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Evolutionary History of Decapod Shrimp Based on Comparative Genomics

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Abstract Decapod shrimps include shrimps, prawns, crayfishes and other groups, and have important research value in terms of biodiversity and evolutionary adaptation. In recent years, with the development of sequencing technology, a large number of shrimp genomes have been deciphered, providing unprecedented opportunities for revealing their evolutionary history based on comparative genomics. This article reviews the diversity and phylogeny of decapod shrimps and the latest progress in shrimp genome resources, focusing on the application of comparative genomics in clarifying the evolutionary relationships, key evolutionary events and environmental adaptation mechanisms of shrimps. For example, through genome comparative analysis, researchers found that the explosive expansion of simple repeat sequences (SSR) in the shrimp genome is closely related to its adaptive evolution; the genomes of eusocial species such as pistol shrimps have significantly expanded due to transposon accumulation. In a case study, we introduce how comparative genomic analysis of the *Alpheidae* family reveals the relationship between social behavior and genome evolution. Finally, the future direction of comparative genomics of decapod shrimps is prospected, such as deepening pan-genome construction and functional genome verification, to further reveal the full picture of shrimp evolutionary history. This article aims to show that comparative genomics has become an indispensable tool in the study of decapod shrimp evolution, providing a new perspective for understanding the evolution and adaptation of marine organisms.

Keywords Decapod shrimp; Biodiversity; Comparative genomics; Evolutionary events; Environmental adaptation

1 Introduction

Decapoda shrimps (hereinafter referred to as "shrimps") are an extremely diverse group of crustaceans, including shrimps, prawns, crayfish, krill and lobsters, and play a key role in marine and freshwater ecosystems (Rutz et al., 2023). There are more than 17 000 known decapoda species worldwide, a considerable proportion of which are shrimps (Wolfe et al., 2019). Shrimp not only plays an important role in ecology, but also is an important target of aquaculture and fisheries. For example, Pacific white shrimp (*LitoPenaeus vannamei*) has become the most produced crustacean cultured species in China in recent years.

However, the research on high-level meta-taxonomy and phylogenetic relationships of shrimps has long been controversial. Traditional morphology and limited molecular markers make it difficult to fully analyze the complex evolutionary relationships of shrimps, and many key evolutionary issues remain unresolved. With the development of high-throughput sequencing technology, breakthroughs have been made in shrimp genomics research. Whole genome sequencing of a large number of shrimp species has been completed, laying the foundation for the use of comparative genomics to study the evolutionary history of shrimp (Zhang et al., 2019; Fu et al., 2024). Comparative genomics can reveal evolutionary signals that cannot be observed by traditional methods, such as whole genome duplication, gene family expansion, adaptive mutation, and convergent evolution patterns, by comparing gene sequences, genome structures, and functional elements of different species at the genome scale. In recent years, this method has been successfully applied to the phylogenetic reconstruction and adaptation mechanism research of decapod crustaceans, and has achieved rich results.

This study aims to review the diversity and phylogenetic framework of decapod shrimps, sort out the main progress in the construction of shrimp genome resources in recent years, analyze the application results of comparative genomics in revealing important evolutionary events, environmental adaptation, and behavioral evolution of shrimps, and take the *Alpheidae* as a case to explore the molecular basis of the evolution of social behavior. Finally, we look forward to the future development direction of this field.

2 Diversity and Phylogeny of Decapod Shrimps

2.1 Classification and morphological diversity of decapod shrimps

Decapod shrimps cover multiple morphologically and ecologically different lineages, showing a high degree of diversity. In taxonomy, decapod shrimps are traditionally divided into *Dendrobranchiata* and *Pleocyemata* based on the morphology of gills and reproductive methods (Figure 1) (Wolfe et al., 2019). The former is commonly known as "shrimps", including marine shrimp families such as *Penaeidae*, with about 540 species described. The latter includes all other decapods, and shrimps are mainly concentrated in the Caridea and Stenopodidea orders; among them, the Caridea includes nearly 4 000 species of "prawns" and freshwater crayfish, while the *Astacidea* and *Axiidea*/*Gebiidea* also belong to the *Pleocyemata*, but their morphology is more like crabs or lobsters.

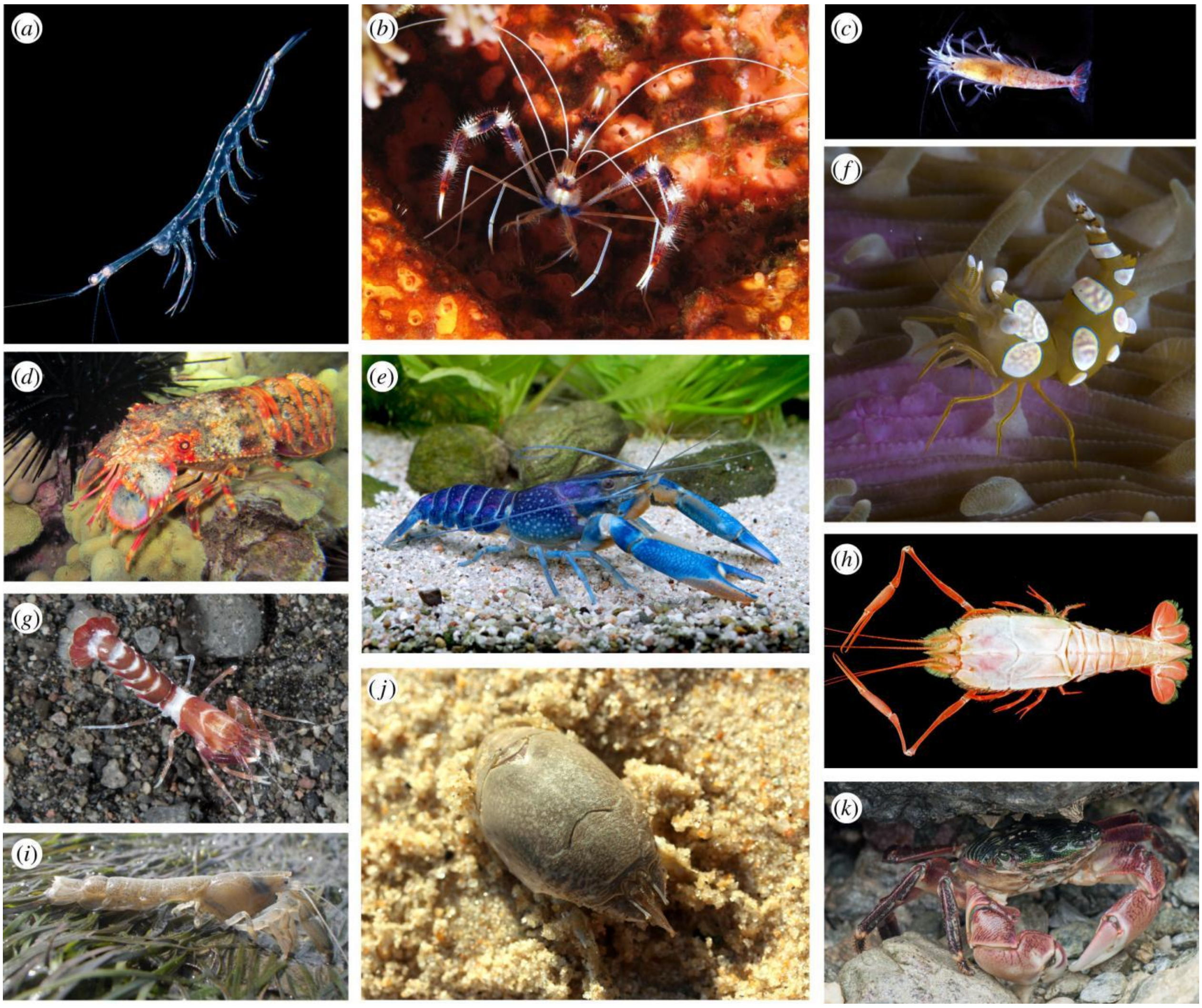

Figure 1 Representatives of major decapod lineages. (a) *Lucifer* sp. (southeast Florida, USA) (*Dendrobranchiata*); (b) *Stenopus hispidus* (Komodo, Indonesia) (Stenopodidea); (c) *Procaris chacei* (Bermuda) (Procarididea); (d) *Arctides regalis* (Maui, Hawaii, USA) (Achelata); (e) *Cherax quadricarinatus* (aquarium specimen) (Astacidea); (f) *Thor amboinensis* complex (Ternate, Indonesia) (Caridea); (g) *Axiopsis serratifrons* (Bali, Indonesia) (Axiidea); (h) *Stereomastis sculpta* (specimen ULLZ 8022) (Polychelida); (i) *Upogebia cf. pusilla* (Arcachon Bay, France) (Gebiidea); (j) *Emerita talpoida* (Westerly, Rhode Island, USA) (Anomura); (k) *Pachygrapsus crassipes* (Catalina Island, California, USA) (Brachyura) (Adopted from Wolfe et al., 2019)

Photo credits: (a) L. Ianniello; (b) A. Vasenin, licence CC-BY-SA; (c) T. M. Iliffe; (d, k) J. Scioli; (e) C. Lukhaup; (f) C. H. J. M. Fransen; (g) A. Ryanskiy; (h) D. L. Felder; (i) X. de Montaudouin; (j) J. M. Wolfe. (Online version in colour.) (Adopted from Wolfe et al., 2019)

2.2 Traditional phylogenetic framework based on morphology and molecular markers

For many years, the study of phylogenetic relationships of shrimps has continued to advance. Research based on molecular data generally supports that the major suborders of the decapod order are monophyletic groups. For example, the latest shrimp phylogenetic tree constructed by large-scale anchored hybrid enrichment shows that each shrimp branch (such as shrimps, true shrimps, crayfishes, etc.) shows a clear monophyletic evolutionary branch. Wolfe et al. (2019) used 410 gene fragments from 94 representative species of decapods to reconstruct the most comprehensive decapod phylogenetic tree to date, which not only confirmed the evolutionary relationship between traditional suborders and superfamilies, but also inferred that the crown group of decapods originated in the Late Ordovician, and the main living lineages rapidly differentiated in the Triassic-Jurassic period. This period coincided with the end-Permian mass extinction event, and the huge environmental changes may have driven the radiation evolution of shrimps.

2.3 Challenges and controversies in solving the evolutionary relationship of decapods

Although the high-level classification of most shrimps has been basically clarified, some more detailed relationships below the family level are still being explored. For example, the position of mud shrimps (formerly classified in the superfamily *Thalassinidea*) has caused a lot of controversy in the past. Later, researchers finally figured out that this group of shrimps should be divided into two independent lineages, the order *Thalassinidae* and the order *Thalassinidae*, by comparing mitochondrial genomes (Lin et al., 2012). Of course, it is not only a classification problem, the species diversity of shrimps themselves is also quite amazing. Take the *Alpheidae* family as an example. The pistol shrimps in it have all kinds of lifestyles, from solitary to truly social groups. This complex behavioral change provides a particularly good example for studying evolution and ecological adaptation.

3 Progress in Decapod Shrimp Genome Resources

3.1 Recent genome sequencing projects and major data sets

For a long time, crustacean genomes have been a headache to sequence, mainly because their genomes are large and complex, with a lot of repetitive sequences (Yuan et al., 2021a). This was basically the case before the mid-2010s. However, things have changed in the past five years. Many whole genome projects for economically and ecologically important shrimp species have been launched internationally, finally pushing shrimp genome resources from zero to a new stage. In 2019, Zhang et al. published the first high-quality shrimp genome, *Penaeus vannamei*, with a total genome length of approximately 1.66 Gb and 25 596 predicted coding genes. Interestingly, in this genome, simple repeat sequences (1~6 bp tandem repeats of SSR) accounted for more than 23.9%, the highest among all species measured at the time. Such a high repetition rate also reveals that the shrimp genome is a bit special, leaving a lot of room for imagination for future studies of their adaptive evolution.

3.2 Development of transcriptome and mitochondrial genome databases

Since then, reference genomes of many important shrimp species have been deciphered and released, including the chromosome-level genome of Japanese shrimp (*Marsupenaeus japonicus*) (Kawato et al., 2021), the chromosome-level genome of black tiger shrimp (*Penaeus monodon*), the improved genome of Chinese shrimp (*Fenneropenaeus chinensis*) (Wang et al., 2022), and the highly continuous genome of Indian shrimp (*Penaeus indicus*). Most of these studies used third-generation long-read sequencing combined with Hi-C-assisted assembly, which significantly improved the assembly quality. For example, the Japanese shrimp genome constructed by Ren et al. (2022) is 1.24 Gb in length, with an N50 of 13.4 Mb, and identified approximately 26 381 genes; the giant tiger shrimp genome released by Uengwetwanit et al. (2021) assisted in the location of growth-related genes. For the shrimp *Penaeus vannamei*, Peng et al. (2023) further used third-generation sequencing and Hi-C technology to assemble its genome to the chromosome level, with the full length increased to 1.87 Gb and the scaffold N50 increased by two orders of magnitude to 39.7 Mb.

3.3 Limitations and future needs of decapod genome data

Although the current level of genome assembly has been greatly improved compared to the past, after all, the genome size of the shrimp, such as the vannamei shrimp, has not yet reached the 2.45 Gb measured by flow cytometry (Fu et al., 2024). However, these achievements are enough to lay a more solid foundation for in-depth research on the genetic mechanism of shrimp. On the other hand, there have been some progress in freshwater shrimp, such as *Macrobrachium rosenbergii*, whose chromosome-level genome was finally released in 2024 (Zheng et al., 2024). Now, more than 20 decapod species have completed genome drafts, and the shrimp genome database is much richer than before. With these data, researchers can compare the genomes of various species to find out which genes are shared by everyone and which are unique, so as to further explore the genetic clues behind shrimp evolution.

4 Application of Comparative Genomics in the Study of Decapod Shrimp Evolution

4.1 Reconstruction of phylogenetic and phylogenetic relationships

The emergence of comparative genomics has provided new ideas for solving many mysteries in evolutionary history. Especially in recent years, with the continuous accumulation of shrimp genome and transcriptome data, researchers can use hundreds of single-copy orthologous genes to perform phylogenetic analysis, and the resolution of phylogenetic trees is much higher than in the past. For example, the shrimp phylogenetic tree built by Wolfe et al. (2019) using hundreds of genes strongly supports the monophyly of lineages such as true shrimp, prawns, and crayfish. In the past, the practice of relying only on mitochondrial genes or a few nuclear genes often struggled to distinguish the relationship between closely related species. Now, with the use of whole genome data, the divergence time can be more clearly inferred, and the evolutionary timeline drawn is more reliable. Of course, comparative genomics not only helps to clarify phylogenetic relationships, but also can correct old classification systems. For example, mud shrimps were not accurately divided in the past, but later confirmed that they should be split into two independent lineages based on genomic evidence (Lin et al., 2012). In general, large-scale genome comparisons have indeed brought shrimp phylogenetic research to a new level.

4.2 Genome evolution patterns and key events

In fact, the genomes of different shrimps have undergone many special changes during their evolution. By comparing the genomes of multiple species, Yuan et al. (2021b) found that simple repeat sequences (SSRs) in the shrimp genome have expanded on a large scale, which is the first time they have been seen in crustaceans. This expansion is likely related to some special genome evolution mechanisms. In addition, there are differences in genome size and the number of repetitive elements between different species. Studies such as Rutz et al. (2023) reveal which factors are driving genome expansion or contraction. Not only between aquatic species, researchers have also compared the genomes of aquatic and semi-terrestrial crustaceans. For example, Veldsman et al. (2021) found that genes related to osmotic regulation and nitrogen waste excretion have undergone significant changes in some groups living close to land. These comparisons help us better understand how shrimps constantly adjust their genomes in different environments.

4.3 Adaptive traits and ecological adaptation mechanisms

The ability of shrimp to adapt to the environment is far more complicated than imagined. From deep-sea hydrothermal vents to extreme salinity, to freshwater and even land, they have evolved many special traits in various environments. Comparative genomics has been very useful in this regard. For example, by comparing shrimps living in hydrothermal environments with closely related species, we can find some genes related to chemosymbiosis and high temperature resistance (Yuan et al., 2020), such as enzymes that can detoxify sulfides. For example, by comparing the genomes of freshwater crayfish and marine shrimp, we can find that freshwater species often have signs of expansion or positive selection in genes related to osmotic pressure regulation (Wang et al., 2022), indicating that these genes are important for their adaptation to low-salinity environments. Even the evolution of social behavior can be explored through comparative genomics, such as analyzing the genomic differences between social pistol shrimp and solitary closely related species to find genes that may be related to social behavior. In short, comparative genomics has now become one of the core tools for understanding the evolutionary diversity and ecological adaptability of shrimp.

5 Key evolutionary Events Revealed by Comparative Genomics

5.1 Changes in genome size and expansion of repetitive sequences

Among decapod shrimps, the difference in genome size can be said to be surprisingly large, with some species less than 2 Gb and others exceeding 40 Gb (Rutz et al., 2023). Such a huge difference is actually largely the result of the increase and decrease of repetitive sequences. For example, Yuan et al. (2021b) studied the vannamei shrimp and the Chinese shrimp (*F. chinensis*) and found that although they are both rich in simple sequence repeats (SSRs), they have continued to expand in independent lineages. This expansion is speculated to have occurred shortly after the genome of the shrimp ancestors had undergone differentiation, which coincided with the time of the dramatic environmental changes at the end of the Paleozoic. In the past, many people regarded microsatellite repeats as "junk DNA", but in shrimps, the large accumulation of SSRs seems to provide genome plasticity and prepare "raw materials" for subsequent adaptive evolution. Changes in the number of transposable elements (TEs) are another factor that leads to different genome sizes. For example, in the family of eusocial shrimps, the genomes of eusocial species are much larger than those of non-social species, mainly due to the accumulation of transposons. Chak et al. (2021) analyzed 33 species of pistol shrimp (genus *Synalpheus*) and found that the stronger the sociality, the larger the genome and the higher the TE content. It seems that the evolution of social behavior not only affects the interaction between individuals, but also indirectly promotes changes in genome structure by accelerating transposon enrichment. This also reminds us that genome expansion is not always "neutral". Sometimes, the increase in repetitive sequences may really be linked to the adaptation of species to new environments and the increase in complexity.

5.2 Gene family expansion and functional innovation

In the evolution of shrimp, gene family expansion is not uncommon, and it is often related to their special physiological adaptations. By comparing the genomes of different shrimp species, we can see at a glance which gene families have expanded particularly strongly in certain lineages. For example, *Penaeus vannamei* has expanded a lot of genes encoding visual proteins. Zhang et al. (2019) speculated that this may be to adapt to the weak light environment on the seabed - multiple copies of rhodopsin protein can help them improve their vision in dim light. In addition, *Penaeus vannamei* molts frequently and has a large demand for chitinase and cuticle protein, so these related genes have also expanded in multiple copies. For example, some marine shrimps living on reefs or substrates have also expanded genes related to adhesion proteins and chitin binding proteins, which may allow them to better adhere to various surfaces. Expansion is certainly a way of adaptation, but there are exceptions. Some genes shrink or even disappear in specific environments. For example, freshwater shrimps lack some genes related to seawater ion transport, which helps them adjust osmotic pressure in low-salt environments. These expansions and contractions, put together, paint a vivid picture of the dynamic evolution of the genome in response to environmental pressures.

5.3 Whole genome duplication and polyploidization events

Whole genome duplication (WGD) in animals is relatively rare in vertebrates and other groups, but has occurred in some invertebrates (such as myriapod insects). For decapod shrimps, no clear whole genome duplication events have been reported. However, there is evidence that individual species may have experienced special polyploidization phenomena. For example, stream crabs and some crayfish have chromosome doubling and parthenogenesis. A famous example is the marbled crayfish (*Procambarus virginalis*), whose genome is a triploid clone that has been widely invasively distributed through parthenogenesis in a very short period of time (Gutekunst et al., 2018). Although crayfish are not typical "shrimp", as a member of the decapod order, their special evolutionary events are worthy of attention. The clonal evolution and rapid spread of this genome were analyzed by Gutekunst et al. (2018), showing another facet of the plasticity of crustacean genomes. Although no similar large-scale doubling events have been found in shrimp and prawns, as the number of sequenced species increases, it is possible that evidence of WGD will be found in some ancient lineages in the future. If found, it will provide new clues for understanding the evolutionary innovation of shrimp.

6 Genomic Characteristics of Environmental Adaptation

6.1 Adaptation to deep-sea chemoenvironment

Decapod shrimps have a wide distribution range, from the darkness of the deep sea to the cold waters of high latitudes, from tropical shallows to freshwater rivers. Such an ecological span naturally forces them to develop a set of unique adaptation strategies in their long evolution. Especially in the extreme environment of deep-sea hydrothermal vents, such as some species of *Alvinocarididae*, the darkness, high temperature, and high sulfide concentration are almost forbidden areas for life. But these shrimps are alive and well, relying on a special symbiotic system that has evolved - a large number of chemoenergetic bacteria parasitize on the gills and obtain energy through bacterial metabolism. The comparison results of the genome and transcriptome also confirm this: this type of deep-sea shrimp has lost a lot of vision-related genes (after all, eyes are not used in a completely dark environment), and genes related to sulfide detoxification and metabolism have expanded or positively selected (Yuan et al., 2020). Other studies have found that their hemocyanin genes have also undergone adaptive changes, improving their oxygen-carrying capacity in low-oxygen environments (Choi et al., 2025). These changes in the genome support the ability of deep-sea shrimp to survive and reproduce in extreme environments at multiple levels.

6.2 Salinity and water conversion adaptation

Of course, the adaptation story of shrimp is not just as simple as the deep sea. It is also common for shrimp to independently invade freshwater from seawater many times, or simply take root in intertidal zones and brackish water areas. Unlike the seawater environment where their ancestors lived, the low ionic strength in freshwater places higher demands on osmotic regulation ability. Through comparative genomic studies, scientists have found that some freshwater shrimps (such as freshwater crayfish and freshwater prawns) have expanded many gene families related to osmotic pressure regulation, such as Na^+/K^+-ATPase and calmodulin, which are significantly richer than marine species (Liu et al., 2020). In addition, the endocrine system that controls molting and shelling has also been quietly adjusted in freshwater populations to cope with changes in the water chemical environment. For example, when Wang et al. (2022) compared the genomes of Chinese shrimp and *Penaeus vannamei*, they found that Chinese shrimp had unique copy number changes or amino acid substitutions in genes related to low-salinity stress. These "little moves" in genes may be the secret to their ability to adapt to the low-salinity environment near the Yellow Sea. As for the shrimps that stay in the intertidal zone, such as the shrimps living in the mangroves, they also expand their antioxidant and anti-interferon protein genes in order to cope with the pressure of alternating dry and wet conditions and freshwater flushing. In general, different salinity environments pose different survival challenges to shrimps, and the changes in the shrimp genome are the key behind their success.

6.3 Adaptation to terrestrial and semi-terrestrial environments

There are a few shrimp relatives in the Decapoda (strictly speaking, they belong to the suborder Anomura, such as crabs) who have evolved terrestrial habits after landing, but most typical shrimps are still aquatic. However, some cases are worth learning from, such as the coconut crab (*Birgus latro*), which is a completely terrestrial species evolved from hermit crabs. Although it is not a shrimp, it is closely related to shrimp, and its genome comparative study provides a useful reference. Veldsman et al. (2021) compared the genomes of coconut crabs with those of closely related aquatic crabs and shrimps and found that the coconut crab genome had a significant expansion of genes in functional categories such as amino acid metabolism and nitrogen waste treatment. It is speculated that this is the result of adapting to the high-ammonia environment on land and a lifestyle such as feeding on plants. At the same time, the coconut crab genome shows a unique pattern of alternative splicing, and many genes produce different transcripts through splicing, which helps to flexibly regulate physiology in dry and wet season environments. These findings suggest that if real landed shrimps are found in the future (such as some intertidal crayfish that stay out of water for a long time), their genomes may also show similar adaptive changes, such as functional enhancement of genes such as respiratory proteins and epidermal proteins. Although decapod shrimps are currently mainly confined to aquatic environments, the experience of genomic research on semi-terrestrial adaptation is inspiring for understanding environmental transformation.

6.4 Pathogen resistance and immune adaptation

In the process of adapting to the environment, shrimps are not only faced with physical and chemical conditions such as temperature and salinity, but also biological pressure, especially the threat of pathogens and viruses, which also forces them to constantly adjust themselves. Along the way of evolution, shrimps have launched an endless arms race with various viruses and bacteria, and many immune-related genomic features are the product of this confrontation. From the perspective of comparative genomics, the changes in immune genes of different shrimps are quite obvious. For example, compared with wild species, those selected and disease-resistant Vannamei shrimp strains have more duplications in pattern recognition receptor and lectin genes (Fu et al., 2024). It may be this amplification that gives them stronger broad-spectrum immunity. However, the situation is not the same for all shrimp populations. Comparisons between shrimp populations found that shrimp living in densely populated waters have higher polymorphisms and evolution rates of immune-related genes, after all, there are many types of pathogens and high pressure; while small populations in isolated waters have relatively low immune gene diversity. It can be seen that genome comparison can not only help us understand how shrimps resist diseases, but also provide a lot of references in disease-resistant breeding.

7 Case Study: Comparative Genomic Analysis of *Alpheidae*

The *Alpheidae*, commonly known as pistol shrimp or pistol shrimp family, is a striking group of decapod shrimps. Species in this family are known for their ability to close their claws at high speed to make a popping sound, and are peculiar in behavior and ecology: some species of the genus Synalpheus have evolved an insect-like eusocial group structure, that is, a breeding "queen" and many infertile workers form a group to raise the larvae together. This sociality is quite rare in invertebrates. The uniqueness of the *Alpheidae* provides a good example for comparative genomics studies to explore the association between behavioral evolution and genomic changes.

7.1 Genome size and social evolution

Pistol shrimps have a wide range of lifestyles, from solitary to eusocial, and there are quite a few species. Chak et al. (2021) did a very interesting study, measuring the genome size of 33 species of pistol shrimps in the family Pleurotus eryngii to see if there is any relationship between their genomes and social behavior (Figure 2). The results were quite unexpected: the pistol shrimps that developed eusociality generally had larger genomes than solitary species, about 1.5 times larger on average. However, it was not the number of coding genes that expanded, but the number of copies of transposable elements, such as LINE and ERV, that increased sharply. After further reconstruction of the ancestral state, the study found that once a lineage evolved sociality, the genome size and transposon content continued to rise; while those that lived alone did not change much. This trend makes people begin to wonder whether highly socialized life reduces the natural selection pressure at the individual level, thereby giving "selfish" transposons an opportunity to take advantage. This discovery not only reveals the possible linkage between social behavior and genome evolution, but also allows us to see the potential of comparative genomics in studying non-model species.

7.2 Comparison of social-related genes

Of course, social evolution is not just about genome expansion. From the molecular details, the genome comparison of the family of shrimp has also found many interesting changes. Because eusociality is accompanied by complex reproductive division of labor and cooperative care, researchers speculate that genes in the fields of neural development, hormone regulation, and immune defense should also be somewhat special. After comparing eusocial species with solitary species, some candidate genes were indeed found. For example, genes that control neurotransmitter receptors showed traces of positive selection in eusocial pistol shrimps, suggesting that they may have been adjusted to adapt to group life. In addition, pattern recognition receptors related to immune recognition have also expanded or specialized in function, perhaps to avoid treating individuals in the same group as enemies. A more special point is that some studies have reported that some antimicrobial peptide genes in eusocial pistol shrimps are downregulated (Guryanova et al., 2023), which is speculated to be because group life reduces the chance of individuals being exposed to pathogens. Although these results are still preliminary, they at least provide some molecular clues to explain the evolution of sociality.

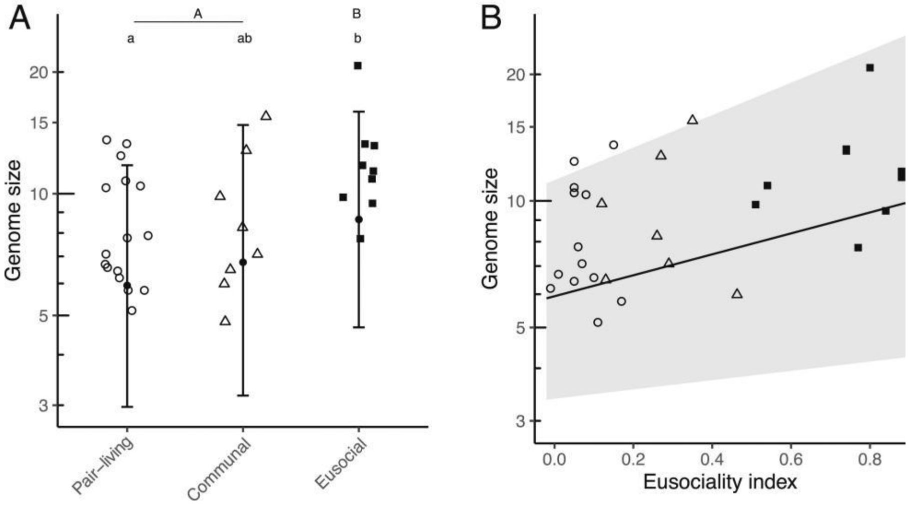

Figure 2 Relationships between genome size and categorical forms of social organization (A) and the eusociality index (B). In A, shapes represent raw values, closed circles and error bars represent posterior means and 95% CI. In B, solid line and gray shade represents the predicted linear relationship and 95% CI. The models control for the effect of egg and body size. In A, letters indicate significant differences in the posterior means in pair-wise comparisons between the three forms of social organization observed in Synalpheus snapping shrimps (a and b) and planned comparisons between eusocial and noneusocial species (pair-living and communal species combined) (A and B) (pMCMC < 0.05). Symbols represent pair-living (○), communal breeding (△), and eusocial species (■) (Adopted from Chak et al., 2021)

7.3 Phylogeny and diversification of the family Pulmonidae

The family of lobsters is actually quite complex. Not only are there many species, but also their lifestyles are very varied. It is difficult to clarify their relationships based on morphology alone. Therefore, the comparative genomic method comes in handy. By measuring the genomes or transcriptomes of various lobsters, researchers are drawing a more detailed molecular phylogenetic tree and trying to superimpose some key evolutionary events, such as genome expansion and the time nodes of the emergence of sociality. Current evidence shows that true sociality has evolved independently in the family of lobsters many times, and it occurred relatively late. Each emergence of sociality is almost accompanied by similar genomic changes - mainly the accumulation of transposons. This phenomenon of parallel evolution is equivalent to nature doing an evolutionary experiment itself, which is very rare. In terms of taxonomy, genomic data also exposes many problems. For example, some geographically separated pistol shrimp populations have surprisingly large genomic differences, which may actually be hidden new species, and subsequent re-evaluation needs to be combined with morphological and molecular data.

8 Future Directions of Comparative Genomics of Decapod Shrimps

8.1 Expanding the scope of genome sampling

Currently, the sequenced shrimp genomes are mainly concentrated in economically cultivated species and very few deep-sea species, and many taxa are still blank. For example, only a few Penaeidae species of the suborder *Cladobranchia* have genomes, and the genomes of the infraorder Gammaridae and some special ecological niches (such as polar cold-water shrimp) have not yet been explored. In the future, a diverse layout of genome projects should be carried out, especially for sequencing key node species on the phylogenetic tree (such as primitive true shrimps, unexplored freshwater crayfish, etc.). With the reduction of sequencing costs and the improvement of technology, this goal is technically feasible. A wider range of species genomes will build a more comprehensive shrimp comparative genome framework, avoid the limitations of inference caused by sampling bias, and thus more accurately reconstruct the evolutionary history of shrimp.

8.2 In-depth analysis of genomic functional elements

Past comparative studies have focused on the gains and losses of coding genes and sequence variations, but a large number of non-coding regions in the genome (such as regulatory elements and repetitive sequences) also play an important role in evolution. In the future, multi-omics methods should be used to integrate transcriptome and epigenomic data on the basis of genome comparison to analyze the evolution of gene expression regulation. For example, the comparison of tissue-specific expression profiles of different shrimps can reveal how gene regulatory networks evolve new functions; the contribution of microRNAs and long non-coding RNAs unique to crustaceans to adaptability is also worth studying. In addition, for previously discovered important repeat sequence expansions (such as SSRs and transposons), population genomics and molecular experiments should be combined to verify their specific mechanisms of action in adaptation. For example, transgenic lines containing different SSR lengths can be constructed to test their effects on gene expression and phenotype. In short, expanding from focusing on "genes" to focusing on "genomic elements" will make the conclusions of comparative genomics more comprehensive.

8.3 Establishing pan-genomes and population comparisons

Traditional comparative genomes mostly use a single reference genome to represent species, but a single genome is difficult to cover all genetic diversity within a species. To solve this problem, a "pan-genome" can be constructed for important shrimp species in the future, that is, a collection of genomic variations that integrate multiple individuals. The pan-genome can more comprehensively display the gene pool of species and help discover genes or structural variations that are missing in the reference genome. For example, pan-genome research on *LitoPenaeus vannamei* has been put on the agenda in order to discover variations related to traits such as stress resistance and growth (Chen et al., 2023). When comparing different species, population-level genome comparisons can also be used, that is, comparing the variation spectrum within each species and then comparing it with other species. This method can distinguish between conserved functional elements and rapidly evolving fragments, and more keenly capture adaptive evolutionary signals. For example, by comparing the population selection sweep areas of closely related shrimps, genes that adapt to different environments can be located and changes left over from common ancestors can be distinguished from changes that have evolved independently. With the increase in sequencing throughput, population-scale comparative genomics will become possible.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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