Reports

Neodymium and Strontium Isotope Evidence for Crustal Contamination of Continental Volcanics

Abstract. Combined neodymium and strontium isotope studies on Tertiary volcanics from northwest Scotland indicate that their parental mantle isotopic compositions have been substantially modified in many instances by contamination with the Precambrian continental crust through which they were erupted. The occurrence of samarium-neodymium and rubidium-strontium "pseudoisochrons" of different ages in these contaminated continental volcanics indicates that they are artifacts of the contamination processes and have no temporal significance with respect to mantle fractionation events.

In view of the current active investigations of mantle differentiation and continental growth it is important to establish the extent to which the isotope and trace element characteristics of continental volcanics are inherited from the mantle or imposed through crustal contamination (1). It has been observed in several Sr isotope studies that certain continental volcanic sequences display positive correlations between 87Sr/86Sr and 87Rb/86Sr, simulating poorly defined isochrons that imply ages significantly greater than the ages of eruption (2). Proponents of crustal contamination (3)have interpreted such correlations as the result of mixing continental crust with mantle-derived magmas in varying proportions. However, recent papers by Brooks et al. (4) and Brooks and Hart (5) suggest that these "pseudoisochrons" reflect ancient differentiation events that produced variably enriched subcontinental mantle. With recent developments in Nd isotope geochemistry (6-9) it has now become possible to make a clear distinction between enriched mantle and at least some types of continental crust material. If crustal contamination is of negligible importance in continental volcanics and Rb-Sr isotopic variations provide information about the timing of mantle differentiation events, then it follows that compatible chronological information should be provided by complementary Sm-Nd isotopic studies.

The initial ¹⁴³Nd/¹⁴⁴Nd ratios of Archaean igneous and metaigneous rocks have demonstrated that the bulk earth has a Sm/Nd ratio indistinguishable from 0.31 (7, 10), the cosmic abundance ratio (11). The present ¹⁴³Nd/¹⁴⁴Nd ratio of ma-SCIENCE, VOL. 202, 17 NOVEMBER 1978 terial with the chondritic Sm/Nd ratio is known with high precision from measurements on meteorites (12, 13). This, together with the correlation of ¹⁴³Nd/ ¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr in oceanic volcanics (14), allows the present-day ⁸⁷Sr/⁸⁶Sr ratio and, in turn, the Rb/Sr ratio of the bulk earth to be inferred (15, 16). The range of ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios in recent oceanic volcanics is compared with this bulk earth Rb/Sr and Sm/Nd evolution in Fig. 1 (17).

The continental crust is a highly differentiated body. Granulite facies rocks stable in the lower crust generally have much lower contents of heat-producing elements (K, U, and Th) as well as other incompatible elements such as Rb than upper crustal rocks (18). Thus the Rb/Sr and ⁸⁷Sr/⁸⁶Sr ratios of granulite facies rocks are more akin to those of the mantle than those of the upper crust. In contrast, there is no evidence for significant fractionation of the Sm/Nd ratio between the lower and upper crusts, which therefore have similar ¹⁴³Nd/¹⁴⁴Nd ratios. This aspect of crustal differentiation in the continents is well illustrated by a Rb-Sr and Sm-Nd isotopic study of the Precambrian Lewisian basement in northwest Scotland (19). The differential isotopic evolution of the Lewisian granulite and amphibolite facies gneisses is compared with the predicted evolution of the bulk earth in Fig. 2. Because of these large differences in Sr and Nd isotopic characteristics, contamination of basalts by either granulite or amphibolite facies basement should be readily recognizable.

The work reported here was centered on the Tertiary igneous province of northwest Scotland (20-22). The ¹⁴³Nd/ ¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios and the Rb, Sr, Sm, and Nd contents were measured on a series of fresh lavas from the islands of Skye, Mull, Muck, and Eigg (Table 1), using previously described analytical techniques (23). The ⁸⁷Sr/⁸⁶Sr and ¹⁴³Nd/ ¹⁴⁴Nd ratios were computed for the time of eruption of the volcanics by applying a 60 million year age correction for the posteruption decay of ⁸⁷Rb and ¹⁴⁷Sm.



Fig. 1. Comparison of the development of ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr in the bulk earth, in depleted mantle as determined from oceanic volcanics, and in the granulite and amphibolite facies components of continental crust in northwest Scotland. The bulk earth evolution is represented by the solid line from T = 4.55 to T = 0 gigayears (*Gy*). Depletion of the suboceanic mantle has resulted in recent oceanic volcanics with respectively higher and lower ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios than the present bulk earth composition. The continents have formed as highly differentiated bodies, as exemplified by the present isotopic variations within the Lewisian basement, which formed at about 2.9 gigayears.

Initial ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios are compared in Fig. 2 with the range of values reported for unaltered oceanic volcanics (6-9) and the inferred range for suboceanic upper mantle 60 million years ago. Whereas most of the Mull volcanics have ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios consistent with the trend defined by the oceanic basalts and may therefore be derived from a source with a similar evo-

lutionary history, many of the basalts from Skye, Muck, and Eigg do not plot on this trend. Their deviation requires either that they were generated from a mantle source in which Rb/Sr and Sm/ Nd did not fractionate coherently, or that they have been contaminated with continental crust.

Table 1. Rubidium-strontium and samarium-neodymium data from Tertiary lavas of northwest Scotland.

Sam- ple	Rock type	Rb (ppm)	Sr (ppm)	⁸⁷ Sr/ ⁸⁶ Sr* †	Sm (ppm)	Nd (ppm)	¹⁴³ Nd/ ¹⁴⁴ Nd*
				Skye			
P1	Basalt	7.73	353	0.70351 ± 5	4.69	19.2	0.51251 ± 2
P2	Basalt	8.20	356	0.70361 ± 4	4.42	22.3	0.51248 ± 3
P3	Basalt	4.11	436	0.70353 ± 5	4.84	19.9	0.51251 ± 2
P4	Basalt	6.65	374	0.70393 ± 5	4.46	18.2	0.51244 ± 3
P5	Basalt	5.23	404	0.70369 ± 4	3.92	17.5	0.51205 ± 2
P6	Basalt	6.29	482	0.70378 ± 6	5.71	26.5	0.51262 ± 2
				Mull			
ML1	Basalt	4.38	763	0.70314 ± 4	7.50	29.2	0.51293 ± 2
ML3	Basalt	8.78	1096	0.70277 ± 4	11.0	51.4	0.51307 ± 2
ML4	Basalt	9.20	296	0.70339 ± 4	3.98	14.7	0.51282 ± 2
ML5	Basalt	3.42	378	0.70315 ± 5	4.63	15.8	0.51287 ± 2
ML6	Basalt	6.22	562	0.70302 ± 4	4.90	22.1	0.51184 ± 2
				Muck			
M9	Basalt	51.8	323	0.70549 ± 4	12.1	62.9	0.51157 ± 2
M11	Basalt	5.45	428	0.70441 ± 4	7.68	27.5	0.51237 ± 3
M17	Basalt	3.46	475	0.70320 ± 6	4.55	22.3	$0.51248~\pm~3$
				Eigg			
E3	Basalt	55.6	719	0.70618 ± 4	14.3	84.5	0.51162 ± 2
E7	Basalt	4.69	262	0.70483 ± 5	4.46	15.9	0.51267 ± 2
E10	Basalt	8.24	318	0.70493 ± 4	3.72	15.2	0.51232 ± 2
E26	Felsite	95.6	34.5	0.71261 ± 6	8.41	45.3	0.51146 ± 2

*Initial ratios were computed for 60 million years ago. Errors are 2 standard errors of the mean based on within-run precision. \uparrow Normalized to the Eimer and Amend SrCO₃ ratio of 0.70800; the measured mean in this laboratory was 0.70808.



Fig. 2. Comparison of the ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios in Tertiary plateau lavas of northwest Scotland and in recent oceanic volcanics. Solid lines enclose 90 percent of the isotopic ratios determined in recent oceanic volcanics. Arrows indicate the present bulk earth values (*15*, *16*). Initial ratios of the Tertiary volcanics computed for 60 million years ago have been plotted, and the dashed line represents the hypothetical values of the oceanic volcanics at this time. Four of the Mull samples fall within these 90 percent boundaries, which indicates that they and the oceanic volcanics are derived from similarly depleted mantle. However, most of the other samples fall well below this trend, with lower ¹⁴³Nd/¹⁴⁴Nd ratios, indicating a more complex origin.

It is convenient to compare the isotopic composition of the volcanics with the inferred bulk earth composition using the parameters ΔND and ΔSR . These Δ values are defined as the percentage of deviations of the time-integrated parentdaughter ratios from the bulk earth values (24). The Δ SR and Δ ND values computed for the Tertiary volcanics are compared with those of Recent oceanic basalts in Fig. 3. It should be noted that in this diagram the origin $(\Delta SR = \Delta ND)$ = 0) represents the bulk earth composition (15). Whereas oceanic volcanics primarily occupy the $-\Delta SR/+\Delta ND$ quadrant and are derived from source regions with time-integrated Rb/Sr and Sm/Nd ratios that are respectively lower and higher than the bulk earth values, the Tertiary volcanics also occupy the two $-\Delta ND$ quadrants. The source regions of these volcanics therefore have time-integrated Sm/Nd ratios lower than those of the bulk earth. On the other hand, the Δ SR values of these volcanics are both positive and negative, implying sources with time-integrated Rb/Sr ratios both higher and lower than the bulk earth values. The deviation of Δ SR and Δ ND for these lavas from those of oceanic volcanics is the result of either crustal contamination or derivation from enriched mantle.

To distinguish between these possibilities, the Δ ND and Δ SR values for the Skye, Mull, Muck, and Eigg lavas are compared with the granulite and amphibolite components of the Lewisian basement and presumed modern seawater in Fig. 3. Seawater contains a large component of continent-derived Sr and Nd (25), and its location in the $+\Delta SR/$ $-\Delta ND$ sector requires that average continental crust also plot in this sector, although almost certainly not in the same position. Since Rb/Sr and Sm/Nd fractionation is qualitatively similar in the production of both continental crust and enriched mantle, and thus complementary to that in the depleted mantle sampled by oceanic volcanism, the enriched mantle will lie somewhere in the $+\Delta SR/-\Delta ND$ quadrant. Continental volcanics with $+\Delta SR$ and $-\Delta ND$ values, which in the case of Fig. 3 include some of the Scottish Tertiary basalts and Roccamonfina volcanics of the Italian province, are subject to ambiguous inter-SCIENCE, VOL. 202 pretations. They may be the uncontaminated products of enriched mantle with $+\Delta SR$ and $-\Delta ND$ values. If contamination is present, the Δ SR and Δ ND values of the primary mantle-derived magma cannot be readily specified. In marked contrast, the Tertiary lavas that have $-\Delta SR$ and $-\Delta ND$ values are not subject to the same ambiguous interpretations. They can only be generated by contamination of mantle-derived magmas with Lewisian granulite facies basement.

Lead isotope analyses of Skye basalts (26) have demonstrated the existence of a Pb component with an isotopic composition indistinguishable from that of Lewisian basement. In view of these results and the Nd and Sr isotope data presented above, there is now no doubt that some of the Tertiary volcanics of northwest Scotland have been markedly contaminated by the Lewisian granulite facies basement through which they were erupted, and it also seems probable that others have been contaminated by Lewisian amphibolite facies basement. Simple mass balance calculations indicate that between 5 and 50 percent of the Sr and Nd in the various lavas has been derived from the Lewisian basement. Since the most contaminated lavas do not have SiO₂ contents commensurate with the bulk assimilation of a corresponding proportion of Lewisian basement, it appears that Sr and Nd were extracted from basement rocks preferentially with respect to SiO_2 (27). This lends support to the concept of contamination by partial melts of basement rocks in at least some cases.

The origin of acid and intermediate Tertiary rocks occurring in intrusive complexes in northwest Scotland has been a much debated question and one closely related to the contamination processes discussed above. The acid rocks have been variously interpreted as crystallization differentiation products of basaltic magmas by Moorbath and Bell (21), as partial melts of Lewisian basement, or as mixtures of both (28). The marked similarity of the Pb and Sr isotope compositions of Tertiary acid intrusives and Lewisian basement gneisses led Moorbath and Welke (26) to reject the crystallization differentiation model in favor of an origin by partial melting of Lewisian basement. The unusually low ¹⁸O/¹⁶O ratios of many of the acid rocks (29) has provided a clear demonstration of large-scale interactions between acid rocks and heated meteoric waters. This led Taylor and Forrester (29) to suggest that Pb and Sr may have been exchanged between the acid rocks and the Lewisian 17 NOVEMBER 1978

basement. The ¹⁴³Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios and the Rb, Sr, Sm, and Nd contents have been measured on a series of Skye Tertiary intrusive rocks (Table 2) (30), including four granites, one gabbro, and one intermediate marscoite (31). The

 Δ ND and Δ SR values for these samples are compared with those of the Lewisian basement in Fig. 3. It is clear from these relationships that the intrusive rocks were not derived entirely from either a mantle source or the Lewisian amphibo-



Fig. 3. Comparison of the ΔND and ΔSR parameters (24) in the Tertiary volcanics, Lewisian basement, Roccamonfina volcanics (8), and seawater (25) relative to the bulk earth composition. The range of oceanic volcanics is represented by the 90 percent boundaries.



diagram for the Tertiary volcanics of northwest Scotland. (a) All samples are plotted. Overall there is a significant correlation, but there is little internal correlation in the Skye and Mull samples. (b) Averages for each island are plotted together with the Mull averages of Beckinsale et al. (22), marked B. With the exception of the Muck average there is a good



correlation corresponding to an age of about 1.6 gigayears. The Muck average is strongly influenced by the exceptionally high Rb/Sr sample M9. This pseudoisochron is composed of averages containing lavas contaminated by Lewisian basement. Fig. 5 (right). Samariumneodymium evolution diagram for the Tertiary volcanics and intrusives of northwest Scotland. (a) All samples are plotted. The Skye and Mull samples do not reveal internal correlations, although overall there is a significant positive correlation. (b) Averages of the samples from each locality are plotted and show a strong positive correlation corresponding to an age of about 6.2 gigayears. This age is significantly different from that in the Rb-Sr evolution diagram (Fig. 4). This pseudoisochron is composed of uncontaminated lavas, lavas contaminated by Lewisian basement, and intrusives containing large proportions of Lewisian amphibolite facies material.

Table 2. Rubidium-strontium and samarium-neodymium data from Skye intrusives.

Sam- ple	Rock type	Rb (ppm)	Sr (ppm)	⁸⁷ Sr/ ⁸⁶ Sr* †	Sm (ppm)	Nd (ppm)	¹⁴³ Nd/ ¹⁴⁴ Nd*
91	Granite	167	79.8	0.71156 ± 5	7.67	37.5	0.51149 ± 2
163	Granophyre	137	90.7	0.71436 ± 5	8.65	50.3	0.51129 ± 3
GL	Epigranite	105	105	0.70889 ± 4	8.14	44.5	0.51177 ± 2
B905	Marsco granite	125	90.3	0.71073 ± 4	17.4	76.5	0.51168 ± 1
B903	Marscoite	37.1	279	0.70981 ± 4	12.3	55.0	0.51169 ± 2
B898	Marsco gabbro	37.8	330	0.71027 ± 8	10.9	47.9	0.51167 ± 3

*Initial ratios were computed for 55 million years ago. Errors are 2 standard errors of the mean based on within-run precision. †Normalized to the Eimer and Amend SrCO₃ ratio of 0.70800.

lites; approximately 50 to 75 percent of the Nd and Sr in these intrusive rocks is derived from the amphibolites, while the remainder is of mantle derivation. Although the end-differentiation products are much more enriched in silica than the basalts, these data provide a clear example of interaction between mantle-derived basic magma and Lewisian amphibolite facies basement. A felsite from Eigg (Table 1) has Δ SR and Δ ND values similar to those of the Skve intrusives (Fig. 3). It thus seems that its parental magma was also a mixture of mantle-derived magma and a large proportion of Lewisian amphibolite basement.

Contamination of continental basalts, such as those in the Tertiary lavas of northwest Scotland, obscures the primary mantle-derived Nd and Sr isotope composition of the basalts. Four of the Mull samples have a Nd and Sr isotope composition similar to that of oceanic basalts, and these lavas must have experienced minimal crustal contamination. Furthermore, they indicate the presence of depleted mantle at the initial opening of the North Atlantic. Although the remainder of the samples have evidently been contaminated by Lewisian basement, it is conceivable that their parental magmas were also derived from depleted mantle. The episodic nature of mantle evolution inferred from pseudoisochrons implies that any interaction of mantle-derived magmas with the continental crust is negligible. Brooks and Hart (5) claimed that the average Rb/Sr and 87Sr/ ⁸⁶Sr ratios of lavas from different provinces provide information about the timing of a mantle-wide fractionation event.

To further examine the effects of crustal contamination on Rb-Sr systematics of basic volcanics, the averaging procedure of Brooks and Hart (5) has been applied to the contaminated Tertiary basalts discussed above. Although the Skye and Mull samples exhibit poor internal correlations, the averages from each island (with the exception of Muck) are remarkably well correlated on a Rb-Sr evolution diagram (Fig. 4). The bestfit line to these averages corresponds to an age of about 1.6 gigayears, coincidentally the same age obtained by Brooks and Hart (5) for Gondwanaland volcanics. This pseudoisochron is, however, an artifact of mixing between continental crust and mantle-derived magmas and does not provide meaningful information concerning mantle evolution. The same procedure has been adopted for the Sm-Nd isotope data, and these are presented on a Sm-Nd evolution diagram in Fig. 5. Also included in this diagram is the average value for the Skye intrusives. Again, the averages form a pseudoisochron that corresponds to an age of about 6.2 gigayears. As with the covariation of 87Sr/ ⁸⁶Sr and Rb/Sr, this pseudoisochron is formed by volcanics and intrusives that contain varying proportions of Lewisian basement and does not have any significance with respect to mantle evolution. The occurrence of pseudoisochrons in these contaminated volcanics should serve as a caution against the indiscriminate use of isotopic data from continental volcanics. Although enriched mantle may exist beneath the continents, it is questionable whether all the data utilized by Brooks and Hart (5) are actually indicative of such, rather than of contamination processes.

In summary, the primary Nd and Sr isotope compositions of some of the continental lavas forming part of the Tertiary igneous province in northwest Scotland have been substantially modified by contamination with the Precambrian Lewisian basement. Because of the similar Sm/Nd ratios but markedly lower Rb/Sr ratio of the Lewisian granulites compared with the amphibolites, it has proved possible to distinguish between basalt magmas contaminated by Lewisian granulites and those contaminated by lower-grade amphibolites.

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References and Notes

- 1. A basic difficulty in assessing possible crustal contamination is that of finding geochemical parameters that can be used as tracers to distinguish mantle and crustal components in volcan-ics. Strontium-87 is concentrated in continental crust relative to the mantle, and crustal con-tamination of mantle-derived magmas is predict-ed to produce anomalously high ⁸⁷Sr/⁸⁶Sr ratios tamination of mantle-derived magmas is predict-ed to produce anomalously high ⁸⁷Sr/⁸⁶Sr ratios in the erupted basalts. The ⁸⁷Sr is produced by the β -decay of ⁸⁷Rb, which has a decay constant $\lambda = 1.42 \times 10^{-11}$ year⁻¹. The isotopic ratio ⁸⁷Sr/⁸⁶Sr ratio in the system. Similarly, ¹⁴³Nd is produced by the α -decay of ¹⁴⁷Sm ($\lambda = 6.54 \times 10^{-12}$ year⁻¹) and the ¹⁴⁸Nd/¹⁴⁴Nd is a function of the time-integrated ¹⁴⁷Sm/¹⁴⁴Nd. R. J. Pankhurst, J. Geol. Soc. London **134**, 255
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 The ¹⁴8Nd/¹⁴⁴Nd and ⁸⁷Sr/⁸⁶Sr ratios in recent, unaltered oceanic volcanics show a strong nega-
- tive covariation (6-9). In mantle regions rela-tively low ⁸⁷Sr/⁸⁸Sr ratios are accompanied by relatively high ¹⁴³Nd/¹⁴⁴Nd ratios and vice versa. Because ${}^{87}Sr$ and ${}^{149}Nd$ are the daughter prod-ucts of ${}^{87}Rb$ and ${}^{149}Nd$ are the daughter prod-ucts of ${}^{87}Rb$ and ${}^{147}Sm$, respectively (1), this co-variation requires that Rb/Sr and Sm/Nd have fractionated coherently during mantle differentiation
- 15. Geochemical parameters for the bulk earth [as used by Carter *et al.* (8) and O'Nions *et al.* (16)] are Rb/Sr \approx 0.031; present-day ⁸⁷Sr/⁸⁶Sr \approx 0.7047; initial ⁸⁷Sr/⁸⁶Sr \approx 0.69898 [D. A. Papa-Sci Lett. 5, 361 (1969)]; Sm/Nd = 0.308 [A. Ma-suda, N. Nakamura, T. Tanaka, *Geochim. Cos*-suda, N. Nakamura, T. Tanaka, *Geochim. Cos*mochim. Acta 37, 239 (1973)]; present-day $^{143}Nd/^{144}Nd = 0.51265$; initial $^{143}Nd/^{144}Nd =$
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- The Lewisian basement was stablized approxi-19. mately 2.9 gigayears ago and consists of both granulite and amphibolite facies gneisses. Sama-rium-neodymium dating of Lewisian amphibo-

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lite and granulite facies rocks has yielded an age of 2.92 ± 0.05 gigayears (mean ± 2 standard deviations) (P. J. Hamilton, S. R. Carter, N. M. Evensen, R. K. O'Nions, J. Tarney, in preparation). The granulites have very low Rb/Sr ratios (0.005 to 0.009) and Sm/Nd ratios less than 0.31, whereas the amphibolites facies have similar Sm/Nd ratios but much higher Rb/Sr ratios (0.07) 0.0.19)

- The North Atlantic Tertiary province was formed during the initiation of sea-floor spread-20. ing between Greenland and Eurasia and com-prises plateau lavas and central intrusive complaces of granite, gabbro, and peridotite. Lavas cover approximately 2000 km² and have a present stratigraphic thickness of 2000 m in Mull and about 1000 m in Skye. Alkali olivine basalts pre dominate but are associated with tholeiites, ha waiites, mugearites, and trachytes. Recent K-Ar studies on samples from Mull indicate a mean extrusion age of about 60 million years for the lavas of this province (22). The youngest reliable age obtained on intrusive centers in Skye by the Rb-Sr method is 55 million years (21). Samples were collected from areas outside the known zones of hydrothermal alteration
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 The Rb, Sr, Sm, and Nd were separated from the sep
- spiked and unspiked sample portions by ion ex-change techniques. Concentrations and isotopic ratios were determined on a Vacuum Generators Micromass 30. The chemical and instrumental techniques have been described previously (9). The Δ parameter (for Sm-Nd systematics) is de-24

fined by

$$\Delta ND(\%) = \frac{R_{\text{single stage}} - R_{\text{bulk earth}}}{R_{\text{bulk earth}}} \times 10^2$$
where $R = {}^{147}\text{Sm}/{}^{144}\text{Nd}$ and
 ${}^{147}\text{Sm}/{}^{144}\text{Nd}_{\text{single stage}} =$

$$\frac{{}^{143}\text{Nd}/{}^{144}\text{Nd}_{\text{measured}} - 0.50682}{\exp(\lambda^{147} \times T) - 1}$$
where $T = 4.55$, significant the measured

The parameter gigayears.

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- weathering and alteration processes (references below) and the markedly different Nd isotope compositions of Lewisian gnesisses and the least-contaminated Tertiary basic volcanics suggest that Nd isotope studies may aid in the reso-lution of these various viewpoints concerning lution of these various viewpoints concerning the origin of the acid intrusives [A. G. Herrman, M. J. Potts, D. Knake, Contrib. Mineral. Petrol.
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- Marscolle is a hybrid, intermediate, intrusive rock thought to be the result of mixing between basic and acidic magmas [L. R. Wager, E. A. Vincent, G. M. Brown, J. D. Bell, *Philos. Trans. R. Soc. London Ser. A* 257, 273 (1965)].
 W. I. Ridley and J. Tarney kindly supplied some of the samples. G. Weisselman and R. Cohen are thanked for their technical help and J. Tar-ney for valuable discussions. Supported by NSE
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Shark Skin: Function in Locomotion

Abstract. Hydrostatic pressure under the skin of sharks varies with swimming speed. Stress in the skin varies with the internal pressure, and the skin stress controls skin stiffness. Locomotory muscles attach to the skin which is thus a whole-body exotendon whose mechanical advantage in transmitting muscular contraction is greater than that of the endoskeleton.

Sharks, we find, are supported in part by hydrostatic pressure. Their internal pressure increases more than tenfold from slow to fast swimming. This increase in pressure causes the skin to become stiffer. Because the skin shortens and lengthens with the muscles when the fish bends and because the muscles are as securely attached to the skin as they are to the backbone, the skin acts as an external tendon by transmitting muscular force and displacement to the tail.

We measured internal hydrostatic pressure of 7 to 14 kN m⁻² just under the skin in a lemon shark (Negaprion brevirostris, 87 cm long) resting on the tank floor (1). While swimming slowly, the shark bent its body in left and right bends of 38 cm radius of curvature, and the pressure varied between 20 and 35 kN m⁻². During bursts of fast swimming, tighter bends of 20 cm radius were produced, and pressure rose to 200 kN m^{-2} once each tail beat—that is, the pressure rose on both concave and convex sides of the fish.

The cause of the pressure increase is unknown, and it may be derived from more than one source: change in muscle surface area compared to skin area or an active increase in blood pressure. The latter might be bought about by the posterior displacement of blood from the cardinal sinuses by contraction of the constrictor muscles that encircle the body behind the head (2).

The white, inner, thickest layer of shark skin is a sheath of fabric cut on the bias: it consists of layers of collagen fibers that lie in helices around the shark's body (3). In alternating layers, the fibers describe right- and left-handed helices. The angle these helices make with the long axis of the shark is called the fiber angle, and in all selachians that we studied (4) and studied by others (3), it varies between 50° and 70° between the pectoral and anal fins and between 45° and 50° in the thin caudal peduncle just in front of the tail (Fig. 1). Collagen fibers in shark skin, which are mechanically similar to those in mammalian tendon (5), are very stiff in tension but flexible in bending. Pressurized cylinders, such as the bodies of worms and sharks, are reinforced with helically wound collagen fibers. This allows flexibility for undula-

tion and reinforces the body wall against embolisms and bursting (6). It also prevents wrinkling on the concave side.

Hydrostatic pressure of 21 kN m⁻² in the cruising shark induces a circumferential stress of 0.3 MN m⁻² in the skin (7). When we held a constant circumferential stress of 0.3 MN m⁻² in a specimen of shark skin while pulling it longitudinally in a biaxial testing machine (8), we found (Fig. 2, lower curve) a great longitudinal extensibility of the skin. Results of an experiment in which we held circumferential stress at the fast swimming value of 2.8 MN m⁻² (Fig. 2, upper curve) show that the stress in the unstretched skin at zero extension has increased 13-fold and that a given longitudinal extension requires very much more stress than it does in the lower pressure, slower swimming situation.

The slope of such a curve at any point is a measure of the stiffness of the material under those conditions. In slowly swimming sharks, we measured ± 10 percent longitudinal and ± 3 percent circumferential extensions (9). At pressures recorded at different speeds, the stiffness of the shark skin is thus apparently 0.8 MN m^{-2} for the slowly swimming shark and 3.0 MN m^{-2} for the fast one. The area under the force-extension curve is a measure of the energy required for and recovered from skin deformation, and the area between the loading and unloading parts of the curve is a measure of the energy lost during the deformation cycle. The energy stored by the skin is much higher over the physiological range of ± 15 percent extensions occurring during fast swimming than it is over the ± 10 percent extensions occurring during slow swimming (Fig. 2). Large energy losses occur only when the skin is stretched more than 20 percent. The very small energy loss over the physiological extensions support the notion that viscous reorganization of interfiber matrix is not important in the living fish.

If the mechanical properties of shark skin were due simply to the properties of the collagen fiber array without contributions from an interfiber matrix or other morphological features, the instantaneous ratio of circumferential to longitudinal stresses at any point on the shark would be equal to the square of the tangent of the fiber angle. Such a predictive

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