VIRUSES IN IXODES URIAE (ACARI: IXODIDAE) FROM SEABIRD COLONIES AT RØST ISLANDS, LOFOTEN, NORWAY

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Abstract. A total of 1929 Ixodes uriae collected from Røst Islands, Lofoten, Norway, in July 1974, was divided into 204 pools and inoculated into suckling mice and chick embryo cell cultures for virus isolation. Virus was detected in 6.6% of the laboratory-molted female ticks, 5.4% of the males and 1.8% of the nymphs. No isolates were obtained from 149 unengorged adult ticks. Of 50 viral strains recovered, 30 belonged to the Uukuniemi group, 13 to the Kemerovo group, and 1 was a strain of Tyuleniy of Group B. Of 6 untyped strains, 1 was orbiviruslike and 1 resembled a coronavirus in a negative-staining electron microscopy. The infection rates of I. uriae in Lofoten were similar to those reported in the Murmansk area in the northern USSR.

Ixodes (Ceratixodes) uriae White [=I. putus (Pick.-Cambr.)], whose mass occurrence in vast seabird colonies creates favorable conditions for circulation of arthropod-transmitted agents, has in recent years been actively studied for arboviruses (for reviews see L’vov et al. 1975, Yunker 1975, Main et al. 1976b). So far, arboviruses belonging to the serological groups B (L’vov et al. 1971, Clifford et al. 1971), Sakhalin (L’vov et al. 1972, Ritter & Feltz 1974, Doherty et al. 1975, Main et al. 1976a), Uukuniemi (L’vov et al. 1973a, Thomas et al. 1973, Traavik et al. 1974), and Kemerovo (L’vov et al. 1973b, Yunker et al. 1973, Main et al. 1973, 1976b, Main 1978, Ritter & Feltz 1974, Doherty et al. 1975) have been reported. In addition, 2 ungrouped viruses, Paramushir (L’vov et al. 1975) and Runde (Traavik et al. 1977), have been isolated from I. uriae.

To study the presence of arboviruses in I. uriae in Scandinavia, a survey was made at Røst Islands, Lofoten, Norway, where the presence of this tick species was reported earlier (Mehl 1968).

MATERIALS AND METHODS

Ticks were collected on 5–6 July 1974 at Røst Islands (68°30’N, 12°04’E), Lofoten, Norway. Detailed descriptions of the study area have been published elsewhere (Wagner 1958, Pomeroy 1966). The area is a breeding place for about 2 million pairs of birds, of which the Atlantic Puffin, Fratercula arctica, Black-legged Kitiwake, Rissa tridactyla, Common Murre, Uria aalge, and Razorbill, Alca torda, are the prevalent species. Unengorged female ticks were found in the active foraging state; unengorged males, engorged nymphs and larvae were collected from crevices in stones or from soil under the bird colonies. Ticks were transported on ice to the laboratory where they were kept alive up to 6 months at 6 ° or 15 °C until isolation attempts were made. Engorged specimens were allowed to molt. Ticks were triturated in pools averaging 5 adults or 20 nymphs and were inoculated into 0- to 3-day-old mice (Brummer-Korvenkontio et al. 1973). Negative pools were further tested in chick embryo cell cultures (Saikku 1974). Presumptive identification of isolates by negative-staining electron microscopy was done with cell culture supernatant or by touching the wet cut surface of the mouse brain with a grid that was then stained with uranyl acetate (pH 5.8) or sodium phosphotungstate (pH 7.0). Preliminary serological typing was done by complement fixation with crude, 2nd- or 3rd-passage suckling mouse brain extracts centrifuged at 10,000 g for 60 min as antigens. The following sera or immune ascitic fluids were used: Uukuniemi group isolate from Røst (NorAr V-697), Great Island (CanAr 41) of the Kemerovo Group, polyvalent Sakhalin group and group B.

Further serological identification of 3 Uukuniemi group and 3 Kemerovo group isolates by cross-complement fixation was done with sucrose-ace-tone extracted mouse brain antigens and immune mouse ascitic fluids supplied by the World Health...
Organization Reference Centre at the Yale Arbovirus Research Unit. The group B isolate was tested both in cross-complement-fixation and hemagglutination-inhibition tests with 49 flaviviruses; it was compared further in suckling mouse neutralization tests with 2 group B isolates, Tyuleniy (L'vov et al. 1971) and Saumarez Reef (St. George et al. 1977).

RESULTS

A total of 50 strains was isolated, 48 in mice and 2 in chick embryo cell cultures. Virus was recovered from 2.6% of the ticks tested (TABLE 1). Unengorged, seemingly overwintered adults yielded no isolates. The infection rates in laboratory-molted males and females were similar, 5.4% and 6.6%, respectively, and 3-fold greater than the rate (1.8%) in molted nymphs. The ratio of Uukuniemi to Kemerovo group viruses was 2:1 in molted nymphs and males and 4:1 in molted females. There was no difference in infection rates in ticks held at 6 ° and 15 °C in the laboratory.

Viruslike particles were seen by negative-staining electron microscopy (FIG. 1) in 12 of 22 mouse brain dips or cell culture supernatants. Of these, 10 were in the 1st passage. Uukuniemi viruslike particles were seen in 4 of 7 mouse brain preparations and in 1 of 2 cell cultures; orbiviruslike particles were detected in 1 of 4 mouse brains and 4 of 6 cell cultures. Most of the strains yielded enough antigen in the 2nd mouse passage to be tentatively classified by complement fixation. Of serologically untyped isolates, 1 was orbiviruslike and 1 resembled a coronavirus. In no case was there a discrepancy between results of serology and electron microscopy.

TABLE 1. Virus isolations from *Ixodes uriae* collected at Røst Islands, Lofoten, Norway in July 1974.

| STAGE           | NO. Ticks | UUKUNIEMI GROUP | KEMEROVO GROUP | B GROUP | UNTYPED | ALL STRAINS |
|-----------------|-----------|-----------------|----------------|---------|---------|-------------|
| Unengorged ♂    | 114       |                 |                |         |         |             |
| Unengorged ♀    | 35        |                 |                |         |         |             |
| Molted ♂        | 10 (3.6)* | 5 (1.8)         |                |         | 15 (5.4)|             |
| Molted ♀        | 197       | 8 (4.1)         | 2 (1.0)        | 1 (0.5) | 2       | 13 (6.6)    |
| Molted nymphs   | 1305      | 12 (0.9)        | 6 (0.5)        |         | 4**     | 22 (1.8)    |
| Total           | 1929      | 30 (1.5)        | 13 (0.7)       | 1 (0.05)| 6       | 50 (2.6)    |

* Number of pools positive; % of ticks infected in parentheses.
** Including coronavirus- and orbiviruslike isolates by electron microscopy.
TABLE 2. Comparison of 3 Uukuniemi group isolates from Ixodes uriae in Norway with other members of the serogroup, based on results of complement-fixation tests.

| ANTIGEN | ASCITIC FLUID |
|---------|--------------|
| NorV-707 | 512/256* | 512/256 |
| NorV-820 | 512/256 | 512/256 |
| NorV-868 | 512/256 | 512/256 |

Uukuniemi group viruses were readily reisolated. Their mean incubation time (about a week) did not markedly shorten in successive mouse passages. Most of the isolates reacted in early passages in complement-fixation tests with antibody prepared against the first Uukuniemi group virus isolated (NorAr V-697). This serum reacted with Zaliv Terpeniya and NorAr V-697 antigens to identical titers, but weakly, or not at all, with Uukuniemi (strains S 23, Jomala A 21, Potepli) and Grand Arbaud antigens. The relationships of 3 representative isolates of the Uukuniemi group are presented in Table 2.

Chick embryo cell cultures seemed to be more susceptible to Kemerovo group isolates than were mice because isolation of 2 strains and reisolation of 2 additional strains were successful in cell cultures only. Isolates were readily adapted to mice with a reduction in incubation time. In preliminary screening, all strains reacted with Great Island and

Table 3. Comparison of 3 Kemerovo group isolates from Ixodes uriae in Norway with other members of the serogroup, based on results of complement-fixation tests.

| VIRUS  | STRAIN | ASCITIC FLUID |
|--------|--------|--------------|
| NorV-808 | — | 256/1024* | 256/1024 |
| NorV-873 | — | 128/256 | 128/256 |
| NorV-962 | — | 128/64 | 128/64 |

* Heterologous titer/homologous titer.
Table 4. Comparison of NorV-724 and other group B viruses by complement-fixation and hemagglutination-inhibition tests.

| Virus                              | NorV-724 ANTIAGEN CF | NorV-724 ANTIAGEN HI | NorV-724 ANTIBODY CF | NorV-724 ANTIBODY HI |
|------------------------------------|----------------------|----------------------|----------------------|----------------------|
| Tyuleniy                           | 64/64                | 320/160              | 128/128              | 160/2560             |
| Saumarez Reef                      | 32/128               | 160/320              | 128/128              | 320/2560             |
| Kadam                              | 8/64                 | 80/80                | 16/6512              | 80/2560              |
| Kyasanur Forest disease            | 32/512               | 320/160              | 8/512                | 80/2560              |
| Karshi                             | 32/512               | 160/1280             | 16/128               | 80/2560              |
| Langat                             | 0/256                | 160/640              | 16/512               | 80/2560              |
| Louping ill                        | 64/≈1024             | 160/640              | 8/512                | 80/2560              |
| Omsk hemorrhagic fever             | 16/2560              | 80/160               | 0/512                | 40/2560              |
| Powassan                           | 32/312               | 20/160               | 16/512               | 80/2560              |
| Tick-borne encephalitis—Far East   | 4/1024               | 80/320               | 0/512                | 80/2560              |
| Tick-borne encephalitis—Central European | 16/1024            | 160/160              | 0/512                | 80/2560              |
| Alfuy                              | 0/64                 | 20/40                | 32/512               | 160/2560             |
| Banzi                              | 8/64                 | 20/40                | 8/512                | 320/2560             |
| Bussaquara                         | 256/≈1024            | 160/640              | 32/512               | 160/2560             |
| Dengue 1                           | 16/512               | 160/1280             | 0/512                | 40/2560              |
| Dengue 2                           | 0/32                 | 0/20                 | 16/512               | 160/2560             |
| Dengue 3                           | 256/≈1024            | 640/1280             | 0/512                | 80/2560              |
| Dengue 4                           | 0/128                | 20/2560              | 32/512               | 160/2560             |
| Edge Hill                          | 0/64                 | 20/40                | 32/512               | 160/2560             |
| Ileus                              | 0/128                | 40/—                 | 32/512               | 160/2560             |
| Japanese B encephalitis            | 32/512               | 160/2560             | 0/512                | 640/2560             |
| Kokobera                           | 0/16                 | 40/20                | 16/512               | 160/2560             |
| Kunjin                             | 8/128                | 80/160               | 32/512               | 320/2560             |
| Murray Valley encephalitis         | 0/128                | 40/320               | 64/512               | 1280/2560            |
| Ntaya                              | 0/64                 | 20/640               | 16/512               | 640/2560             |
| St. Louis encephalitis             | 256/≈1024            | 640/1280             | 32/512               | 160/2560             |
| Spondweni                          | 8/256                | 80/160               | 16/512               | 80/2560              |
| Stratford                          | 16/512               | 80/2560              | 16/512               | 80/2560              |
| Tembusu                            | 32/512               | 80/2560              | 32/512               | 160/2560             |
| Uganda S                           | 0/32                 | 20/20                | 16/512               | 0/2560               |
| Usatu                              | 128/≈1024            | 320/320              | 64/512               | 160/2560             |
| Wesselsbron                        | 0/64                 | 20/40                | 32/512               | 320/2560             |
| West Nile                          | 128/≈1024            | 320/—                | 16/512               | —/2560               |
| Yellow fever                       | 0/128                | 40/40                | 32/512               | 80/2560              |
| Zika                               | 0/256                | 40/512               | 32/512               | 160/2560             |
| Apoi                               | 0/128                | 20/10                | 16/512               | 40/2560              |
| Cowbone Ridge                      | 20/20                | 8/512                | 80/2560              |
| Dakar bat                          | 0/64                 | 20/20                | 8/512                | 40/2560              |
| Entebbe bat                        | 8/20                 | 8/512                | 80/2560              |
| Jutiape                            | 8/≈1024              | 40/160               | 0/512                | 40/2560              |
| Israel turkey meningitis           | 20/160               | 32/512               | 160/2560             |
| Modoc                              | 0/16                 | 20/40                | 0/512                | 20/2560              |
| Montana Mystis leukoencephalitis    | 32/1024              | 40/—                 | 0/512                | —/2560               |
| Negishi                            | 40/512               | 8/512                | 40/2560              |
| Phnom Penh bat                     | 32/256                | 160/320              | 0/128                | 80/2560              |
| Saboya                             | 8/512                | 160/2560             |
| U.S. (Burns) bat                   | 64/512               | 160/80               | 0/512                | 40/2560              |
| Yokose                             | 32/256                | 256/2560             | 0/128                | 2560/2560            |
| Sokuluk                            | 0/512                | 80/2560              |
| Group B ascitic fluid              | 16/64—128            | 320/40—320           |

*Heterologous serum titer/homologous serum titer. Initial dilution: Sera—CF 1:8, HI 1:10; Antigen—CF 1:4.

Okhotskiy ascitic fluids. Results of cross-complement-fixation tests with 3 isolates and Kemerovo group agents are presented in Table 3.

One strain (NorAr V-724), from a pool of 3 molted female ticks, was found to be similar to or identical with Tyuleniy virus by hemagglutination-inhibition, complement-fixation and neutralization tests (Table 4, 5). Of the untyped isolates, 1 strain (NorAr V-958) morphologically resembled a coronavirus by electron microscopy (Fig. 1). It was isolated from a pool of 20 nymphs collected as larvae and held in the laboratory for 6 months. This
strain was reisolated and caused a cytopathic effect in both chick embryo and baby hamster kidney (BHK/WI-2) cells (Vaheri et al. 1967).

**DISCUSSION**

Studies on the ecology of *I. uriae* at Lofoten are lacking, although they have been published from the Murmansk area of the USSR (Flint & Kostyrko 1967, Karpovich 1970), which is at the same latitude but with a much cooler winter temperature due to the diminished effect of the Gulf Stream. At Murmansk, the Thick-billed Murre, *Uria lomvia*, replaces the Common Murre as a primary host for this tick.

Engorged female *I. uriae* were not collected in early July, suggesting that they had not completed their engorgement. Males, which do not feed, and engorged larvae and nymphs were found tightly packed in crevices in the rocks. Virus was not isolated from unengorged adult ticks that apparently had overwintered. This is compatible with the hypothesis that an arbovirus in a hibernating vector can go into an "invertebrate" cycle in which the virus is difficult to detect in vertebrates or in vertebrate cells at higher temperatures (Schlesinger 1975). Evidence of this phenomenon has been presented in studies on transovarial transmission of Japanese encephalitis virus in mosquitoes (Rosen et al. 1978). The easily detected isolates from engorged and molted ticks in our studies may be due to recently acquired virus of the "vertebrate" type, to alterations in tick physiology during feeding and molting, or to exposure during engorgement to the body temperature of the bird. The isolates, although not proven arboviruses, were recovered from molted ticks and thus were maintained and passed transstadially in *I. uriae*.

The spectrum of viruses isolated from this species in different parts of the world varies considerably (L'vov et al. 1975, Yunker 1975, Main 1976). The high infection rates of viruses in *I. uriae* may have led to some mixed isolates, but overall ratios of Uukuniemi and Kemerovo group viruses and Tyuleniy virus were similar to those reported in the Murmansk region but differed from those observed in the Far East (L'vov et al. 1975). Viruses of the Kemerovo and Sakhalin groups, but not the Uukuniemi group, were isolated from *I. uriae* in eastern Canada and the Faeroe Islands (Main et al. 1976a, b), despite similar host species and connecting bird migratory pathways between the Faeroe Islands and Lofoten. A comparison can be made only by matching the status of ticks and isolation methods. Chick embryo cell cultures were more sensitive to Kemerovo group viruses than were mice.

Electron microscopy was a simple and rapid method for preliminary classification of these viruses and worthy of wider application in arbovirus studies.

The isolation of a coronaviruslike agent, transmitted transstadially and maintained for 6 months in *I. uriae*, is interesting. Runde virus, morphologically a coronaviruslike agent, was reported from *I. uriae* in southern Norway (Traavik & Mehl 1975, Traavik et al. 1977). This is an unusual structural group among the arboviruses. These isolates must await biologic verification of an arbovirus cycle and biochemical characterization of nucleic acid and polypeptide composition before final classification is attempted.

Complement-fixation tests on the Uukuniemi and Kemerovo group viruses produce complexes that often reflect the origin of the isolates (Main 1976). For example, within the Kemerovo serogroup there are 4 such groupings: the Chenuda complex associated with argasid vectors, the Wad Medani complex from ixodid ticks of the subfamilies Amblyomminae and Rhipicephalinae, the Kemerovo complex from the *Ixodes ricinus* complex...
plex, and the Cape Wrath complex from *I. uriae* (Main et al. 1976b). The Uukuniemi and Kemero
vo group viruses isolated in our studies fall into the complexes associated with *I. uriae*. Neutral-
ization tests reveal a variety of serotypes of Kemero
vo group viruses circulating in the same bird col-
ony (Main et al. 1973, Main 1978); therefore,
cross-neutralization tests must be completed be-
fore final classification of the isolates is made.

The complex pattern of viruses recovered from the ecosystem involving *I. uriae* and seabirds, with a
limited number of variables, presents a suitable
model for the study of virus evolution.

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**LITERATURE CITED**

Brummer-Korvenkontio, M., P. Saikku, P. Korhonen & N.
Oker-Blom. 1973. Arboviruses in Finland. I. Isolation of
tick-borne encephalitis (TBE) virus from arthropods, ver-
tebrates, and patients. *Am. J. Trop. Med. Hyg.* 22: 382-89.

Clifford, C. M., C. E. Yunker, L. A. Thomas, E. R. Easton &
D. Corwin. 1971. Isolation of a group B arbovirus from
*Ixodes uriae* collected on Three Arch Rocks, National Wild-
life Refuge, Oregon. *Am. J. Trop. Med. Hyg.* 22: 461-68.

Doherty, R. L., J. G. Carley, M. D. Murray, A. J. Main, B. H.
Ray & R. Domrow. 1975. Isolation of arboviruses (Kem-
erovo group, Sakhalin group) from *Ixodes uriae* collected at
Maquarrie Island, Southern Ocean. *Am. J. Trop. Med.
Hyg.* 24: 521-26.

Flint, V. E. & I. N. Kostyorko. 1967. On the biology of *Ixodes
putus* Pick-Camb. tick. *Zool. Zh.* 46: 1253-56. (In Russian,
English summary.)

Karpovich, V. N. 1970. Properties of *Ceratixodes putus* Pick-
Camb. parasitism on birds. *Parasitologia* 4: 545-51. (In
Russian, English summary.)

L'vov, D. I., A. A. Timopheeva, V. I. Chervonski, V. L. Gro-
mashevsky, G. A. Klisenko, V. G. Gostinschikova & I. N.
Kostyorko. 1971. Tuleniy virus; a new group B arbovirus isolated from
*Ixodes (Ceratixodes) putus* Pick-Camb. 1878 collected in Tuleniy Island, Sea of Okhotsk.
*Am. J. Trop. Med. Hyg.* 20: 456-60.

L'vov, D. R., A. A. Timopheeva, V. L. Gromashevski, V. I.
Chervonski, A. I. Gromov, Yu. M. Tsyrkin, A. G. Pogreb-
benko & I. M. Kostyorko. 1972. “Sakhalin” virus—a new
arbovirus isolated from *Ixodes (Ceratixodes) putus* Pick-
Camb. 1878 collected on Tuleni Island, Sea of Okhotsk.
*Arch. Gesamte Virolog.* 38: 133-38.

L'vov, D. R., A. A. Timopheeva, V. L. Gromashevski, G. V.
Gostinschikova, O. V. Veselovskaya, V. I. Chervonski,
K. B. Fomina, A. I. Gromov, A. G. Pogrebkeno & V. Yu.
Zhezmer. 1973a. “Zaliv Terpenyia” virus, a new Uuku-
niemi group arbovirus isolated from *Ixodes (Ceratixodes)
putus* Pick-Camb. 1878 on Tuleni Island (Sakhalin re-
ion) and Commodore Islands (Kamchatka region). *Arch.
Gesamte Virolog.* 41: 165-69.

L'vov, D. K., A. A. Timopheeva, V. L. Gromashevski, Yu. M.
Tsyrkin, O. V. Veselovskaya, G. V. Gostinschikova, N. V.
Khytoretskaya, A. G. Pogrebkeno, V. A. Aristova, A. A.
Sazonov, V. I. Chervonski, G. A. Sidorova, K. B. Fomina
& V. Yu. Zhezmer. 1973b. “Okhotskiy” virus, a new ar-
biovirus of the Kemero group isolated from *Ixodes (Cer-
attxodes) putus* Pick-Camb. 1878 in the Far East. *Arch.
Gesamte Virolog.* 41: 160-64.

L'vov, D. K., A. A. Timopheeva, V. A. Smirnov, V. L. Gro-
mashevsky, G. A. Sidorova, L. P. Nikiforov, A. A. Sazo-
nov, A. P. Adreev, T. M. Skyortsova, L. K. Beresina & V.
A. Aristova. 1975. Ecology of tick-borne viruses in col-
onies of birds in the USSR. *Med. Biol.* 53: 325-30.

Main, A. J. 1976. Seabirds and *Ixodes uriae* as reservoirs in the
Witless Bay Seabird Sanctuary, Newfoundland, Canada.
Dr. P.H. Dissertation, Yale University, New Haven, Con-
nnecticut. 115 p.

1978. Tindholmur and Mykines: Two new Kemero group orbiviruses from the Faeroe Islands. *J. Med.
Entomol.* 15: 11-14.

Main, A. J., W. G. Downs, R. E. Shope & R. C. Wallis. 1973.
Great Island and Baulline: Two new Kemero group orbiviruses from *Ixodes uriae* in eastern Canada. *J.
Med. Entomol.* 10: 229-35.

1976a. Avian orbiviruses of the Witless Bay Seabird San-
cuary, Newfoundland, Canada. *J. Wildl. Dis.* 12: 182-94.

Main, A. J., R. E. Shope & R. C. Wallis. 1976b. Cape Wrath:
A new Kemero group orbivirus from *Ixodes uriae* (Acari:
Ixodidae) in Scotland. *J. Med. Entomol.* 13: 304-08.

Mehl, R. 1968. Lopper og lundelus på sjøfugl på Røst.
*Fauna, Oslo* 21: 197-98.

Pomero, D. 1966. The birds of Røst, Lofoten Islands, with
special reference to a visit in August, 1960. *Sterna, Stavan-
ger 7*: 19-92.

Ritter, D. G. & E. T. Feltz. 1974. On the natural occurrence of
California encephalitis virus and other orbiviruses in
*Alaska. Can. J. Microbiol.* 20: 1559-66.

Rosen, L., R. B. Tesh, J. C. Lien & J. H. Cross. 1978. Trans-
ovarial transmission of Japanese encephalitis virus by mos-
quitos. *Science* 199: 909-11.

Saikku, P. 1974. Passerine birds in the ecology of Uukuniemi
virus. *Med. Biol.* 52: 98-103.

Schlesinger, R. W. 1975. Sindbis virus replication in verte-
brate and mosquito cells: An interpretation. *Med. Biol.*
53: 295-301.

St. George, T. D., H. A. Standfast, R. L. Doherty, J. G. Carley,
C. Fillipich & J. Brandsma. 1977. The isolation of Sau-
marez Reef virus, a new flavivirus, from bird ticks *Ortho-
daro* opensini and *Ixodes esuytides* in *Australia. Aust.
J. Exp. Biol. Med. Sci.* 55: 493-99.

Thomas, L. A., C. M. Clifford, C. E. Yunker, J. E. Keirans, E.
R. Patzer, G. E. Monk & R. C. Wallis. 1973. Tickborne
viruses in western North America. I. Viruses isolated from
*Ixodes uriae* in coastal Oregon. *J. Med. Entomol.* 10:
165-68.

Traavik, T. & R. Mehl. 1975. Tick-borne viruses in Norway.
*Med. Biol.* 53: 321-24.

Traavik, T., R. Mehl & E. Kjeldsberg. 1977. “Runde” virus, a
coronavirus-like agent associated with seabirds and ticks.
*Arch. Virol.* 55: 25-38.

Traavik, T., R. Mehl & M. Petterson. 1974. The isolation of
an agent related to Uukuniemi virus from Norwegian
*Ixodes ricinus* ticks. *Acta Pathol. Microbiol. Scand. Sect.
B* 82: 297-98.

Vaheri, A., W. D. Sedwich & S. Plotkin. 1967. Growth of rubella virus in HK-21 cells. I. Production, assay and ad-
apation of virus. *Proc. Soc. Exp. Biol. Med.* 125: 1086-92.

Wagner, G. 1958. Die Brutfägel von Röst (Lofoten). *Sterna,
Stavanger* 3: 59-72.

Yunker, C. E. 1975. Tick-borne viruses associated with sea-
birds in North America and related islands. *Med. Biol.*, **53**: 302-11.

Yunker, C. E., C. M. Clifford, J. E. Keirans, L. A. Thomas & J. Cory. 1973. Tick-borne viruses in western North Amer-
ica. II. Yaquina Head, a new arbovirus of the Kemerovo group isolated from *Ixodes uriae*. *J. Med. Entomol.*, **10**: 264–69.