ments with localized iron sources within the sediment[21,25]. This view is supported by the lack of a negative correlation between strontium and iron values, which could be predicted if recrystallization were prevalent[26].

Manganese concentrations increase progressively towards pore centres in hardground 1. This trend is associated with a change in the cathodoluminescence emission of bladed cements from nonluminescent (with some very dull luminescence) to brightly luminescent. Inclusions with seawater salinities exist in both nonluminescent and brightly luminescent crystals, indicating that the manganese trend toward pore centres may also be a result of seawater precipitation in oxic to suboxic microenvironments (probably as a result of progressive pore restriction combined with continuing decay of organic carbon). This hypothesis is supported by stable isotope data which show δ^{18}O values similar to other hardground cements but δ^{13}C values ~0.4‰ more negative. Bladed cements within hardgrounds 2 and 3 show very dull luminescence or none at all.

We measured ^{87}Sr/^{86}Sr in bladed cements from hardgrounds 1 and 3, normalizing them to a value of 0.71014 for NBS 987. Normalized values were 0.708958 for hardground 3 and 0.708970 for hardground 1 (±0.00003 at the 95% confidence level). These are very close to those previously estimated for the Late Cambrian to Early Ordovician interval[6]. Again, this is evidence that the cements have not recrystallized appreciably (within an open system) and that they, and their contained fluid inclusions, preserve primary marine signatures from the early Palaeozoic.

Petrographic relationships indicating early (syndepositional) erosional truncation of these cements, with the preservation of inclusion-rich areas that are confined by former growth surfaces, provide strong evidence that they were initially precipitated during the Cambrian-Ordovician. Our analyses yield no definitive evidence of significant recrystallization and in fact provide evidence against it. No single geochemical signature can be considered 'definitive', but in combination they provide strong evidence that the cements and their fluid inclusions are relatively pristine. We conclude that the cements formed as low-magnesium calcite marine precipitates at (and below) the sediment-water interface and have not undergone significant recrystallization.

Our results support the hypothesis that the dominant mineral precipitating from sea water has changed through time[7-10], which implies that some chemical parameter in the atmosphere-seawater system (significant with respect to calcite precipitation) has changed between Cambrian time and the modern. The partial pressure of CO_2 may be one such parameter, with modelling studies suggesting that it was much higher during the Cambrian and Ordovician than at any other time in the Phanerozoic[4]. Changes in the Mg/Ca ratio of sea water have been proposed as an alternative mechanism[18,27]. Samples of ancient sea water preserved as fluid inclusions could provide a direct means of answering these and other questions. □

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Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic

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THE cause of extinction of the woolly mammoth, *Mammuthus primigenius* (Blumenbach), is still debated. A major environmental change at the Pleistocene–Holocene boundary, hunting by early man, or both together are among the main explanations that have been suggested. But hardly anyone has doubted that mammoths had become extinct everywhere by around 9,500 years before present (BP). We report here new discoveries on Wrangel Island in the Arctic Ocean that force this view to be revised. Along with normal-sized mammoth fossils dating to the end of the Pleistocene, numerous teeth of dwarf mammoth dated 7,000–4,000 yr BP have been found there. The island is thought to have become separated from the mainland by 12,000 yr BP. Survival of a mammoth population may be explained by local topography and climatic features, which permitted relictual preservation of communities of steppe plants. We interpret the dwarfing of the Wrangel mammoths as a result of the insularity effect, combined with a response to the general trend towards unfavourable environment in the Holocene.

The woolly mammoth was well adapted to the rigorous climate of the Ice Age. As recently as 15,000-20,000 yr ago it inhabited northern and temperate latitudes of the Northern Hemisphere. At the end of the Pleistocene, about 10,000-12,000 yr ago, it disappeared from all the three continents almost simultaneously. No reliable radiocarbon (^{14}C) dates younger than 12,000 yr BP obtained directly on woolly mammoth fossils are known from Europe or North America[1-6], but there are 11 ^{14}C dates within the range 12,000 to 9,600 yr BP from the Siberian Arctic (A.V.S. and L. D. Sulerzhitzky, manuscript in preparation). On Wrangel Island (Fig. 1), an abundance of mammoth fossils was reported long ago[7,8], but they have only been specifically collected since 1989 (by S.L.V.). Mammoth fossils were mainly picked from the surface and at a small depth in slope or valley-bottom sediments; some were found just in river channels. The first set of ^{14}C dates from four tusk samples and one tibia bone (produced by the Laboratory of the Geographic Research Institute, St Petersburg (Leningrad) State University (LGU)) fall within the range 7,380 to 4,740 yr BP[9]. Later, L. D. Sulerzhitzky (Geological Institute, Russian Academy of Sciences, Moscow (GIN)) dated a tusk fragment, previously brought from Wrangel, to 5,980 ± 90 yr BP (GIN-6310).

The LGU and GIN laboratories have now produced a total of 30 dates on mammoth tusks and bone samples collected by

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S.L.V. on Wrangel. Twenty-nine are of Holocene age (3,730–7,620 yr BP) and the remaining sample, 12,750 yr BP (S.L.V., L. D. Sulerzhitzky and T. V. Tertychnaya, manuscript in preparation).

In 1991, S.L.V. collected a series of mammoth cheek teeth which were then studied by V.E.G. and A.V.S. The teeth are moderately preserved, about half are virtually undamaged, and many just slightly abraded. The whole sample (29 teeth and fragments) falls into two size classes. One comprises 5 specimens of relatively large size, the other 24 of very small size, though belonging to adults (Fig. 2; Table 1*a*).

The larger teeth from Wrangel are the size of normal Late Quaternary mammoths from north-east Siberia, including the neotype of *Mammuthus primigenius*, the Taimyr mammoth skeleton[10]. The small teeth from Wrangel are about 20–25% smaller. The hypothesis suggested by this important size difference was that the small teeth from Wrangel belonged to the Holocene survivors previously dated by the tusks. This was

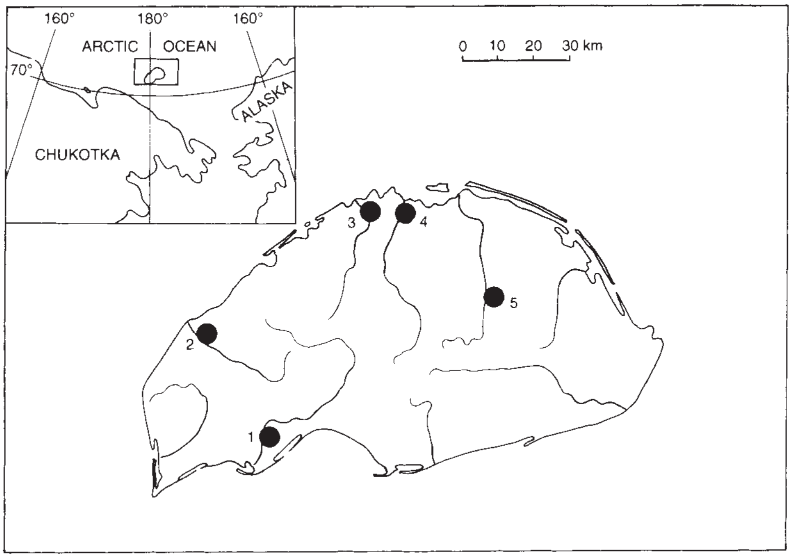

FIG. 1 Wrangel Island and the main areas of collecting mammoth teeth. (1) Mamontovaya River; (2) Goosinaya River; (3) Tundrovaya River; (4) Neizvestnaya River; (5) Krasnyy Flag River. The island is separated from the mainland, Chukotka, by Long's Strait with a minimum width of 150 km and maximum depth of 50 m. The central part of the island consists of low mountains (up to 1,000 m). Plateaus elevated up to 200–400 m lie west and east of the mountains; the lowland Tundra of Academy (up to 60 m) occupies the north of the island. Quaternary deposits of Wrangel Island are rather shallow and poorly studied. Marine sediments of uncertain age make up the northern lowland. Gravels, sands and silts, deposited by fluvial and slope processes, cover the plain surfaces and fill valley bottoms. Sometimes they include thick peat layers[26]. There are no traces of extensive glaciation of the island (S.L.V. manuscript in preparation).

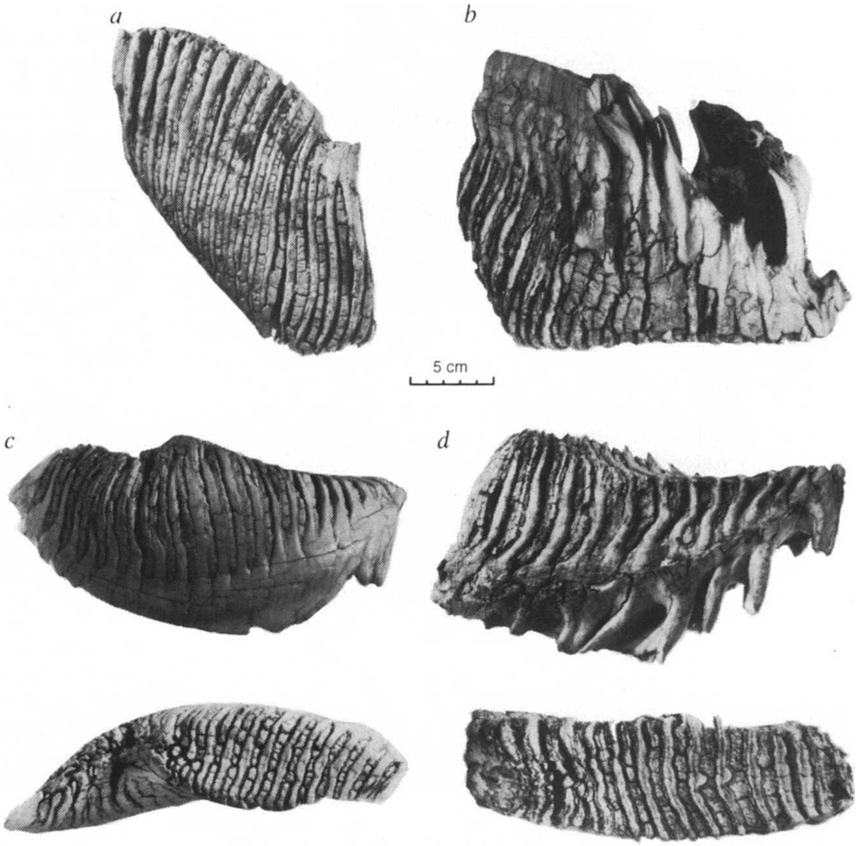

FIG. 2 Last molar teeth (M3) of two forms of mammoth from Wrangel Island. *a*, Upper M^3 of dwarf form, no. MAM-4, Mamontovaya River, in lateral view. This is one of four upper M^3 teeth of the dwarf form in the collection. The tooth was just coming into wear when the animal died. Similar dental stage in living elephants (eruption of the last generation of molars) suggests an age of not less than about 30 yr[24,27]. Two more upper teeth (not illustrated) belong to the last but one generation (M^2); a further one is either M^2 or M^3. The pictured specimen, MAM-4, is the best preserved one, though several plates at the posterior end are missing (18 are preserved). The estimated total length of the crown was hardly more than 220 mm. Three teeth of similar size from Mamontovaya River have ^{14}C ages of 4,000–5,000 yr BP. *b*, Upper M^3 of large form, no. KRF-1, Krasnyy Flag River, in lateral view. The tooth is deeply worn: the anterior roots have been resorbed and the corresponding part of the crown is lost. Only 20 plates are preserved, but their original number is estimated to have been 26 or 27 (ref. 28). The original crown length was more than 300 mm (268 mm preserved). The left M^3 of the same individual (KRF-2) is dated as 12,980 ± 80 yr BP. *c*, Lower M_3 of dwarf form, no. GUS-10, Goosinaya River, in medial (image here reversed to facilitate comparison) and occlusal views. There are 15 measurable lower teeth of dwarf form in Wrangel collection; 12 of them, including GUS-10, certainly belong to the last generation (that is M_3). The tooth GUS-10 is the best preserved one and has the maximum number (23) of preserved plates. Two anterior plates seem to be absent due to rather deep wear. All the other M_3s of the dwarf form are much more deeply worn, and belong to old or senescent individuals. Because of this their crown length and total number of plates cannot be reconstructed. *d*, Lower M_3 of large form, no. KRF-3, Krasnyy Flag River, in medial and occlusal views. The large tooth KRF-3 is also quite worn and lacks at least 10 plates (14 preserved).

TABLE 1 Results of analysis of mammoth teeth

(*a*) Maximum crown width of last molars of mammoth (mm)

	Upper M^3			Lower M_3		
	Range	Mean	*n*	Range	Mean	*n*
Wrangel, small	63–72	68.0	4	54–74	64.6	12
Berelyokh, small	64–80	74.6	10	72–85	78.8	6
Berelyokh, whole sample	64–90	77.2	12	72–96	83.2	9
Other NE Siberian localities	66–102	88.7	18	71–96	82.8	14
Wrangel, large	88–94	91.3	3	88; 88	88.0	2
Neotype *M.p.*, Taimyr	99; 99			87; 91		

(*b*) Radiocarbon dates of mammoth teeth from Wrangel island

		Small form:		
LU-2798	4,010 ± 50	Mamontovaya R.	last upper molar	MAM-6
LU-2808	4,040 ± 30	Mamontovaya R.	tooth fragment	MAM-2
LU-2794	5,110 ± 40	Mamontovaya R.	last lower molar	MAM-5
LU-2799	6,260 ± 50	Goosinaya R.	last lower molar	GUS-9
LU-2810	6,890 ± 50	Goosinaya R.	tooth fragment	GUS-7
LU-2809	7,250 ± 60	Tundrovaya R.	last(?) lower molar	PIK-1
		Large form:		
LU-2792	12,980 ± 80	Krasnyy Flag R.	last upper molar	KRF-2
LU-2807	20,000 ± 110	Neizvestnaya R.	last upper molar	NZV-1

a, Crown width was used as the main size parameter because of either deep wear or fragmentation of most specimens. Berelyokh 'mammoth cemetery' in the lower Indigirka is one of the latest large samples of Siberian mammoth (12,850 ± 110–12,000 ± 130 yr BP). Most mammoth last molars from the Berelyokh collection are relatively small (particularly evident in small crown width[23]), but some are larger, close to normal late north-east Siberian mammoth. It is debated whether all the small-sized mammoth fossils from Berelyokh belong to females, or some are dwarfed males (see ref. 24 for references). The latter hypothesis may suggest that the large fossils are of earlier geologic age. That is why we present the whole Berelyokh sample and the small-sized teeth separately. Whether the small teeth from Berelyokh represent females only, or a whole dwarfed population, the Wrangel teeth are notably smaller in size even than them. *b*, The datings were made in the LGU laboratory on collagen by standard precedures[25]. As far as most samples were collected on the surface, the issue of possible contamination by younger carbon was carefully studied. Extensive methodological research entailing sequential assays (L. Sulerzhitzky, personal communication) has demonstrated that the thorough procedures of collagen extraction and cleaning removed all extraneous carbon from the samples before measurement. The validity of the Wrangel dates is further confirmed by comparison with more than 50 mainland mammoth fossils from Taimyr peninsula (A.V.S. and L. D. Sulerzhitzky, manuscript in preparation). Although these were also surface finds, none gave a date younger than 9,500 yr BP, and some proved to be older than 50,000 yr BP. Only the small Wrangel remains, of analogous provenance and preservation, and using the same techniques, gave dates younger in the range 7,000–4,000 yr BP. We are therefore confident in ruling out the great contamination which would be required spuriously to produce such young dates.

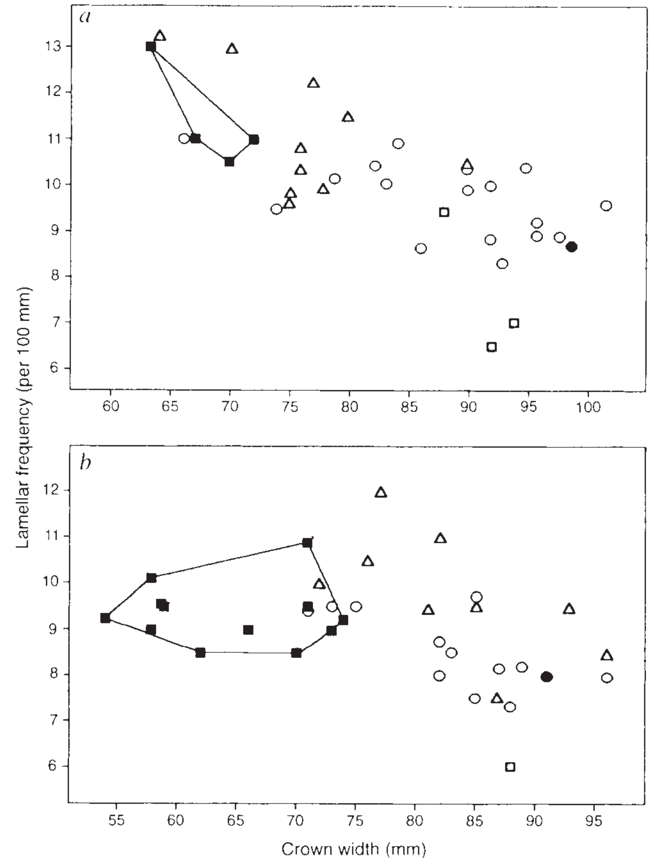

FIG. 3 Comparison of small and large forms of mammoth from Wrangel Island with some mainland samples. Maximum crown width is plotted against lamellar frequency (average number of plates in 100 mm of crown length). *a*, Last upper molars M^3; *b*, last lower molars M_3. Wrangel Island, small form (■); Wrangel Island, large form (□); Berelyokh 'Mammoth Cemetery' (△); other late Pleistocene localities of the Indigirka-Kolyma Lowland from A.V.S. collection (○); Taimyr Mammoth, neotype of *Mammuthus primigenius* [10] (●). Original data by V.E.G. and A.V.S. Measuring methods from ref. 29. Upper teeth of small Wrangel form display a very high lamellar frequency, like those from Berelyokh, which can be related to their small size and resulting lamellar compression[30]. Relatively low values of this index in lower teeth of the Wrangel dwarf are related to their deep wear (in lower teeth the plates diverge to the base of the crown, resulting in fewer plates per 100 mm on heavily worn teeth, that is, in lower lamellar frequencies).

confirmed by the ^{14}C dating of six teeth and measurable fragments of the small form, and two of the large (Table 1*b*).

Because all dated small teeth are Holocene, and both large ones are late Pleistocene, there is no reason to suggest that they belong to males and females in the same population. Small last molars (M3) from Wrangel are among the smallest known for *Mammuthus* (Fig. 3). Though we have no evidence on the size of limb bones, the small mammoth from Wrangel can be considered as a dwarfed form.

The existence of dwarfed forms of Pleistocene elephants on islands is well known[11]. Pigmy forms of straight-tusked elephant, *Palaeoloxodon*, inhabited some islands in the Mediterranean[12,13]. *Mammuthus exilis*, a dwarfed descendant of the North American mammoth *M. columbi*, existed on Santa-Rosa and other islands off the Californian coast at the end of the Pleistocene[14,15]. The existence of dwarfed woolly mammoth in northern Siberia at the end of the Pleistocene or even in early Holocene had been suggested by other workers[16], but could not be proved.

It is not possible to reconstruct the body size of the Wrangel small form based on teeth alone. Note, however, that these teeth are about 30% smaller than those of the type *M. primigenius* from Taimyr, which was rather small itself (2.65 m shoulder height[17]). In many dwarfed forms body size was reduced to a much greater extent than the teeth[18]. This suggests that we can consider the 30% tooth reduction as only a minimum estimate for body size, and that the Holocene Wrangel mammoth was very small.

During the late Pleistocene, until at least 16,000 yr BP, Wrangel Island together with the coastal lowlands of Arctic East Siberia, Alaska and what is now the vast and shallow Arctic shelf, was a part of the extensive land of Beringida[31]. According to reconstructions based on age estimation of submerged shorelines in the Bering Strait area[19], Wrangel Island could still have been joined with the mainland as late as 13,000 yr BP, but by 12,000 yr BP that connection had been broken. The normal size of Wrangel mammoth teeth dating from the Pleistocene agrees with these estimates: it seems that the local population was not isolated from the main range until 12,000 yr BP. Later there is a gap in the mammoth record on the island until 7,000 yr BP, when the dwarfing had already occurred. This seems to have been enough time for insular dwarfing, comparable to the dwarfing of red deer on the island of Jersey (UK), which took less than 6,000 years[18]. But the trend of general environmental change must also be considered. As early as about 12,000 yr BP, that trend resulted in the disappearance of mammoth over most of its vast range, and survival only in the High Arctic, north of 70° N (A.V.S. and L.D. Sulerzhitzky, manuscript in preparation and ref. 20). At that time at least some Arctic mainland populations, such as that of the Berelyokh in the lower course of the

Indigirka River, show a reduction in body size (Table 1*a*). The period 9,500–8,000 yr BP is considered as the Holocene 'optimum' for this region, marked by increased temperature and humidity, and related turnover in plant communities[20]. By 9,500 yr BP, mammoth had vanished totally from the mainland and most of the Arctic islands, and it is likely that this time was also critical for the Wrangel Island mammoth.

How was a single mammoth population able to survive such hard times and why just on Wrangel Island? A possible explanation comes from present-day botanical observations[21,22]. Unlike the other islands within the Arctic Tundra subzone, Wrangel retains a much higher diversity of herb species, steppe plants in particular. Grasses, sedges and forbs, mainly xerophytes and cryoxerophytes in their ecology, play an important role in cryophyte steppe and tundra meadows. These herbaceous communities occupy some favourable habitats on the island, mostly in the basins and plateaus of its mountainous part, supported by more continental climate and abundance of carbonate rocks, and are considered as depauperated relicts of the Pleistocene grassland (tundra-steppe)[22]. It is likely that the island provided a relict of tundra-steppe habitat in the early Holocene too, but that is still to be proved.

Although oppressed and dwarfed, woolly mammoth could exist on Wrangel Island until at least 3,700 years ago. There is no evidence that it was hunted by man. The extraordinary fact is not that mammoth eventually became extinct on Wrangel like elsewhere, but that, together with some relicts of tundra-steppe flora, it was able to survive the early Holocene environmental revolution in this Arctic island refuge. ☐

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A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks

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THE Lyme disease spirochaete, *Borrelia burgdorferi s.l.*, is the only *Borrelia* known to infect both mammals and birds[1]. The main vertebrate reservoirs of *B. burgdorferi* are thought to be various small and intermediate size mammals[2], but the importance of birds as a reservoir has not been thoroughly explored. In the Northern and Southern Hemispheres the seabird tick, *Ixodes uriae*, is prevalent and closely associated with many species of colony-nesting marine birds[3]. Here we report the presence of spirochaetes, demonstrated by immunofluorescent assay, by polymerase chain reaction and in culture, in *I. uriae* infesting razorbills on an island in the Baltic Sea. This island is free from mammals. The protein profile of the spirochaetes and the sequences of their flagellin and *ospA* genes are identical to those of the Lyme disease spirochaete, *Borrelia burgdorferi s.l.*, previously isolated from *I. ricinus* on a nearby island. In biopsies from the foot web of razorbills, *B. burgdorferi*-specific DNA was detected after amplification by polymerase chain reaction. Our results suggest that birds play an important part in the maintenance of *B. burgdorferi* and that mammals may not be a prerequisite for its life cycle.

There are several seabird colonies in the Baltic Sea and one of the largest is on the island of Bonden (63° 26′ N, 20° 03′ E; surface area, 0.45km^2) 12 km from the Swedish mainland. During the breeding season this island holds about 4,000 pairs of razorbill (*Alca torda*), 800 pairs of guillemot (*Uria aalge*), 500 pairs of black guillemot (*Cepphus grylle*), and 50 pairs of gulls (*Larus* spp)[4]. The vegetation is dominated by herbs and grasses. Bonden is not inhabited by terrestrial mammals[5].

During bird ringing on Bonden in July in 1991 and 1992, 145 razorbills, 223 guillemots, two black guillemot nestlings and five herring gull (*Larus argentatus*) fledglings were checked for ticks. Twenty-three adult female and fourteen nymphal fed *I. uriae* were collected from the feet of 13 razorbills and 2 guillemot

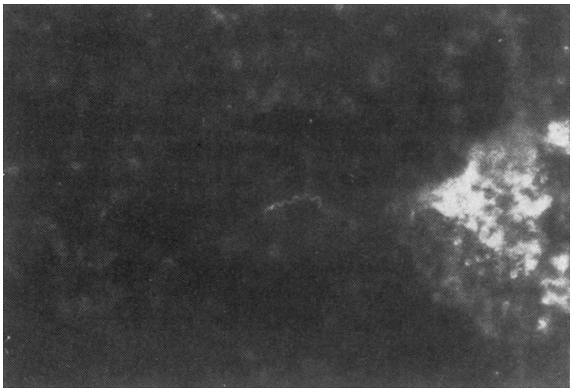

FIG. 1 Borreliae in mid-gut tissues of *Ixodes uriae*. After immersion in 70% ethyl alcohol, each tick was washed in sterile water. The content of the tick's idiosoma was excised aseptically into a few drops of sterile phosphate-buffered saline on a glass slide. Smears remaining on the slides after microscopy were dried and fixed and stained by indirect immunofluorescence using the anti-flagellum monoclonal antibody H9724 (ref. 8). After incubation for 30 min at 37 °C, slides were washed and incubated with goat anti-mouse (Becton Dickinson, UK) fluorescein isothiocyanate-labelled conjugate.