INFECTION AND IMMUNITY, June 1996, p. 2295–2299 Vol. 64, No. 6
0019-9567/96/$04.00+0

Infection of Cesarean-Derived Colostrum-Deprived 1-Day-Old Piglets with *Arcobacter butzleri*, *Arcobacter cryaerophilus*, and *Arcobacter skirrowii*

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Received 29 November 1995/Returned for modification 22 January 1996/Accepted 26 March 1996

Neonatal piglets have been used as models to study human campylobacteriosis and helicobacteriosis. The purpose of this study was to determine the relative pathogenicities, on the basis of the duration of fecal shedding and colonization of tissues, of three *Arcobacter* species in 1-day-old cesarean-derived colostrum-deprived piglets. Two experiments were conducted. In experiment 1, two piglets each were infected per os with either *Arcobacter butzleri* ATCC 49616, *Arcobacter cryaerophilus* 1B ATCC 43159, *Arcobacter skirrowii* CCUG 10374, or the three field strains of *A. butzleri* (~5×10^9 CFU per piglet). Rectal swab samples were taken prior to infection and daily thereafter for up to 7 days. *Arcobacter* spp. were detected at least once in rectal swab samples of all but one of the experimentally infected piglets but not in the control. At necropsy, *A. butzleri* was recovered from the lung, kidney, ileum, or brain tissues of the four infected piglets which had received either the field strain or the ATCC type strain of *A. butzleri*. *A. cryaerophilus* 1B was detected in rectal swab samples for up to 7 days postinfection but was not cultured from tissues at necropsy. Arcobacters were detected in the rectal swab sample of the *A. skirrowii*-infected piglet only on day 3 postinfection; no isolates were obtained from tissues at necropsy. No gross pathological lesions were consistently noted in the experimentally infected piglets. In experiment 2, two piglets each were infected per os with *A. butzleri* ATCC 49616, *A. cryaerophilus* 1A ATCC 43158, *A. skirrowii* CCUG 10374, or the single *A. butzleri* field strain Yard J/c (~5×10^9 CFU per piglet). *Arcobacter* spp. were cultured from rectal swab samples of all but one of the experimentally infected piglets at least once. At necropsy *Arcobacter* spp. were cultured from the liver, kidney, ileum, or brain tissues of two of the four *A. butzleri*-infected piglets. However, no severe gross pathology was noted. These data suggest that *Arcobacter* spp., especially *A. butzleri*, can colonize neonatal pigs.

Arcobacter species (*Campylobacter cryaerophila*) display campylobacter-like motility and morphology but are aerotolerant and grow at 30°C (20). *Arcobacter butzleri*, *Arcobacter cryaerophilus*, and *Arcobacter skirrowii* have been recovered from humans and livestock (10, 13, 29) and from the environment (4). Consumption of contaminated water during travel and person-to-person transmission have resulted in human enteritis attributed to *A. butzleri* (14, 29). In one study, *A. butzleri* accounted for 16% of the *Campylobacter*-like isolates obtained from cases of diarrhea in Thai children (27). *A. butzleri* has also been cultured from diarrheic macaques with colonic lesions; however, no isolates were obtained from normal animals (1).

Aerotolerant campylobacter-like organisms have been isolated from aborted and normal porcine fetuses (7), sows with reproductive problems, and clinically healthy specific-pathogen-free pigs (3, 20–23). In one study, 90% of *Campylobacter* spp. isolated from fetuses and 78% of *Campylobacter* spp. isolated from porcine vaginal swabs were identified as *C. cryaerophila* (18). That strains from reproductively impaired and from normal sows were similar antigenically suggested that strains associated with infertility were opportunistic pathogens which colonize the fetus after placental damage (24). Late-term abortions (at 90 to 105 days of gestation), repeat breedings, and a "higher than usual rate of stillbirths" were observed in North Carolina pig herds from which *Arcobacter* spp. were recovered from fetal kidneys and livers. Antibiotic therapy provided limited improvement; an autogenous vaccine was effective (8).

Prior to 1992, the species of *Arcobacter* recovered from livestock were designated aerotolerant *Campylobacter*, *C. cryaerophila*, or *Campylobacter*-type Neill strain. Attempts to establish experimental infections in livestock have led to conflicting results in part because of the multiple species used. Experimental infection of sows with *C. cryaerophila* lowered conception rates (12). Intraperitoneal inoculation of 10 neonatal piglets (1 to 11 days old) with three strains of *Campylobacter*-type Neill (10^6 to 10^{11} CFU) produced no clinical disease; no campylobacter-like organisms were recovered from tissues (12). No symptoms and no lesions were observed 2 weeks after intraperitoneal inoculation of nongravid guinea pigs, rabbits, mice, and hamsters with aerotolerant *Campylobacter* (11). However, in another study utilizing eight different strains, *Campylobacter*-type Neill strain caused abortion in 7 of 15 guinea pigs (12). Inflammation followed inoculation of *C. cryaerophila* into the udder of a dairy cow (17). Yet no gross pathology was noted after experimental intravenous or conjunctival infections in calves, although arcobacters were cultured from tissues (30).

Because of the conflicting results obtained from previous attempts to establish experimental infection, a dependable model was sought in which to evaluate the pathogenicities of the *Arcobacter* species. Recent studies have shown that the arcobacters, campylobacters, and helicobacters are closely related (26, 29, 32). The clinical manifestations of both human enteritis and lymphofollicular gastritis have been replicated in neonatal piglets following inoculation with *Campylobacter je-*

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juni (2) and *Helicobacter pylori* (5, 6, 15, 16), respectively. Thus, it would be reasonable to assume that a laboratory animal model suitable for *C. jejuni* and *H. pylori* would also be susceptible to infection with *Arcobacter* spp. The goal of this study was to compare the relative levels of virulence of the three *Arcobacter* species in cesarean-derived colostrum-deprived piglets.

MATERIALS AND METHODS

Bacterial strains. The bacterial strains used in this study included *A. butzleri* ATCC 49616, *A. skirrowii* CCUG 10374, *A. cryaerophilus* hybridization group 1A ATCC 43158, *A. cryaerophilus* hybridization group 1B ATCC 43159, and three field isolates of *A. butzleri* (NADC 1722/f, 1736/c, and Yard J/c), which exhibited restriction fragment length polymorphism (RFLP) when hybridized with a 16S rRNA gene probe that is broadly reactive with all species of *Arcobacter* (32). The field isolates were recovered from a single farm in Iowa whose pigs had reproductive problems. Strains NADC 1722/f and NADC 1736/c were recovered from rectal swabs, and strain Yard J/c was cultured from wastewater collected from the concrete floor of a hog pen. Bacteria were grown (30°C, 48 h) on a biphasic medium consisting of brain heart infusion agar with 10% sheep blood overlaid with brain heart infusion broth. After incubation, the liquid phase was centrifuged (12,000 × *g*, 15 min, 4°C), and the pellet was washed in 0.1 M phosphate-buffered saline (PBS) (pH 7.4), recentrifuged, and resuspended in approximately 2 ml of PBS. Piglets received 4×10^9 to 1.6×10^{10} CFU of each strain in 1 ml per os by feeding tube. In experiment 1, piglets inoculated with the three field strains were given each strain in succession to a total of 3 ml.

Piglets. Two conventionally reared, non-specific-pathogen-free sows were cesarean sectioned at approximately the 115th day of gestation. The health status of the sows for any of the common swine enteric pathogens, such as transmissible gastroenteritis (TGE) virus or *Serpulina hyodysenteriae*, was not known. Cesarean-derived piglets were housed in sterile individual isolation units and fed SPF-LAC (Pet-Ag Inc., Elgin, Ill.) liquid diet three times daily. Rectal swab samples were taken daily, and piglets were observed daily for diarrhea, depression, inappetence, or other signs of disease. Piglets were removed from their cages for experimental inoculation and for daily rectal swabbing. Control animals were handled first in order to minimize cross-contamination.

In experiment 1, 1-day-old piglets ($n = 9$; two piglets per bacterial strain) were each given *A. butzleri* ATCC 49616, *A. skirrowii* CCUG 10374, *A. cryaerophilus* 1B ATCC 43159, or the three *A. butzleri* field isolates NADC 1722/f, 1736/c, and Yard J/c. Piglet 9 served as an uninoculated control. Piglets were euthanized and necropsied if they appeared moribund or necropsied if found dead. Surviving piglets were euthanized on day 7.

In experiment 2, 1-day-old piglets ($n = 10$; two piglets per bacterial strain) were given *A. butzleri* ATCC 49616, *A. skirrowii* CCUG 10374, *A. cryaerophilus* 1A ATCC 43158, or the farm isolate *A. butzleri* Yard J/c. Isolate Yard J/c was the predominant strain recovered in experiment 1 from animals infected with the three *A. butzleri* field strains. Piglets 9 and 10 served as uninoculated controls. Five piglets (one from each group) were euthanized on days 5 and 10 postinfection (p.i.).

Bacterial isolation. Rectal swab samples were taken prior to inoculation (day 0) and daily throughout the experiment. Each swab was placed into Ellinghausen, McCullough, Johnson, and Harris (EMJH) semisolid medium with 5-fluorouracil (100 μg/ml), incubated (30°C, 48 h), and examined by dark-field microscopy for the presence of motile arcobacters (7, 25). Because of the failure of *C. jejuni* or *Campylobacter coli* to grow in EMJH medium (30°C, 48 h), identification of *Arcobacter* spp. was based on growth in this selective medium and a determination of characteristic motility under dark-field microscopy as follows. A drop of EMJH semisolid medium was placed on a slide, and up to 30 microscopic fields (magnification, ×40) were scanned for typical *Arcobacter*-like, motile bacteria. At necropsy, portions of lungs, livers, kidneys, stomach walls or stomach contents, ilea, and brains were cultured in EMJH semisolid medium. After incubation (30°C, 2 to 4 days), cultures were examined by dark-field microscopy as described above.

In experiment 1, at necropsy, rectal, lung, and liver swab samples were plated onto blood agar and MacConkey agar for isolation of *Staphylococcus* spp., *Streptococcus* spp., and coliforms, including *Escherichia coli*. No attempt was made to culture for anaerobes or to isolate viruses.

RFLP analysis. RFLP analysis was used to verify the identities of the inocula with those of organisms recovered in the rectal swab samples or tissues of infected piglets in experiment 1 as follows. An aliquot (100 μl) from the EMJH enrichment medium was placed on a 0.45-μm-pore-size filter (Millipore Corp. Bedford, Mass.) on the surface of blood agar (1 h), the resultant filtrate was streaked for colony isolation, and plates were incubated (30°C, 48 h) microaerophilically (5% O_2, 10% CO_2, and 85% N_2). Bacterial chromosomal DNA was extracted as described previously (31). The RFLP patterns were obtained by hybridization of *Pvu*II-digested chromosomal DNA with a probe broadly reactive for all species of *Arcobacter*. The patterns of the inocula and at least one isolate randomly selected from each infected piglet were obtained, as described previously (32). Sizes (in kilobases) were obtained by using a *Hin*dIII digest of bacteriophage lambda as the standard.

Histopathology. Portions of the lungs, livers, kidneys, stomach walls, ilea, and brains were fixed in 10% buffered formalin, embedded in paraffin, sectioned (diameter, 6 μm), stained with hematoxylin and eosin or with silver, and observed by light microscopy.

TABLE 1. Summary of recovery of *Arcobacter* spp. from rectal swab samples and from tissues (brain, liver, stomach contents, small intestine, or lungs) at necropsy

Isolate	No. of positive pigs/total infected as determined from:	
	Rectal swab samples	Tissues
A. butzleri	8/8	6/8
A. cryaerophilus 1A	1/2	0/2
A. cryaerophilus 1B	2/2	0/2
A. skirrowii	3/4	0/4
None	0/3	0/3

RESULTS

As summarized in Table 1, *Arcobacter* spp. were detected at least once in the rectal swab samples of all but two of the experimentally infected animals. In contrast, *Arcobacter* spp. were not cultured from any of the rectal swab samples of control piglets. Arcobacters were recovered from tissues of six of the eight *A. butzleri*-infected piglets. Arcobacters were not recovered from the tissues of controls, and piglets experimentally infected with *A. skirrowii*, *A. cryaerophilus* 1A, or *A. cryaerophilus* 1B *Arcobacter* spp. were not recovered from the rectal swabs of any piglet prior to infection.

Experiment 1. As summarized in Table 2, the duration of shedding was prolonged in the four *A. butzleri* (piglets 1, 2, 7, and 8)- and in the *A. cryaerophilus* 1B (piglets 3 and 4)-infected animals. The *A. butzleri*-infected piglets (piglets 1, 2, 7, and 8) died within 24 h of appearing weak and inappetent. At necropsy, *A. butzleri* was recovered from kidney, brain, ileum, or lung tissues of these piglets. *A. cryaerophilus* 1B ATCC 43159 was recovered from rectal swabs of piglets 3 and 4 for 7 and 3 days, respectively, but it was not cultured from tissues at necropsy. Arcobacters were recovered once (day 2 p.i.) from the rectal swabs of one (piglet 6) of the two piglets infected with *A. skirrowii* CCUG 10374. No arcobacters were recovered from the rectal swabs of piglet 5, which on the fourth day after receiving the inoculum appeared weak and died. *A. skirrowii* was not isolated at necropsy from any of the tissues cultured.

RFLP patterns verified the identity of the *A. butzleri* inoculum with isolates recovered from the rectal swabs (4 days p.i.) and the kidney, lungs, brain, small intestine, and stomach contents of piglet 1 and from the rectal swabs (4 days PI) and brain of piglet 2. The RFLP pattern of the *A. cryaerophilus* 1B inoculum was identical to that of isolates recovered from the rectal swabs collected 4 days p.i. from piglets 3 and 4. Piglets 7 and 8 received the three *A. butzleri* field strains. Only strain Yard J/c, as determined by RFLP pattern (Fig. 1), was recovered from the lung, brain, and ileum of piglet 7 and from the kidney of piglet 8. The Yard J/c pattern was also seen in isolates cultured from rectal swabs taken 4 days p.i. from piglets 7 and 8. No other isolates from piglets 7 and 8 were available for analysis.

Gross examination. As summarized in Table 2, multiple lesions (1 to 2 mm in diameter) that appeared grossly to be small ulcers or erosions were visible in the mucosae of the glandular stomachs of the *A. butzleri*-infected piglets (piglets 2 and 7). Perforation of the glandular stomach was evident in one *A. skirrowii*-infected animal (piglet 5); the edges of the perforation appeared grossly to be inflamed. *Arcobacter* spp. were not recovered from the stomach contents of animals 2, 5, and 7. No gross lesions were seen in the *A. cryaerophilus* group

TABLE 2. Summary of recovery of *Arcobacter* spp. from experimentally infected piglets and postmortem findings

Experiment	Piglet	Inoculum	Necropsy (day p.i.)	Duration of shedding (days)	*Arcobacter*-positive tissue	Pathology determined by examination type:	
						Gross	Microscopic
1	1[a]	*A. butzleri*	4	4	Lung	None	Purulent pneumonia
					Kidney	None	None
					Brain	None	None
					Small intestine	None	None
					Stomach contents	None	Not examined
	2[a]	*A. butzleri*	5	5	Brain	None	None
					None	Stomach erosions	Purulent gastritis
					None	None	Purulent pneumonia
	3	*A. cryaerophilus* 1B	7	7	None	None	None
					None	None	Purulent pneumonia
	4	*A. cryaerophilus* 1B	7	3	None	None	Purulent pneumonia
	5[a]	*A. skirrowii*	4	0	None	Stomach perforation	Purulent gastritis
	6	*A. skirrowii*	7	1	None	None	None
	7[a]	*A. butzleri* three field strains	5	5	Lung	None	None
					Brain	None	Purulent meningitis
					Ileum	Reddening of ileum	Congested ileum
					None	Stomach erosions	Purulent gastritis
	8[a]	*A. butzleri* three field strains	3	3	Kidney	None	None
	9	None	7	0	None	None	Purulent pneumonia
2	1	*A. butzleri*	10	10	Lung	None	None
					Brain	None	None
					Ileum	Reddening of ileum and of cecum	None
	2	*A. butzleri*	5	4	None	Reddening of ileum	None
	3	*A. butzleri* Yard J/c	10	10	None	Reddening of ileum	None
	4	*A. butzleri* Yard J/c	5	5	Stomach	None	None
					Kidney	None	
					None	Reddening of ileum	None
	5	*A. cryaerophilus* 1A	10	0	None	Reddening of ileum and of cecum	None
	6	*A. cryaerophilus* 1A	5	2	None	None	None
	7	*A. skirrowii*	10	2	None	Reddening of ileum, spiral colon	None
	8	*A. skirrowii*	5	1	None	Reddening of ileum, spiral colon	None
	9	None	10	0	None	None	None
	10	None	5	0	None	None	Purulent pneumonia

[a] Animal found dead.

1B-infected (piglets 3 and 4), *A. skirrowii*-infected (piglet 6), *A. butzleri*-infected (piglets 1 and 8), and control (piglet 9) animals.

Histopathology. As summarized in Table 2, a mild-to-moderate acute lobular purulent pneumonia was evident in the lungs of piglets 1 through 4 and in the control (piglet 9). *Arcobacter* spp. were cultured from the lungs of the *A. butzleri*-infected piglet (piglet 1) but were not observed in situ. However, coccoid and rod-shaped bacteria were seen in silver-stained sections scattered throughout the exudate, but organisms resembling *Arcobacter* spp. (i.e., curved rods) were not observed. A mild-to-moderate acute purulent gastritis characterized by neutrophilic infiltration of the gastric submucosae was observed in the *A. butzleri* (piglets 2 and 7)- and in the *A. skirrowii* (piglet 5)-infected animals. Organisms morphologically resembling *Arcobacter* spp. were not observed in the silver-stained sections of the inflammed gastric submucosae of pigs 2 and 7. The stomach sections of piglet 5 were not silver stained. Arcobacters were not cultured from the stomach contents of piglets 2, 5, and 7. Piglet 7, which received the three *A. butzleri* field strains, had severe acute diffuse purulent meningitis in the cerebrum, cerebellum, and brain stem (Fig. 2). *Arcobacter* spp. were isolated from the brain of piglet 7. No other piglets had discernible lesions in the brain sections examined.

Experiment 2. The duration of fecal shedding was prolonged in the *A. butzleri*-infected piglets which received either the strain ATCC 49616 (piglets 1 and 2) or the field strain Yard J/c (piglets 3 and 4) (Table 2). Only in the *A. butzleri*-infected piglets were arcobacters detected in rectal swab samples for up to 10 days. Except for piglet 2, the *A. butzleri*-infected animals shed the organism until they were euthanized. For two of four *A. butzleri*-infected piglets, arcobacters were recovered from lung (piglet 1), ileum (piglet 1), brain (piglet 1), stomach (piglet 4), or kidney (piglet 4) tissues at necropsy. Arcobacters were not recovered from the tissues of *A. butzleri*-infected piglets 2 and 3. Although arcobacters were cultured from the rectal swabs of an *A. cryaerophilus*-infected piglet (piglet 6), no recoveries were made from tissues. Arcobacters were not cultured from tissues of the *A. skirrowii*-infected piglets (piglets 7 and 8), although the organisms were cultured from the rectal swab samples at least once. *Arcobacter* spp. were not cultured from the rectal swab samples or tissues of control piglets (piglets 9 and 10).

Gross examination. Seven piglets displayed some reddening of the ileum (piglets 1 to 5, 7, and 8). The reddening extended to the ceca (piglets 1 and 5) and to the spiral colons (piglets 7 and 8). No gross lesions were evident in piglet 6 and in control piglets 9 and 10.

Histopathology. No diagnostic lesions were seen in sections of lung, liver, spleen, kidney, small intestine, stomach wall, and brain taken from all the experimentally infected piglets and one control (piglet 9). There was a mild purulent pneumonia in a control piglet (piglet 10).

Staphylococcus saprophyticus, as described previously for cesarean-derived colostrum-deprived piglets (19), was cultured from the rectal swab samples, livers, lungs, kidneys, or stomachs of all animals in both experiments, including the control piglets.

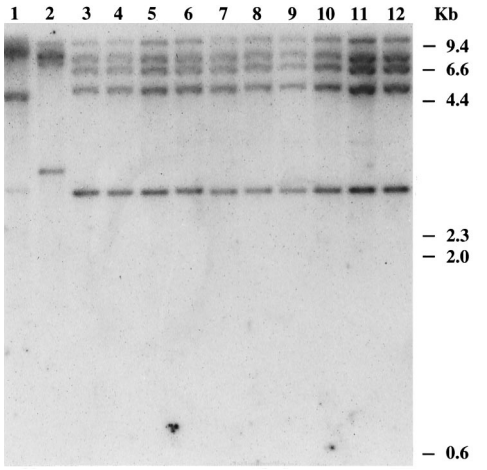

FIG. 1. DNA hybridization patterns of *Pvu*II-digested DNA of *Arcobacter butzleri* field strains 1736c (lane 1), 1722f (lane 2), and Yard J/c (lane 3) inoculated into piglets 7 and 8 in experiment 1. For piglet 7, only field strain Yard J/c was recovered from rectal swab samples 5 days p.i. (lanes 4 and 5) and from the lung (lane 6), ileum (lane 7), intestine (lane 8), and brain (lane 9). For piglet 8, field strain Yard J/c was detected in the rectal swab sample 3 days p.i. (lanes 10 and 11) and from the kidney at necropsy (lane 12). Molecular size markers are noted at the right.

DISCUSSION

Aerotolerant campylobacters, now designated *Arcobacter* spp., have been described in normal pigs and pigs with reproductive problems as well as in normal and aborted porcine fetuses. In a study of livestock abortion cases from which *Arcobacter* spp. were cultured, *A. cryaerophilus* 1A (20%), *A. cryaerophilus* 1B (66%), and *A. butzleri* (9%) were recovered from fetal tissues (25). Taken together, these data suggested that arcobacters are capable of colonizing neonatal piglets. Invasion into HEp-2 cells and a rat ileal loop model have been described to evaluate the pathogenic mechanisms of *A. cryaerophilus* (9). However, an in vivo model is needed to monitor fecal shedding patterns and colonization of tissues.

In these studies, cesarean-derived colostrum-deprived piglets experimentally infected with *A. butzleri* shed arcobacters in their feces for up to 10 days, which indicates intestinal colonization and multiplication of the organism. Piglets shed *A. butzleri* in their feces until necropsy, at which time the organism was cultured from the ilea, livers, kidneys, or brains of six of the eight *A. butzleri*-infected piglets. Although the number of experimental animals was small, that *A. cryaerophilus* 1B was detected in the feces more frequently than *A. cryaerophilus* 1A may indicate its greater pathogenicity. The short duration of fecal shedding observed in piglets inoculated with *A. cryaerophilus* 1A and *A. skirrowii* may indicate either a less invasive species or loss of virulence upon laboratory adaptation. *A. skirrowii*, *A. cryaerophilus* 1A, and *A. cryaerophilus* 1B were recovered from rectal swabs but were not recovered from tissues of any of the experimentally infected piglets. This may suggest failure to penetrate the intestinal barrier. Thus, on the basis of duration of shedding and recovery of organisms at necropsy, *A. butzleri* may be relatively more virulent than either *A. cryaerophilus* 1A, *A. cryaerophilus* 1B, or *A. skirrowii*.

RFLP patterns of the inoculum were compared with the strains recovered from infected animals in experiment 1. In

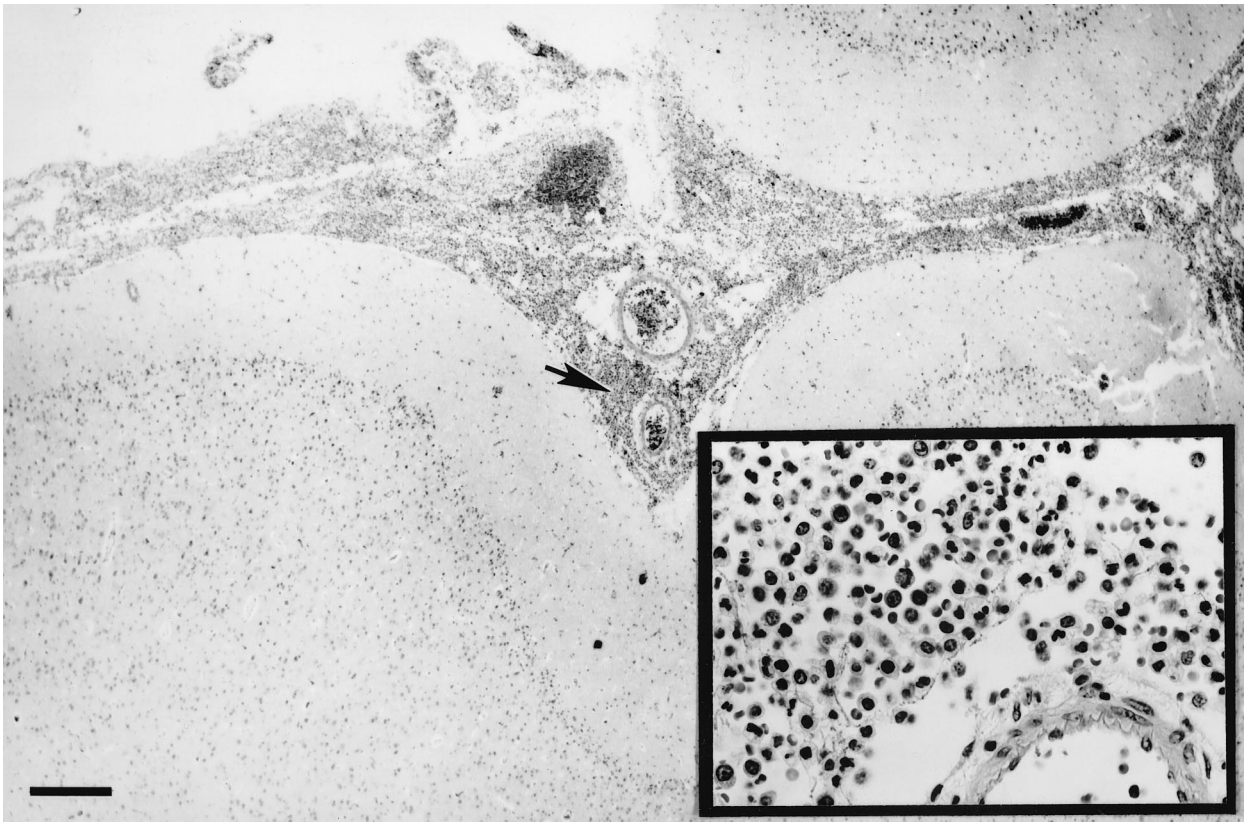

FIG. 2. Photomicrograph of purulent exudate in the cerebral meninges of *A. butzleri*-infected piglet 7 from experiment 1. Bar, 100 μm. Sections were stained with hematoxylin and eosin. The arrow indicates the area magnified in the inset (magnification, ×20).

order to determine possible virulence differences, three field strains of *A. butzleri* recovered from an Iowa pig farm with reproductive problems were given to piglets. The single strain Yard J/c predominated in the 10 isolates available for study from rectal swabs and tissues. This suggested that strain Yard J/c may be better adapted to swine intestines than the two other field strains examined. However, when the three strains were inoculated into biphasic culture for 2 days, to simulate passage in the pig, and an aliquot was subsequently placed in the EMJH enrichment broth for four days, 12 of the 13 randomly selected colonies displayed the strain Yard J/c pattern. This suggests that the in vitro enrichment methods used to recover *Arcobacter* spp. may have preferentially selected for the *A. butzleri* Yard J/c strain.

Although sows were cesarean sectioned on approximately the 115th day of gestation, the piglets used in experiment 1 appeared to have been younger than those used in experiment 2. That the mortality observed in experiment 1 in five of eight piglets, four of which received *A. butzleri*, was not observed in the second trial may be attributed to the greater susceptibility of the piglets used initially. *Arcobacter* spp. were recovered in rectal swab samples and from tissues after enrichment in EMJH medium, but were not visible in the tissue sections of any lesions observed. Thus, no correlation could be consistently made between the recovery of *Arcobacter* spp. from tissues and gross or histopathological lesions.

The results from this study indicate that neonatal swine can be infected with *Arcobacter* spp. and suggest that, on the basis of fecal shedding and reisolation from tissues, *A. butzleri* is better able to colonize piglets than either *A. skirrowii*, *A. cryaerophilus* 1A, or *A. cryaerophilus* 1B strains. It is of interest that in a parallel study, *A. butzleri* ATCC 49616 did not colonize 3-day-old chicks, as determined from cloacal swabs and cecal culture (30a).

Neonatal piglets have been used to study the pathogenicities of *C. jejuni* (2) and *H. pylori* (5, 6, 15, 16). It is possible that the virulence attributes of *A. butzleri* associated with human infections also may be evaluated in the porcine model.

ACKNOWLEDGMENTS

The veterinary assistance of LaWayne Nusz in performing the cesarean sections and in assisting in the necropsies is acknowledged. The technical assistance of Roger Spaete, Ellen Bates, and Sydney Hartman of the NADC Animal Resources Division is appreciated. We thank Sharon Franklin for her technical support.

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Editor: P. E. Orndorff