Transmission of Hog Cholera Virus by Horseflies (Tabanidae: Diptera)

Mac A. Tidwell, Ph.D.; W. D. Dean, D.V.M.; Margaret A. Tidwell, M.S.; Gary P. Combs, D.V.M.; D. W. Anderson, D.V.M., M.P.V.M.; W. O. Cowart, D.V.M., M.S.; R. C. Axtell, Ph.D.

SUMMARY

Epidemiologic evidence indicates that insects, specifically flies (Diptera) may disseminate hog cholera virus (HCV). Two species of horseflies (Tabanidae), *Tabanus lineola* Fabricius and *Tabanus quinquevittatus* Wiedemann, experimentally transmitted HCV to susceptible swine within 2 hours after biting a virus-source pig. Three other *Tabanus* species were incriminated. An apparent 24-hour delayed transmission of the virus by horseflies occurred. Transmission attempts using 6 species of mosquitoes were unsuccessful.

Laboratory diagnostic tests used for the detection of HCV were the fluorescent-antibody tissue section technique (FATST) for tonsillar tissue and the fluorescent-antibody cell culture technique (FACCT) for splenic tissue. The fluorescent-antibody serum-neutralization test (FASNT) was used for the detection of serum antibody against hog cholera (HC).

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From the Animal Health Division, Agricultural Research Service, U.S. Department of Agriculture, Raleigh, N. Car. 27601 (Dean and Anderson), Hyattsville, Md. 20782 (Combs), and Elba, Ala. 36323 (Cowart); and the Department of Entomology, North Carolina State University, Raleigh, N. Car. 27607 (Tidwell, Tidwell, and Axtell). Dr. and Ms. Tidwell's present address is Department of Zoology and Physiology, Louisiana State University, Baton Rouge, La. 70803.

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Little research has been conducted on the possible role that insects have in the transmission of HCV.[1,3,6,7] Dorset *et al.*[4] were able to contaminate houseflies and stable flies with HCV by placing them in contact with, or allowing them to feed on, infectious eye secretions or blood of affected pigs. Flies were homogenized in saline solution and injected in susceptible pigs. Transmission took place most often during the first 24-hour period, although one transmission was achieved 7 days after a fly had become contaminated. Transmission without injection was successful when houseflies previously exposed to eye secretions of affected pigs were touched within 24 hours to the eyes of susceptible pigs. The bite of the stable fly resulted in transmission for periods up to 24 hours.

TABLE 1—Tabanidae (Horseflies and Deerflies) and Culicidae (Mosquitoes) Collected on Premises Known To Have Herds Infected with Hog Cholera*

Species	Percentage of total** collected	Species	Percentage of total** collected
Tabanidae		Culicidae	
Chlorotabanus		*Aedes*	
crepuscularis (Bequaert)	1.3	*atlanticus* Dyar & Knab	9.6
		canadensis (Theobald)	3.8
Chrysops		*sollicitans* (Walker)	0.4
flavidus Wiedemann	1.3	*vexans* (Meigen)	4.2
hinei Daecke	0.4		
reicherti Fairchild	0.6	*Anopheles*	
vittatus Wiedemann	0.6	*crucians* complex	2.5
		quadrimaculatus Say	0.8
Diachlorus			
ferrugatus (Fabricius)	0.2	*Culex*	
		pipiens complex	19.6
Tabanus		*salinarius* Coquillett	12.5
americanus Forster	1.5		
atratus Fabricius	0.5	*Culiseta*	
calens Linnaeus	0.4	*melanura* (Coquillett)	0.8
fuscicostatus Hine	5.2		
gladiator Stone	6.2	*Psorophora*	
lineola Fabricius	43.6	*ciliata* (Fabricius)	0.8
molestus Say	0.7	*confinnis* (Lynch-Arribalzaga)	40.4
mularis Stone	1.4	*ferox* (Humboldt)	4.6
petiolatus Hine	2.9		
quinquevittatus Wiedemann	16.9		
subsimilis Bellardi	14.5		
sulcifrons Macquart	1.7		
zythicolor Philip	0.1		

* Gates and Perquimans Counties, N. Car., Aug. 26–Sept. 3, 1970. ** Total number of tabanids, 839; total number of mosquitoes, 210.

Recently, dissemination of HC by insects has been suspected due to an apparent increase in the number of explosive epizootics in localized areas. Characteristically, this localized spread cannot be associated with any known transmission factor, and its peculiar nature promotes the suspicion that other factors are responsible. Hog cholera eradication teams in North Carolina and elsewhere frequently noted a pattern in the localized spread of the disease. Cholera was often first detected in herds located at the margins of woods or swamps. Its spread usually followed the courses of forests and streams. Most area spread occurred during June through September, the period of fly abundance. Suspicion of insect transmission was increased by observations of horseflies, deerflies, and mosquitoes in the vicinity of swine herds. Composite suspensions prepared from some of these flies were injected in specific-pathogen-free swine. Of 3 swine, 2 developed HC, and the viral isolates from these swine were of low virulence.

Horseflies seemed to prefer larger swine, and most often, adult swine were the first affected with HC. Horseflies seen feeding on swine in herds test positive for HC occasionally included a specimen of *Tabanus americanus* Forster and *Tabanus atratus* Fabricius. The flies were seen feeding most frequently on the back, head, and ears. Closer examination revealed *T. quinquevittatus* (approx. 4 per swine) on the ventral surfaces, especially on the udders of sows. *Tabanus lineola* averaged less than 1 per swine and was not observed to have a feeding site preference. Two specimens of *Tabanus molestus* Say landed on the backs of the swine. These observations were made in September during the final portion of the fly season. The abundance of flies at this time would not be indicative of the numbers or species during other portions of the season. Horsefly and mosquito species collected from premises where cholera-infected herds were located are listed (Table 1).

In light of (1) the field observations, (2) the suspected role of insects, and (3) the substantial numbers of both individuals and species of horseflies and mosquitoes in the vicinity of cholera-

infected herds, the present study was made to determine the capability of horseflies and mosquitoes to transmit HCV.

Materials and Methods

Experimental Housing.—The site of the experiment was the former Naval Auxiliary Air Station near Edenton, N. Car. On an isolated portion of the air base, a series of 5 bomb bunkers were utilized as shelters for some of the experimental pigs. The pigs were individually kept in 14 pens (1.2 by 1.2 by 1.2 m.) with fine 32-mesh screen tops. One pen was in each of 3 bunkers, and 2 were in each of 2 large bunkers. The remaining pens (with plastic rain covers) were placed outdoors 20 m. apart. An insectary and a fly-feeding house (2.4 m. long by 1.2 m. wide by 2.1 m. high) had fine-mesh screen on the top and on 3 sides. A quarantine house (3 by 3 by 2.1 m. high) held the virus-source pigs and was located 80 m. from the nearest experimental pigs.

Pigs.—Ten susceptible pigs were obtained from outside the areas containing known HC-infected pigs. Blood samples and tonsillar biopsies from these 10 pigs were submitted for FASNT and FATST. Additional pigs were subsequently obtained from the same source. Three infected pigs were obtained from a local herd determined to be test positive for HC. These 3 pigs had clinical signs of HC, and tonsillar tissue was test positive by the FATST. Additional infected pigs were acquired to provide a continuing source of the virus.

Quarantine Security Measures.—All foot gear was cleaned and disinfected, and disposable gloves were used or hands were washed in disinfectant between the handling of each pig. Precautions were taken to prevent the accidental entry of insects into cages when doors were opened. Coveralls worn while in contact with contaminated pigs were removed and placed in plastic bags for laundering. All straw bedding and other wastes were incinerated or buried. A minimal distance of 20 m. was maintained between each pen, except when susceptible pigs, designated as controls, were placed in the same bunker with a principal pig.

Collection of Insects.—Only female horseflies and mosquitoes were used in the transmission studies, as blood feeding is limited to this sex. The flies were collected from areas lacking swine. Horseflies were collected primarily by the use of a modified Manitoba trap similar to one described by Catts.[2] The horseflies were transferred individually to 155-Gm. vials with gauze lids and were placed in an insulated cooler. Mosquitoes were collected with an aspirator and transferred to a 450-ml. freezer carton before being placed in the cooler. At the insectary (24 C.), the mosquitoes were kept in individual glass vials (13.6 Gm.) with gauze covers and containing a cotton pad soaked in 10% sugar solution.

Insect Feeding Technique.—The pig used as the source of virus was tied on a restraining table. In general, the infected pig used for insect feeding was one that had the highest fever and maximal leukopenia. For feeding, the horseflies were transferred from the 155-Gm. vials to shorter, wide-mouth plastic cups with index cards used as covers. The cup was inverted on the pig, and the card was removed. To induce the fly to feed on the pig, the surface of the skin was moistened with water, and occasionally, CO_2 was provided by holding a small piece of dry ice near the plastic cup. After feeding, the fly was transferred to an oviposition chamber. This chamber was a 155-Gm. vial a quarter filled with moist sand and covered with a piece of gauze. A cotton pad impregnated with a 10% sugar solution was provided, and a sprig of grass was placed in the sand for use as a site for oviposition. After the eggs were deposited, the fly was generally receptive for a second feeding. Approximately 20% of the flies fed when first offered the blood source. Those flies initially refusing to feed were retained and repeatedly offered a blood source until they fed or were discarded after 5 or 6 unsuccessful attempts.

The individual mosquitoes were fed directly from their vials which were inverted on the pig, allowing the mosquito to probe through the gauze cover. After a blood meal, the mosquito was transferred to a 58-Gm. vial for oviposition and was provided with moist sand, a layer of damp filter paper, and a sugar water pad.

Transmission Experiments.—Insects were allotted to 3 experimental groups.

Group 1 (Immediate Transfer Feeding Group).—Insects in this group were interrupted during feeding on a diseased pig and were removed before a complete blood

meal was taken. Within 2 hours, insects were allowed to complete their meal on a susceptible pig. Four pigs were exposed to horseflies in this manner, and 1 pig was exposed to mosquitoes.

Group 2 (Twenty-Four-Hour Delayed Feeding Group).—Flies in this group were treated like those in group 1, except that a 24-hour delay was imposed before feeding was resumed on a susceptible pig. Three pigs were exposed to horseflies in this manner.

Group 3 (Postoviposition Feeding Group).—Insects in this group were permitted to feed to completion either on a virus-source pig alone or on both a virus-source pig and a susceptible pig. In the latter case, these were insects which had been used in other transmission experiments (group 1). After a complete blood meal was taken, all insects in this group were placed in chambers to deposit eggs. After oviposition, they were allowed to bite a susceptible pig. In a few instances, some insects did not oviposit and were allowed to feed on the susceptible pig after a minimal lapse of 4 days. One pig was exposed to horseflies in the manner just described. A 2nd pig was exposed only to the flies which had fed on the 1st pig and had oviposited a 2nd time. A 3rd pig was exposed to 1 fly which had fed on the 2nd pig and had oviposited a 3rd time. A 4th pig was exposed to mosquitoes, most of which had oviposited once.

Control Pigs.—Four pigs were maintained as controls. Two were submitted on 6 occasions to a similar regimen as pigs used in the immediate transfer feeding experiments. That is, horseflies and mosquitoes which had fed on or had otherwise had contact with virus-source pigs, were placed in contact with, but were not permitted to feed on, these 2 control pigs. The 2 remaining control pigs were not exposed to insects but were kept in pens adjacent to 2 of the principal pigs.

Challenge Inoculation.—All pigs remaining at the termination of the study were moved into a large bunker 33 days after the last transfer insect feeding. Each pig was intramuscularly inoculated with 2 ml. of serum containing the Ames strain of HCV.

Results

Pigs on Which Group 1 Insects Fed.—Four pigs (No. 4, 9, 10, and 13) on which horseflies had fed contracted HC and were shown to be test positive by the FATST. One pig (No. 6) on which mosquitoes had fed remained healthy throughout the study and later proved susceptible to the virus in the challenge inoculum.

Pig 4 was bitten by 34 horseflies (days 0 through 5) representing 4 species, including *Tabanus calens* Linnaeus (2 specimens), *T. lineola* (19 specimens), *T. quinquevittatus* (11 specimens), and *Tabanus sulcifrons* Macquart (2 specimens). These flies had been exposed to diseased pigs 1 and 3 (Table 2). First signs of the disease were observed on day 9 when body temperature of the pig was 40.6 C. On day 11, the virus was detected in tonsillar tissue by the FATST, and the white blood cell (WBC) count was 7,500/cmm. Necropsy on day 12 revealed ecchymotic and petechial hemorrhages of the diaphragmatic lobes of the lungs, petechiation of the surface of the kidney, splenic infarction, and peripheral congestion of the cervical, splenic, superficial inguinal, and popliteal lymph nodes. The spleen contained HCV as determined by FACCT; 4 plaque-forming units (PFU) per milliliter were detected.

Pig 9 was bitten by 5 *T. lineola* (day 0) which had fed on virus-source pig 16 (Table 2). At 4 days after transfer fly feedings, the WBC count was 8,100/cmm., and on day 6, HCV was detected in tonsillar tissue by the FATST. On day 7, pig 9 was transferred to the quarantine house to replenish the supply of virus-source pigs. Signs of HC continued until day 21 when body temperature decreased to 38.9 C. A WBC count taken on day 26 was 20,100/cmm., and tonsillar tissue was test negative for HCV. This pig was resistant to challenge inoculation with the Ames strain of HCV, and splenic and tonsillar tissues were test negative for HCV on the 7th day postinoculation. The postmortem examination at this time revealed slight petechiation of the heart and urinary bladder, slight peripheral congestion of the mandibular and lumbar lymph nodes, and a splenetic infarct.

Pig. 10 was bitten by 5 *T. lineola* (day

TABLE 2—Transmission Results Obtained by Transfer Feeding of Horseflies and Mosquitoes (Group 1) Within Two Hours of a Partial Blood Meal on a Hog Cholera-Infected Pig

Susceptible pig No.	No. of insects biting	Species of insects	Result of FATST (tonsil)	Virus-source pig No.	No. of days until first clinical signs	White blood cell count (No./cmm.)	Susceptible to challenge inoculation
4	2	*T. calens*	Positive	1 and 3	4 to 9	7,500 (11)	
	19	*T. lineola*					
	11	*T. quinquevittatus*					
	2	*T. sulcifrons*					
9	5	*T. lineola*	Positive	16	4	8,100 (4)	No
10	5	*T. lineola*	Positive	2	9	8,500 (9)	
13	20	*T. quinquevittatus*	Positive	16	7	7,600 (8)	
6	8	*A. atlanticus*	Negative	2, 3, and 16	**		Yes
	2	*A. infirmatus*					
	35	*A. sollicitans*					
	10	*A. taeniorhynchus*					
	3	*A. triseriatus*					
	13	*P. ferox*					

No. in parentheses = No. of days after transfer fly feedings; *T.* = *Tabanus*; *A.* = *Aedes*; *P.* = *Psorophora*; FATST = fluorescent-antibody tissue section technique.
** Remained healthy.

0) which had fed on virus-source pig 2 (Table 2). At 9 days after transfer fly feedings, tonsillar tissue was determined to be test positive by the FATST, and clinical signs seen at this time included body temperature of 40.1 C. and WBC count of 8,500/cmm. Necropsy on day 10 revealed petechiation of the urinary bladder, infarction of the spleen, and peripheral congestion of the renal and hepatic lymph nodes. Hog cholera virus (28 PFU/ml.) was isolated from the spleen by the FACCT.

Pig 13 was bitten by 20 *T. quinquevittatus* (day 0) which had fed on virus-source pig 16 (Table 2). At 7 days after transfer fly feedings, HCV was detected in tonsillar tissue by the FATST. The WBC counts decreased from 15,800/cmm. on day 0 to 7,600/cmm. on day 8. Temperatures increased from 39.6 C. on day 7 to 40.6 C. on day 9 and remained high until the pig was killed and necropsied on day 11. Lesions seen on necropsy included infarction of the spleen, petechiation of the urinary bladder, peripheral congestion of the mandibular and inguinal lymph nodes, and congestion of the visceral and parietal surfaces of the stomach. The spleen contained HCV (8 PFU/ml.) as determined by the FACCT.

Pig 6 was bitten by 71 mosquitoes (days 0 through 13) representing 6 species, including *Aedes atlanticus* Dyar and Knab (8 specimens), *Aedes infirmatus* Dyar and Knab (2 specimens), *Aedes sollicitans* (Walker) (35 specimens), *Aedes taeniorhynchus* (Wiedemann) (10 specimens), *Aedes triseriatus* (Say) (3 specimens), and *Psorophora ferox* (Humboldt) (13 specimens). These mosquitoes had fed on virus-source pigs 2, 3, and 16 (Table 2). Pig 6 remained healthy throughout the study, and tonsillar tissues examined by the FATST were test negative for the virus. This pig later proved susceptible to the virus used for challenge inoculation.

Pigs on Which Group 2 Insects Fed.—Pigs 21, 25, and 27 apparently remained healthy after transfer fly feedings. Pig 21 was bitten by 6 flies (days 0 through 3) representing 3 species, including *T. lineola* (2 specimens), *T. quinquevittatus* (3 specimens), and *Tabanus nigrovittatus* Macquart (1 specimen). These flies had fed on virus-source pigs 9 and 22 (Table 3). Pig 21 remained healthy and later proved susceptible to the virus used for challenge inoculation.

Pig 25 was bitten by 2 *T. quinquevittatus* (day 0) which had fed on virus-source pig 23 (Table 3). Pig 27 was bitten by 2 *T. lineola* (day 0) which had

TABLE 3—Transmission Results Obtained by Transfer Feeding of Horseflies (Group 2) After a Twenty-Four-Hour Delay Following a Partial Blood Meal on a Hog Cholera-Infected Pig

Susceptible pig No.	No. of insects biting	Species of insect	Feeding period in days	Virus-source pig No.	Health status	Susceptible to challenge inoculation
21	2	*T. lineola*	4	9 and 22	Remained healthy	Yes
	3	*T. quinquevittatus*				
	1	*T. nigrovittatus*				
25	2	*T. quinquevittatus*	1	23	Remained healthy	No
27	2	*T. lineola*	1	23	Remained healthy	No

T. = *Tabanus.*

TABLE 4—Transmission Results Obtained by Transfer Feeding of Horseflies and Mosquitoes (Group 3) After Oviposition Delay Following a Blood Meal on a Hog Cholera-Infected Pig

Susceptible pig No.	No. of insects biting	Species of insect	Av. period of delay (days)	Virus-source pig No.	Health status	Susceptible to challenge inoculation
12	1	*T. calens*	8	1, 2, 3, and 16	Remained healthy	Yes
	10	*T. lineola*				
	2	*T. nigrovittatus*				
	24	*T. quinquevittatus*				
	2	*T. sulcifrons*				
20	3	*T. lineola*	15	1, 3, and 16	Remained healthy	Yes
	1	*T. nigrovittatus*				
	6	*T. quinquevittatus*				
	1	*T. sulcifrons*				
19	1	*T. nigrovittatus*	20	16	Remained healthy	Yes
7	7	*A. sollicitans*	10	3 and 16	Remained healthy	Yes
	1	*A. triseriatus*				
	5	*P. ferox*				

T. = *Tabanus; A.* = *Aedes; P.* = *Psorophora.*

fed on virus-source pig 23 (Table 3). Pigs 25 and 27 both apparently remained healthy; however, they later resisted challenge inoculation with the Ames strain of HCV at 7 days after inoculation. Tonsillar tissue from both pigs was test positive for HCV by the FATST 5 days after inoculation. However, body temperatures remained normal, and spleen was test negative for HCV by the FACCT. Before challenge inoculation, WBC counts for pigs 25 and 27 were 26,700 and 19,500/cmm., respectively. At the time of necropsy, WBC counts for both pigs were 16,200/cmm. Blood serums of these pigs at a 1:4 dilution (FASNT) caused approximately a 75% reduction in the plaque count of the test dose of HCV. Although this reduction was less than the 90% required to satisfy the criterion of the test, it indicated the presence of very low antibody levels.

Pigs on Which Group 3 Insects Fed.—Three pigs (No. 12, 19, and 20) on which horseflies fed and 1 pig (No. 7) on which mosquitoes fed all remained healthy throughout the study and later proved susceptible to challenge inoculation.

Pig 12 was bitten by 39 horseflies which had fed on virus-source pigs 1, 2, 3, and 16 (Table 4). Five species oviposited and subsequently fed on pig 12. Oviposition occurred from 5 to 12 days (mode, 7 days) after the initial blood meal. In general, most flies accepted a blood meal within 36 hours after oviposition. Species feeding on this pig included *T. calens* (1 specimen), *T. lineola* (10 specimens), *T. nigrovittatus* (2 specimens), *T. quinquevittatus* (24 specimens), and *T. sulcifrons* (2 specimens). Pig 12 remained healthy throughout the study and later proved susceptible to challenge inoculation.

Pig 20 was bitten by 11 horseflies representing 4 species, including *T. lineola* (3 specimens), *T. nigrovittatus* (1 specimen), *T. quinquevittatus* (6 specimens), and *T. sulcifrons* (1 specimen). These flies had fed on virus-source pigs 1, 3, and 16 (Table 4). Pig 20 remained healthy and later proved susceptible to challenge inoculation.

Pig 19 was bitten by a single fly, *T. nigrovittatus*, which had fed on a virus-source pig (No. 16) 20 days previously. This pig remained healthy and later proved susceptible to challenge inoculation.

Pig 7 was bitten by 13 mosquitoes representing 3 species, including *A. sollicitans* (7 specimens), *A. triseriatus* (1 specimen), and *P. ferox* (5 specimens). These mosquitoes had fed on virus-source pigs 3 and 16 (Table 4). Pig 7 remained healthy and later proved susceptible to challenge inoculation.

Control Pigs—All 4 pigs remained free of cholera throughout the study and later proved susceptible to challenge inoculation.

Challenge Inoculation.—Pigs 2, 9, and 23 (virus-source pigs) from the quarantine house had apparently recovered from HC. Tonsillar tissue collected at this time was test negative for all pigs (control, principal, and virus-source pigs) by the FATST, and WBC counts were more than 19,000/cmm. Pigs, with the exception of No. 2, 9, 23, and No. 25 and 27 (on which group 2 insects fed) developed HC. All pigs which contracted the disease had HCV in tonsils, body temperatures greater than 40.6 C., and leukopenia within 7 days after inoculation.

Typical lesions of HC (peripheral congestion of lymph nodes; petechiation of the epiglottis, heart, lungs, and urinary bladder; infarction of the spleen; and pneumonia) were observed on these pigs at necropsy. Spleen of all pigs contained HCV as determined by the FACCT, and serums were test negative at the 1:4 dilution for HC antibodies by the FASNT.

Pigs 2, 9, and 23 which had recovered from HC were resisting challenge infection at 7 days after inoculation, at which time they were killed. These pigs had high WBC counts, and tonsillar and splenic tissues were test negative for HCV by the FATST and FACCT, respectively. Serums of these pigs had antibodies against HCV, as determined by the FASNT both before and after challenge inoculation.

Discussion

The results of this investigation indicate that tabanids are capable of transmitting hog cholera. *Tabanus lineola* and *T. quinquevittatus* transmitted the disease, and 3 other *Tabanus* spp. were incriminated. The results of the 24-hour delayed transmission experiment were not conclusive. The resistance of 2 of these pigs to the challenge virus gives evidence that these pigs had probably been exposed to the HCV by the bite of the tabanids.

The results of the postoviposition feeding group represent some evidence that biological transmission of HCV does not occur in the species used in the present experiment. However, the data are too meager for final analysis. Most of the insects in this group had obtained only a partial meal on the virus-source pig, since these flies were also used in the immediate transfer experiments. The possibility therefore exists that these flies may not have obtained a sufficient quantity of virus to become infected. The amount of virus in the source pigs and available to the flies at the time of feeding was not determined. It is possible that some of the source pigs were not viremic when exposed to the flies.

Transmission by mosquitoes was not demonstrated; however, only 3 species participated in the postoviposition feeding test. In view of the frequency with which arboviruses are found associated with mosquitoes, further studies are needed to clarify their potential as biological vectors of HC.

Other kinds of flies may be capable of disseminating HCV. *Culicoides* spp., vectors of bluetongue virus, are suspects for

biological transmission. *Hippelates* spp., or eye gnats, may be carriers of HCV because of their predilection for mucous secretions; and as previously mentioned, houseflies and stable flies should also be considered.

When mosquitoes or other bloodsucking flies are extremely numerous in nature, mechanical transmission may contribute to explosive dissemination of a virus.[5] This type of transmission could occur in the ecologic situations in which localized epizootics of HC are found. Tabanids are usually numerous throughout much of the fly season; they readily feed on swine, are strong fliers, and are capable of experimentally transmitting the virus. Tabanids are prime suspects for natural dissemination of HCV.

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