with iodine (*4*); and (iii) by gas-liquid chromatographic separation of the methyl derivatives of nonvolatile organic acids extracted with ether from the incubation mixtures (*5*). When, however, a further attempt was made to strengthen the chemical evidence for the identity of lactic acid by means of an enzymatic method based on the use of nicotinamide adenine dinucleotide (NAD) and muscle L(+)-lactate dehydrogenase, a negative result was obtained. This alerted us to the possibility that the lactic acid produced by the spermatozoa is not L(+)-lactic acid.

On the assumption that the lactic acid formed by the octopus spermatozoa may be D(−)-lactic acid, we made use of a preparation of D(−)-lactate dehydrogenase from *Lactobacillus leichmannii* and were able to show that, in fact, the lactic acid produced by these spermatozoa was present in the D(−) enantiomorphic form. The rate at which the spermatozoa produced this lactic acid varied, but on the average, at 10°C, about 1 mg of D(−)-lactic acid was produced by 10^9 spermatozoa during 48 hours of anaerobic incubation.

We have good reason to believe that the formation of D(−)-lactic acid also occurs under conditions in vivo. On two occasions, after copulation had been allowed to proceed to completion, we dissected the mated females 24 hours later and recovered from their oviducts the remnants of spermatophores together with a large dilute mass of motile spermatozoa. In this material we found in one instance 5 mg, and in the other 25 mg, of D(−)-lactic acid per 100 ml; L(+)-lactic acid was absent. In this particular type of experiment in vivo, it still remains to be established how much of the D(−)-lactic acid is derived from semen and how much is contributed by the female reproductive tract.

Following the identification of D(−)-lactic acid as a metabolite, we turned our attention to the possibility that the octopus spermatozoa may also contain a D(−)-lactate dehydrogenase. We have, therefore, examined the dehydrogenase activity of aqueous, centrifuged extracts made from homogenized spermatozoa, using an assay system composed of either reduced nicotinamide adenine dinucleotide (NADH) and pyruvic acid, or NAD in combination with either L(+)-, D(−)-, or DL-lactic acid. We were able to demonstrate that the sperm extracts contain a highly active D(−)-lactate dehydrogenase, namely, about 50,000 enzyme units per 10^9 spermatozoa, and that they are capable of both reducing pyruvic acid in the presence of NADH as well as oxidizing D(−)- and DL-lactic acid, but not L(+)-lactic acid, in the presence of NAD. On electrophoretic examination, most of the D(−)-lactate dehydrogenase was found to migrate as a band in a position quite distinct from the multiisozyme pattern of the L(+) enzyme.

Oxamic acid ($10^{-3}M$), a well-known inhibitor of L(+)-lactate dehydrogenase (*6*), had no effect on the D(−)-lactate dehydrogenase of spermatozoa. The *p*H optimum of the sperm enzyme, examined in a system consisting of D(−)-lactic acid and acetylpyridine-NAD, was above 9, which is nearer to the *p*H optimum of the D(−)-lactate dehydrogenase from *Lactobacillus* (*7*) than to that of the L(+)-lactate dehydrogenase prepared from beef heart or skeletal muscle.

The following conclusions may be drawn from the above observations. The lactic acid produced anaerobically by the spermatozoa of *O. dofleini martini*, is D(−)-lactic acid, as we have been able to prove by using a combination of chemical and enzymatic assay methods for the purpose of identification and determination. We would have missed this interesting fact had we relied solely on the conventional L(+)-lactate dehydrogenase assay method. We have shown, moreover, that the octopus spermatozoa possess a highly active, stereospecific, NAD-dependent D(−)-lactate dehydrogenase, which in some properties resembles the D(−)-lactate dehydrogenase of certain microorganisms, but clearly differs from the L(+)-lactate dehydrogenase commonly encountered in animal tissues and body fluids.

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Probable Fijian Origin of Quartzose Temper Sands in Prehistoric Pottery from Tonga and the Marquesas

Abstract. *Quartzose temper sands included within fired clay bodies of certain prehistoric potsherds from Tonga and the Marquesas have mineralogical compositions wholly different from those of indigenous sands that occur as temper in other potsherds from the same sites but are indistinguishable from sands in potsherds collected from the Rewa Delta of Viti Levu in Fiji.*

Men who travel in boats leave no footprints but may transport with them geologically identifiable artifacts that bear a record of their origins. This fact is significant for reconstructing the migration paths of early islanders across the Pacific. We have traced unusual temper sands in prehistoric potsherds from Tonga in western Polynesia and from the Marquesas in eastern Polynesia to an apparently common source in Fiji (Fig. 1a).

Small islands in the western and southern Pacific are virtual point sources of sand (*1*). On each island, sands available for collection as temper for the manufacture of earthenware by insular potters have restricted mineralogical compositions governed by the limited range of rock types exposed. The limited compositional range prevails across a spectrum of textural types including littoral beach deposits, alluvial and colluvial sands, ash beds, and diverse placers (*2*). The varied tectonic settings of different archipelagoes also allow classification of the potential tempers from various island groups into general categories within which the character of indigenous

sands is predictable in a regular manner (*1, 2*): (i) oceanic basalt tempers in island clusters like the Marquesas within the Pacific basin proper; (ii) andesitic arc tempers in island chains of active magmatic arcs like Tonga standing parallel to trenches or active subduction zones; (iii) volcano-plutonic orogen tempers in dormant or quiescent magmatic arcs that are deeply eroded like Fiji; and (iv) tectonic highland tempers in large, geologically complex islands like New Caledonia along the fringe of the Pacific Ocean. Only calcareous sand tempers collected from coastal sands made of reef detritus are common to all the tectonic settings. Oceanic basalt and andesitic arc tempers are composed dominantly of volcanic rock fragments plus grains of feldspar and ferromagnesian minerals derived also from the local volcanic rocks. Quartz is absent or rare, although amounts of the order of 10 percent of the total sand grain population occur exceptionally in some andesitic arc tempers. By contrast, quartz derived from granitic rocks or metasedimentary rocks is common and locally abundant in tempers of the volcano-plutonic orogen and tectonic highland types. Similarly, potash feldspar is rare or absent in the former two temper types but common in the latter two.

Petrographic examination of thin sections of more than 500 potsherds collected by a number of archeologists from various sites in 12 different island groups (*3*) discloses that most sherds are fragments of locally made pottery containing temper sands of types specifically indigenous to the island on which they were found, or at least generally indigenous to the island group within which they were found (*2*). The ability to detect sherds of pottery exotic to a given island group on a mineralogical basis was confirmed by study of imported Spanish-made potsherds left at abandoned village sites on two different islands in the Solomons by survivors of the Mendaña expedition of A.D. 1595 (*4*). One Tongan sherd selected at the Bernice P. Bishop Museum, Honolulu, as being atypical in the collections of A. L. Kaeppler from the islet of Tungua in Ha'apai, and three Marquesan sherds collected by R. C. Suggs and Y. H. Sinoto at Ha'atuatua on Nuku Hiva in the Marquesas, contain quartzose temper sands wholly unlike plainly indigenous tempers in other sherds from the same sites. The anomalous tempers have compositions exotic to both Tonga and the Marquesas, but are texturally and mineralogically indistinguishable from each other, and are likewise indistinguishable from the apparently indigenous tempers in two Fijian sherds collected by E. Shaw at Nasilai from deltaic deposits of the Rewa River on Viti Levu (Table 1). We interpret the sherds with exotic tempers as fragments of pots imported from Fiji. The tempers are moderately sorted, subangular to subrounded sands of fluvial type. We have not encountered temper sands of similar composition elsewhere in the Pacific region (Fig. 1b).

The volcanic islands of Tonga are dominantly mafic and felsic andesite with lesser dacite and some basalt (*5*). Examination of about 50 prehistoric potsherds in thin section shows that the sand tempers commonly used by potters in the island group are volcanic sands derived from such sources (*6*). Sand grains in these indigenous andesitic arc tempers are dominantly pyroxene and plagioclase mineral grains plus volcanic rock fragments of varied texture, in part glassy. Opaque iron oxides are subordinate constituents, olivine and hornblende occur in trace amounts in some sherds, and quartz occurs in minor amounts in most sherds, but all sherds lack potash feldspar in petrographically detectable amounts. This composition is markedly more restricted and in part qualitatively different from that of the exotic temper.

The Marquesas are a typical intraoceanic archipelago composed of eroded volcanoes of alkaline olivine basalt and basanite with minor trachytic differentiates exposed locally (*7*). To avoid destruction of the few sherds ever found in the Marquesas, we used a special technique, developed by R. V. Laniz at Stanford University, for preparing thin sections. Instead of sawing sherds, Laniz merely took scrapings from the least valuable edges, then impregnated the scrapings with epoxy and ground them. Although the texture of the paste cannot be observed in this fashion, mineral grains generally

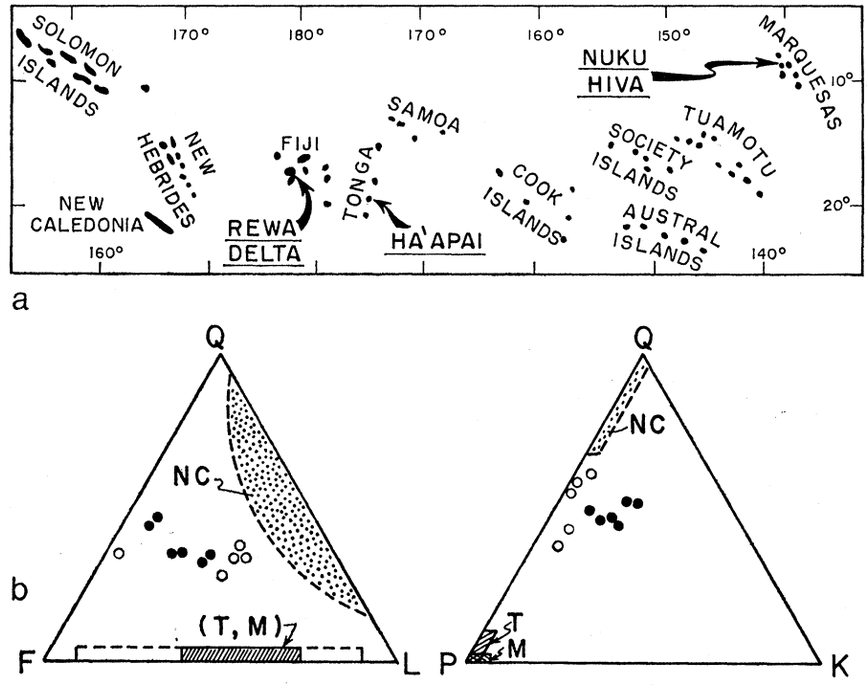

Fig. 1. (a) Sketch map showing locations of sites from which sherds of Table 1 were collected in relation to various island groups as discussed in the text. (b) Triangular diagrams showing relative proportions of certain categories of sand grains in tempers discussed: (left) quartz (*Q*), feldspars (*F*), and polycrystalline lithic (*L*) fragments (of fine-grained rocks); (right) quartz (*Q*), plagioclase (*P*), and alkali (potash) feldspar (*K*). Closed circles represent temper sands of Table 1. Open circles represent mean values for other volcano-plutonic orogen tempers from Fiji (*9*). Stippled areas indicate fields (our unpublished data) for quartzose temper sands in sherds from New Caledonia (*NC*). Shaded bars indicate schematically the fields for andesitic arc tempers from Tonga (*T*) and oceanic basalt tempers from the Marquesas (*M*); the dashed bar on the left indicates the approximate additional range known for similar tempers elsewhere (note, however, that quartz is wholly lacking in oceanic basalt tempers). Quartzose tempers from New Caledonia are distinctive from those of Fiji in that rock fragments are mainly metasedimentary rather than volcanic.

Table 1. Compositions of closely comparable tempers in selected prehistoric potsherds from Fiji, Tonga, and the Marquesas. Results are given as percentage frequencies of sand grain types as determined by transverse counts of N grains in thin section; identification was aided by feldspar staining (*15*). Samples 24-2 and 24-3 were collected at the surface at Nasilai, Rewa Delta, Viti Levu, Fiji, by E. Shaw. Sample D4529-1 from Tungua, Ha'apai, Tonga, was selected by R. Shutler, Jr., from the collection of A. L. Kaeppler at the Bernice P. Bishop Museum, Honolulu. Samples M-23b and M-23c from Ha'atuatua, Nuku Hiva, Marquesas, were collected by Y. H. Sinoto from the surface at Location M, Ha'atuatua; they were loaned by the Bishop Museum. Sample 550 was collected by R. C. Suggs at site Ha'a-1 and loaned by the American Museum of Natural History, New York. A trace amount of biotite mica was found in samples 24-3, D4529-1, and 550.

Sand grain type	Percentage of sand grain type in sample from					
	Fiji		Tonga	Marquesas		
	24-2 $N = 403$	24-3 $N = 475$	D4529-1 $N = 335$	M-23b $N = 280$	M-23c $N = 158$	550 $N = 160$
Plagioclase	25	26	21	23	26	22
Potash feldspar	7	11	11	17	15	19
(Total feldspar)	(32)	(37)	(32)	(40)	(41)	(41)
Quartz	31	31	28	43	33	42
(Quartz + feldspar)	(63)	(68)	(60)	(83)	(74)	(83)
Clinopyroxene	3	4	5	1	1	1
Hornblende	4	6	6	5	2	4
Epidote	2	2	1	2	4	2
Opaque oxides	1	1	4	1	1	2
(Total ferromagnesian)	(10)	(13)	(16)	(9)	(8)	(9)
Igneous rocks	23	16	20	6	15	6
Metasedimentary rocks	4	3	4	2	3	2
(Total rock fragments)	(27)	(19)	(24)	(8)	(18)	(8)

are not broken, although some breakage of polycrystalline rock fragments may account for somewhat lower percentages reported for that component. Of five sherds studied, one from Ua Huka and one from Nuku Hiva contain indigenous oceanic basalt tempers composed dominantly of pyroxene and opaque iron oxide mineral grains. Subordinate volcanic rock fragments of basalt as well as minor plagioclase and rare olivine grains are also present. To our knowledge, no quartz has been reported from any rocks in the Marquesas, and the exotic temper also contains other foreign elements.

In Fiji, the Rewa River drains a deeply dissected and geologically complex highland in the interior of Viti Levu. Varied rock types are exposed within the drainage basin (*8*): intrusives ranging in composition from gabbroic to granitic rocks, volcanics ranging in composition from basaltic lavas to felsitic tuffs, sedimentary sequences of varied grain size and provenance, and metamorphics of both metavolcanic and metasedimentary types. The diversified composition (Table 1) of the temper sands in the two sherds found embedded in deltaic deposits at Nasilai near the river mouth is expected for detritus eroded from the Rewa drainage, and these tempers have been interpreted as indigenous to the Rewa Delta (*9*).

The similarity of the exotic Tongan and Marquesan tempers to the indigenous Nasilai temper in Fiji extends beyond the quantitative correspondence in proportions of grain types to close qualitative similarities for each grain type as well. In all six sherds studied (see Table 1): (i) quartz includes both ordinary plutonic varieties with vacuoles and clear, unstrained volcanic types; (ii) plagioclase includes a range of compositions from calcic or intermediate to albitic, the latter dusty, as well as both zoned and unzoned plutonic and volcanic types; (iii) two feldspars are consistently present in significant amounts; (iv) clinopyroxene is mainly green augite; (v) amphibole is mainly green-brown hornblende; (vi) epidote is commonly aggregated; (vii) sedimentary and metasedimentary rock fragments include chert or metachert on the one hand and quartz-mica schist or hornfels on the other; and (viii) igneous rock fragments include a whole spectrum of types from granular granitic and intermediate plutonic varieties occurring as aggregates of a few discrete grains, through microgranular hypabyssal varieties presumably from dikes and sills, to microcrystalline volcanic varieties including mainly fragments with felsitic texture, but some microlitic (pilotaxitic to hyalopilitic) grains as well. No grain types, however subordinate, appear to be unique to any one of the three sets of sherds.

Moreover, several diagnostic rock types, present as rock fragments in the exotic tempers, are wholly foreign to Tonga or the Marquesas but present in Fiji: (i) quartzo-feldspathic aggregates representing pieces of hypidiomorphic granular granite rock containing both quartz and microcline in two sherds from the Marquesas, (ii) a felsite fragment with quartz phenocrysts and an impure indurated quartzite fragment in the other sherd from the Marquesas, and (iii) a fragment of quartz-mica schist in the sherd from Tonga.

Suggs (*10*) places the exotic Marquesan sherds in his Settlement Period (150 B.C. to A.D. 100), during which the material culture was Melanesian in character, as migration from Fiji would allow. The presence of some indigenous pottery in the Marquesas suggests that an attempt was made to carry on the pottery-making tradition locally for some time. Sinoto (*11*) has reinterpreted Suggs' material, terming the initial settlement, to which the exotic pottery belongs, as Phase I and dating it as A.D. 300 to 600. If the Marquesas were the end of the line for the Fijian-made pottery, Tungua in Tonga was presumably an intermediate stopover (Fig. 1a). Since the exotic Tungua sherd came from the surface, there is no way of dating it.

The history of the Fijian pots that arrived in the Marquesas by A.D. 300 is unknown. The group carrying them was probably only one of many such groups arriving in Tonga from Fiji over a long period of time. The ceramic history of Tonga belongs to the tradition of Lapita pottery, both decorated and undecorated. We could accept the finding of Melanesian and Lapita sherds together in Tonga as evidence of a group of Melanesians who left Fiji and made a landfall among Lapita people of Tungua, but were forced for one reason or another to take to the sea again and became the discoverers of the Marquesas. Alternative situations are possible, including a direct voyage from Fiji to the Marquesas. It is also conceivable that a group from Fiji landed on Tungua and traded some pots to people who went to the Marquesas, or that people from Tungua had gone to Fiji and brought back the pots that were eventually taken to the Marquesas. There is also the possibility that the movement from Fiji or Tonga to the Marquesas was via Samoa (Fig. 1a). However, Samoan pottery of comparable age is plain, but different from the Marquesan sherds. A straight line from Tonga to the Marquesas would also be within sight of the Society Islands.

Lapita pottery-making people were in Tonga by 1140 B.C. (*12*) and in Samoa perhaps as early as 800 B.C. (*13*). If we accept A.D. 300 as about the time that our exotic sherds (in the form of pots) arrived in the Marquesas, then the people carrying them were probably too late in time to be proto-Polynesians. The early Lapita people of Tonga and Samoa were no doubt in this stage of development, but by A.D. 300 the cultures of Tonga and Samoa were Polynesian. The implication for Polynesian origins is a continuing infusion of Melanesians into Polynesia from Fiji (and perhaps elsewhere), and supports indirectly the suggestion that Fiji was the homeland of the proto-Polynesians (*14*). If our conclusions are valid we have, in any case, demonstrated the movement of pottery from Fiji to both eastern and western Polynesia at an early date.

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2 May 1974

Lateral Diffusion of Visual Pigment in Photoreceptor Disk Membranes

Abstract. *Visual pigment molecules are found to move transversely, but not longitudinally, in both rod and cone outer segments of mud puppy and frog. This is consistent with the idea that they are immersed in a two-dimensional fluid disk membrane. The diffusion coefficient for the motion is about* 5×10^{-9} *square centimeters per second at 20°C, corresponding to a root-mean-square molecular displacement of 0.3 micrometer in 1 second.*

A variety of evidence supports the concept of a two-dimensional fluid mosaic structure for biological membranes (*1*). In particular, rhodopsin has been shown to exhibit fluid-like behavior in retinal rod disks (*2*). A quantitative measure of fluidity in several artificial and natural membranes has been made through the use of spin-labeled lipid probes. Values of the lateral diffusion coefficient estimated in this way range from 1×10^{-8} to 6×10^{-8} cm^2/sec (*3*). Microscopic observations of the spread of fluorescent labels attached to proteins in two types of biological membrane yield values for these proteins of 5×10^{-11} to 2×10^{-9} cm^2/sec (*4*). In this report, we describe evidence for lateral diffusion of visual pigment in rod disk membranes from experiments we did but could not interpret in 1964 (*5*), together with new work that provides a value for the diffusion coefficient (*6*).

Rhodopsin is a hydrophobic glycoprotein with a molecular weight of 36,000, which is known to be embedded in disk membranes of rod outer segments (ROS) (Fig. 1a). The diameters of the ROS range up to 8 μm in frog (*Rana pipiens*) and up to 13 μm in mud puppy (*Necturus maculosus*). Because of their great size and accessibility, the ROS can be readily isolated and visualized in the light microscope. Techniques have been developed for directly measuring absorption spectra of small regions of these organelles. Measuring and reference microbeams as small as 1 by 5 μm are projected onto a microscope stage and aligned with the ROS before being sent on to a photomultiplier and associated electronics for detection.

In our early work, with a split-beam microspectrophotometer of this general design, we found that we could determine visual pigment spectra in single outer segments if the measuring light was made sufficiently dim to limit loss of the photosensitive pigment by bleaching during the measurement (*5*). We could also determine the photosensitivity of the visual pigment by measuring the rate of loss of absorption in beams of higher intensity and constant wavelength. We were surprised to find that, although the bleaching rates of rods and cones 1 to 2 μm in diameter were nearly identical in beams 1 to 2 μm wide, the bleaching rate of larger amphibian rods was much slower in these beams. Moreover, the rate increased in direct proportion to

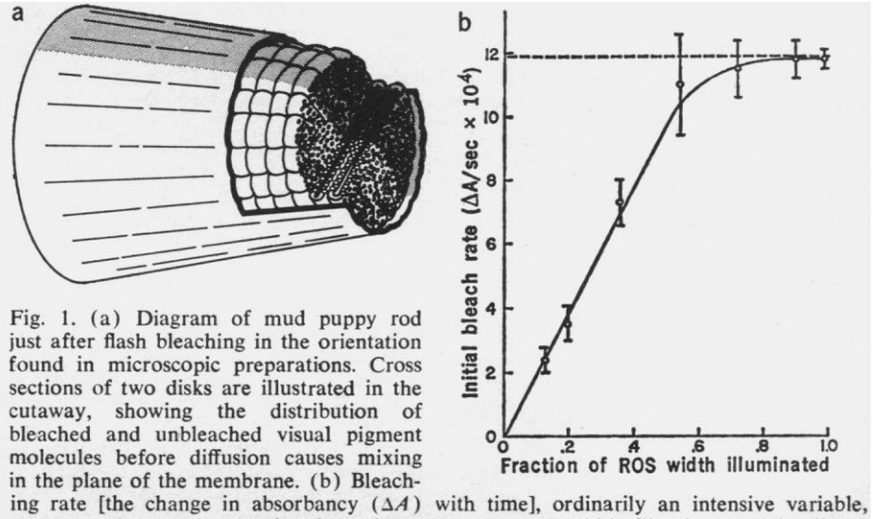

Fig. 1. (a) Diagram of mud puppy rod just after flash bleaching in the orientation found in microscopic preparations. Cross sections of two disks are illustrated in the cutaway, showing the distribution of bleached and unbleached visual pigment molecules before diffusion causes mixing in the plane of the membrane. (b) Bleaching rate [the change in absorbancy (ΔA) with time], ordinarily an intensive variable, seems to depend on the fraction of mud puppy rod width illuminated. The linear dependence is due to rapid diffusional redistribution of unbleached molecules. Molecules are bleached by the measuring beam. The dotted line is for glutaraldehyde-fixed cells.