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Evolutionary Background Entities at the Cellular and Subcellular Levels in Bodies of Nonhuman Vertebrate Animals §

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Abstract

During the past two decades, it has been revealed by culture-independent approaches that individual bodies of normal animals are actually inhabited by subcellular viral entities and membrane-enclosed microentities, prokaryotic bacterial and archaeal cells, and unicellular eukaryotes such as fungi and protists. However, the relationship between animals, including human beings, and their environmental micro-entities or microorganisms reflected in such phenomenon cannot be accounted for by our traditional pathogenic recognition in human medicine and veterinary medicine. It is well known that as one of humans' environmental macroorganisms, some nonhuman animal species were initially concerned for their practical values in nutrition, medicine, and economy, and have been studied within the scope of traditional macrobiology for a long time. Our primary interest in the microorganisms of nonhuman animals has been for their potential risk of zoonotic transmission of pathogenetic bacteria and viruses from animals to humans. In recent novel evolution theories, the relationship between animals and their environments has been deciphered to be the interaction between animals and their environmental evolutionary entities at the same and/or different evolutionary levels;[1-3] and evolutionary entities of lower evolutionary levels are hypothesized to be the evolutionary background entities of entities at higher evolutionary levels.[2-3] As more and more pathogenic microorganisms are identified in diseases of nonhuman animals, it is becoming the first priority to elucidate the normal ecological and evolutiological relationships between microorganisms and nonhuman macroorganisms for the development of our existing theoretical systems of modern human medicine and veterinary medicine. In this paper, I try to briefly review the evolutionary background entities at the cellular and subcellular levels for several selected nonhuman vertebrate animal species.

Key words: Evolutionary background entities (EBE); Evolution; Diversity; Animals; Symbiosis; Eukaryote; Prokaryote; Vertebrate; Mammals; Bacteria; Archaea; Fungi; Viruses; Membrane-enclosed microentities

CONTENTS

1. Background

Pasteur’s Germ Theory, Cell Theory, and Koch’s Postulates at the end of the 19th century established a pathogenic relationship between prokaryotic bacterial cells and eukaryotic host cells of humans and nonhuman animals, which, since then, has become one of the theoretical cornerstones of our modern human medicine and veterinary medicine. However, such a pathogenic relationship at the cellular level hadn’t been linked with Darwin’s evolution theory until bacterial antibiotic resistance gradually became a clinical problem in the 1960s-1970s [4-8] and the emergence of multiantibiotic-resistant strains of bacterial cells was finally accounted for to be the consequence of natural selection, which, for the first time from a clinical perspective, combined Darwin’s evolution theory with modern medicine.[9,10]

During the past two decades, studies using culture-independent approaches have revealed that normal individual bodies of macroorganism such as humans, nonhuman animals, and plants are actually not only constituted by host eukaryotic cells, but also inhabited by prokaryotic bacterial cells and unicellular eukaryotes such as fungi and protists, which the traditional recognition of pathogenic relationship between prokaryotic bacterial cells and eukaryotic host cells of humans, nonhuman animals, and plants cannot account for, as Augustin and colleagues pointed out “for a long time, the main purpose of microbiology and immunology was to study pathogenic bacteria and infectious disease; the potential benefit of commensal bacteria remained unrecognised.” [11] Modern Darwinian evolution theories propose that there is an evolutionary relationship between prokaryotic cells and eukaryotic cells. In recent papers,[1,2] a new notion has been proposed: (i) animals are not only inhabitants of natural habitats, but also are the “niches” or “habitats” of evolutionary micro-entities including bacteria, viruses, and fungi; (ii) the interaction between an evolutionary entity and its environment is actually the interaction between the entity and its environmental evolutionary entities at the same and/or different evolutionary levels; and (iii) entities of lower evolutionary levels are the evolutionary “background entities” of entities at higher evolutionary levels.[1,2]

Nonhuman animals are one of humans’ environmental macro-entities. Our initial interest in the microorganisms of nonhuman animals is the potential risk of zoonotic transmission of pathogenetic bacteria and/or their toxins from animals to humans.[12-19] Later, such attention has been extended to the potential risk of zoonotic transmission of antimicrobial resistance and animal viruses to humans,[20-24] viral transmission to biological experiment systems,[25] pathogenic bacteria and viruses in nonhuman animals,[26-32] alterations of microbial compositions during depuration and storage,[33-37] antibacterial function,[38] leech therapy,[39-42] and biological control.[43-45] However, from the fimpological perspective, the following questions such as “how do nonhuman animal species interact at different evolutionary levels?” “how do nonhuman animal species interact with humans at different evolutionary levels?” and “what are the evolutionary background entities of nonhuman animals?” are urgent to be answered; moreover, among which, knowing what constitutes the evolutionary background entities is one of prerequisites. In this paper, I try to briefly review the evolutionary background entities at the cellular and subcellular levels for several selected nonhuman animal species.

2. Mammalia in the Phylum Chordata

To date, most data of mammalian evolutionary background entities has come from studies on mammalian fecal microbiota, except in human beings. And mammal species-specific variations, diversities, and dynamics of microbes have been revealed mainly in the gut in recent studies. For instance, Ley and colleagues compared the fecal microbiota of humans and fifty-nine other mammalian species, and found that the fecal bacterial diversity increases from carnivore to omnivore to herbivore.[46] Leser and Molbak revealed that Firmicutes and Bacteroidetes were two dominant prokaryotic cellular entities in the guts of all mammal species.[47] Moreover, Furet and colleagues compared fecal microbiota in farm mammals, such as rabbits, goats, horses, pigs, sheep, and cows with that of humans and showed that Bacteroides/Prevotella, Clostridium coccoides, and Bifidobacterium were three dominant bacterial groups in animal species, with species-specific variations.[48] Traditionally, the pathogenic role of microorganisms is our major research attention. However, during the past decades, the relationships between microorganisms and mammal species (except human beings) have been gradually studied from the ecological and evolutiological perspective, although it is still in its infancy.

2.1 Artiodactyla

2.1.1 Swine in the genus Sus

Bacteria

Breastmilk

Bacterial communities in pigs have been investigated from different anatomic perspectives during the past decades. Diverse bacterial species belonging to the genera of Lactobacillus, Enterococcus and Weissella were detected in sow milk.[49,50] For more information, please see the recent review.[51]

Gastrointestinal tract

Bacterial culture-based methods and cultivation-independent microbial molecular analysis of gut bacteria have indicated that the microbial community harboring the gastrointestinal tract in pigs is dynamic, diverse, developmental, and unknown in many aspects.[52,53] Studies have revealed that bacterial species in the guts of normal pigs belong to the phyla Firmicutes, Bacteroidetes, Proteobacteria, Fusobacteria, Actinobacteria, and Synergistetes, and the different genera including Arcobacter, Bacteroides, Butyrivibrio, Eubacterium, Lactobacillus, Peptostreptococcus, Selenomonas, and Streptococcus.[54-56] Despite pathogenic Arcobacter spp. found in aborted pig fetuses,[57,58] some Arcobacter species including Arcobacter butzleri, Arcobacter cryaerophilus, and Arcobacter skirrowii in the genus Arcobacter of the Campylobacteraceae were isolated from the feces of healthy pigs,[56] and their establishment was proposed to be the consequence of vertical and horizontal transmission in pigs.[59,60] The number of lactobacilli in the esophagus, stomach, duodenum, jejunum, and ileum of piglets increased 10-fold during their first ten postnatal days.[61] Lactobacillus sobrius and Lactobacillus reuteri were predominant in the ileal samples of 2-day-old piglets, and after starting weaning between 21 and 28 days of life, the predominant microbiota changed in composition and metabolic activities with the emergence of clostridia and E. coli in the gut of the piglets.[53] Lactococcus lactis, which was altered to express biologically active epidermal growth factor stimulated the intestinal development of early-weaned pigs.[62] Moreover, differences between luminal and mucosa-associated microbiota have been revealed in pigs.[63,64]

Experimental studies have shown that the postnatal colonization of normal gut microbiota in piglets is influenced by different rearing environmental factors.[65,66] Even in adult pigs, the composition of their microflora and metabolic activities in the gastrointestinal tract are dynamic and easily affected by various cellular, subcellular, and molecular entities in food, such as antibiotics,[67,68] probiotics,[69,70] yeast,[71] dietary protein,[72] dietary fiber,[72,73] prebiotic oligosaccharides,[74] the weaning diet,[75] organic acids including formic acid and gluconic acid,[76,77] plant extracts,[78,79] flaxseed,[80] raw potato starch,[81] and trace elements.[82,83]

Reproductive system

Diverse bacterial species were isolated from boar semen samples and they belonged to the genera Escherichia, Proteus, Serratia, Enterobacter, Klebsiella, Staphylococcus, Streptococcus, and Pseudomonas.[84] Moreover, diverse bacterial species were isolated from the anterior vagina of healthy sows, and those belonging to the genera Streptococcus, Escherichia, Staphylococcus, and Corynebacterium were predominant.[85]

Viruses

Shan and colleagues showed that healthy piglets normally have different mammalian viruses and 99% of them are RNA viruses belonging to the families Picornaviridae, Astroviridae, Coronaviridae, and Caliciviridae, while the remnants are DNA viruses belonging to the families Circoviridae and Parvoviridae.[23] Moreover, four classes of porcine endogenous retroviruses (PERV-A, PERV-B, PERV-C, and PERV-E) have been identified in the pig genome.[86-88] In addition, swine torque teno virus (TTV) has been detected in swine colostrum.[51,89]

Exosomes

As one of membrane-enclosed microentities, exosome have been detected in boar semen [90] and in porcine milk.[92,91] Membrane-enclosed micro-entities are structurally subcellular and have been discussed from the fimpological perspective recently.[93]

2.1.2 Cow, Cattle, and Buffalo in the genera Bos and Bubalus

Bacteria

Breastmilk

The bacterial species in cow milk are an important and interesting natural phenomenon that has attracted increasing attention in recent decades. For more information, please see the recent review.[51]

Gastrointestinal tract

Studies have clearly shown that the bacteria within the gut of cows consist of unattached bacteria and bacteria that attached to the epithelium.[94-97] Unattached bacteria can be further classified into bacteria found in rumen fluid and bacteria associated with food particles.[98] Bacterial species in the genus Arcobacter, including Arcobacter butzleri, Arcobacter cryaerophilus, and Arcobacter skirrowii, which are members of the Campylobacteraceae, have been detected in meat and fecal samples of healthy cattle.[99,100] Bacterial diversity in rumen fluid has been shown in several studies,[101,102] and bacterial species belong to the phyla Bacteroidetes, Firmicutes, Spirochaetes, and Proteobacteria.[102,103] Russell and Rychlik showed that in the rumen, there are more than 10^{10} bacterial cells per gram of contents, including various bacterial species such as Ruminococcus albus, Ruminococcus flavefaciens, Fibrobacter succinogenes, Butyrivibrio fibrisolvens, Streptococcus bovis, Lactobacillus fermentents, Peptostrptococcus anaerobius, Selenomonas ruminantium, Prevotella ruminicola, Clostridium aminophilium, Fusobacterium necrophorum, and Megasphaera elsdenii.[104] Moreover, some bacterial species are believed to be animal species-specific bacteria.[102] In addition, the ruminal bacterial composition has been shown to be influenced by some environmental factors, such as high temperature and humidity,[105] ruminal acidification,[106] diets, and time of feeding.[107-110] Fecal bacterial communities have also been studied recently.[109,111] Ziemer reported that the fecal bacterial species of cows belong to the phyla Firmicutes, Bacteroidetes, Proteobacteria, Actinobacteria, Synergistetes, and Fusobacteria.[111] Inter-individual variation in the fecal bacterial community has been observed in dairy cows.[109]

Reproductive tract

Chlamydophila abortus, Chlamydophila pecorum, Mycoplasma bovis, Mycoplasma bovigenitalium, and Ureaplasma diversum have been detected in genital tract swabs of dairy cattle.[112] Fungal species including Penicillium and yeast have been isolated from the vaginas of pregnant and non-pregnant healthy cows.[113] Actinomyces pyogenes, Bacteroides spp., and Fusobacterium necrophorum are predominant species and have been isolated from the uteri of post-partum dairy cows.[114] Moreover, Bekana and colleagues found an interesting phenomenon: the postpartum intrauterine bacterial species in dairy cows disappear from the uteri within three weeks of postpartum.[114] McDougall showed that the bacterial species isolated from the uteri of dairy cows failing to conceive or maintain pregnancy are diverse and belong to the genera Arcanobacterium, Escherichia, Fusobacterium, Haemophilus, and Streptococcus.[115]

Archaea

Methanogenic archaeal species such as Methanobrevibacter ruminantium, Methanobrevibacter millerae, Methanobrevibacter smithii, Methanobrevibacter wolinii, Methanobrevibacter gottschalkii, Methanosphaera stadtmanae, and Methanomicrobium mobile have been detected in the rumen of mammal species including cows, cattle, and Yak in the genera Bos, Bubalus, and Syncerus;[116-121] and the ruminal archael variation has been observed between yak and cattle.[122] Moreover, the archael communities in the rumen are affected by diet type.[121,123]

Fungi

Studies have shown that there are diverse fungal species in cow milk and they belong to different fungal genera. For more information, please see the recent review.[51]

Viruses

Our knowledge of the relationship between viruses and cow, cattle, or buffalo is mainly based on our understanding of viral pathogenesis. For example, bovine papular stomatitis virus and orf virus are etiologic agents of cattle diseases.[124,121] However, non-pathogenic viral species or strains have also been found in cows, cattle, or buffalo. Bovine herpesvirus type 5 (BHV-5) was isolated from samples of frozen semen and fresh semen from apparently healthy bull.[125] Genes of bovine endogenous retrovirus K1 (BERV-K1) and BERV-K2 were identified in the bovine genome, [126] and the expression of endogenous retrovirus elements was recently identified in bovine trophoblastic cells.[127] Bovine papillomavirus (BPV) DNA was detected in BPV-infected cattle blood, reproductive and embryonic tissues, as well as in milk, urine, seminal fluid, and spermatozoa.[128].

Cattle have been showed to be persistently infected with bovine viral diarrhea virus 1 (BVDV 1), a viral strain in the pestivirus genus of the Flaviviridae family.[129-131] Passler and colleagues found that host species-crossing transmission of BVDV could occur between cattle and deer,[129,130] between cattle and goats, or among goats.[132] Goats-specific BVDV can be vertically transmitted from parental goats to their offspring.[132] Moreover, torque teno viruses (TTV) were detected in the milk of water buffaloes (Bubalus bubalis).[133]

Exosomes

Exosomes were isolated from cow milk.[134-137]

2.1.3 Sheep or Goat in the genera Ovis and Capra

Bacteria

Breastmilk

Diverse bacterial species, including Enterococci, Lactococci, Staphylococci, Streptococci, and Lactobacilli, were identified in sheep and goat milk. For more information, please see the recent review.[51]

Gastrointestinal tract

Diverse bacterial species were identified in the rumen of sheep. For example, a diverse range of hyper-ammonia-producing bacteria were detected in the rumen of sheep,[138] and a diverse group of proteolytic and peptidolytic bacteria, such as Clostridium spp. were present in the rumen of sheep and goats.[139] The intra-species variation of sheep in the concentration of cellulose-digesting bacteria in the rumen microbial population was great and influenced by the change in ration.[140] Moreover, two previously uncultured Gram-positive bacterial strains with sizes ranging from 0.5 to 0.8 μm were isolated from the sheep rumen.[141] Bacteria within the gut of sheep consist of unattached bacteria and adherent bacteria that attached to the epithelium.[142-144]

Differences between luminal and mucosa-associated microbiota are a special question in studies on gut-associated bacteria in goats. Three decades ago, Bauchop, Clarke and Newhook already showed that a specific bacterial species existed on the rumen epithelial surface.[142] Using bacterial culture methods, Mead and colleagues isolated 161 strains of adherent bacteria from the rumen epithelial surface of sheep, and the bacterial species belonged to the genera Butyrivibrio, Bacteroides, Selenomonas, Succinivibrio, Streptococcus, Propionibacterium, Treponema, Eubacterium, Lachnospira, Ruminococcus, and Lactobacillus.[144,145] Moreover, Mosoni and colleagues showed that cellulolytic bacteria, such as Fibrobacter succinogenes, Ruminococcus albus, and Ruminococcus flavefaciens in the rumen of sheep were decreased by adding fermentable carbohydrates in the diet, while adding live yeast resulted in a significant increase in Ruminococci.[146]

Reproductive tract

Bacterial species in the genera Staphylococcus, Streptococcus, and Micrococcus, and Mycoplasma were isolated from the vaginal tract of goats.[147] Escherichia coli, Staphylococcus aureus, and Micrococcus spp. were isolated from the postpartum uteri of goats.[147,148]

Archaea

Archaeal species including Methanobrevibacter gottschalkii and Methanobrevibacter millerae in the Methanobrevibacter genus were identified in the rumen contents of sheep.[149,150] Snelling and colleagues showed that the rumen archaeal communities of sheep in Scotland belong to several genera, including Methanobrevibacter, Methanosphaera, and Methanobacteria within the order of Methanobacteriales.[151] Ohene-Adjei and colleagues revealed that supplementation of ruminant diets with essential oils increased the diversity of methanogenic archaea.[152]

Fungi

Fungal species in sheep and goat were studied in milk and cheeses samples and belonged to diverse fungal genera including Aspergillus, Candida, Cladosporium, Cryptococcus, Debaryomyces, Engyodontium, Fusarium, Geotrichum, Kluyveromyces, Malassezia, Mucor, Penicillium, Pichia, Torrubiella, Trichosporon, and Rhodotorula.[51]

Viruses

Ovine herpesvirus-2 DNA has been detected in the nasal secretions from all lambs during the first two postnatal months.[153] proviral-DNA of caprine arthritis-encephalitis virus was found in non-spermatic cells, the seminal plasma, and the periphery of the epididymal epithelium from male goat that were naturally infected with caprine lentivirus.[154] Several strains of Bovine papular stomatitis virus and orf virus in the genus Parapoxvirus of the Poxviridae, were isolated from goat and sheep.[124] Endogenous betaretroviruses were identified in the ovine genome and they were found to be highly related to two exogenous oncogenic viruses (Jaagsiekte sheep retrovirus (JSRV) and Enzootic nasal tumor virus).[155,156] These endogenous retroviruses were highly expressed in the ovine uterus.[156] Viruses in milk samples from sheep and goats are especially interesting and they have been reviewed recently.[51]

2.1.4 Deer species in the genera Rangifer, Cervus and Capreolus

Bacteria

Our knowledge of the relationship between deer species and viruses is mainly from the recognition of bacterial pathogenesis. For example, Mycobacterium avium subsp. paratuberculosis was associated with paratuberculosis in a captive tundra reindeer (Rangifer tarandus tarandus).[157] Anaplasma spp. involves sudden death of reindeer.[158] Bacteroides, Fibrobacter, Streptococcus, Clostridium, and Prevotella were found to be the dominant members of bacterial community in the rumen fluid of reindeer and the rumen and fecal bacterial composition was influenced by environmental factors such as foods and seasons.[159-161] In the fecal samples of semi-domesticated reindeer (Rangifer tarandus tarandus), Escherichia coli, and Enterococcus species were dominant members of their bacterial communities, and Yersinia species and Campylobacter species were also detected.[12] Moreover, E. coli and Yersinia species were shown not being pathogenic strains.[12] Oscillospira species were detected in the rumen of Norwegian reindeer.[162] Bacterial species in the Prevotella genus were dominant in the rumen of domestic Sika deer (Cervus nippon).[159] Mycobacterium spp. were isolated from reindeer in northern China.[163] Escherichia fergusonii were isolated from the fecal samples of a captive reindeer herd.[164] Clostridium perfringens was isolated in the fecal samples from free-ranging reindeer.[165]

Campylobacter hyointestinalis subsp. hyointestinalis was the only Campylobacter species isolated from reindeer (Rangifer tarandus).[166] Mycoplasma ovis was detected in blood samples from white-tailed deer (Odocoileus virginianus).[167] The geographic variation of rumen bacterial diversity has been described in Svalbard reindeer (Rangifer tarandus platyrhynchus).[168] The rumen bacterial community of the reindeer contained bacterial species belonging to the phyla Firmicutes, Bacteriodetes, Verrucomicrobia, and Proteobacteria;[169] bacterial species from the phyla Bacteroidetes, and Firmicutes were dominant in the rumen,[168,170] and the seasonal and geographic dynamics of the rumen bacterial composition were observed in reindeer.[168] Moreover, the rumen bacterial community of reindeer was influenced by probiotic bacteria.[171]

Archaea

Ruminal archaea belonging to the orders Methanobacteriales, Methanomicrobiales, and Methanosarcinales were detected in Svalbard reindeer.[172]

Protozoal fauna

Reindeer-specific Entodinium spp., such as Entodinium anteronucleatum, Entodinium bicornutum, Enoploplastron confluens, and Epidinium gigas, were described in the ciliate fauna by Imai and colleagues.[173]

Viruses

Our knowledge of the relationship between deer species and viruses is mainly based on the recognition of viral pathogenesis. For example, cervid herpesvirus 2 causes infectious keratoconjunctivitis,[174,175] parapoxviruses cause contagious stomatitis and contagious ecthyma,[176,177] cervid herpesvirus 2 causes respiratory and fetal infections in semidomesticated reindeer,[178] West Nile virus causes reindeer lymphohistiocytic encephalomyelitis,[179] and Orf virus causes papular stomatitis.[180] However, some strains of pestivirus, papillomavirus, alphaherpesvirus, betaherpesvirus, and gammaherpesvirus have also been detected in the rumen, trigeminal ganglia, nasal swabs, fetal tissues, blood, and eye swabs of healthy reindeer (Rangifer tarandus tarandus).[174,175,181-184] Rimstad, Krona and Hyllseth showed that reindeer herpesvirus is a species-specific viral group within the family Herpesviridae.[185]

2.2 Perissodactyla

2.2.1 Horses in the genus Equus

Bacteria

Even in recent years, the pathogenic roles of microbial entities in their relationship with horses are still a major concern. For example, etiological actinomycetes species have been found to cause nocardioform placentitis-mediated abortions in horses,[186] Salmonella Oranienburg is a pathogenic agent in Salmonella infection,[187] and Clostridium perfringens acts as an etiological factor in severe colitis in horses.[188] Some investigations have revealed that bacterial species normally exist in different anatomic locations of healthy horses. For example, microorganisms including bacteria and fungi have been detected or isolated from normal equine synovial fluid,[189] stomach,[190] intestinal tract,[191,192] and blood,[193]

Skin

An interesting finding reported by Cook and colleagues has revealed that cocci were found on the surface and within noninflamed hair follicles of skin biopsy specimens from horses with healthy skin.[194]

Conjunctiva

Johns and colleagues studied the bacterial community in the normal conjunctiva of horses and found that bacterial species in the genus Acinetobacter were the most dominant. [195]

Gastrointestinal tract

The diversity and dynamics of the gut microbial community in horses have been revealed in recent years. Many bacterial species have been isolated from different regions or segments of the gastrointestinal tract of horses, such as the esophagus, stomach, small intestine, ileum, and colon;[190,192,196-198] and the majority of the isolated bacterial species belong to the phyla Firmicutes, Verrucomicrobia, Proteobacteria, Bacteroidetes, Actinobacteria, and Cyanobacteria.[196,197,199-201]

Bacteria and fungi are normally found to cover the epithelium of the equine esophagus, in which, bacteria species belonging to the genera Streptococcus, Prevotella, Fusobacterium, and Actinobacillus are dominant.[197] And the bacterial communities in the stomach of feral horses mainly consist of Lactobacillaceae, Streptococcaceae, Veillonellaceae, and Pasteurellaceae.[190] Bacterial species detected in biopsy specimens from the gastric mucosa mainly belong to the genera Actinobacillus, Moraxella, Prevotella, and Porphyromonas.[196] The core microbiota species in the feces of healthy Irish thoroughbred racehorses includes Clostridium, Fibrobacter, Faecalibacterium, Ruminococcus, Eubacterium, Oscillospira, Blautia Anaerotruncus, Coprococcus, Treponema, and Lactobacillus spp.[199] Moreover, the gut core bacterial community has a regional characteristic in its composition.[192] Steelman and colleagues found that at the individual level of horses, there is individual variation in bacterial communities.[200] Bacteria were found to adhere to the apical membrane of the enterocytes in the ileum of horses under scanning electron microscopy.[198]

Bacterial communities in different anatomic locations of the gut of horses vary not only in their composition, but also in their metabolic activities.[201,202] For example, the fatty acids and purine profiles of bacterial populations in the cecum are different from those in the colon.[202] Age-related changes in the bacterial community have been detected in the feces of foals.[203] Moreover, alterations in fecal bacterial composition are accompanied by changes of in metabolic activities.[204] Changes in cecal and fecal bacterial communities after dietary alterations have been described in horses.[205-208] In addition, antimicrobial-resistant bacteria are another reason for our studies on horse-associated bacterial species.[209-212]

Reproductive tract

Many bacterial species belonging to the genera Taylorella, Streptococcus, Lactobacillus, Enterococcus, and Staphylococcus have been isolated from the reproductive tracts of horses.[213-216] the bacterium Taylorella asinigenitalis in the phylum Proteobacteria was isolated from the reproductive tracts of mares.[213] Aerobic bacterial species without any potential pathogens were isolated from vaginal swab specimens of normal mares.[217] Moreover, Streptococcus zooepidemicus is normally isolated from the genital tract of horses,[214,215] which however, differs genetically from Streptococcus equi subsp. zooepidemicus isolates from equine infectious endometritis.[215] Vaginal lactic acid bacteria and lactobacilli, such as Lactobacillus spp. and Enterococcus spp. were isolated from mares.[218] Aerobic bacterial species isolated from uterine swab specimens of normal mares were nonpathogenic organisms.[217,219] The fertility problem of mares was associated with the appearance of abnormal bacterial species in the uterus.[220] Coagulase-negative staphylococci, alpha-hemolytic streptococci, and coryneforms are dominant aerobic and anaerobic bacterial species in the sheath of the penis, the urethral fossa, the urethral opening, and semen in stallions.[216]

Archaea

Archaeal species belonging to the phyla Methanomicrobiales and Methanoplasmatales were detected in the hindgut of horse and ponies.[221] The variation of fecal methanogen compositions was observed between the feces of horses and ponies.[221] An external probiotic was observed to affect hindgut microbial communities and their polysaccharidase and glycoside hydrolase activities in horses.[222,223]

Protozoa

Protozoal entities were detected in the cecum and colon of horses.[224,225]

Fungi

Fungal species have been detected in different anatomic locations of healthy horses. For example, fungal species that were isolates from conjunctival swabs of the normal conjunctiva of healthy horses in the UK belonged to three genera: Mucor, Absidia and Aspergillus.[195] Fungal concentrations in the colon of horses were higher than those in the cecum.[224] The anaerobic fungal compositions were similar in the feces of horses and ponies.[221] Fungal species belonging to the genera Penicillium, Aspergillus, Scopulariopsis, Trichosporon, and Mucoracee were isolated from the urethra of healthy stallions.[226]

Viruses

In the existing literature, our research interests have focused on those pathogenic viruses including Venezuelan equine encephalitis virus,[227] equine encephalosis virus,[228] equine infectious anemia virus,[229] equine H3N8 influenza A virus,[230,231] and African horse sickness, [232] as well as viral diseases of horses such as equine influenza.[233] In addition, antibodies against West Nile virus have also been detected in horses.[234,235]

Microvesicles

Membrane-enclosed micro-entities such as microvesicles and exosomes have been detected in equine ovarian follicular fluid.[236]

2.2.2 Donkeys in the Genus Equus

Bacteria

Although antimicrobial-resistant bacteria are currently our major concern in studies on donkey-associated bacterial species,[237-239] increasing research attention has been paid specifically to donkey-associated microbial communities normally existing in different anatomic locations of healthy donkeys.

Breastmilk

Many bacterial species including Escherichia coli, Lactobacillus plantarum, and diverse bacterial species in the genera of Enterococcus, Streptococcus, and Pediococcus, have been isolated from donkey raw milk.[51]

Conjunctiva

Bacterial isolates from swabs obtained from the normal conjunctiva of donkeys belonged to nine bacteria genera, in which, Staphylococcus and Enterobacter were the most dominant two genera.[237]

Nares

Staphylococcus delphini and Staphylococcus pseudintermedius are dominant in the nasal carriage in healthy donkeys.[239] Moreover, nasal Methicillin-resistant strains of Staphylococcus aureus have been isolated from the swabs of healthy donkeys.[238]

Oral cavity

In the study on bacteria in the oral cavity of donkeys, Takada and colleagues reported that novel Gram-negative bacterial strains of Prevotella dentasini belonging to the genus Prevotella were isolated from the oral cavity of donkeys.[240] Moreover, novel Gram-positive bacterial strains of Streptococcus orisasini and Streptococcus dentasini, as well as other strains of Streptococcus criceti were also isolated from the oral cavity of donkeys.[241] Human infection with Staphylococcus hyicus subspecies hyicus following a donkey bite was reported.[242]

Gastrointestinal tract

The diversity and dynamics of gut bacteria communities were described in healthy donkeys.[199,243,244] Liu and colleagues showed that the bacterial species in the feces of healthy donkeys belonged to 21 phyla and 183 genera including the phyla Firmicutes, Bacteroidetes, Verrucomicrobia and Proteobacteria, and the genera Akkermansia, Sporobacter, Methanobrevibacter, and Treponema.[243] Diverse Escherichia coli strains, including Shiga toxin-producing Escherichia coli, were isolated from the ruminant of donkeys, raw milk, and traditional dairy products in Iran.[245] E. coli from the feces of foals was low at birth but increased within 24 hours, and the similar dynamic patterns can also be observed in bacterial species of the genera Enterococcus, Streptococcus, and Staphylococcus.[244]

Reproductive tract

Bacterium Taylorella asinigenitalis in the phylum Proteobacteria was isolated from the reproductive tracts of donkeys.[213,246] A 20-year-old man was diagnosed with lymphogranuloma venereum after sexual contact with a mare.[247]

Fungi

Conjunctiva

Fungal species in the genera Aspergillus, Penicillium, Cladosporium, and Acremonium were detected in conjunctival swabs from both eyes of healthy donkeys.[249]

Viruses

Equine arteritis virus was detected in semen samples from a naturally infected South African donkey.[248] H3N8 *equine influenza virus*[231,250] and rabies virus (RABV) were isolated from donkeys.[251] A novel papillomavirus was detected in healthy skin of a white donkey.[252] Avian influenza virus subtype H5N1 was detected in donkeys, which is another example for viral jumping via crossing species barriers from poultry to another mammalian host, in this case donkeys.[253] Antibodies against *West Nile virus* were detected in donkeys.[235] *Equine arteritis virus* was isolated from the semen of naturally seropositive donkey stallions.[254]

2.3 Carnivora

2.3.1 Dogs in the genera Canis and Nyctereutes

Bacteria

Oral cavity

Bacterial species in the oral cavity of dogs were recently studied by Sturgeon and colleagues using cultural-independent approaches.[255] *Bacteroidetes*, *Proteobacteria*, *Firmicutes*, *Fusobacteria*, and *Spirochaetes* were the dominant phyla; and *Porphyromonas*, *Fusobacterium*, *Capnocytophaga*, *Derxia*, *Moraxella*, and *Bergeyella* were the most abundant genera in canine oral bacterial communities.[255] Moreover, there was a core microbiome in all samples.[255]

Gastrointestinal tract

Bacterial diversity in the gastrointestinal tract of dogs showed high intra- and inter-individual variations.[256-261] In the jejunal fluid samples of beagle dogs, the portions for cultured aerobic/facultative and anaerobic bacteria were equal, and the bacterial community was dominated by *staphylococci*, nonfermentative gram-negative rods, and yeasts, which were higher than in the fecal samples.[260] The dominant bacterial phyla in fecal samples of dogs are *Firmicutes*, *Bacteroidetes*, *Proteobacteria*, and *Fusobacteria*.[256,262,263] The intestinal lactic acid bacteria isolated from dogs belong to many genera, including *Lactobacillus*, *Bifidobacterium*, *Enterococcus*, and *Streptococcus*.[259] Mucosa-adherent commensal bacteria in duodenal biopsies from dogs have been found to belong to seven bacterial phyla: *Proteobacteria*, *Firmicutes*, *Bacteroidetes*, *Actinobacteria*, *Fusobacteria*, *Tenericutes*, and *Verrucomicrobia*.[257]

Damborg, Sorensen, and Guardabassi first reported that they isolated ampicillin-resistant *Enterococcus faecium* strains from fecal samples of healthy dogs.[264,265] Ghosh, Dowd and Zurek further revealed that *Enterococcus faecium* strains isolated from dogs treated with antibiotics were frequently resistant to enrofloxacin, ampicillin, tetracycline, doxycycline, erythromycin, gentamicin, streptomycin, and nitrofurantoin; in contrast, canine fecal *Enterococcus faecalis* strains were resistant to tetracycline, erythromycin, doxycycline, and enrofloxacin.[266] Tremblay and colleagues also showed that some ampicillin-resistant *Enterococcus faecium* strains isolated from canine clinical cases were also resistant to ciprofloxacin, lincomycin, tetracycline, macrolides, gentamicin, kanamycin, and streptomycin; moreover, some strains were related to human hospital-associated lineage.[267] Igarashi and colleagues showed that the fecal bacterial composition of healthy dogs can be altered by oral administration of metronidazole.[268] Suchodolski and colleagues revealed that the composition and diversity of bacteria in jejunal intestine of healthy dogs were altered by antibiotic tylosin. [269]

Dietary changes, for example adding fibers, had a detectable impact on the canine gut microbial communities.[262,263,270] For example, Kerr and colleagues showed that after 4 weeks of dietary intervention, the Phylum *Firmicutes* was increased in fecal samples of healthy dogs while the Phyla *Actinobacteria* and *Fusobacteria* were decreased.[270]

Reproductive tract

The most predominant vaginal bacteria during estrus were *Bacteroidaceae*, and the number of aerobes was almost equal to that of anaerobes in healthy dogs.[271,272] *Bacteroidaceae*, *streptococci*, *Pasteurella* spp, and *mycoplasmas* were the common bacterial species isolated from the vaginas of mature dogs.[273] *Pasteurella multocida*, beta-hemolytic *streptococci* group G, and *Escherichia coli* were the most common bacteria isolated from vagina of bitches.[274] The canine vaginal lactic acid bacteria belong to the genera *Lactobacillus* and *Enterococcus*.[275] Some strains or species of vaginal bacteria were dynamic from the prepuberal period to the postpuberal period.[276] Moreover, methicillin-resistant *Staphylococcus pseudintermedius* was isolated from vaginal swabs taken from healthy bitches.[272]

Bacterial species in the genera *Staphylococci* and *Mycoplasmas* were also isolated from uterine contents of adult dogs.[273] In another study, bacteria including *Escherichia coli*, *Haemophilus* species, alpha-hemolytic *streptococci*, *Corynebacterium* species, *Streptococcus canis*, *Alcaligenes faecalis*, *Bacteroides species*, *Pasteurella* species, and *Proteus mirabilis* were isolated in the uterus of normal bitch during pro-oestrus and oestrus.[277]

Skin and mucosal surfaces

Rodrigues and colleagues, using culture-independent approaches, revealed that the microbial diversity and abundance was observed in samples from different haired skin sites and mucosal surfaces of healthy dogs, in which bacteria in the phylum *Proteobacteria* and the family *Oxalobacteriaceae* were the most abundant.[278] Moreover, they found that the portion of bacterial species in the genus *Betaproteobacteria* Ralstonia in the skin of allergic dogs was decreased compared to healthy dogs.[278]

Archaea

Swanson and colleagues reported on their study of archaeal species in dogs that the most abundant and diverse archaeal species in the canine gut were the members of *Crenarchaeota* and *Euryarchaeota*.[263]

Fungi and Yeasts

Yeasts were cultured in the jejunal fluid samples of beagle dogs.[260]. Handl and colleagues showed that the identified fungal species in the fecal microbiota of 12 healthy pet dogs belonged to several fungal phyla including *Ascomycota, Basidiomycota*, *Glomeromycota*, and *Zygomycota*; *Nacaseomyces* was the most abundant genus in the fecal fungi of canines.[256]

Viruses

Endogenous retroviral DNA occupied 0.15% of the dog genome.[279] *Canine parvovirus* was detected in the feces of dogs.[280] The diversity of *canine parvovirus* in domestic dogs and *canine distemper virus* in raccoon dogs (Nyctereutes procyonoides) was observed.[281,282] Carnieli and colleagues revealed that geographic variations in the genes of rabies virus lineages were observed in dogs from areas of the North and Northeast of Brazil.[283]

2.3.2 Cats in the genus Felis

Bacteria

Breast milk

Some bacterial species in the genus *Enterococcus* were identified in feline milk.[49,51]

Oral cavity

Recently, Sturgeon and colleagues showed that most bacterial species in the healthy feline oral cavity belonged to the bacterial phyla *Proteobacteria, Bacteroidetes, Firmicutes, Spirochaetes, Fusobacteria,* and *Actinobacteria,* and the various bacterial genera including *Pasteurella, Moraxella,* and *Neisseria*.[284]

Gastrointestinal tract

Bacterial species in the phyla *Firmicutes*, *Proteobacteria*, *Bacteroidetes*, *Fusobacteria*, and *Actinobacteria* were identified in luminal samples from the gastrointestinal tract of cats.[256,285] High numbers of bacteria were found in the proximal part of the small intestine of healthy cats.[286] The fecal bacterial community of the domestic cat was shown to be altered by different diets.[287]

Reproductive tract

Aerobic bacteria including species in the genera *Acinetobacter*, *Actinomyces*, *Corynebacterium*, *Escherichia*, *Haemophilus*, *Klebsiella*, *Lactobacillus*, *Staphylococcus*, and *Streptococcus*, and anaerobic bacterial species in *Bacteroides* and *Peptococcus* were isolated from vaginal samples of healthy female cats,[288] in which, coagulase-negative *Staphylococcus*, *Streptococcus canis*, and *Escherichia coli* were the most abundant and dominant.[288] In addition, a *Lactobacillus* spp. was also isolated from uterus of cat.[288]

Fungi

Handl and colleagues reported that species in the fungal phylum *Ascomycota*, and in the genera *Saccharomyces* and *Aspergillus* were detected in cats.[256]

Viruses

Troyer and colleagues reported that specific strains of Gammaherpesviruses belonging to *Gammaherpesvirinae*, a subfamily of *Herpesviridae* were detected in blood cell DNA samples from domestic cats (Felis catus) as well as from bobcats (Lynx rufus), and pumas (Puma concolor).[289] Zhang and colleagues revealed that there were diverse viral strains and species from both mammalian and bacterial sources in the guts of domestic cats and they belonged to the viral families of *Astroviridae*, *Coronaviridae*, Parvoviridae, *Circoviridae*, *Herpesviridae*, *Anelloviridae*, *Caliciviridae*, and *Picobirnaviridae*.[290] Pacitti, Jarrett and Hay once reported that the *feline leukemia virus* (both FeLV antigen and infectious virus) was detectable in milk sample of cats.[51,291]

2.3.3 Bears in the Genera Ursus and Helarctos

Bacteria

While bacterial diseases of bears, such as *Bordetella bronchiseptica*-associated tracheitis,[292] *Clostridium sordellii*-caused septicemia,[293] and *Clostridium perfringens type A* strains-associated necrotic and hemorrhagic intestinal lesions, [294] still attract our attention, some bacterial species that were found in the following anatomic locations of normal bears may reflect their non-pathogenic relations with bear hosts.

Oral cavity

Sixteen anaerobic bacterial species in nine genera, including *Peptostreptococcus prevotii*, *Streptococcus constellatus*, and *Porphyromonas gingivalis* were isolated from the oral swabs of hunter-killed black bears (Ursus americanus).[295] *Gibbsiella dentisursi* spp. was isolated from the oral cavity of bears.[296] A novel *streptococcal* species in the genus *Streptococcus* was isolated from the oral cavities of bears.[297]

Gastrointestinal tract

Enterobacteriaceae and *enterococci* were the dominant fecal bacterial populations in wild bear feces while fecal *Enterobacteriaceae* were predominant in captive grizzly bears.[298] *Mycobacterium avium subsp. paratuberculosis*, the causative agent of paratuberculosis in ruminants, was isolated from the intestinal mucosa of brown bears (Ursus arctos).[299] Hemotropic *Mycoplasma* was detected in a free-ranging black bear (Ursus thibetanus japonicus).[300] The bacterial diversity in feces from polar bears was revealed in recent studies.[301,302] The majority of bacterial species in faeces from polar bear (Ursus maritimus) in Arctic Svalbard belonged to the genus *Clostridium* in the order *Clostridiales* of the phylum *Firmicutes*;[301 and the dominant fecal bacterial species of captive polar bears belonged to the phylum Firmicutes.[303] Moreover, the fecal microbiota composition of grizzly bears (Ursus arctos) was shown to be influenced by bears' diet, except the core members of animal species-specific bacterial species.[304]

Viruses

While viral diseases in bear are still our major concern, for example, *equine herpesvirus 9* causing meningoencephalitis,[305] *West Nile virus* being a pathogenic agent in paraparesis, [306] *Ursid herpesvirus 1* acting as an oncogenic factor in oral squamous cell carcinoma,[307] *equine herpesvirus 9* being associated with progressive encephalitis,[308] *neurotropic equine herpesvirus (EHV) 1* strains playing a role in epizootics,[309] increasing evidence has revealed some non-pathogenic viral species or strains normally exist in host bears. Papillomaviral DNA was detected in the tissue sample from the oral mucosa of a polar bear (Ursus maritimus).[310]

Recently, Mayer and colleagues first reported that a novel endogenous retrovirus named *Ursus maritimus endogenous retrovirus (UmaERV)*, with the highest similarity to the human endogenous retrovirus group HERV-K, was identified in polar bears (Ursus maritimus).[311] And the authors believed that UmaERV in extant bear species "exist as genomic fossils of viruses that no longer have exogenous counterparts."[311] This is the same view as the recent articles stating that "the ancient viral polyribonucleotide, which left within the genomes of extant prokaryotes and eukaryotes, could be named 'viral fossils', one class of molecular fossils left within extant cells." [1,93,312]

2.3.4 Sea lions in the genera Zalophus, Eumetopias, Otaria and Neophoca

Bacteria

One of the original purposes of studies on microorganisms in sea lions was to find potential zoonotic bacteria for diseases in humans and nonhuman animals. For example, Q fever in humans is a zoonotic disease caused by the pathogenic strain of bacterium *Coxiella burnetii*. *Coxiella burnetii* was detected by polymerase chain reaction in the placentas of Steller sea lions that were collected in the Pacific Northwest.[313] And moreover, the high antibody prevalence of *Coxiella burnetii* was showed in Steller sea lions of Alaska.[314] *Salmonella* may cause gastrointestinal disease in marine mammals, and diverse species and strains of *Salmonella* were found in the feces of captive and free-range California sea lions (Zalophus californianus).[315]

Leptospirosis of California sea lions (Zalophus californianus) is believed to be caused by pathogenic spirochetes in the genus *Leptospira*.[316] *Leptospira interrogans serovar Pomona* was isolated from samples of the kidney and urine in California sea lions (Zalophus californianus).[317] Prager and colleagues found that during the epizootic season of Leptospirosis, 39% free-ranging sea lions were asymptomatic and chronic carriage of *Leptospira interrogans serovar Pomona*.[316]

80% bacterial species of the gut microbiome of an Australian sea lion (Neophoca cinerea) belonged to the phylum *Firmicutes*, and 10% belonged to the genera *Proteobacteria* and *Actinobacteria*.[318] Australian sea lion (Neophoca cinerea)-specific bacterial species in the family *Helicobacteraceae* were detected in gastric biopsy specimens of an Australian sea lion with chronic gastritis and in the feces of normal Australian sea lions.[319,320]

Fungi

The information about fungal species in sea lions is mainly from studies on sick individuals.[321-324] *Cryptococcus albidus*, a ubiquitous fungal species, was detected in a California sea lion (Zalophus californianus).[322] Cystofilobasidiales DNA was detected in a California sea lion (Zalophus californianus) with systemic mycosis.[323] *Trichophyton mentagrophytes* was detected in a Steller sea lion (Eumetopias jubatus) with dermatophytosis.[325] *Malassezia pachydermatis* was isolated from a South American sea lion (Otaria byronia) with dermatitis.[326]

Viruses

In the recent study on the fecal virome in healthy California sea lions of different ages, Li and colleagues uncovered the viral diversity, dynamics, and abundance in the feces of California sea lion (Zalophus californianus).[327] The fecal virome of California sea lions consisted of mammalian viral species, including various RNA and DNA virus families and bacteriophages, including phages in the family *Microviridae*.[327] *Canine adenovirus 1* is believed to cause viral hepatitis in dogs.[328] An independent lineage and species of *adenovirus*, with some similarity to *Canine adenovirus* 1 and 2 were isolated from California sea lions.[328] Diverse strains of *polyomavirus* and *Zalophus californianus papillomavirus 1* were identified in different proliferative lesions of California sea lions.[329,330] *Steller sea lion reovirus* was identified in an aborted mid-gestational male fetus of Steller sea lion.[331] *California sea lion polyomavirus 1* was detected in a free-ranging California sea lion (Zalophus californianus) with intestinal T-cell lymphoma.[332] Diverse strains of *San Miguel Sea Lion Virus*, a small RNA virus in the genus *Vesivirus*, were identified in California sea lions.[333] Viral species of the *copiparvovirus* genus which have been identified in pigs and cows, were recently detected in the feces of a California sea lion pup.[334] Wright and colleagues recently examined whether corneal lesions in stranded pinnipeds were associated with viral infections and found that several viruses existed in the ocular tissues of clinically normal animals.[335] *Rotavirus* RNA and antibodies to rotavirus were detected in Galapagos sea lion pups (Zalophus wollebaeki).[336]

2.4 Rodentia

2.4.1 Murine in the genera of Mus and Rattus

Bacteria

Gastrointestinal tract

Bacterial species belonging to the phyla *Bacteroidetes*, *Firmicutes*, and *Acinetobacter* were identified in the small and large intestines (tissue and luminal contents) of mice.[337] Del Chierico and colleagues found that a bacterial community with prevalent species in the *Lactobacillaceae* family of *Firmicutes* and the *Enterobacteriaceae* family of *Proteobacteria* already formed in the gut of newborn mouse.[338] The healthy gastrointestinal microbiota, which contributes to host resistance to infection, is vital to many aspects of normal host physiology.[339] For example, the interaction between bacterial microorganisms and murine host cells, whcih displayed microbiota-dependet immune regulatory features, was identified in a murine model.[340] Kuwahara and colleagues reported the complete genome sequence of non-culturable mouse segmented filamentous bacteria, in which, there were no “genes for the biosynthesis of almost all amino acids, vitamins/cofactors and nucleotides,” but there was “a full set of genes for sporulation/germination and, unexpectedly, for chemotaxis/flagella-based motility.”[341] The altered fecal bacterial compositions in mice were found to be associated with different functional and structural status in innate and adaptive immunity.[342] Moreover, there were some similarities in the fecal bacterial composition at the genus and the phylum levels between mice and humans.[343]

The influence of diets on the intestinal microbiota of mice has been a hot topic for over a decade.[344-346] It has been shown that normal gut microbiota of healthy mice is shaped in microbial composition by various dietary components, such as high-flavonoid apple,[345] soy foods,[347] and dietary fat sources.[348,349] Using the telemetry technique, Lesniewska and colleagues showed that chicory inulin, *Lactobacillus rhamnosus*, and *Bifidobacterium lactis* as dietary supplements caused changes in the gastrointestinal microflora of rats. [350] And these changes included an increase in the number of bifidobacteria, a decrease in the number of enterobacteria in the jejunum, ileum, caecum, and colon, and an increase in the number of total anaerobes and lactobacilli in both the caecum and colon.[350] It has also been shown that a low residue diet introduces greater homogeneity of fecal bacterial communities in mice.[351] Other influencing factors include indomethacin,[352] antibiotics,[353,354], delivery mode,[355] fasting,[356] and acidic water.[357]

Reproductive tract

Studies using traditional culture methods in different laboratory murine species have shown that the vaginal flora is different in many conventionally reared laboratory animals species and that even in same murine animals, the vaginal bacterial community is dynamic during the estrous cycle.[271,358] For example, Noguchi**,** Tsukumi, and Urano showed that vaginal aerobes are more predominant than vaginal anaerobes in mice, while in contrast, anaerobes were more predominant than aerobes in hamsters.[271] Some bacterial species in the genera *Staphylococcus*, *Streptococcus*, *Pasteurella*, and *Proteus* are dominant in the bacterial community of the female rat genital tract.[359] Moreover, predominant vaginal bacteria increase during estrus, resulting in an increase in the total number of bacteria in the vagina.[271]

Fungi

Fungal species in the genera *Acremonium*, *Monilinia*, *Cryptococcus/Filobasidium*, *Fusarium*, *Spizellomyces*, *Neocallimastix*, *Entophlyctis*, *Mortierella* and Smittium, and the order *Mucorales* were identified in the small and large intestines (tissue and luminal contents) of mice.[360] Moreover, the murine fungal community is shaped by antibiotic treatment.[361]

Viruses

Murine cytomegalovirus (MCMV) was detected in the breastmilk of mice and there was a vertical transmission of viruses between breastmilk and exposed suckling offspring.[362] Endogenous retrovirus K-type family (ERV-K) with genetic polymorphisms was detected in the rat genome.[363] The fecal viral strains belonging to the mammalian viruses families *Circoviridae*, *Picobirnaviridae*, *Picornaviridae*, *Astroviridae*, *Parvoviridae*, *Papillomaviridae*, *Adenoviridae*, and *Coronaviridae* were showed in wild rodents.[364] Some novel viruses were also identified in murine animals. For instance, Ehlers and colleagues detected novel betaherpesviruses and gammaherpesviruses in Mus musculus.[365] Wu and colleagues reported that *Mojiang Paramyxovirus*, as a novel Henipa-like virus, was identified in rats (Rattus flavipectus) in China.[366]

Exosomes

Masyuk and colleagues reported that “saucer-shaped” exosomes were identified in rat bile.[367] Moreover, Colino and Snapper showed that murine bone marrow dendritic cells, under the induction of an intact protein (diphtheria toxoid (DT), were able to produce exosomes.[368]

3. Aves in the Phylum Chordata

3.1 Order: Galliformes

3.1.1 Chickens in the genus Gallus

Gastrointestinal tract

Traditionally, the intestinal microbiota of the chickens or chicks has been analyzed by using bacteriological culture methods. However, approximately 90% of the bacterial cells detected by microscopy do not grow on media.[369] The development of cultural-independent molecular methods, including 16S rRNA gene and DGGE, has made it possible to identify different bacterial populations in samples from chickens without cultivation.[370-372] Although *Campylobacter jejuni* was detected in the cecal contents of newly hatched chicks by using DNA-DNA hybridization, [373] and *Campylobacters* spp. are generally considered commensal organisms in avians,[374] a report using PCR and DGGE failed to detect a bacterial community in the intestinal tract of newborn chicks.[375] Pedroso and colleagues revealed that the newly hatched chicks carry a complex community of bacteria in the small intestine, detectable by PCR followed by DGGE.[376] The abundant bacterial community in the small intestine of newly hatched chicks is attributed to several possible origins:[377] (i) external origins, including bacteria transmitted horizontally from hens, hatchery basket debris,[376, 378] or from water, in which Campylobacter can exist in a viable but nonculturable form,[379,380] and can infect chickens;[381] (ii) vertical transmission from semen and the hen’s reproductive tract;[382] and (iii) indirect evidence suggests that bacteria-related events can occur during the chicken embryonic stage.[376,383]

The recent study on chicken fecal microbiota by Sekelja and colleagues suggested that gastrointestinal origin may be the main determinant for the composition of the chicken fecal microbiota.[384] Campylobacters are gram-negative, thermophilic, obligate microaerophilic bacteria that colonize avians as a commensal organism.[374] Campylobacter DNA was present in the intestine and yolk contents of day-of-hatching chicks before they began to consume food or water.[373,385] The genomic diversity of Campylobacter has been revealed in *Campylobacter jejuni* and *Campylobacter coli*.[386-388] Geographical and seasonal variations of bacterial diversity were also described in *Campylobacter* spp.[389-391] In addition, bacterial species in the genus *Arcobacter* such as *Arcobacter butzleri*, *Arcobacter cryaerophilus*, and *Arcobacter skirrowii*, were also detected in the intestinal ract of breeding hens.[60,392-394] Previous culture-based studies showed that after hatching, the previously sterile alimentary tract was rapidly colonized by external microorganisms from the mother and the surrounding environment. Anaerobic bacteria capable of decomposing uric acid appeared 3 to 6 h post-hatch, and streptococci and enterobacteria became the dominant microbial members during the first 2-4 days after hatching.[372]. After the first week, Lactobacilli, such as *Lactobacillus acidophilus*, *Lactobacillus reuteri*, *Lactobacillus crispatus*, *Lactobacillus buchneri*, and *Lactobacillus salivarius*, were the most abundant microorganisms present in the gastrointestinal tract of 5- to 6-week-old broiler birds.[369,395] The population of Bifidobacteria became more dominant in the ceca at older age.[372] The novel species *Anaerostipes butyraticus* was isolated from the cecum of chicken by Eeckhaut and colleagues.[395]

It was showed that there was a remarkable difference in microbial composition between the cecum the small intestinal locations, and in the former, species belonging to the *Clostridiales* order and *Bacteroidetes* phylum were dominant, while in the latter, species of the *Actinobacteria* class and *Bacillales* order were aboudant.[396] Moreover, the diversity of the microbial community in the population cecum of chicken was found to be accompanied by functional diversity in metabolism.[388]

Reproductive system

It was usually attributed to the consequence of contamination that *Campylobacter jejuni* were detected from the inner membranes of the eggs and egg contents.[397] *Campylobacter* spp. were isolated from semen samples and from the ductus deferens and testes of commercial turkeys and roosters using traditional bacterial cultivation methods.[398,399] *Campylobacter* spp. were isolated from the vagina, ovarian follicles, spleen, liver-gallbladder, ceca, shell gland, isthmus, magnum, and infundibulum of hens.[340,398] Like *Campylobacter*, bacterial species in the genus *Arcobacter*, such as *Arcobacter butzleri*, *Arcobacter cryaerophilus*, and *Arcobacter skirrowii*, were also detected in the oviduct of breeding hens.[60,392-394]

Viruses

The sequences of three endogenous retroviruses were identified in chromosome 1, 2, and 3 of White Leghorn chickens.[401] Some strains of H5N1 *avian influenza virus* were detected in chickens and were not pathogenic to chickens. However, some strains of H5N1 avian influenza viruses in other birds were shown to be highly pathogenic to chickens.[402]

Influencing Factors

Age

The compositions of bacterial molecular species (referring to those bacterial species detected using culture-independent methods) in the ilea and ceca of chickens showed a region-specific profile, which also changed as the birds aged.[370,403]

Gender

The compositions of bacterial molecular species in the digesta of the ileum revealed two gender-specific profiles, with less than 30% similarity between populations. Moreover, even within the same gender, the inter-individual variety of the intestinal bacterial community increased as the chickens aged.[404]

Litter materials

Environmental factors, such as different types of litter materials, can influence the cecal bacterial molecular species communities.[403]

Diets

Diets have different effects on *Salmonella* colonization in the ceca of broilers.[405] A 16S rRNA gene-based analysis showed that chicken intestinal microbial communities are altered by feed withdrawal and diets containing additives such as CuSO4 or bacitracin. As the tome of feed withdrawal increases, the uniformity of intestinal microbial populations decreases.[406] Dietary supplementation with *Lactobacillus* culture increases *Xanthophyll* content in the shank skin of chickens.[407] Bjerrum and colleagues found that when broilers infected with a rifampicin-resistant *Salmonella Typhimurium* strain at 15 days of age are fed whole wheat, it significantly reduces the numbers of *Clostridium perfringens* in the intestinal tract of the birds compared to pellet-fed group.[408]. The microflora in the gastrointestinal tract of chickens is dynamic and can be easily affected by biological factors in food, such as caprylic acid and other medium-chain fatty acids. For example, caprylic acid, an 8-carbon medium-chain fatty acid, has been reported to be effective in killing various bacteria, including *Campylobacter jejuni*.[409]

Competitive exclusion bacteria

Oral administration of a combination of Citrobacter diversus, *Klebsiella pneumoniae*, and *E. coli* reduced *Campylobacter jejuni* colonization in chickens. [410] Stern and colleagues isolated a *Lactobacillus salivarius* strain from more than 1,200 isolates of different lactic acid bacteria and showed that its bacteriocin inhibited *Campylobacter jejuni* growth in the chicken gastrointestinal system.[411] Nazef and colleagues isolated 45 strains of lactic acid bacteria from poultry feces in the Nantes area of France and found that only one *Enterococcus faecalis* strain exhibited clear antilisterial activity and slight anti-Campylobacter activity, and one *Lactobacillus reuteri* strain exhibited only anti-Campylobacter activity.[412] Line and colleagues isolated an *Enterococcus* spp. strain from chicken ceca that was shown to produce an enterocin that inhibited the growth of many bacterial species, including those in the genera of *Salmonella*, *Escherichia*, *Yersinia*, *Citrobacter*, *Klebsiella*, *Shigella*, *Pseudomonas*, *Proteus*, *Morganella*, *Staphylococcus*, *Listeria*, and *Campylobacter*.[413]

Antibiotics

Diets containing growth-promoting antibiotics, such as avilamycin, bacitracin methylene disalicylate, enramycin, bacteriocins, and virginiamycin were shown to influence the composition of the intestinal bacterial community of broiler chickens.[396,414,415] Recent studies also showed that antimicrobial agents may have an impact on the antimicrobial resistance of *Campylobacter* spp. in poultry.[416-418]

Bacteriophage

Bacteriophage is considered a phage-mediated control for *salmonellas* and *Campylobacter jejuni*.[419,420]

3.2 Anseriformes

3.2.1 Geese in the genera Chen and Branta

Bacteria

The pathogenic roles of bacteria in diseases of geese are still a research highlight. For instance, the pathogenic relationship of mycoplasma species in diseases of gees was recently reviewed by Stipkovits and Szathmary.[421] Studies on the diversity and seasonal dynamics of the microbial community in geese have focused on fecal samples and mainly described from the perspective of natural reservoirs for zoonotic pathogens.[422-425] Some species and strains in the genus *Brachyspira* are pathogenic bacteria in diarrhea and colitis in pigs. Rubin and colleagues isolated *Brachyspira* spp., including *Brachyspira hampsonii*, from the feces of lesser snow geese (Chen caerulescens).[422] Some strains of *Campylobacter jejuni* were isolated from the feces of Canada geese (Branta canadensis) by Rutledge and colleagues.[426] Moreover, in an in vitro experiment by Moriarty and colleagues, the survival of *Campylobacter jejuni* and other bacterial species, including *E. coli* and *enterococci*, in Canada goose feces showed a seasonal characteristic.[423] Recently, Dickx and colleagues reported that the bacterium *Chlamydia psittaci* was isolated from pharyngeal swabs of healthy Canada geese (Branta canadensis).[425] In addition, several novel strains of *Pasteurella multocida*, *Lactobacillus brantae*, and *Salmonella enterica* were isolated from the heart, liver and feces of geese.[427-429]

Viruses

Goose calicivirus, *goose parvovirus*, *newcastle disease virus*, *goose herpesvirus*, *goose haemorrhagic polyomavirus*, *goose circovirus*, *goose adenovirus*, *goose flavivirus*, *goose* *tembusu virus*, *avian influenza virus*, and *bornavirus* were detected in geese.[430-438] The pathogenicity of H5N1 *avian influenza virus* was found to depend on the hosts, and some strains were nonpathogenic in geese but pathogenic to chickens and ducks.[402]

3.3 Charadriiformes

3.3.1 Gull in the genus Rissa

Bacteria

The bacterial pollution of gull feces in the beach environment has been a hot topic recently.[439,440] The cloacal bacteria compositions of black-legged kittiwakes (Rissa tridactyla) belong to the phyla *Firmicutes*, *Actinobacteria*, and *Proteobacteria*, and have an age-related dynamics.[441] A recent study on the gull fecal microbial community showed that the most dominant bacterial species belong to the two families *Enterococcaceae* and *Enterobacteriaceae*.[440] The gull gut bacterial community is mainly composed of bacterial populations closely related to *Bacilli*, Clostridia, *Gammaproteobacteria*, *Catellicoccus marimammalium*, and *Bacteriodetes*.[442,443] Moreover, copulation between male and female kittiwakes (Rissa tridactyla) affects the female cloacal bacterial composition.[444]

Viruses

Newcastle disease viruses, *avian influenza virus*, and *gull avian influenza virus* were detected in gulls.[445,446]

3.4 Columbiformes

3.4.1 Pigeons and Doves in the genus Columba

Bacteria

Novel bacterial strains belonging to the genus *Riemerella* of the family *Flavobacteriaceae* were isolated from pharyngeal swabs of domestic pigeons.[447] Bacterial species detected in free-ranging and captive pigeons included *Enterocytozoon bieneusi*, *Encephalitozoon intestinalis*, *Encephalitozoon hellem*, and *Encephalitozoon cuniculi*.[448] Strains in the genera *Escherichia*, *Staphylococcus*, *Streptococcus*, *Campylobacter*, *Mycobacterium*, and *Salmonella* were isolated from pigeons.[449-455] Various strains of *Salmonella typhimurium* and *Salmonella enterica* were isolated from normal feral pigeons (Columba livia).[456] Studies showed that diverse chlamydial species or strains, including *Chlamydia psittaci*, *Chlamydia abortus*, *Chlamydia pecorum*, and *Chlamydia trachomatis* normally exist in pigeons.[454,457-459]

The pathogenicity of a given bacterial species is determined by various factors, including virulence factors, which are host-species specific or host-individual specific. In addition, different strains of a given bacterial species vary in virulence. For example, Shiga toxin 2f, a protein produced by some strains of *E. coli* has been attributed to Shiga toxin 2f-producing *E. coli* (STEC2f) infections in humans, was recently detected in samples of pigeon droppings.[460] Moreover, some enterobacterial species in the genera *Campylobacter*, *Escherichia*, and *Salmonella* were isolated from pigeons, and some strains of these species were believed to be pathogens in infections of other birds, livestock, and humans.[461] Studies indicated that for the strains of *Streptococcus gallolytics* and *Streptococcus bovis* isolated from pigeons, some strains were highly virulent for pigeons, but some strains were moderately virulent or low virulent for pigeons.[451,462,463]

Abundant bacteria were detected on the feathers of woodpigeons.[464] The gut microflora of pigeons can be influenced by the components in pigeon diets.[465,466] In addition, antimicrobial resistance in the fecal bacterial species from pigeons was also investigated. Studies revealed that different bacterial species isolated from pigeons showed different antimicrobial resistance patterns.[449,467-469]

Fungi

Diverse fungal species, including *Candida glabrata*, *Candida famata*, *Cryptococcus albidus*, *Cryptococcus laurentii*, and *Cryptococcus neoformans*, were found in the guts of feral pigeons.[470-472] And they are the dominant fungal species in the feces of normal pigeons.[471,472] Moller and colleagues reported that abundant fungi were detected on the feathers of woodpigeons.[464] Lallo and colleagues showed that *Encephalitozoon hellem*, *Enterocytozoon bieneusi*, *Encephalitozoon intestinalis*, and *Encephalitozoon cuniculi* were the dominant microsporidia species found in the feces of pigeons.[470,474]

Viruses

Avian infectious bronchitis virus, *avian metapneumovirus*, and *newcastle disease virus* were detected in asymptomatic pigeons.[456,476,477] The genetic diversity of *newcastle disease virus* in wild birds and pigeons, which was described by Snoeck and colleagues[478] suggests that different viral strains may vary in virulence. *Pigeon circovirus* was also detected in pigeons,[479,480] as were *avian nephritis virus* and *chicken astrovirus* in the feces of pigeons.[481]

Diverse viral species or strains belonging to the families *Circoviridae*, *Parvoviridae*, *Picornaviridae*, *Reoviridae*, *Adenovirus*, *Astroviridae*, and Caliciviridae were detected in wild pigeon droppings.[475] Two new viruses belonging to the genus *Avastrovirus* in the *Astroviridae* family were detected in feral pigeons and wood pigeons.[482] *Columbid herpesvirus-1*, which normally exists in domestic pigeons, is believed to infect falcons and owls when they eat infected pigeons.[474] Some strains of *avian influenza virus*, such as H7N9, have been found to be low pathogenic to pigeons and doves, while other strains of H5N1, have been found in asymptomatic or mild symptomatic pigeons.[483-485] Other viruses and diseases of interest in pigeons and doves include *West Nile viruses*,[486] *pigeon paramyxovirus type 1*, the pathogen of paramyxovirosis in pigeons,[487] and *avian infectious bronchitis virus*.[488]

Concluding Remarks

Although there have not yet been any specific programs to describe the whole image of non-host cellular and subcellular entities for any nonhuman vertebrate animals, the existing limited information from studies on various vertebrates supports the notion that the bodies of normal nonhuman vertebrate animals are actually inhabited by cellular and subcellular entities. All normal and healthy nonhuman vertebrates should have their species-specific bacterial, archaeal, fungal, protozoal, viral communities, and membrane-enclosed microentities from the ecological and evolutiological perspective, which is supported by evidence obtained by using both culture-dependent and culture-independent approaches, and light and electron microscopes. By putting these existing “pieces” together, we can theoretically find where the missing or incompleted “pieces” are in the puzzle of evolutionary background entities (EBEs) of nonhuman vertebrate animals. However, solving thsi puzzle is just beginning and we are still facing a series of theoretical and technical challenges The topic of evolutionary background entities (EBEs) in invertebrate animals will be discussed in the next issue.

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