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

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Abstract

The novel recognition 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 has been supported by increasing evidence since the emergence of culture-independent approaches. However, understanding the relationship between animal hosts, including human beings, and those non-host microentities that include microorganisms is challenging our traditional understanding of pathogenic relationship in human medicine and veterinary medicine. In recent novel evolution theories, the relationship between animals and their environments has been deciphered as the interaction between animals and their environmental evolutionary entities at the same and/or different evolutionary levels;[1-3] and evolutionary entities of the lower evolutionary levels are hypothesized to be the evolutionary background entities of entities at the higher evolutionary levels.[1,2] Therefore, understanding the normal existence of microentities that include microorganisms in multicellular animal bodies is becoming the first priority for elucidating the ecological and evolutiological relationships between microorganisms and nonhuman macroorganisms. The evolutionary background entities at the cellular and subcellular levels in bodies of nonhuman vertebrate animals have been summarized recently.[4] In this paper, I try to briefly review the evolutionary background entities (EBEs) at the cellular and subcellular levels for several selected invertebrate animal species.

Key words: Evolution; Diversity; Animals; Symbiosis; Eukaryote; Prokaryote; Invertebrate; Bacteria; Archaea; Fungi; Viruses; Protist

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1. Background

In recent novel evolution theories, the relationship between animals and their environments has been deciphered as the interaction between animals and their environmental evolutionary entities at the same and/or different evolutionary levels; [1-3] and evolutionary entities of the lower evolutionary levels are hypothesized to be the evolutionary background entities of entities at the higher evolutionary levels. [1,2] Therefore, understanding the normal existence of microentities that include microorganisms in multicellular animal bodies is becoming the first priority for elucidating the ecological and evolutiological relationships between microorganisms and nonhuman macroorganisms. The evolutionary background entities, including subcellular viral entities and membrane-enclosed microentities, prokaryotic bacterial and archaeal cells, and unicellular eukaryotes such as fungi and protists at the cellular and subcellular levels in bodies of nonhuman vertebrate animals, have been summarized recently. [4] In this paper, I try to briefly review the evolutionary background entities (EBEs) at the cellular and subcellular levels for the following selected invertebrate animal species.

2. The Phylum Arthropoda

2.1 The Class Insecta

Mutualistic interaction between endosymbionts and their host cells

Over half of all described macroorganism species on Earth are insects.[5] Recently, it has been gradually accepted that the symbiotic phnomenon in the Insecta is ubiquitous, although to date, only bacterial symbionts have been well studied in several groups of Insecta;[6] and the information about viral and fungal symbionts of insects is relatively limited. Many insects rely on symbiotic microorganisms to supply nutrients that are required by hosts for their viability and fertility.[7] Although these symbiotic microorganisms have lost the ability to live freely outside the sheltered environment within their host insects,[8] they eventually became essential partners in maintaining their host's life. Therefore, this mutual beneficial relationship was the consequence of evolution, which enabled host organisms to obtain some kinds of advantages for survival. Moreover, even the diversity of the Insecta was believed to be associated with the diverse microbial communities inhabiting insect guts where interactions between symbiotic prokaryotic bacteria and host eukaryotic cells for gene transfer occurred.[9,10]

Despite microbial symbionts being found in different anatomic locations, including the alimentary tract, body cavity and/or eukaryotic cells of insects, researchers have defined two kinds of bacterial symbionts in insects when describing the symbiotic interaction between symbionts and host cells: "primary symbionts" and "secondary symbionts." Primary symbionts have three characteristics: (i) living within specialized host cells called bacteriocytes (or mycetocytes), (ii) inheriting maternally (vertically) by transovarial transmission, and (iii) establishing an obligate mutualistic association.[11-13] For example, Wolbachia is a bacteriocyte-associated symbiont and detected in all of the examined insects.[14] In fact, bacteria living within eukaryotic cells are a natural phenomenon, which also has been revealed in Protozoa and human macrophages.[15,16] The significance of symbiosis in insects has been studied in several insect species. Buchner proposed that the usual role of bacteriocyte-associated symbionts was to provision nutrients to their hosts.[13] Bacterial endosymbionts in the genus Portiera were believed to be the source of carotenoids in whiteflies because no evidence of carotenoid biosynthesis genes was found in whitefly species, but found in the obligate bacterial endosymbiont Portiera from the whitefly Bemisia tabaci.[17] Chlamydiae strain UWE25, as an endosymbiont in protozoa, was found to lack encoding genes for producing ATP,[18] but depends on the host cytosol to obtain energy.[19-21] In contrast, secondary symbionts are those endosymbiotic microorganisms without the strict limitation of the above three characteristics for defining primary symbionts.[11,12] Secondary symbionts may occur both intracellularly or extracellularly and may be both transovarially and horizontally transmitted.[11] For example, some extracellular bacterial symbionts belonging to the genus Burkholderia existed in a specialized symbiotic organ in a posterior region of the midgut in the bean bug Riptortus pedestris.[10] In fact, a secondary symbiont today may be the primary symbiont tomorrow. It is believed by some investigators that symbioses of insects and primary symbionts are the results of ancient infections.[11] For instance, cicadas, leafhoppers, treehoppers, spittlebugs, and planthoppers were found to host species-specific bacterial symbionts belonging to the phylum Bacteroidetes, which was believed to be the consequence of ancient infections occurred at least 260 million years ago.[13] An obligate intracellular bacterium belonging to the subphylum Gammaproteobacteria in the bulrush bug Chilacis typhae was located at the anterior poles of developing eggs and showed to have phylogenetic relationship with several secondary endosymbiotic bacteria including Pectobacterium and Dickeya.[22]

2.1.1 The Order Hemiptera

2.1.1.1 Lygaeoid bugs in the families Blissidae and Lygaeidae

Bacteria

Symbiotic bacteria belonging to the phylum Proteobacteria in the “symbiont ball”, or bacteriocytes, were detected at the anterior pole of developing eggs in the ovary of adult females, or within the abdominal midgut in different lygaeid stinkbug species of the families blissidae and lygaeidae.[11,23-25] Moreover, bacterial symbionts within the cytoplasm of the bacteriocytes in the Lygaeoid bugs Nysius ericae and Nithecus jacobaeae were in both large elongated and small rod-shaped forms.[11] Morphologically, bacteriocytes of the birch catkin bug Kleidocerys resedae were showed to be red-colored and raspberry-shaped.[23] The above description of obligate endosymbionts constitutes the supporting evidence for maternal vertical transmission of endosymbionts to offspring through the ovarial passage.[23,24]

2.1.1.2 Stinkbugs in different genera of the families Alydidae, Pentatomidae, Plataspididae, Parastrachiidae, and Scutelleridae

Bacteria

The host-symbiont relationships were shown to be diverse anatomically and phylogenetically among plataspid stinkbugs, acanthosomatid stinkbugs, pentatomid stinkbugs, and cydnid stinkbugs.[26-29] Primary symbionts in the “symbiont ball”, or bacteriocytes were identified in stinkbugs of the families Plataspididae,[27,30] Acanthosomatidae, [28] and Pentatomidae.[31] Hosokawa and colleagues observed that the mothers of the stinkbugs in the genera Adomerus, Parastrachia, and Megacopta excreted a copious amount of symbiont-containing white mucus from the anus or small particles called “symbiont capsules” onto their laid eggs and after egg hatching, the newborn nymphs immediately ingested the mucous secretion and obtained primary symbionts, which was believed to be the mechanism of vertical symbiont transmission.[32-35] Kikuchi and colleagues showed that symbionts were vertically transmitted via egg surface contamination during oviposition and that surface sterilization of eggs resulted in symbiont-free hatchlings which suffered retarded growth, high mortality, and abnormal morphology.[28] Extensive genome rearrangements of the obligate whitefly endosymbiont Portiera were found within the genome of individual insects of the whitefly Bemisia tabaci and the whitefly Trialeurodes vaporarium.[36] Bacterial symbionts of the stink bug Plautia stali were shown to produce rough-type lipopolysaccharide (LPS), a major component of the outer membrane of Gram-negative bacteria.[37] Recently, Matsuura and colleagues revealed that bacterial symbionts in the stinkbug Antestiopsis thunbergii were diverse and belonged to four distinct bacterial groups: gammaproteobacteria, Sodalis, Spiroplasma, and Rickettsia.[38] Moreover, these symbiotic bacteria existed not only in the stinkbug’s gut, but also infected various cells and tissues of the stinkbug.[38] Although the gut bacterial symbionts were believed to be primary symbiotic with obligate nature in stinkbugs,[12,38,39] Kaiwa and colleagues showed that primary gut symbionts actually consisted of different evolutionary-origin cell lineages for their finding of a stinkbug species-specific gammaproteobacterium in different geographic location.[12,39] More interestingly, Kaiwa and colleagues provided electron microscopic morphological evidence showing that in the midgut crypts of the Scutellerid stinkbug Cantao ocellatus, “convoluted projections from the epithelial cell layer form an intermingled structure, where the symbiont cells are entrapped in narrow extracellular spaces in close association with the host cells.” [12]

Experimental studies indicated that primary symbiotic bacteria play a physiological role in the normal development and growth of host insects. The symbiont-deprived stinkbug Sibaria englemani after treating with egg surface sterilization exhibited significant developmental retardation.[40] Moreover, deprivation of the bacterium from the nymphs of the stinkbug Megacopta punctatissima was also found to cause various abnormalities in development, growth and body coloration of the host insect.[41] Bacteria in food were experimentally shown to be an external source for secondary bacterial colonization in first instars of the stinkbug Nezara viridula.[42] A dense population of a bacterial symbiont belonging to the genus Burkholderia was found in the crypts at a posterior midgut region of the stinkbug Riptortus clavatus, and the symbiont was not vertically transmitted but was environmentally acquired.[43] The study on symbiont acquisition during nymphal development showed that a beneficial Burkholderia symbiont was detectable as early as in 2nd instar nymphs of the alydid stinkbug Riptortus pedestris.[44] The increase of external temperature was shown to associate with gut symbiont loss while accompanying a decrease in host fitness in stink bugs, such as Acrosternum hilare, Murgantia histrionica, and Nezara viridula L.[31,45] In addition, studies on bugs-associated bacterial symbionts have revealed their roles in other aspects such as in bacterial symbiont-mediated insecticide resistance [46] and in extracellular bacterial symbiont-mediated insect gene expression.[10]

Viruses

Insect-associated viruses have not attracted much research attention yet. Plautia stali intestine virus was found in stinkbugs Plautia stali, Nezara viridula, and Halyomorpha halys.[47] Nezara viridula virus type 1 and type 2 were isolated from the stinkbug Nezara viridula with severe disease symptoms.[48]

2.1.1.3 Whitefly in the genera Aleurocanthus, Bemisia, Siphoninus, and Trialeurodes of the family Aleyrodidae

Bacteria

Diverse bacterial endosymbionts belonging to the genera Arsenophonus, Arthrobacter, Bacillus, Bhargavae, Brevibacillus, Curtobacterium, Erwinia, Kocuria, Listeria, Micrococcus, Paenibacillus, Pantoea, Portiera, Pseudomonas, Psychrobacillus, Rhodococcus, Rummellibacillus, Serratia, and Wolbachia were detected in the whiteflies of the genera Trialeurodes,[49] Aleurocanthus[50] and Bemisia.[51] For instance, the secondary bacterial symbionts in the whitefly Trialeurodes vaporariorum were showed to belong to the genera Hamiltonella, Arsenopnohus, Rickettsia, Wolbachia, and Cardinium, while those bacterial symbionts in the whitefly Siphoninus phillyreae belonged to the genera of Hamiltonella, Wolbachia, Cardinium, and Arsenophonus.[52] The study on bacterial symbionts in the whitefly Bemisia tabaci showed that symbiotic bacteria belonging to the genus Hamiltonella were involved in the development of the host insect.[53]

Viruses

Currently, our understanding on viruses in whiteflies mainly focusses on the role of whiteflies as vectors for many plant viruses such as begomovirus, carlavirus, crinivirus, ipomovirus, and torradovirus.[54,55] A recent study by Rosario and Capobianco suggested that the complexity and diversity of viruses carried in whiteflies may extend beyond our existing knowledge.[54]

2.1.1.4 Moss bugs in the genus Gondwanan of the family Peloridiidae

Bacteria

An endosymbiotic, intranuclear bacterium as an Alphaproteobacterium of the genus Rickettsia in bacteriomes and the “symbiont ball” of developing oocytes was described for the first time by Kuechler and colleagues.[56]

Santos-Garcia and olleagues revealed that the primary endosymbiont of moss bugs belonged to Candidatus Evansia muelleri and Portiera.[57]

2.1.1.5 Pirate bugs in the genus Orius of the family Anthocoridae

Bacteria

Bacterial symbionts belonging to the genera Spiroplasma and Wolbachia were detected in pirate bugs in the genus Orius of the family Anthocoridae; and the Spiroplasma population was showed to be dynamic in the development of the host insect.[58]

2.1.1.6 Leafhopper in the genus Orosius of the family Cicadellidae

Bacteria

The obligate bacterial symbionts belonging to the genera Rickettsia, Wolbachia, Sulcia, Nasuia, and Arsenophonus of the phylum Proteobacteria were detected in different leafhopper species.[59,60] A study comparing the genomes of symbionts in the leafhopper Homalodisca vitripennis and Graphocephala atropunctata revealed that the genome of the anciently acquired symbiont "Candidatus Sulcia muelleri" differed from that of the more recently acquired symbiont "Candidatus Baumannia cicadellinicola" in genome stability and evolutionary rate.[61]

2.1.1.7 Firebugs in the genus Pyrrhocoris of the family Pyrrhocoridae

Bacteria

Bacterial species in the gut of the red firebug Pyrrhocoris apterus were shown to belonge to the phyla Actinobacteria, Firmicutes, and Proteobacteria, and the genera Coriobacterium, Gordonibacter, Clostridium, Lactococcus, Klebsiella, and Rickettsiales.[62]

2.1.1.8 Chinch bug in the genus Cavelerius of the family Blissidae

Bacteria

The symbiont-contamination on egg surfaces as the mechanism of vertical transmission and the environmental acquisition as the mechanism of horizontal transmission for acquiring Burkholderia symbionts were revealed in the oriental chinch bug Cavelerius saccharivorus.[63]

2.1.1.9 Potato psyllid in the genus Bactericera of the family Triozidae

Bacteria

The primary bacterial symbiont Candidatus Carsonella ruddii and many secondary bacterial symbionts in the bacterial genera Wolbachia, Sodalis, and Pseudomonas were detected in Potato psyllids.[64]

2.1.2 The Order Phthiraptera

2.1.2.1 Louse in the genera Columbicola of the family Philopteridae, the genus Pedicinus of the family Pedicinidae, and the gunus Lepidophthirus of the family Echinophthiriidae

Bacteria

Although lice, including the head and the body lice, and lice-transmitted pathogenic bacteria in diseases such as epidemic typhus, trench fever, and relapsing fever, are still major research concerns,[65-67] increasing attention has been paid to the relationship between symbiotic bacteria and host lice in resent years.[68-73] The symbiont-associated disk-shaped structure (mycetoma or bacteriocytes) was first observed by Robert Hooke 350 years ago.[66] Intestinal endocellular symbiotic bacteria in lice were found to be louse species-specific.[71] Moreover, those bacteriocyte-associated symbionts in the macaque louse Pedicinus obtusus and the slender pigeon louse Columbicola columbae belonged to gammaproteobacteria,[70,71] and they were diverse and dynamic.[68]

Viruses

The study on viruses in lice is limited, and existing literature about louse-associated viruses mainly focuses on a few lice species such as the salmon louse Lepeophtheirus salmonis [74,75] and the louse Lepidophthirus macrorhini.[76] The southern elephant seal (SES) virus, the first arbovirus of marine mammals, was described by La Linn and colleagues in the elephant seal louse Lepidophthirus macrorhini.[76] Okland and colleagues showed that five rhabdovirus-like sequences were detected in the salmon louse (Lepeophtheirus salmonis), with two viral sequences observed for the first time.[75] Moreover, the vertical transmission of viruses in the salmon louse Lepeophtheirus salmonis was suggested by Okland and colleagues.[75]

2.1.3 The Order Coleoptera

2.1.3.1 Beetles in different genera of the families Carabidae, Cerambycidae, Curculionidae, Elateridae, Passalidae, Scarabaeidae, Staphylinidae, and Tenebrionidae

Bacteria

The composition and diversity of the beetle's gut microbial community has attracted increasing research attention in recent decades. Diverse bacterial species belonging to the phyla Firmicutes, Proteobacteria, and Actinobacteria were found in the guts of larvae and adults of different beetle species;[77-85] and it was shown that there were inter- and intra-specific variations of bacterial composition in the larvael gut of humivorous scarab beetles in the genus Pachnoda.[86] Lehman, Lundgren and Petzke estimated that direct cell counts were 1.5×10^8 bacteria per milliliter of the gut in the beetle Poecilus chalcites.[78] Specific bacteria were found in the wood-feeding beetle Anoplophora glabripennis and the dung beetle Onthophagus taurus. And these bacterial symbionts were believed to be from both vertical and horizontal sources.[87,88]

Rod-shaped pleiomorphic symbiotic bacteria were identified by Fluorescence in situ hybridization in the oocyte and bacteriocytes of Hylobius species belonging to the Molytinae subfamily.[89] In the gut microbiota of larval Holotrichia parallela, bacterial species were diverse and the dominant species belonged to the phyla Firmicutes and Proteobacteria, and the families of Ruminococcaceae, Lachnospiraceae, Enterobacteriaceae, Desulfovibrionaceae, and Rhodocyclaceae.[90] Diverse bacteria were detected in the larval gut microbial community of Pachnoda ephippiata, and the dominant bacteria belonged to the orders Lactobacillales, Clostridiales and Bacillales, and the phylum Cytophaga-Flavobacterium-Bacteroides.[91] The comparison of bacterial communities in the guts of larva and adults of the beetles Melolontha hippocastani revealed that although the beetles experienced a huge environmental switch from below-ground to above-ground, some bacterial species belonging to Beta-, Delta-, and Gamma-proteobacteria, Clostridia, Bacilli, Erysipelotrichi, and Sphingobacteria were detected in both the larval midgut and the adult gut.[81] Moreover, the core microbiome of the mycangium was found in six beetle species in the genera Dendroctonus, Xyleborus, and Xylosandrus.[92] Scanning electron microscopy showed that cocci were found as early as in the first-instar larvae, and morphological changes of symbiotic bacterial community continued during larval development.[93] In addition, the diversity of symbiotic microbial communities was influenced by environmental factors.[94] The different roles of bettle-associated bacterial symbionts have been revealed, such as nitrogen fixation,[95] food digestion, [96,97] suppressing plant defenses,[98] insect development,[80] and biological control.[99]

Archaea

The archaeal community was detected in the larval gut microbial community of the beetles Pachnoda ephippiata, but less diverse than bacteria.[91] Archael species belonging to the genus Methanobrevibacter were detected in the hindgut of Melolontha melolontha larvae.[100]

Fungi

Diverse fungal species or yeasts belonging to different genera and families were detected in eggs, larvae, and adults of different beetle species such as cerambycid beetles,[101] carrion beetles,[102] costa rican beetles,[85] red turpentine beetles,[103] ambrosia beetles,[104-106] mountain pine beetles,[107] and bark beetles.[108] For example, fungal species belonging to the genera Grosmannia, Leptographium, Ophiostoma, Pesotum, and Ambrosiellawere were detected in root-feeding beetles in the genera Hylastes, Pachylobius, Hylobius, and Dendroctonus;[109] fungal species in the genus Penicillium of the family Trichocomaceae, the genus Trichoderma of the family Hypocreaceae, and the genus Ophiostoma of the family phiostomataceae were detected in the bark beetle Ips typographus;[108] and symbiotic Leptographium longiclavatum and Grosmannia clavigera of the family Ophiostomataceae were detected in the mountain pine beetle Dendroctonus ponderosae Hopkins.[110] Moreover, studies revealed that obligate fungal community in the beetle Doubledaya bucculenta was shown to be developmental and physiological dependence [111] and that fungal species in the bark beetle Dendroctonus ponderosae were dynamic and shown to associate with environmental factors.[112]

2.1.3.2 Weevils in the genera Conotrachelus, Curculio, Lissorhoptrus, Otiorhynchus, Sitophilus, Sphenophorus, and Rhynchophorus of the family Curculionidae

Bacteria

Bacterial species in both bacteriocyte-associated primary symbionts and environment-associated secondary symbionts have been detected in weevils,[113-120] and their roles in nutrition, reproduction, development, evolutionary adaptation, and immunity have been studied at the cellular and molecular levels in recent years.[115,119-124] However, some essential questions dealing with their origination, dynamics, diversity and evolution remain largely unanswered. The study of the interaction between bacterial symbionts and host eukaryotic cells, or among weevils-associated bacterial symbionts is largely unknown.[119,123,125] For instance, it has been revealed that there are four different prokaryotic genomes from nuclear, mitochondrial, principal endosymbiont, and Wolbachia respectively within somatic and germ cells of the weevil Sitophilus oryzae, but we know little about their interactions.[126] Diverse bacteria belonging to the phyla of Proteobacteria, Firmicutes, and Bacteroidetes were isolated from larvae or larval guts of different weevil species including the red palm weevil Rhynchophorus ferrugineus Olivier,[116] the weevil Lissorhoptrus oryzophilus Kuschel,[127] the sugarcane weevil Sphenophorus levis, [122] and the weevil Otiorhynchus species.[128] Diverse Wolbachia strains with curculio-host and geographic variations have been uncovered in the plum curculio Conotrachelus nenuphar.[114] Moreover, at the weevil individual level, diverse bacterial species belonging to the genera of Fusobacterium, Staphylococcus, Bacillus, Corynebacterium, Arthrobacter, Serratia, Vibrio, and Flavobacterium were detected in the gut of the kola nut weevil Balanogastris kolae.[117] The gut bacterial community in larvae of the red palm weevil Rhynchophorus ferrugineus Olivier was found to be mainly from the phyla of Proteobacteria, Bacteroidetes and Firmicutes, and the families of Enterobacteriaceae, Porphyromonadaceae, and Streptococcaceae.[116,129] Although sibling weevil species compete for the same resource, they were found to have a clearly distinct community of secondary endosymbionts, including bacterial species or strains in the genera of Rickettsia, Spiroplasma, and Wolbachia.[119] In addition, seasonal alteration of the dominant bacterial species, such as Klebsiella pneumoniae in November and Lactococcus lactis in July, was found in the digestive tract of the red palm weevil Rhynchophorus ferrugineus.[130] The finding of the primary symbiont “Candidatus Curculioniphilus buchneri” in the germalia at the tip of each overiole of Curculio weevils provided another evidence supporting vertical transmission of endocellular bacteria via ovarial passage.[113]

2.1.4 The Order Blattodea

2.1.4.1 Termite in the genus Coptotermes of the family Rhinotermitidae

Bacteria

Termite guts harbor a high density of diverse bacterial microorganisms, including bacterial species in the genera of Staphylococcus, Streptococcus, Enterobacter, Enterococcus, and Lactococcus.[131-134] Since the combination of traditional methods with modern molecular techniques, accumulating evidence has revealed that not only have the roles played by bacteria in the physiological function of termite guts been ignored, but also that the bacterial abundance, diversity, and distribution have been severely underestimated.[135,136] New symbiotic bacteria have been gradually identified in termite guts during the past decades. For example, bacterial species belonging to the order Bacteroidales were identified in the gut of the termite Coptotermes formosanus.[132] “Elusimicrobium minutum” was first cultivated as the representative of the termite group 1 phylum.[137] Moreover, the comparison of the intestinal bacterial communities in fungus-growing termites at the genus level indicated that termite species-specific core microbiota may exist in extant termites.[138]

Archaea

Methanogenic archaeal species, including those in the orders of Methanobacteriales and Thermoplasmales, were identified in the guts of termites.[139-143]

Protists

Protists, as a member of gut microbes, were identified in termites.[142]

2.1.4.2 Cockroaches in the genus Cryptocercus of the family Cryptocercidae, the genera Periplaneta and Shelfordella of the family Blattidae, and the genus Blattella in the family Blattellidae

Bacteria

The gut symbiotic bacteria of cockroaches have attracted increasing research attention in recent years.[144-146] The bacterial community in the gut of the American cockroach Periplaneta americana was found to consist of those in the phyla of Proteobacteria, Bacteroidetes, Firmicutes, Fusobacteria, and unclassified bacterial species.[147] Bacterial species belonging to the phyla of Bacteroidetes, Firmicutes and Proteobacteria were dominant in the gut of the Cockroach Shelfordella lateralis.[148] Bacterial species belonging to the genera Pseudomonas and Serratia were the most common and abundant bacterial species in external surfaces and alimentary tract of the German cockroach Blattella germanica.[149] In the gut of the wood-feeding cockroach Cryptocercus punctulatus, the dominant microorganism species is Formyltetrahydrofolate synthetase.[150] The bacterial species belonging to the phyla of Bacteroidetes, Firmicutes and Proteobacteria were dominant in the gut of the cockroach Shelfordella lateralis.[148] As an endosymbiotic bacterium, Blattabacterium is found in all cockroaches except one cave-dwelling genus.[145] For example, Blattabacterium cuenoti, an endosymbiont is found within mycetocytes in the American cockroach, Periplaneta americana.[151] Interestingly, Park, Park and Takeda revealed that starved cockroaches do not digest bacterial endosymbionts for recycling of nutrients,[151] reusing uric acid, glycogen and lipids stored in the fat body.[151-153] In the recent study, the core bacterial species was detected in the gut of Shelfordella lateralis.[154]

In addition, the role of bacterial symbionts in cockroaches has been gradually uncovered during the past years. Bacterial symbionts participating in lignocellulose digestion was revealed in the wood-feeding roach Cryptocercus punctulatus [155] and the enteric bacterium Shimwellia blattae coenzyme isolated from a cockroach was shown to produce B12.[156] Moreover, the interaction between the bacterial community of cockroaches and their environmental bacterial entities at the cellular and subcellular levels have also attracted much attention. For instance, food-driven shifting in the gut bacterial community was shown in the gut of Periplaneta americana;[157] transmission of antibiotic resistance was found in different cockroach species;[158-160] and vectors of environmental pathogenic bacteria, including Staphylococcus aureus, Enterobacter sakazakii, Escherichia coli, Proteus vulgaris, and some specific species in the genera of Bacillus, Salmonella, Streptococcus, Klebsiella, and Citrobacter were detected in cockroaches.[149,161-166]

Protists

Microscopy revealed that protists existed in the gut of the wood-feeding roach Cryptocercus punctulatus.[155]

Archaea

Methanogenic archaea were identified from the gut of cockroaches.[143,167]

Viruses

Viral strains or species belonging to the genus Cyclovirus of the family Circoviridae were detected in the Florida woods cockroach Eurycotis floridana.[168] Blattella germanica densovirus was detected in in the German cockroach Blattella germanica.[169] Moreover, viral particles were also identified under microscopy in the gut of the wood-feeding roach Cryptocercus punctulatus.[155]

2.1.5 The Order Lepidoptera

2.1.5.1 Silkworms in the genus Bombyx of the family Bombycidae

Bacteria

The intestinal bacterial community of silkworm mainly consists of species belonging to the genera of Arthrobacter, Bacillus, Brevibacterium, Corynebacterium, Escherichia, Klebsiella, Lactobacillus, Micrococcus, Pseudomonas, Staphylococcus, and Stenotrophomonas.[170,171] The gut bacterial community of the silkworm Bombyx mori was showed to be impacted significantly by diet and the rearing way. [171,172] Eukaryotic initiation factor 4E-1, BmFOXG1, MBF2-related genes in the silkworm Bombyx mori were shown to be induced by bacteria.[173]

Fungi

Diverse fungal species of Beauveria bassiana were isolated from the silkworm Bombyx mori.[174]

Viruses

Bombyx mori nucleopolyhedrosis virus and Autographa californica multiple nucleopolyhedrovirus were isolated from a diseased larva of the wild silkworm, Bombyx mandarina.[175] Some viruses that were identified in silkworms are pathogenic, which includes Bombyx mori cytoplasmic polyhedrosis virus,[176] Bombyx mori densovirus type 1,[177,178] and infectious flacherie virus.[179]

2.1.5.2 Moth species in different genera of the families Sphingidae, Saturniidae, and Noctuidae

Bacteria

Studies on the microbial community of moth species mainly focused on Manduca sexta, a tobacco hornworm in the genus Manduca. Brinkmann and colleagues described two kinds of bacterial symbionts from eggs of Manduca sexta: (i) an active Enterococcus relative, and (ii) an inactive Citrobacter sedlakii relative.[180] Bacteria in the gut of the velvetbean caterpillar Anticarsia gemmatalis belonged to the genera Bacillus, Enterococcus, and Staphylococcus. Among these, Bacillus subtilis, Bacillus cereus, Enterococcus gallinarum, and Enterococcus mundtii exhibited protease activity.[181] The “commensal-to-pathogen” switch phenomenon was displayed by Mason and colleagues in the moth Manduca sexta, in which, Enterococcus faecalis, as a commensal bacterium in the gut of Manduca sexta, caused the rapid death of M. sexta larvae after injection of Enterococcus faecalis directly into the larval hemocoel.[182] Moreover, the bacterial community in the midguts of months was shown to be affected by different diets and antibiotics.[183-185]

2.1.5.3 Hepialus gonggaensis in genus Thitarodes of the family Hepialidae

Bacteria

The bacteria belonging to the genera Rahnella and Carnobacterium were dominant in the guts of Hepialus gonggaensis larvae.[186] Moreover, the dynamics of the intestinal microbial community in different instars larvae was associated with their physiological development stages although the mechanism is unclear yet.[187] Feeding with external bacteria can impact the gut microbial community in Hepialus gonggaensis larvae.[188]

Fungi

Diverse and aboundant fungi were detected in the gut of larval Hepialus gonggaensis, in which, fungi belonging to Mortierellaone and Trichosporon were dominant.[189]

2.1.5.4 Galleria mellonella in the genus Galleria of the family Pyralidae

Bacteria

Galleria mellonella is the larvae of the greater wax moth and has been used as in vivo or in vitro model for different laboratory studies dealing with bacterial species. For example, it has been utilized to study the infection-induced antimicrobial activity, such as heat-killed bacterial cells induced immunity,[190] heat-shock enhanced immunity, [191] to test the antimicrobial efficacy of antibiotics, such as antibacterial compounds, [192-195] antifungal compounds, [196,197] and insecticidal proteins, [198] to study the virulence of a wide range of pathogenic microorganisms including Coxiella burnetii, [194] enteropathogenic Escherichia coli (EPEC), [199] uropathogenic E. coli (UPEC), [200] Helicobacter pylori, [201] Klebsiella pneumoniae, [202] Legionella pneumophila, [203] Listeria monocytogenes,[204-206] Proteus vulgaris,[204] Pseudomonas aeruginosa, [207] Serratia marcescens,[204] Staphylococcus aureus,[204] Streptococcus pyogenes, [208] Streptococcus pneumoniae, [209] and fungal species including Aspergillus fumigatus, Candida albicans, Candida tropicalis and Fusarium oxysporum,[197,204] and to evaluate novel antimicrobial molecular or subcelllular entities, such as Synthetic epidermicin NI01,[210] antimicrobial peptides,[211] and bacteriophage,[212]

2.1.6 The Order Hymenoptera

2.1.6.1 Ants in the genera Atta, Azteca, Camponotus, Cephalotes, Crematogaster, Cyphomyrmex, Formica, Mycocepurus, Odontomachus, Paratrechina, Procryptocerus, Solenopsis, Tapinoma, and Trachymyrmex of the family Formicidae

Bacteria

The origin of ants was in Cretaceous [213,214] and their diversity was recently revealed.[215] During the past two decades, ants and their symbiotic bacteria have absorbed much research interest.[216-218] The bacterial symboints belonging to the phyla Acidobacteria, Actinobacteria, Bacteroidetes, Firmicutes, Planctomycetes, Proteobacteria, and Spirochaetes were found in the bacterial community of arboreal ants, and revealed little overlap with the bacteria found on the ants' host plant.[218] Multiple molecular bacterial species of the genus Bacillus were identified as inhabitants of the midgut of red imported fire ant larvae.[219] Blochmannia, an obligate primary bacterial symbiont, was found to live within host bacteriocyte cells, be transmitted vertically from maternal host queens to offspring, and play a role in host nitrogen recycling and nutrient biosynthesis.[220-222] Blochmannia's closest bacterial relative, in the genus Serratia, was found to be a secondary endosymbiont in the guts of the ant Camponotus japonicus Mayr, and it was suggested that diets may be an external source for Camponotus ants to acquire their secondary endosymbionts.[220] Bacteria communities in the guts of red imported fire ant larvae appeared to be influenced by the geographical location and the foods consumed by the ants.[223]

Bacteria have been studied as an important partner in the multilateral symbiotic association of ants, fungi, bacteria, and plant.[224-228] The study of the microbial community structure of leaf-cutter ant fungus gardens revealed that the members of the microbial community were diverse and dominated by Gram-negative bacterial species in the gamma-Proteobacteria and Bacteroidetes.[229] Bacterial species in the orders of Rhizobiales, Burkholderiales, Opitutales, Xanthomonadales, and Campylobacterales were most dominant in the turtle ant Cephalotes varians.[230] And the vertical transmission of the entire community was suggested to play an important role in the evolution of the turtle ants.[231]

The bacterial species in the genera Wolbachia and Arsenophonus of Proteobacteria, the order Entomoplasmatales of Tenericutes, and the fungal Microsporidia were detected in the ant Formica exsecta.[232] Moreover, distributions of Entomoplasmatales bacteria in guts were found unique to the army ants,[233] and their origin may involve vertical and horizontal transmission mechanisms.[231,234,235] Additionally, the gut regional distribution of symbiotic bacteria was shown in the ant Camponotus japonicus.[221] For example, the bacterial species in the genera of Bacillus and Enterococcus were found in the midgut, those in the genus Paenibacillus were identified in the hindgut, and those in the genus Bacillus were detected in the crop.[221]

The bacterial symbionts of turtle ants belonged to the orders Burkholderiales of Betaproteobacteria, Pseudomonadales of Gammaproteobacteria, Rhizobiales of Alphaproteobacteria, Verrucomicrobiales of Thermoprotei, and Xanthomonadales of Gammaproteobacteria.[236] Moreover, some bacteria strains isolated from ants were shown to have antifungal activity and such activity was believed to play a critical role in maintaining multipartite symbiosis.[237-243] Pseudonocardia was a dominant and colony-specific symbiotic bacterium in leaf-cutter ants,[244] and believed to be vertically transmitted and occasionally horizontally transmitted.[234] Pseudonocardia symbionts produce antibiotics that can inhibit the growth of Escovopsis parasites.[234,245] In addition, symbiotic nitrogen-fixing bacteria were consistently isolated from the fungus gardens of leaf-cutter ant colonies [246,247] and core species in bacterial communities were identified in the ant Cephalotes varians.[248]

Fungi

The ant-fungus association has been a hot topic during the past decades despite its recognition in the mid-19th century.[249-253], Fungal symbionts were shown in fungus-growing ants.[254-258] Fungal diversity in ants has been shown in recent studies.[259-265] For example, the fungal species of leaf-cutting ants belonged to the genera Cladophialophora, Cladosporium, Exophiala, Hyaline, Ochroconis, Penidiella, Phaeococcomyces, and Phialophora. [266] However, some pathogenic fungal species carried by ants were a concern for some researchers.[267]

Studies found that the function of fungal species in the fungus-ant association varies. Fungus was utilized as a building material for prey in the plant-ant of the genus Allomerus,[239] served as a food source in ants of different genera including Tetraponera, Petalomyrmex, and Pseudomyrmex.[239,268,269] And it can degrade a large range of plant polymers in Acromyrmex leaf-cutting ants.[257,270] Moreover, in ant-plant symbioses, symbiotic ants can obtain food from their host plants.[253] Endophytic fungi of host plants were shown to influence ants' behavior.[263,327,328] In addition, a recent study showed that the variation of fungal communities between fungus chamber soils and non-nest soils was associated with the existence of leaf-cutting ants.[256,329]

Viruses

Solenopsis invicta virus 1 (SINV-1), SINV-2, and SINV-3 were detected in individual worker ants, and moreover, individuals of Solenopsis invicta ants were shown to have simultaneously all combinations of the S. invicta viruses.[271-276] The Solenopsis invicta virus-1 (SINV-1), a positive-strand RNA virus, was found to affect only Solenopsis species and to infect all caste members and developmental stages, including eggs and instars.[273,277] However, in another study, SINV-1 genome integration had not been found in Solenopsis invicta host genome.[278] Solenopsis invicta virus 2 (SINV-2) with unique genome characteristics was also identified in the red imported fire ant.[279] Solenopsis invicta virus 3, as the third viral species of the red imported fire ant, was found by Valles and Hashimoto in 2009.[272,274] After being infected experimentally with Solenopsis invicta virus 3, the behavior and some biological and reproductive functions of red imported fire ants were shown to be altered.[280,281] Moreover, the host range for Solenopsis invicta virus 3 covered various genera and subfamilies of ants.[282] The significant geographic divergence of Solenopsis invicta virus-1 (SINV-1) nucleotide sequences and the seasonal dynamics of infection rates were observed. [283] In addition, chronic bee paralysis virus (CBPV) was detected for the first time in the ant Camponotus vagus and the ants Formica rufa.[284]

2.1.6.2 Bees in the genera Apis and Bombus of the family Apidae, and the genus Osmia of the family Megachilidae

Bacteria

It is estimated that there are more than 16,000 bee species on Earth, with their origin in African in early to mid-Cretaceous.[285] Recently, the pathogenic agents of microorganisms have been attributed to the loss of bee colonies worldwide.[286]

Therefore, while the topic of bee immunity is still one of our major research interest,[286-288] increasing attention has been paid to bee-associated bacterial, viral and fungal microorganisms.[289] Diverse bacterial species belonging to the bacterial phyla of Proteobacteria, Bacteroidetes, and Firmicutes were found in the gut of different bee species in various genera of the family Apidae.[290-294] Gilliamella apicola (Gammaproteobacteria) and be dominant in the gut symbionts of the honey bee of the genus Apis and bumble bee of the genus Bombus; [293,295,296] and the acquisition of the gut symbionts in corbiculate bees was determined by both environmental transmission and vertical transmission.[293] The diversity and dynamics of the core gut bacteria were shown in honey bee larvae[9,290] and in adults of different honey bee species.[290,292,297-299] Bacterial species in the phyla of Proteobacteria, Bacteroidetes, and Firmicutes were dominant in the guts of the honey bee Apis mellifera ssp. carnica, the bumble bee Bombus terrestris, and the red mason bee Osmia bicornis.[292] Lactobacillus kunkeei and Acetobacteraceae appeared in 1st instar larvae; and in later larval instars, Lactobacillus kunkeei decreased remarkably while Fructobacillus emerged.[290]

Viruses

Many honey bee viruses, including black queen cell virus, chronic bee paralysis virus, deformed wing virus, Kashmir bee virus, and sacbrood bee virus, were detected in the body of healthy queens despite of our attention focusing on those pathogenic viruses.[300-302] The large scale losses of honey bees in recent years were attributed to environmental viral entities from parasitic varroa mites.[303,304] Recently, honey bee viruses such as deformed wing virus, black queen cell virus, and Israeli acute paralysis virus were found to have the ability to replicate in the fungal Ascosphaera apis, a pathogen of honey bee chalkbrood disease.[305] Viruses can be transmitted vertically in honeybees.[302] Overlapping genes, a common characteristic of viruses defined as having nucleotides coding for more than one protein by being read in multiple reading frames, were identified in the genomes of Israeli acute paralysis virus, acute bee paralysis virus, Kashmir bee virus, and Solenopsis invicta virus 1.[306,307] From a fimpological perspective, I hypothesize that overlapping genes may reflect the conserved core viral genes during their evolution.

2.1.6.3 Wasps in the genus Megastigmus of the family Chalcididae

Bacteria

Bacterial symbionts belonging to the genera Rickettsia and Wolbachia of the family Rickettsiaceae, the genus Ralstonia of the family Ralstoniaceae, and the genus Burkholderia of the family Burkholderiaceae were detected in larvae, pupae, and adults of wasp species in the genus Megastigmus of the family Chalcididae.[308,309] Wolbachia are intracellular symbiontic bacteria belonging to the family Rickettsiaceae and were shown to have an association with reproduction in the parasitic wasp Asobara tabida.[310,311]

2.1.7 The Order Diptera

2.1.7.1 Mosquitoes in the genera Aedes, Anopheles, and Culex of the family Culicidae

Bacteria

There are more than 3,500 mosquito species on Earth.[312] The diverse bacterial species in mosquitoes have been one of the hot topics during the past decades, and the function of bacterial symbionts and their relationship with mosquito hosts have been studied at the molecular level and the cellular level recently.[312-317] The halotolerant bacteria Halobacillus litoralis and Staphylococcus cohnii were detected in the midgut of Culex quinquefasciatus mosquito larvae.[315] The bacteria belonging to the phyla of Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes were isolated from the wild mosquito species in different genera.[316,318-320] Mosquito bacterial communities were believed to be acquired from the aquatic environment where larvae developed and can be influenced by diverse environmental entities including diets and antibiotics;[317,320-326] and some of bacteria in adult mosquitoes were detected from eggs.[321]

Viruses

Traditionally, our understanding of mosquito-borne viruses is associated with the human illnesses they caused, such as dengue virus in dengue fever.[330,331] Recently, accumulating viral species or strains have been identified in various mosquito species from different geographic areas, for example, Liao Ning virus, Stretch Lagoon virus, Beaumont and North Creek viruses, and Murrumbidgee and Salt Ash viruses in Australian mosquitoes,[332] Quang Binh virus in Chinese mosquitoes and in Vietnam mosquitoes,[333] mosquito-borne flaviviruses and Ilomantsi virus in Finnish mosquitoes,[334] Omono River virus in Culex species mosquitoes of Japan,[335] Eilat virus in Anopheles coustani mosquitoes in the Negev desert of Israel,[336] Nam Dinh virus,[337] and a viral core community was revealed in different mosquito samples despite the diverse and heterogeneous nature of the viral community from the animal and plant hosts they feed on.[336,339]

2.1.7.2 Flies in Different Genera of the Families Glossinidae, Ephydridae, Nycteribiidae, Psychodidae, Tipulidae, Streblidae, and Sarcophagidae

Bacteria

Symbiontic bacterial species or strains have been identified in various fly species. Diverse bacterial species belonging to the genus Arsenophonus were identified in louse flies and bat flies, [340] and in the larval guts of Tipula abdominalis, they were confirmed by culture, light microscopy and scanning electron microscopy.[341,342] Four bacterial strains belonging to Schineria gen. nov, a new lineage of gamma-Proteobacteria, were isolated from the fly larvae of an obligate parasitic fly, Wohlfahrtia magnifica.[343] The lavael gut of the oil fly Helaeomyia petrolei contained 2×10^5 heterotrophic bacteria per larva, which consisted of non-sporeformers and Gram-negative bacteria.[344] Using Scanning electron microscopy, light microscopy, and direct isolation methods, Klug and colleagues found that the gut tract of larval stages of Tipula abdominalis contained a diverse bacterial community, which even directly attached to the gut wall. Furthermore, the attached microbiota, sloughed during ecdysis, recolonized to the same density and diversity observed before the molt.[341] Diverse bacteria, including those in the genera of Morganella, Providencia, and Acinetobacter, were isolated from the larval gut of the oil fly Helaeomyia petrolei. [344,345] Moreover, the dynamics of the bacterial community was found in the different developmental stages and larval organs of the fly Wohlfahrtia magnifica.[346] Recently, accumulating novel symbiontic bacterial species or strains from various fly species have been reported. For example, a novel Serratia glossinae strain was isolated from the midgut of the tsetse fly Glossina palpalis gambiensis;[347] a novel Klugiella xanthotipulae strain was isolated from the hindgut of the larvae of the aquatic crane fly Tipula abdominalis;[348] Bartonella DNA was detected in the bat fly Cyclopodia greefi,[349] and a novel Arsenophonus bacterium and a novel strain of Rickettsia were detected in the bat fly Trichobius major.[350]

Bacterial endosymbionts in the gut of Tsetse flies of the family Glossinidae were classified by some researchers into primary endosymbionts residing intracellularly within specialized cells (bacteriocytes) and secondary endosymbionts relating to the free-living bacteria of the phylum Proteobacteria.[8,351] Sodalis glossinidius, as a secondary endosymbiont of tsetse flies, was believed to be transmitted maternally, and its coding capacity of chromosome was found to be reduced significantly,[352] which was attributed to the influence of the host environment.[353]

Recently, Drosophila has been utilized as a model in the study on microbiota-induced host structural and functional alterations.[354,355] Wolbachia, intracellular bacteria detected in Drosophila species, is associated with host reproduction in Drosophila.[356-358] Moreover, diverse Spiroplasma strains, another wide spreading symbiont in Drosophila species, were also found to be involved in reproduction.[359-361] In addition, diversity of larvael bacteria belonging to the phyla Actinobacteria, Firmicutes, and Proteobacteria was described in the sand fly Deanemyia maruaga; [362-364] and some Alphaproteobacteria and Gammaproteobacteria were detected in bat flies of the families Nycteribiidae and Streblidae.[340,349,365-369]

Viruses

Toscana virus in the genus Phlebovirus was identified in the sand flies Phlebotomus perniciosus and Phlebotomus perfiliewi.[370] In addition, Nora virus was recently identified in Drosophila melanogaster;[371] and West Nile virus was detected in the louse fly Icosta Americana.[372]

2.2 The Class Arachnida

2.2.1 The Order Parasitiformes

2.2.1.1 Ticks in the genera Ixodes, Amblyomma, Dermacentor, Haemaphysalis, Hyalomma and Rhipicephalus of the family Ixodidae, and the genus Ornithodoros of the family Argasidae

Bacteria

Ticks were believed to be the most important vectors of disease-causing pathogens in nonhuman animals and humans.[373,374] During the past years, increasing studies have been done on tick-associated microorganisms such as pathogenic and endosymbiotic bacteria. Various tick-borne microorganisms in different genera including Anaplasma, Bacillus, Bartonella, Borrelia, Coxiella, Ehrlichia, Francisella, Midichloria, Mycobacterium, Neoehrlichia, Propionibacterium, Rickettsia, Theileria, and Wolbachia have been detected in a range of tick species of various genera including Amblyomma, Carios, Dermacentor, Haemaphysalis, Hyalomma, Ixodes, and Rhipicephalus.[375-384]

There are variations in the tick species-specific and geographic distribution of the tick-associated bacterial community,[376,378,380,382-384] which should be attributed to the close biological, ecological, and evolutiological relation with their macroorganism hosts such as bears, cattle, sheep, goats, horses, or dogs.[378] Several endosymbiotic bacterial species were identified in hard ticks,[380,385] and the origin of the tick-associated bacterial community was suggested to be the consequence of horizontal transmission from the environment during ticks' sterile larvael development[376] and to be vertically transmitted.[380,385]

Viruses

Although recently tick-borne encephalitis-virus was detected in ticks from migratory birds,[386] we still know very little about tick-specific non-pathogenic viruses.

2.3 The Class Malacostraca

2.3.1 The Order Decapoda

2.3.1.1 Shrimps in different genera of the families Axiidae, Penaeidae, Callianassidae, and Palaemonidae

Bacteria

The complex bacterial species belonging to various genera from the phyla Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes, and Fusobacteria were detected in various shrimp species of the genera including Artemia, Litopenaeus, Marsupenaeus, Neotrypaea, Penaeus, and Rimicaris, which however, exhibited shrimps' inter- and intraspecies variations.[387-393] For instance, Cytophaga-Flavobacteria-Bacteroides, proteobacteria, and gram-positives were three major features of the bacterial community in the hindguts of the shrimp Neotrypaea californiensis.[394] Bacterial species in the gut of the deep-sea Alvinocarid shrimp Rimicaris exoculata mainly belonged to Epsilonproteobacteria, Entomoplasmatales, and Deferribacteres.[395] And the Gammaproteobacteria were dominant in eggs of the shrimp Rimicaris exoculata.[391] Moreover, Beardsley and colleagues showed that there were 0.6-7 × 10^{10} bacteria in one gram fresh feces of the Pacific white shrimp Penaeus (Litopenaeus) vannamei, in which 61% of bacteria belonged to the genus Vibrio.[392] Most of the bacteria associated with shrimp are uncultured and novel species, and increasing novel species or strains have been found in the guts of healthy shrimps. For example, a novel strain of Bacillus pumilus was isolated from the mid-gut of the healthy black tiger shrimp Penaeus monodon.[396] The bacterial community composition in the guts of shrimps is dynamic in different growth stages,[397,398] and influenced by many factors such as starvation and probiotic bacteria.[393,399] For example, after a long period of starvation, the dominant Deferribacteres in the gut of the shrimp Rimicaris exoculata were replaced by the dominant Gammaproteobacteria.[393] Morphologically, it has been observed that filamentous bacteria are inserted between microvilli of gut epithelial cells of shrimps.[393] Recently, the genome of Pacific white shrimp, Litopenaeus vannamei was shown for the first time to have horizontally transferred genes from bacteria and fungi,[400] which, however, is a novel supporting evidence for the hypothesis of the evolutiological role of microorganisms played in shrimp evolution.

Viruses

Shrimp-associated viruses have been accounted for mainly from the pathogenic perspective. Some pathogenic viruses, including white spot syndrome virus, hypodermal and hematopoietic necrosis virus, Penaeus monodon densovirus (formerly called hepatopancreatic parvovirus), spawner-isolated mortality virus, lymphoid organ parvo-like virus, Laem-Singh virus, Macrobrachium rosenbergii nodavirus, and extra small virus, were identified to infect different shrimp species.[401-403] However, some symbiotic viruses were also detected in healthy shrimps. For example, yellow-head virus was found to be a symbiotic virus in the shrimp Palaemonetes pugio despite some pathogenic strains of yellow-head virus.[403,404]

2.3.1.2 Crabs in the genera Scylla and Callinectes of the family Portunidae

Bacteria

The culture-dependent and culture-independent approaches have revealed that the diversity of intestinal bacteria belonging to the phyla of Proteobacteria, Firmicutes, Tenericutes, Bacteroidetes, Fusobacteria, and unidentified or unclassified bacteria exist in different crab species of various genera including Eriocheir,[405,406] Scylla,[407-409] and Callinectes.[410] The most abundant bacterial species within Chionoecetes (snow crab) internal organs belong to the genera of Acinetobacter, Bacillus, Pseudomonas, Stenotrophomonas, Agreia, Microbacterium, Rhodococcus and Agrococcus.[411] Moreover, crab-associated bacterial compositions have been shown to be influenced by different environmental factors.[405,408,409] The intestinal bacterial compositions of pond-raised crabs aree different from that of wild crabs.[405,408] Despite the pathogenic role of bacteria in diseases of crabs, the question, “what are their roles in healthy crabs?” has been attracting increasing attention.[406-408,412,413]

Viruses

Studies on crab-associated viruses have revealed that the complexity of the relationship between crabs and viruses is far beyond our existing understanding. Crab-associated viruses belong to different virus families, including Reoviridae, Bunyaviridae, and Roniviridae.[414] More and more novel viral species or strains in crabs have been described during the past decades, such as a reo-like virus in blue crab Callinectes sapidus,[415] Scylla serrata reovirus in mud crab Scylla serrata,[416] and novel reoviruses in the Chinese crabs.[417-419] Although our primary interest in crab-associated viruses was their pathogenicity,[416,420-424] accumulating evidence has suggested that their role may not be so simple. For example, white spot syndrome virus and Infectious hypodermal and hematopoietic necrosis virus are pathogenic,[421,425,426] however, both viruses are also detected in normal crabs,[427] and the heart of freshwater crab Paratelphusa hydrodomous was showed to be a good tissue for replication of white spot syndrome virus.[428] In addition, how to account for the species-variation in response to similar external viruses is another challenge that needs further exploration.[429]

Fungi

Crab-associated fungi have not attracted much attention in the past decades when compared to crab-associated bacteria and viruses. However, the recent study on fungi Lethargic Crab Disease by Vicente and colleagues suggested that crab-associated fungi should become one of hot topics in the near future, despite its focus on fungal pathogenicity.[430]

2.4 The Class Maxillopoda

2.4.1 The Order Siphonostomatoida

2.4.1.1 Lice in the genus Lepeophtheirus of the family Caligidae

Bacteria

Bacterial species such as Tenacibaculum maritimum, Pseudomonas fluorescens, and Vibrio spp. were isolated from sea lice.[431] Despite its parasitic characteristics in salmon,[432,433] the salmon louse Lepeophtheirus salmonis was found to be a vector for the transmission of aquatic bacteria [431] and viruses, such as salmonid alphavirus, infectious salmon anaemia virus, infectious haematopoietic necrosis virus, and rhabdovirus.[74,75,434-436] However, the study on sea lice-associated bacteria and viruses focused on their pathogenicity, and therefore, the roles of sea lice-associated bacterial and viral species or strains in the existing literature were mainly accounted for from a pathogenic perspective.

3 The Phylum Annelida

3.1 The Class Polychaeta

3.1.1 The Order Canalipalpata and Sabellidae

3.1.1.1 Tubeworms in the genera of Escarpia, Lamellibrachia Ridgeia, Riftia and Sclerolinum of the family Siboglinidae, and the genus Hydroides of the family Serpulidae

Bacteria

Diverse bacterial species belonging to the phyla of Proteobacteria, Bacteroidetes, Actinobacteria, Chloroflexi, Firmicutes, Planctomycetes, Verrucomicrobia, and Deinococcus-Thermus have been detected in the vestimentiferan tubeworm Ridgeia piscesae.[437] Chemolithotrophic sulfur-oxidizing bacteria were found to be endosymbionts of tubeworms in the genera of Riftia, Lamellibrachia, Oligobrachia, and Sclerolinum that live near the volcanic deep-sea vents, which enable the tubeworm to utilize sulfide for its metabolism.[438,439,440,441] Therefore, sulfide-oxidizing bacterial symbionts have been believed to supply tubeworms food.[442,443] In addition, a specialized worm tissue where the chemoautotrophic symbionts live intracellularly is called the trophosome.[443,444] It has been gradually revealed during the past decades that symbiotic bacteria are involved in the development of invertebrate larvae. For example, the settlement of invertebrate larvae is actually bacteria-dependent.[445,446] It was showed that the entering and colonizing of bacterial symbionts occurred during the development of the settled larvae and the formation of trophosome, which was a horizontal endosymbiont transmission.[444] Recently, a strain of the bacterium Pseudoalteromonas luteoviolacea was showed to induce metamorphosis in the larvae of the marine tubeworm Hydroides elegans. [445] Moreover, the bacterium Pseudoalteromonas luteoviolacea participated in the development of Hydroides elegans larvae by producing phage tail-like structures to trigger metamorphosis of the tubeworm.[447] These experimental evidences reveal for the first time how this novel form of bacterium-animal interaction at the cellular and subcellular levels cooperates physiologically during larvael development.

Fungi

A novel yeast species, Rhodotorula benthica, was isolated from the tubeworm in the genus Lamellibrachia.[448]

3.2 The Classes Clitellata and Hirudinea

3.2.1 The Orders Arhynchobdellida, Hirudinida, and Gnathobdellida

3.2.1.1 Leech in the genera of Hirudo, Placobdella, and Myzobdella

Bacteria

One of the reasons for the study on leech microorganisms is that medicinal leeches used in plastic and reconstructive surgery can cause bacterial infection.[449-454] Studies have revealed that commensal bacterial species exist in various anatomic locations of leeches, such as the skin,[455-457] the digestive tract,[458-464] bladder,[465] viscera,[466] and eggs.[465] For example, a bacterial species belonging to the genus Rickettsia was found in various tissues including the epidermal, esophageal, and intestinal tissues of two species of Japanese glossiphoniid leeches.[467] Recently, Rio and colleagues showed that bacterial symbionts appeared within the cocoon immediately following deposition, grew dynamically, and displayed diverse temporal colonization during leech embryogenesis;[465] and the authors attributed the synchronization of host development with the establishment of particular members of the microbial community to vertical transmission and the dynamic nature of symbiont invasion.[465] Leech-associated symbiotic bacteria belong to the phylum Bacteroidetes, Proteobacteria, Verrucomicrobia, and unclassified Bacteria,[466,465] in which, new members including novel species of the genera Niabella and Devosia have been added recently.[468,469]

In addition, endosymbiotic bacteria belonging to the subphyla Alphaproteobacteria and Gammaproteobacteria have been isolated from specialized structures or organs, variously termed bacteriocytes or mycetomes, such as the esophageal organ in leeches.[463,464, 470] Studies also revealed that the leech-associated bacterial community is dynamic, despite unclear functions of the bacterial symbionts. For instance, a study showed that bacteria belonging to the genus Psychromonas were undetectable in cocoons or 2-16 week-old juveniles of the deep-sea leech species, but became dominant in later developmental stages, which was suggested to be obtained from the environment of the leeches.[471] Moreover, molecular analysis revealed that the dominant gammaproteobacteria of the leeches were inter-species different.[471]

Viruses

It has been recognized for a long time that leeches are potential virus reservoirs. Leech-associated viruses have been shown to come from external sources. For example, mammalian Myxoma hog cholera viruses, bovine parvovirus, feline calicivirus, equine arteritis virus, and herpesvirus type 1 can survive in leeches.[472,473] Recently, the viral hemorrhagic septicemia virus and mimivirus were detected in leeches.[474,475]

3.3 The Classes Oligochaeta and Clitellata

3.3.1 The Orders Haplotaxida and Megadrilacea

3.3.1.1 Earthworms in the genus Amynthas of the family Megascolecidae, the genus Eudrilus of the family Eudrilidae, and the genera Aporrectodea, Eisenia, and Lumbricus of the family Lumbricidae

Bacteria

Earthworms are saprotrophic invertebrates. Although the question “how do earthworms interact with soil environmental microbes for survival?” still a major concern in the study of earthworms,[476-480] increasing attention has been paid to the question “what are the symbiotic microorganisms of earthworms?” It was estimated that the bacterial number was 5.43×10^5 cfu per milliliter content in the gut of earthworms.[481] Diverse earthworm-associated bacteria belong to different phyla including Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Cyanobacteria, Firmicutes, Gemmatimonadetes, Nitrospirae, Planctomycetes, Proteobacteria, Tenericutes, and Verrucomicrobia, and various genera including Acinetobacter, Azotobacter, Bacillus, Clostridium, Flavobacterium, Halobacterium, Lactobacillus, Micrococcus, Pseudomonas, Spirocheata, Staphylococcus, Streptococcus, and Verminephrobacter.[481-488] Bacteria belonging to the phylum Bacteroidetes and the subphyla of Alphaproteobacteria and Betaproteobacteria were detected in the nephridia of basal Crassiclitellata.[482] Bacterial symbionts belonging to the genus Verminephrobacter were identified in the excretory organs (the nephridia) of different earthworm species,[487,489] which was suggested to be transmitted vertically.[490]

Fungi

Several studies have showed that some fungal strains or species were isolated from earthworms in the past years.[484,488,491] Fungal strains or species belonging to the genera of Aspergillus, Candida, Fusarium, Penicillium, Pichia, Pytium, Rhizopus, Saccharomyces, and Rhizopus were detected in the earthworm Libyodrillus violaceous.[488] The interaction between earthworm and fungi is thought to play an important role in the diversity and recycling organic matter.[488,491]

4. The Phylum Cnidaria

4.1 The Class Hydrozoa

4.1.1 The Order Anthomedusae

4.1.1.1 Hydra in the genus Hydra of the family Hydridae

Bacteria

Hydra is one of the first “witnesses” when humans began to step into the microorganism world because it was first observed by Antoni van Leeuwenhoek in 1702.[492,493] Since 1744, Hydra has been used as a subject of study in experimental biology.[493,494] While our attention on the relationship between Hydra and bacteria is still focusing on Hydra’s antimicrobial mechanism at the cellular and molecular levels,[495,496] and the role of symbiotic bacteria in the physiology and homeostasis of Hydra,[497,498] some researchers have begun to try to understand the role their relationship plays in evolution. [494,497,499] Moreover, some new questions such as “What causes species-specific bacteria to be maintained in Hydra species grown in different environments?” and “What are the underlying mechanisms?” need to be answered.[499,500] The diversity, complexity, and dynamics of Hydra-associated bacteria after hatchlings were described in Hydra.[500] Recently, Hydra’s microbial communities were reviewed from a non-pathogenic perspective by Bosch and colleagues.[501,502] Some bacterial species in the bacterial community of the basal metazoan Hydra were endosymbionts.[499,503] The early embryogenesis of the basal metazoan Hydra requires specific bacterial colonization.[495] Invertebrate embryos often develop in an environment full of microorganism, including potential pathogens.[495] However, the interaction of embryo-bacterial endosymbionts occurs normal embryogenesis is still a paradoxical phenomenon, despite the discovery of many antimicrobial mechanisms or factors.[495]

Viruses

Three decades ago, two research groups described an interesting phenomenon: viral particles with 185 nm in diameter emerged in the nuclear region of the algae within several hours after the algae were isolated from the Hydra. Moreover, “the source of the virus is unknown since it has not been detected in thin sections of intact hydra or in algal cells immediately after their isolation.”[504-506] Such virus synthesis induced by the isolation of symbiotic Chlorella-like algae was confirmed in different green Hydra and the protozoan Paramecium bursaria.[505,506] In the recent study, Grasis and colleagues found that each species of Hydra harbors a diverse host-associated virome, in which, bacteriophages are the most abundant subcellular viral entities and belong to the virus families Myoviridae, Siphoviridae, Inoviridae and Herpesviridae.[507]

4.2 The Class Anthozoa

4.2.1 The Order Alcyonacea, Gorgonacea, Scleractinia, and Zoantharia

4.2.1.1 Corals in different genera of the families Acroporidae, Alcyoniidae, Gorgoniidae, Fungiidae, Oculinidae, Faviidae, Mussidae, Plexauridae, Pocilloporidae, Poritidae, Siderastreidae, Dendrophylliidae, and Parazoanthidae

Bacteria

Bacterial species in the coral-associated bacterial community are diverse and belong to different bacterial phyla, including Cyanobacteria, Firmicutes, and Proteobacteria. Moreover, in the phylum Proteobacteria, and the dominant bacterial species are shown to be distribute over various subphyla, such as Alphaproteobacteria, Betaproteobacteria, Deltaproteobacteria, Gammaproteobacteria, and Epsilonproteobacteria, which associate with both coral species-specificity and geographic environmental variability.[508-516] Cultivable actinobacteria belonging to different genera, including Agrococcus, Dietzia, Micromonospora, Nocardia, Nocardiopsis, Pseudonocardia, Rhodococcus, Saccharomonospora, Saccharopolyspora, Streptomyces, and Verrucosispora, were isolated from gorgonian coral species.[517] Gammaproteobacteria, Alphaproteobacteria, and Actinobacteria are dominant cultivable bacterial groups in the mucus of the healthy Red Sea coral Fungia scutaria.[518] Roseobacter was shown to be coral-specific in the coral Pocillopora meandrina;[519,520] cyanobacteria were found to exist in 93% healthy species of the coral Pocillopora damicornis;[521] and the bacterial community composition of the South China Sea reef corals Porites lutea, Galaxea fascicularis, and Acropora millepora was found to be different in some bacterial species.[522] Moreover, tissue-specific bacteria at the individual level were found in diverse coral host tissues. For example, Endozoicomonas bacteria were abundant in the endodermal tissues of the coral Stylophora pistillata,[523] and some intracellular bacterial symboints have been observed.[523-526]

Both geographic- and species-specificity of coral-associated bacterial communities hace been recognized in different coral species worldwide including Acropora hyacinthus, Acropora millepora, Alcyonium gracillimum, Galaxea fascicularis, Lophelia pertusa, Madracis decactis, Madrepora oculata, Montastrea franksi, Mussismilia hispida, Palythoa caribaeorum, Pocillopora damicornis, Porites lutea, Stylophora pistillata, and Tubastraea coccinea. [508,511,512,521,522,527-533] However, an interesting fact which our existing theories cannot account for is that Frias-Lopez and colleagues found that there was less than 5% similarity in the bacterial community composition between seawater and the healthy, black band diseased, and dead coral surfaces.[534] Studies have shown that the coral-associated bacterial community can be influenced by environmental factors [535-537] such as seawater depth, salinity and pH, temperature, geographic location, coastal pollution, fish farm effluents, algae, and DNA extraction protocols.[511,538-546] Recently, a normally transient alteration in bacterial associations of the gorgonian Paramuricea clavata was reported[513] and a seasonal dynamic bacterial community was revealed in Caribbean reef-building corals.[547]

A macro-ecological relationship between coral and fish has been found to associate with coral diseases, although the mechanisms haven not been elucidated clearly.[548,549] For instance, although several diseases have been recognized in the coral genera of Porites, Montipora, and Acropora,[550] their etiology is largely unclear and may associate with environmental factors.[550] In fact, although coral-associated bacterial community has been shown to play a physiological role in maintaining coral health, [551,552] the shift of the coral-associated bacterial community has been mainly studies from a pathological perspective already. [508,516,552] Some coral diseases, including dark spot syndrome, white syndrome, yellow band disease, white plague disease, and black band disease, have been found to be associated with the alteration of the coral-associated bacterial and/or fungal communities.[546,547,553-555] Some bacterial species, such as Vibrio coralliilyticus, have been proposed as potential causative agents in both coral bleaching and coral diseases.[508,556]

Archaea

Diverse archaeal species have been identified in corals.[509,515,520,547,557-559] Geographic- and species-specificity archaea have been shown in corals from the Gulf of Eilat, Red Sea, [560] and in corals from the South China Sea.[515] A seasonal dynamic archaeal community has been shown in Caribbean reef-building corals.[547] The roles or functions of archaea are largely unknown. Sato, Willis and Bourne showed that archaea played a role in black band disease of corals.[561]

Fungi

Corals have been found to harbor fungi, in addition to diverse and abundant communities of prokaryotic cells, eukaryotic zooxanthellae, endolithic algae, and protists.[508,518,536,558,562] Geographic- and species-specificity fungi belonging to different genera have been shown in healthy South China Sea gorgonian corals.[517,563] However, the study of coral-associated fungi is still limited and infantile.

Viruses

Coral-associated viruses are attracting more and more attention, partially because of their pathogenic and non-pathogenic roles.[564,565] Virus-like particles have been identified in the coral Pocillopora meandrina during early development.[519] Herpes-like sequences have been detected in healthy and bleaching corals.[565] Moreover, viral sequences similar to some algae- and plant-pathogenic viruses have also been identified in corals.[565]

5. The Phylum Porifera

5.1 The Classes Demospongiae and Calcarea

5.1.1 The Orders Agelasida, Astrophorida, Chondrosida, Clathrinida, Dictyoceratida, Hadromerida, Halichondrida, Haplosclerida, Homosclerophorida, Poecilosclerida, and Verongida

5.1.1.1 Sponges in different genera of the families Ancorinidae, Aplysinidae, Astroscleridae, Chalinidae, Chondrillidae, Clathrinidae, Coelosphaeridae, Dictyonellidae, Geodiidae, Ianthellidae, Irciniidae, Niphatidae, Petrosiidae, Plakinidae, Suberitidae, Spongiidae, and Thorectidae

Bacteria

Sponges are animals belonging to the phylum Metazoa, the oldest of the multicellular animals which emerged around 1.3 billion years ago.[566-569] The members of sponge-associated microorganisms have been revealed to consist of bacteria, archaea, microalgae, and fungi.[569-572] Bacterial communities have been found in sponge species and show ubiquity, geographic heterogeneity, and diversity.[573-582] It is estimated that up to 40% of the total volume of an individual sponge is contributed by sponge-associated bacteria.[583] The number of bacterial phyla in sponge-associated bacterial community increased from 15 in 2007 to 43 in 2013.[584-587] For example, cultivable bacterial communities in the South China Sea sponge includ Alpha-, Gamma-, Delta-Proteobacteria, Bacteroidetes, and Firmicutes.[588] Moreover, the concentration of sponge-bacterial communities usually exceed that of seawater by 2 to 4 orders of magnitude.[589]

Sponge-specific Microorganism Community

After studying sponge-bacterial association and interactions, the novel concept of the sponge-specific microorganism community, or sponge-specific microbiota, was first proposed by Wilkinson in his 1984 study.[569,590] This was supported by later investigations.[508,576,584-587,591-594] Inter-individual variation of bacterial symbiont communities was found in the same sponge species or in different sponge species from the same environment.[595] Webster and colleagues demonstrated that 48% of the 33 previously described “sponge-specific” bacterial clusters existed exclusively in adults and larvae, which implied vertical transmission of bacterial symbionts.[595] The question “where did sponge-specific bacteria come from?” seems simple, but it is not. In fact, after several decades of effort, we still have not found the final answer to it, except that several mechanisms have been proposed around this question.[569,590,596,597] However, after comparing sponge-associated bacterial communities with those in the aquatic surrounding, some bacterial species and archaeal species of the sponge-associated microbial communities were less abundant, or even different from those in the surrounding seawater,[576,587,594,595,598] which cannot be accounted for only by horizontal transmission from an aquatic surrounding source despite of other environmental influences such as seawater temperature.[599] Lee and colleagues revealed that the bacterial communities in sponge adults and embryos were highly similar to each other, but completely different from those in the surrounding seawater, which they believed supported the vertical transfer hypothesis.[576] Therefore, except horizontal transmission from the aquatic environment, vertical transmission of bacterial symbionts has became another source of sponge-specific microorganism communities.[600]

The phenomenon of bacteria inside the larvae of the sponge was first described by Levi and Porte in 1962.[576,589,601] The presence of bacteria in maternal sponges, oocytes, or larvae has been confirmed morphologically via transmission and scanning electron microscopes in a series of studies.[576] Recently, vertically transferred sponge-specific microorganisms have been phylogenetically analyzed using molecular techniques.[576,585,587,595,602-604] Lee and colleagues found that “a dominant proportion of sponge-specific bacteria present in the tissues of Svenzea zeai are maintained through vertical transfer during embryogenesis rather than through acquisition from the environment (horizontal transfer).”[576] The inter-individual or intra-species variation and the dynamics of bacterial communities in healthy tissues have been observed among sponge individuals.[605] Sponge bacterial symbionts have been shown to play a role in the release of nitrogen gas [606] and in coral abnormality.[605]

Archaea

Sponges are host to microorganisms not only from the domain Bacteria, but also from the domain Archaea.[586,587,607] Sponge-associated filamentous Archaea were first described by Webster and colleagues in 2001.[607] And a similar description of this novel association was also reported by Margot and colleagues in 2002 in three Mediterranean species of sponges from the family Axinellidae (Porifera: Demospongiae),[608] and by Lee and colleagues in 2003 in eight sponges from Korea.[609] Moreover, ammonia-oxidizing archaea have been identified in marine sponges,[610] despite the fact that the roles of most sponge-associated microorganisms are largely unknown.[584] The microbial community of sponges Inflatella pellicula sampled from a depth of 2,900 meters was found to be archaeal dominant, in contrast, archaeal communities in the surrounding seawater were less abundant.[587] Crenarchaeota was shown to be a dominant archaeal community in two sponge species, Stylissa massa and Xestospongia testudinaria.[611]

Fungi

Since 2002, when Morrison-Gardiner isolated many fungal species from marine sponges, increasing attention has been paid to the study on sponge-associated fungi.[571,612-614] In 2005, Maldonado and colleagues found that symbiotic yeast cells were transmitted vertically through oocytes to fertilized eggs for the first time.[571] Differences in fungal communities have been found among different sponge species and between sponges and seawater.[604] In a further phylogenetic study of marine sponge-associated fungal communities, cultivable fungal communities of the Hawaiian sponges Gelliodes fibrosa, Haliclona caerulea, and Mycale armata were found to belong to at least 26 genera of the phyla Ascomycota and Basidiomycota.[615] Species-specificity and inter-species variation of fungal symbionts were described in South China Sea sponges, and cultivable fungal communities of these sponges covered at least 17 genera of the phyla Ascomycota and Basidiomycota.[616] In addition, current research interest in sponge-associated fungal species includes the discovery of novel secondary metabolites such as antimicrobial compounds and cellulases.[612,616,617]

6. The Phylum Mollusca

6.1 The Class Bivalvia

6.1.1 The Orders Arcoida and Veneroida

6.1.1.1 Clams in the genus Codakia of the family Lucinidae, the genus Calyptogena of the family Vesicomyidae, and the genus Anadara of the family Arcidae

Bacteria

The internal organ of the quahog clam has been shown to contain high density of bacteria.[618] Endosymbiotic bacteria were found in the ovarial tissue of three species of vesicomyid clams belonging to the genus Calyptogena[619] and in the gill tissues of Calyptogena magnifica.[620] Diverse cellular size of the sulfur-oxidizing symbiont were identified in the clam Codakia orbicularis.[621] Moreover, novel bacterial species were detected in clams. A novel species of Aliivibrio finisterrensis was isolated from the cultured Manila clam Ruditapes philippinarum in the north-western coast of Spain.[622] Bacterial symbionts in clams are the consequence of vertical transmission from adults and horizontal transmission from environment, although some researchers believ that the vertical transmission of bacterial symbionts might not exist in clam species in the genus Codakia of the family Lucinidae.[623] Intracellular bacteria in deep-sea clams of the family Vesicomyidae are believed to be the evolutionary consequence of lateral symbiont acquisition.[624] The experimental studies using starvation as an experimental factor to elucidate the dynamics and acquisition of symbionts in adult specimens of the lucinid clam species in the genus Codakia have shown that starvation of clams resulted in the decrease of bacterial symbionts to an undetectable level as the consequence of being digested for nutrition;[625,626] after being returned to their natural environments, the reacquisition of symbionts in the starved clams was from environmental sources; [626] and such bacterial recolonization was associated with host tissue regeneration.[627]

6.1.2 The Orders Ostreoida and Pterioida

6.1.2.1 Oyster in the genera of Crassostrea and Saccostrea of the family Ostreidae, and the genus Chama of the family Chamidae

Bacteria

Bacterial diversity has been revealed in different oyster species, including Crassostrea gigas, Crassostrea virginica, Saccostrea glomerata, Chama pacifica, Chama savignyi, and Louisiana oysters.[628-634] Oyster-associated bacterial species belong to different phyla, including Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria, Planctomycetes, and Verrucomicrobia.[628,635] Moreover, increasing nymbersof novel bacterial species have been detected in oyster tissues. For example, a novel species of Bacillus nanhaiensis was isolated from an oyster collected from Naozhou Island in the South China Sea;[636] and Vibrio vulnificus was isolated from oyster tissue.[637] Oyster-associated Pseudomonas stutzeri, P. alcaligenes, and P. aeruginosa were isolated from tissues and mantle fluid of the Eastern oyster (Crassostrea virginica) and the surrounding environment.[638] A novel species named Bizionia hallyeonensis was isolated from seawater collected in an oyster farm.[639]

Moreover, the bacterial community of oysters has also shown to exhibit a seasonal dynamic,[630,634] which is, however, associated with external environmental factors such as heat stress and temperature.[640,641] Interestingly, Azandegbe and colleagues found that the bacterial community in the sediment of two Pacific oyster farming sites did not show a seasonal dynamic, but it can be influenced by the presence of oysters.[641] The oyster-adapted Vibrio species has been shown to increase in number rapidly and maintain a large, stable population to prevent colonization by exogenous Vibrio vulnificus.[642]

Protozoa

Protozoa of the genus Ancistrocoma have been found to exist normally in oysters of the genus Crassostrea.[643]

Viruses

Noroviruses genogroup I and genogroup II, detected in oysters, were believed to associate with acute epidemic gastroenteritis in industrialized countries.[644-647] Although hepatitis A virus Sapoviruses were detected in oysters, they were believed to be the consequence of contamination.[645,648] Moreover, Savin and colleagues showed that a new herpesvirus causing ganglioneuritis in abalone shared ancestry with oyster herpesvirus.[649] Ostreid herpes virus was detected in the pacific oyster, Crassostrea gigas, and it was suggested to play a role in Crassostrea gigas mortalities.[650]

6.2 The Class Gastropoda

6.2.1 The Order Archeogastropoda

6.2.1.1 Abalone species in the genus Haliotis of the family Haliotidae

Bacteria

Abalone-associated bacteria have been described in several abalone species in the genus Haliotis.[651-655] Bacterial species belonging to the genus Vibrio, such as Vibrio neonatus, Vibrio ezurae, and Vibrio halioticoli were found in the guts of the abalones.[652,656] A novel motile, rod-shaped, pink-orange pigmented bacterial strain of Shewanella haliotis was isolated from the gut microflora of abalone.[653] Moreover, a novel, strictly aerobic, Gram-stain-negative, yellow-orange-pigmented, rod-shaped bacterial strain of Wandonia haliotis was isolated from the abalone Haliotis discus.[654]

Viruses

Abalone shriveling syndrome-associated virus, a double-stranded DNA virus has been detected in healthy abalones although some strains were believed to be associated with a fatal disease in abalones in China.[657,658]

6.3 The Class Cephalopoda

6.3.1 The Order Teuthida

6.3.1.1 Squid in the genus Loligo of the family Loliginidae

Bacteria

Diverse bacteria exist in squid, among which, the marine bacterium Vibrio fischeri is the most studied.[659-662] One of the recognized roles played by symbiotic bacteria in macoorganism-hosts is the function of symbiotic bioluminescent bacterium Vibrio fischeri in the light-emitting organ of squid.[659-662] In the past decades, the symbiotic relationship between animals and their environmental bacteria has been well studied at different evolutionary levels in the experimental model of the Hawaiian bobtail squid Euprymna scolopes and the bioluminescent bacterium Vibrio fischeri.[660-666] Theoretically and experimentally, bacterial symbiont Vibrio fischeri in the light organ of the Hawaiian bobtail squid Euprymna scolopes has been indicated to come naturally from the surrounding seawater.[659,661,666,667] More interestingly, natural seawater and Gram-negative bacteria (either living or dead) were shown to stimulate the newly hatched squid Euprymna scolopes to secrete a viscous material from the pores of its organ, but filtered seawater cannot.[667] The viscous material or mucus is believed to be a critical environmental factor for colonization and aggregation of external bioluminescent Vibrio fischeri in the squid Euprymna scolopes.[659,668,669] It has been observed that under simulated microgravity, the luminescent bacterium Vibrio fischeri-induced apoptosis and regression in the host squid Euprymna scolopes are accelerated.[665] However, if we consider that the capability of light-emitting is the consequence of evolution in the squid Euprymna scolopes,[664,666,670] the mechanisms behind the formation of the mutualism between squid and bioluminescent bacteria may be more complicated than our current understanding, which has been hinted at in recent studies.[663,670]

In addition, bacterial symbionts in other anatomic locations of squid have also been investigated in the past decades. Symbiotic bactera have been revealed within the squid accessory nidamental gland using transmission and scanning electron microscopy,[671] and molecular approaches.[672] However, their exact roles are unknown. Intense bacterial communities have also been found within the reproductive system of sexually mature female squid, in which Alpha- and Gamma-proteobacteria were the major constituents.[673]

7. The Phylum Echinodermata

7.1. The Class Echinoidea

7.1.1 The Order Echinoida, Camarodonta, and Temnopleuroida

7.1.1.1 Sea Urchin Species in the genera of Colobocentrotus and Echinometra of the family Echinometridae, the genus Echinus of the family Echinidae, the genera Hemicentrotus and Strongylocentrotus of the family Strongylocentrotidae, and the genus Tripneustes of the family Toxopneustidae

Bacteria

Sea urchin-associated bacteria have attracted increasing research attention since the 1970s [674-676] and it has been revealed that there were N2-fixing bacteria identified in the normal gastrointestinal microflora of sea urchins.[675] Diverse bacteria belonging to different genera including Aeromonas, Acinetobacter, Alteromonas, Bacillus, Bacteroides, Brachybacterium, Brevibacterium, Enterobacter, Enterococcus, Flavimonas, Flavobacterium, Halobacillus, Halomonas, Moraxella, Nocardiopsis, Oceanobacillus, Piscibacillus, Planococcus, Pontibacillus, Pseudomonas, Pseudonocardia, Salinicoccus, Salinivibrio, Serratia, Staphylococcus, Vibrio, and Virgibacillus have been isolated from sea urchin species in various genera.[674,676-678] Moreover, diverse bacterial species have also been isolated from the lantern and gonads of healthy echinoids.[677] Recently, novel bacterial species or stains have been identified in different sea urchin species, such as a novel Gram-staining-negative, facultatively anaerobic, and motile bacterial strain of Echinimonas agarilytica in the sea urchin Strongylocentrotus intermedius,[679] a novel Gram-staining-positive anaerobic rod-like bacterium of Bacillus hemicentroti in the sea urchin Hemicentrotus pulcherrimus,[680] a novel Gram-staining-negative aerobic rod-like bacterium of Halomonas zhanjiangensis in the sea urchin Hemicentrotus pulcherrimus,[681] and a novel Gram-staining-positive coccus of Jeotgalicoccus marinus in the sea urchin Hemicentrotus pulcherrimus.[682]

Fungi

Kajikazawa and colleagues revealed that diverse fungal species including Candida albicans, Candida sake, Debaryomyces hansenii, Pichia anomala, Rhodotorula mucilaginosa, and Trichosporon mucoides were detected in processed fresh edible sea urchins obtained from seven countries including Russia, USA, Canada and China. Yeast concentration varied with the range from 45 to 7×10^4 cfu per gram of processed fresh edible sea urchin.[683]

Viruses

Upon the fact that “there are currently no described viruses of echinoderms”, [684] Gudenkauf and colleagues first revealed that bacteriophages and densoviruses belonging to the family Parvoviridae were detected in tissues of three sea-urchins, Colobocentrotus atratus, Tripneustes gratilla and Echinometra mathaei in the Hawaiian archipelago.[684]

8. The Phylum Nematoda

8.1 Nematodes in the genus Steinernema of the family Steinernematidae, the genera Rhabditis, Caenorhabditis, and Heterorhabditis of the family Rhabditidae

Bacteria

Although the nematode Caenorhabditis elegans is usually utilized as a model to investigate host-microbiota interactions,[685] how to avoid the interference from the interaction between a testing bacterial species and nematode-specific microbiota at different evolutionary levels is a challenge. The bacterial community of nematodes has been shown to contain different bacterial species, including those in the genera of Achromobacter, Alcaligenes, Bacillus, Ewingella, Flavobacterium, Leifsonia, Microbacterium, Providencia, Pseudomonas, Rheinheimera, Rhizobium, Serratia, Staphylococcus, Stenotrophomonas, Wolbachia, and Xenorhabdus.[686-690] Nematodes-associated bacterial symbionts are believed to be transmitted vertically from parent to offspring and horizontally from the environment.[692,691] For example, symbiotic bacteria belonging to the genus Xenorhabdus in nematode host were found within a specific host-intestinal structure called “bacterial receptacle” or “bacterial vesicle”.[693-695] Recently, Chaston and colleagues argued that bacterial colonization in a host species-specific manner occurred not only in the nematode infective juvenile stage, but also in other nematode developmental stages.[696,697] Although the role of nematodes-associated bacterial symbionts is largely unknown, during the past decades, the symbiotic bacteria of many nematode species have been found to be utilized by nematodes to kill insects.[698]

9. Concluding Remarks

The evolutionary background entities including subcellular viral entities and membrane-enclosed microentities, prokaryotic bacterial and archaeal cells, and unicellular eukaryotes such as fungi and protists at the cellular and subcellular levels are largely uncharacterized in many invertebrate species. However, to date, there have not been any specific programs to describe the whole image of microbial, fungal, viral, and protozoal entities for any invertebrate animals. The existing limited information from studies on various invertebrates selected in this article is enough to clearly express the following notion: (1) the evolutionary background entities (EBEs) of any given invertebrate animal exhibit both host intra- and inter-species-specificity and geographic environmental variability, and (2) all normal and healthy invertebrates should have their species-specific bacterial, archaeal, fungal, protozoal, and viral communities from an ecological and evolutiological perspective. This has been supported by solid evidence obtained using both culture-dependent and culture-independent approaches. By putting our existing pieces together, we can theoretically easily find where the pieces are still missing, uncompleted, or outdated in the puzzle of evolutionary background entities

(EBEs) of invertebrate animals. However, solving the puzzle is just the beginning, and we are still encountering a series of theoretical and technical challenges, which will be partially discussed in the next issues.

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