control	Adrenal RNA	Testis RNA	Control	Testis RNA			
Progesterone	3,800	8,560	8,500	13,300	13,000			
Testosterone	3,000	2,820	3,080	333	417			
Androstenedione				559	506			
Deoxycorticosterone	12	763	240					
Corticosterone	48	210	23					

Table 3. Radioactive steroid products, expressed as counts per minute per milligram of tissue. isolated from cell-free incubations of adrenals or ovaries, previously exposed to RNA from either adrenal or testis. The substrate was pregnenolone- $7_{\alpha}$ -<sup>3</sup>H (0.5  $\mu$ c per milligram of tissue).

	Amounts (count min <sup>-1</sup> mg <sup>-1</sup> )							
	Mouse adrenals		Rat adrenals		Rat ovaries			
Product	oduct Control Testis Adrenal Testis RNA RNA RNA	Testis RNA	Control	Human adrenal RNA				
Testosterone	8,480	12,500	671	2,170				
Corticosterone	53,000	6,580	37,500	32,900	82	217		
Cortisol					70	848		
Estrone					11,700	14,200		
Progesterone					4,550	8,120		

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Table 4. Radioactive steroid products, expressed as counts per minute per milligram of adrenal, isolated from cell-free incubations of mouse adrenals, previously exposed saline or to an inactive fraction of testicular RNA eluted from a methylated-albumin column. The substrate was pregnenolone- $7\alpha$ -<sup>3</sup>H (0.5  $\mu$ c per milligram of adrenal).

Control	Inactive RNA 4,910	
5,310		
755	844	
55,900	48,000	
164,400	175,000	
	Control 5,310 755 55,900 164,400	

reports (3) which indicate that preparations of RNA administered by one or another route to tissues in vivo may alter the morphology or enzyme activity of the recipient cells. The present experiments extend these observations to cells in organ culture. It should be emphasized that the preparation of RNA used is a crude one and a small contamination with protein or DNA has not been ruled out. The type of RNA molecule that may be responsible for the biological effect has not yet been defined.

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# Pediplain in Northern Chile and the Andean Uplift

Abstract. A pediplain in the Chilean Atacama Desert formed during Oligocene and Miocene time when the aridity of the region started and was later displaced by north-trending faults associated with the Andean uplift. Block basins and some horsts were later concealed by Upper Tertiary and Quaternary orogenic sediments and ignimbrites.

Late Tertiary block faulting, associated with the Andean uplift in northern Chile, displaced a Tertiary pediplain that had formed in the preceding 30 million years and initiated deposition of orogenic sediments and ignimbrites in large areas of the Atacama Desert. The

<sup>4.</sup> Supported by USPHS grant AM-08026.

structural relations between the pediplain and north-trending faults indicate that the faulting began before deposition of the orogenic sediments and ig-



nimbrites, even though movement continued intermittently thereafter. These conclusions have been determined by mapping a 30-minute quadrangle (1)and a 15-minute quadrangle (2), in which the faulted pediplain and the overlying orogenic deposits and tuffs are included. These observations are new and extend the previous results of the writer and of Ruiz-Fuller (3).

The region studied is on the Andean Range at the latitude of Iquique (Fig. 1) where north-trending ridges of Paleozoic and younger rocks, partly eroded to a pediplain in early Tertiary time, were broken by late Tertiary northtrending faults to form a basin-andrange structure. The grabens and some horsts of the structure were then concealed by orogenic conglomerates and sandstones and by associated rhyolitic ignimbrites, collectively known as the Altos de Pica Formation of late Tertiary and Pleistocene age (4). In certain localities where the pediplain was not concealed, such as the surface on

Fig. 1. Location of Iquique and of the Tarapacá, Violeta, and Juan de Morales ridges. Late Tertiary faults are shown.



Fig. 2. Diagrammatic section across the Juan de Morales Ridge.

the southeastern flank of the Juan de Morales Ridge, erosion has cut deep canyons. The Altos de Pica Formation is relatively less faulted by tensional faults that developed during uplift of the Andean Range. The north-trending ridges acted as barriers to the westward spread of the Altos de Pica Formation from the Andean uplift and locally prevented or diminished deposition, particularly west of the Juan de Morales, Tarapacá, and Violeta ridges.

The orogenic deposits of the Altos de Pica Formation overlie a well-developed surface of erosion (Fig. 2), which is here named the "Choia Pediplain." To the west of the Juan de Morales and Violeta ridges the Choja Pediplain is a rock-cut surface sloping 2° to 3°W, marked locally by residual bornhardts or inselbergs surrounded by the Altos de Pica Formation. Partly buried inselbergs and the associated pediplain are well exposed in deep, second-cycle canyons that cut the Altos de Pica Formation (5). Several higher rock-cut surfaces on the southeastern flank of the Juan de Morales Ridge and on the western flank of the Violeta Ridge are thought to be related to the Choja Pediplain, because these relict surfaces probably were uplifted by faults and by differential movements of the horsts. The altitude of these surfaces is approximately 400 m higher than the concealed Choja Pediplain of the basins. The relict surfaces resemble the Choja Pediplain in that they also present deep weathering, a thin veneer of mantling gravels, and a gently rolling surface, although the surfaces are partly eroded by canyons (6).

The formation of the Choja Pediplain is related to a prolonged period of aridity that is thought to have existed during the Tertiary in northern Chile where the Andean Range is now located. Although Brüggen (7) was not generally impressed by pediment-forming processes in the Atacama Desert, he was the first to conclude that the beginning of the arid climate of northern Chile took place after the Eocene.

Other workers have arrived at similar conclusions from observations in the San Bartolo area; about 400 km farther south-southeast ". . . the tectonic activity which warped the early Tertiary planation surface and which produced much of the present Andean relief . . . began shortly before and continued after the period of ignimbrite eruption" (8).

In summary, erosion of the Choja

Pediplain in the Juan de Morales region in Northern Chile might have occurred during the Oligocene and Miocene epochs in a period of 30 million years. Because pediplains are common in deserts, such an erosion surface supports Brüggen's idea that northern Chile has been arid since the Oligocene Epoch. The uplifting of some relatively high fault blocks of the Choja Pediplain at the same time as the other Andean tectonic blocks precluded deposition of younger orogenic materials that were transported from eastern source areas, which indicates that the aggradation of the block basins is younger than the north-trending block-fault system associated with the Andean uplift.

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# Fracture Planes in an Ice-Bilayer

## **Model Membrane System**

Abstract. Experiments with transferred stearate layers were performed to determine the location of fracture planes in frozen ice-lipid systems. Bilayers and multilayers of carbon-14-labeled stearate were frozen in contact with an aqueous phase and then fractured. The distribution of radioactivity on both sides of the fracture showed that the stearate layers were cleaved apart predominantly in the plane of their hydrocarbon tails. Because bilayers split in this manner, it was possible to measure time-dependent exchange of label between the layers. Exchange occurred with a half-time of 50 minutes in the presence of calcium and 25 minutes in the absence of calcium. Since stearate bilayers and multilayers are models of hydrophobically stabilized structures, the strong influence of their hydrophobic region on the fracture plane provides an explanation of how the freeze-etch technique of electron microscopy can expose inner, hydrophobic faces of cell membranes.

The freeze-etch method of preparing biological specimens for electron microscopy has provided evidence that fractures in frozen tissues split inner, hydrophobic regions of biological membranes (1). For freeze-etching, specimens are frozen and then fractured under vacuum. A small amount of ice is allowed to sublime from the fractured face and this etched surface is then shadowed and replicated. Examination of the replica by usual electron microscopic techniques reveals extensive structures which evidently represent membranous portions of cells.

This technique was first applied to biological materials by Steere (2) and later developed by Moor *et al.* (3). 3 NOVEMBER 1967 Moor and Mühlethaler (4) proposed that fracturing occurs along exterior faces of membranes to expose true membrane surfaces. Branton and coworkers (1, 5, 6) have presented evidence for the alternative possibility that fractures in frozen tissues may split membranes in their inner, hydrophobic regions rather than along their hydrophilic surfaces. It is generally accepted that two of the major forces stabilizing lipoprotein membranes in aqueous environments are entropic (hydrophobic) bonding and van der Waals interactions (7); it was reasoned (6) that upon freezing entropic bonding would no longer be important and only relatively weak van der Waals forces would stabilize membranes in

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- 3. C. Ruiz-Fuller, Geología y yacimientos metaliferos de Chile (Instituto de Investigaciones Geológicas, Santiago, 1965). Ruiz, on the contrary, concluded that the diastrophism that resulted in uplift of the Andean Range in northern Chile began after the deposition of the orogenic sediments and the ignimbrites.
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   Young canyons and eastward migration of
- Young canyons and eastward migration of nickpoints are indications of an active second-cycle erosion that followed the Andean uplift.
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hydrophobic regions. Such regions could therefore represent weak areas in the frozen structure, since strong charge-dipole interactions between hydrophilic portions of the membrane and the surrounding ice would be less affected by freezing.

In the present investigation a model system was employed to test this reasoning. The model consisted of a bimolecular layer of stearate on glass, deposited according to the multilayer technique first described by Blodgett (8). The bilayer is composed of two successive monolayers of stearate as shown in Fig. 1. Although this model is not analogous to biological membranes, it is similar in that there exists an extensive hydrophobic region, consisting of hydrocarbon chains, and a hydrophilic region composed of carboxylate groups. If the water (Fig. 1) is frozen and the glass split away from the ice, several fracture modes are possible: (i) there is no preferred fracture plane; (ii) the fracture occurs between the glass and the bilayer; (iii) the fracture occurs between the ice and the bilayer; (iv) the fracture cleaves the bilayer down the middle. Using C14-labeled stearic acid, we determined that the last-mentioned fracture mode is preferred and that approximately half the stearic acid was left on the glass and half on the ice.

Stearic acid (99.8 percent, Applied Science Laboratories, Inc., State College, Pa., 1 mM in n-hexane) was spread on 1 mM CaCl<sub>2</sub>-NaHCO<sub>3</sub> solution, pH 8.5, until a lens of hexane solution formed, indicating that the surface was covered with a monolayer. Blodgett (8) found that the presence of calcium or barium ions was necessary for production of multilayers. At pH 8.5, the spread monolayer is predominantly present as stearate (9). Divalent cations apparently link together carboxylate groups of the stearate molecules (10) and facilitate multiple transfers of layers from the water surface to the slide. The solutions were contained in a 2-liter Teflonlined trough with approximately 300 cm<sup>2</sup> of surface area. After spreading was completed, a drop of methyl laurate was placed at one end of the trough to act as a piston oil (8). Glass cover slips that had previously been cleaned in chromic acid and immersed in the trough were slowly withdrawn ( $\sim 2$  cm/minute) and reimmersed at the same speed by means of a small hydraulic lift (Fig. 1, a and b). This caused a bilayer of calcium stearate to