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Origin and Evolutionary History of Oysters Based on Comparative Phylogenomics and Fossil Evidence

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Abstract Oysters represent a biologically and ecologically significant group of marine bivalves with a complex evolutionary history. This study integrates comparative phylogenomics and fossil evidence to explore the origin, diversification, and morphological evolution of oysters. We examined recent advances in phylogenomic methodologies, including high-throughput sequencing and ortholog identification, to resolve oyster lineages and their adaptive traits. In parallel, we assessed the rich fossil record of oysters to trace evolutionary trends and provide calibration points for molecular clocks. Through synthesis of these two complementary datasets, we addressed consistencies and discrepancies in evolutionary timelines, reconstructed key trait evolution, and analyzed biogeographical dispersal patterns. A focused case study on the genus *Crassostrea* highlights the power of integrated approaches in uncovering lineage-specific evolutionary events. This study underscores the importance of combining genomic and paleontological data to achieve a more comprehensive understanding of oyster evolution and provides a framework for future research leveraging multidisciplinary approaches and advanced analytical tools.

Keywords Oyster evolution; Phylogenomics; Fossil record; *Crassostrea*; Comparative genomics

1 Introduction

Walking along the beach, you can often see rows of oysters attached to the reefs. This bivalve is basically found along the coasts of the world, active in intertidal zones or not too deep waters (Zhang et al., 2024). People may not pay much attention to their existence, but they are actually a key part of coastal ecology - they purify water quality, provide hiding places for other marine life, and are also important targets for aquaculture. In fact, oysters rely on more than just "toughness" to survive well and widely in such a complex and changeable marine environment. They have strong adaptability and rich genetic background. Some can float, while others stay in one place for their entire lives. Different species have their own set of shell shapes and reproduction methods, and their appearance changes quickly and they adapt to the environment quickly (Li et al., 2021; Li et al., 2022).

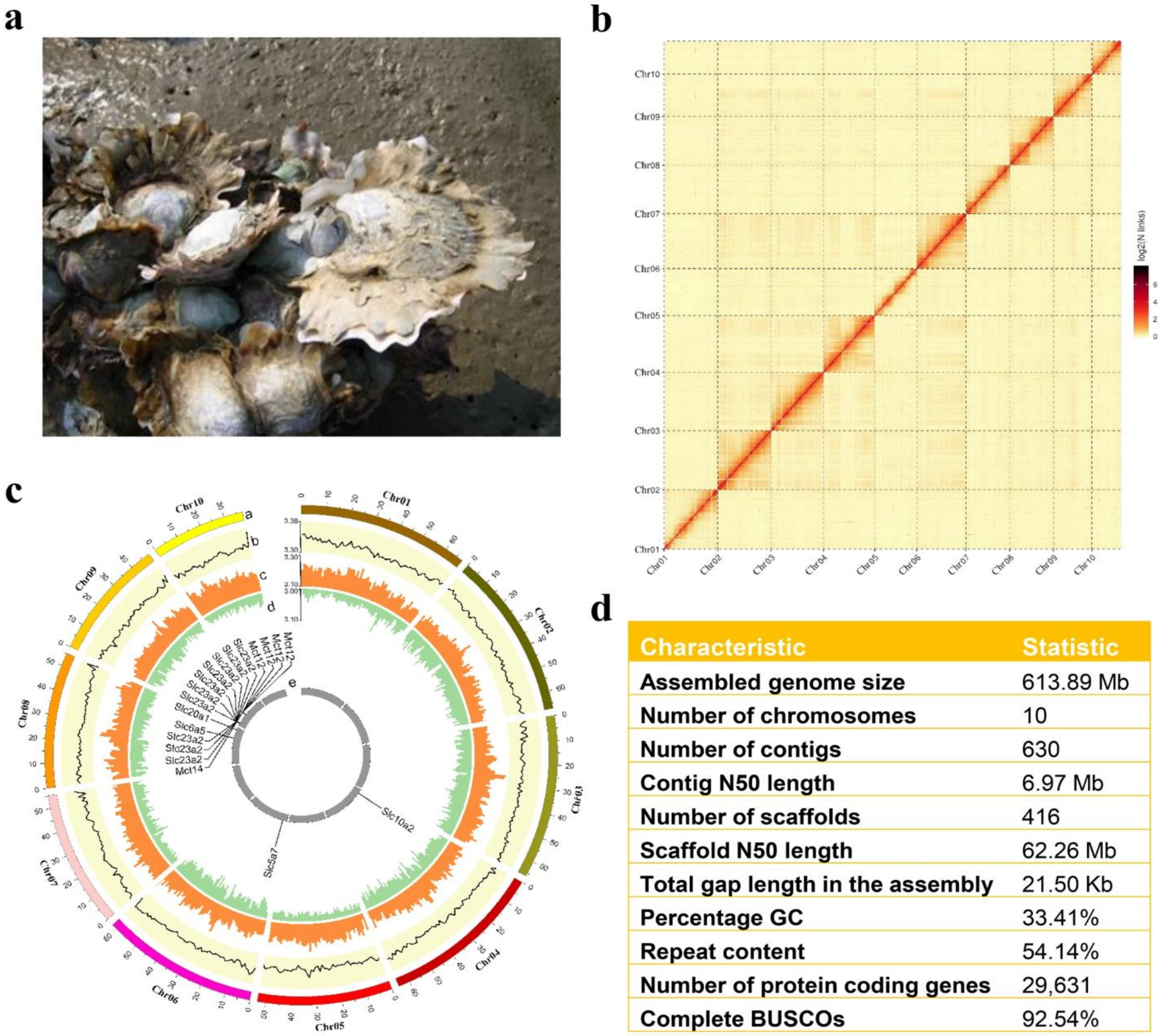
However, when it comes to their "origin"-that is, where they came from and how they became what they are today, things are not so clear. Many people think that they can judge their species by looking at their shells, but the shells change all the time, and their appearance is not reliable. Previous classification methods often leave people confused (Hautmann, 2006; Guo et al., 2018). Now scientists no longer rely solely on appearance. They begin to pull out genomic data and study them together with clues from fossils. Genes tell us about their genetic changes and ways of adaptation, while fossils allow us to look back at the traces they left in ancient strata (Márquez-Aliaga et al., 2005; Liu et al., 2024). Together, the two are expected to give us a more complete understanding of the evolution of oysters.

So this study intends to start from two perspectives: genomics and fossils. We want to figure out how different types of oysters are divided and whether there are any regularities in their geographical distribution. We also want to know which genes have changed and which morphologies have changed in the process of adapting to the environment, and how they interact with environmental changes. We hope that in this way, we can provide some more reliable references for future research on the classification, evolutionary mechanism, and protection strategies of oysters.

2 Comparative Phylogenomics in Oyster Evolution

2.1 Phylogenomic methods and datasets applied to oysters

To understand how oysters evolved, it is not something that can be solved by just looking at the shell. Especially now, many studies are no longer satisfied with traditional methods. Scientists prefer to use genome-level methods for analysis, and they have indeed accumulated a lot of technology over the years. Whole genome resequencing and chromosome-level assembly sound complicated, but in fact they are just to see more clearly which genes are changing and how they are changing. Sometimes, just by looking at a few marker sites in mitochondrial or nuclear DNA, you can find obvious differences between different species (Li et al., 2021b). However, there are exceptions. The genetic changes in some lineages are not obvious, and they can only be seen by comparing them on a larger scale (Figure 1). Through these new tools, people have found that the gene families of some oysters have become very large, which may be the result of the "duplication" of certain specific genes. Some structures have also changed, and these changes seem to be related to their adaptation to the environment (Li et al., 2022). Of course, this speculation still needs more experimental evidence to support it. Whether it is sequencing technology or data analysis methods, it is now more detailed and deeper than before, providing us with a new path to study oyster evolution.



Characteristic	Statistic
Assembled genome size	613.89 Mb
Number of chromosomes	10
Number of contigs	630
Contig N50 length	6.97 Mb
Number of scaffolds	416
Scaffold N50 length	62.26 Mb
Total gap length in the assembly	21.50 Kb
Percentage GC	33.41%
Repeat content	54.14%
Number of protein coding genes	29,631
Complete BUSCOs	92.54%

Figure 1 Chromosome-level assembly of the estuarine oyster *Crassostrea ariakensis* genome (Adapted from Li et al., 2021b)

Image caption: a Estuarine oyster (photo by Lumin Qian). b Hi-C interaction heatmap showing 10 chromosomes of the estuarine oyster. c CIRCOS plot showing 10 chromosomes. d Summary statistics of the genome assembly (Adapted from Li et al., 2021b)

2.2 Insights into oyster lineage diversification

Phylogenomic analysis has found that oysters have great genetic differences at the species, population and even genome levels. These differences can sometimes reveal some hidden species that cannot be seen from the outside, and can also show some species differentiation processes that are taking place. For example, the evolution of different oyster species (such as Pacific oysters and European oysters) coincides with some geological changes, such as the expansion of the Atlantic Ocean, changes in the Paleo-Tethys Ocean, and major climate fluctuations in the past (Guo et al., 2018). The diversification of oysters is mainly not based on larval dispersal, but on their local adaptability and different reproduction methods (Li et al., 2021a). Some groups are very different, and some seem to be one species, but actually contain multiple genetically different groups, all of which indicate that they may be differentiating into new species.

2.3 Comparative genomics and adaptive traits

Studies have also found that oysters have many genes related to stress response, immune defense, and environmental adaptation. These genes have been significantly expanded in their gene families (Takeuchi et al., 2016). For example, some solute carrier families and genes involved in energy metabolism and shell formation are very numerous. These expansions help oysters adapt to different salinities, temperatures, and other pressures. Studies have also found that oysters are very flexible in phenotype, especially gene expression can change according to the environment. This flexibility is related to their evolutionary direction, indicating that in a changing environment, this variability in gene expression is actually an advantage (Li et al., 2018a; Li et al., 2018b). However, this adaptation also has a price. For example, in order to have stronger stress resistance, oysters may have to sacrifice growth rate or metabolic efficiency (Li et al., 2017; Li et al., 2020). In addition, some special genomic features, such as the positional changes of *Hox* genes and gene expansion caused by transposable elements, have also helped different oyster species to form their own unique characteristics and adaptability during evolution.

3 Fossil Record and Morphological Evolution of Oysters

3.1 Overview of the oyster fossil record

Oysters have a very rich fossil record. They first appeared in the early Triassic, shortly after the Permian extinction (Figure 2) (Hautmann et al., 2017). Early oysters, such as the species called Liostrea, had some special features, such as the left shell being fixed to a hard object and a unique ligament structure. The fossils of these early oysters are generally found in open marine environments, sometimes wrapped in ammonites. Judging from the fossils, oysters are distributed in many places and at many times. Especially in the Jurassic and Cretaceous periods, their species became very diverse. Scientists have discovered many different oyster populations in Central Europe, the Tethys Sea, and the Americas (Anzai et al., 2024).

3.2 Evolutionary trends inferred from fossils

Looking at fossils is not always about finding the oldest one. Often, what is really interesting is to see the changes, such as oysters. Their evolutionary pace is quite fast in some periods, especially in the way they cope with different environments. For example, the ribs of the shell are sometimes obvious and sometimes almost invisible. This is not entirely accidental, but has something to do with the conditions of the seabed at the time. When the seawater flows slowly and there is fine sand underneath, the shells of oysters often have more obvious patterns (Rantuch, 2023). But once the water flow becomes faster and the environmental energy is high, their shells become thicker and larger, and look more "hardcore" (Moneer et al., 2024). Of course, not all fossils are so regular, and there are occasional exceptions. The morphology changes, and the lifestyle also changes. Some species used to lie directly on the seabed, but later they became able to "live" close to the rocks. This change from "lying to attaching" actually left traces in the stratigraphic record, and it is quite obvious (Márquez-Aliaga et al., 2005). Not only did the depth change, some even moved from shallow seas to deeper places, and also changed their body shape (Hook et al., 2012). So sometimes, a fossil is not an isolated piece of information. Behind it, there may be a story of environmental change and adjustment of survival strategies.

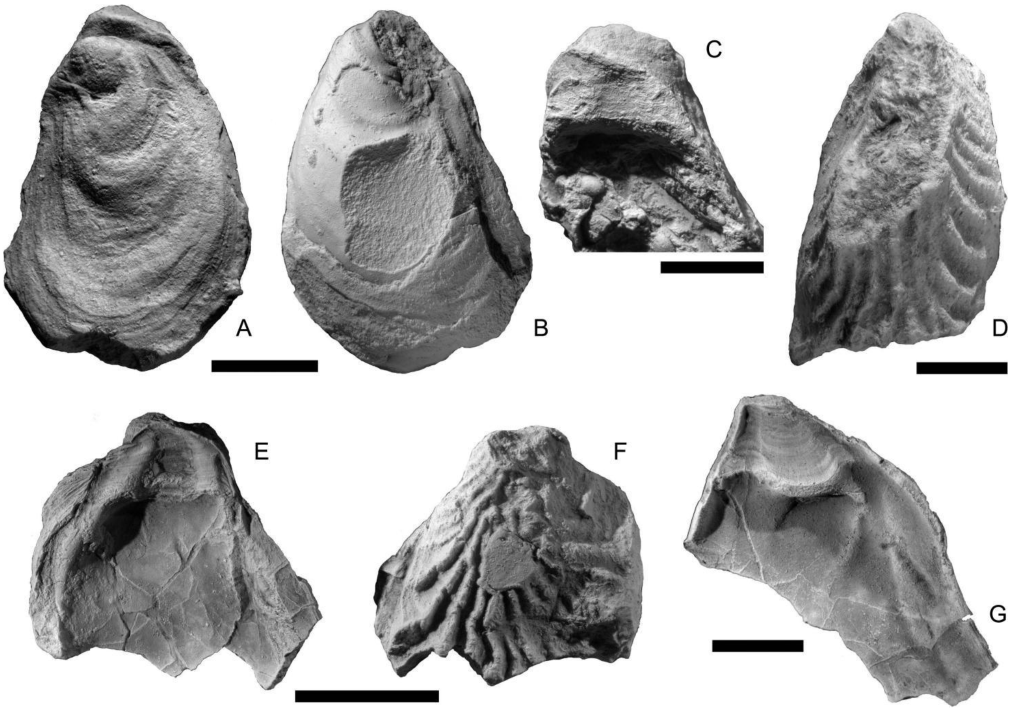


Figure 2 Examples of previously described Liostrea (A, B) and Lophinae (C-G) from the Middle and early Late Triassic. A, B.Ostrea pictetiana Mortillet, 1858, SNSB BSPG AS XVI 14, right and left valve of specimen with conjoined valves. C, D.Ostrea calceoformis Broili, 1903. C. SNSB BSPG 1903 IX 200, ligament area of left valve. D. SNSB BSPG 1903 IX 1364, exterior of left valve, showing attachment scar and plicae. E-G.Ostrea montiscaprilis Klipstein, 1843. E, F. SNSB BSPG AS XVI 32, interior and exterior of left valve; note ligament area with broad resilifer and narrow, ridge-like bourrelets and plicate shell. G. SNSB BSPG AS XVI 33, interior of right valve with depressed bourrelets and relatively elevated resilifer (note that true relief may appear inverted in figure). All specimens are housed in collection of Bayerische Staatssammlung für Paläontologie und Geologie, Munich. Scale bars: A, B, E, F=10 mm; C, D, G=5 mm (Adapted from Hautmann et al., 2017)

3.3 Fossil calibration of molecular clocks

Fossils are also useful for "molecular clocks". The so-called molecular clock is to estimate the time of species differentiation through the rate of genetic mutation. Fossils can provide a reference point in time, helping scientists to analyze evolutionary history more accurately (Hautmann, 2006). For example, when studying the pearl oyster (Pinctada), Bayesian analysis was used to measure that it originated around the Miocene, and this result also matches the time of the fossils (Cunha et al., 2011). By combining molecular data and fossil records, scientists can confirm the time of some major events, such as the origin of the oyster family in the early Jurassic, or the rapid differentiation in the Cretaceous and Paleogene. These changes are often related to geological movements and environmental changes (Li et al., 2021a). Fossil data can allow us to draw a more accurate timeline of oyster evolution, and also help us understand how they migrate and form different species.

4 Integration of Phylogenomics and Fossil Evidence

4.1 Concordance and conflicts between molecular and fossil evidence

Phylogenomics and fossil data together can help us better understand the evolution of oysters. The two methods sometimes agree, but there are also many places where there are conflicts. For example, molecular studies using mitochondrial and nuclear DNA markers have estimated that oysters appeared in the early Jurassic period, which is consistent with the time of some important fossils. At that time, geological events such as the expansion of the Atlantic and Tethys Oceans may have driven the diversification of oysters. However, in some details, the molecular analysis and the traditional classification based on appearance are not exactly the same. Especially for shellfish like oysters, their shell morphology is very changeable and the fossil record is not very complete, so it is sometimes difficult to classify accurately (Salvi and Mariottini, 2016). Genetic data also found some lineages that had not been noticed before, which led researchers to reclassify some genera. These changes were not obvious in the previous classification system based mainly on fossils.

4.2 Evolution of key traits in an integrative framework

By combining molecular data with fossil records, we can more clearly see the changes in some important traits of oysters, such as their reproduction methods and shell morphology. Studies have found that the ancestors of oysters first reproduced by spreading eggs, and some species later evolved the method of raising chicks. Fossils can also provide some support for this. Genome analysis also found that there are many gene duplications and structural changes in oysters. These changes may help them better cope with stress, such as changes in salinity, high temperature, lack of oxygen and other problems (Li et al., 2020; Gundappa et al., 2022). Fossil records can also support these conclusions, such as changes in shell shape, shell thickness, and attachment methods found in different strata. These findings provide us with a timeline, telling us when these adaptive characteristics probably appeared (Wang et al., 2014).

4.3 Biogeographical patterns and historical dispersal

Not all organisms rely on "running far" to spread around the world. Oysters are a typical example. They have a wide distribution range, but they are not good at long-distance diffusion-at least common species such as *Crassostrea* and *Saccostrea* are like this (Foighil and Taylor, 2000). According to current research, oysters may have originated in areas near the Arctic, around the early Jurassic. This is not a random guess, genetic data and fossil evidence are concentrated on this time point and place (Li et al., 2021a). Things later were much more complicated. Some geological events around the world-such as plate movement and climate fluctuations-seem to have paved the way for the spread of oysters. It is not that they actively spread quickly, but that the environment "carries" them away slowly. There is a point that is easily overlooked: whether the larvae can drift far is actually not that critical. On the contrary, how they adapt to the local environment and how they reproduce really determines whether they can stay and develop. Changes in the earth's crust and the transfer of habitats are the main drivers of their diffusion patterns. So, looking at molecular and fossil data together is more than just supplementary information. They can verify each other and help us better piece together the full picture of oyster spread and diversification-just like superimposing two pictures together, and only when they match up can we know that we are right.

5 Case Study: *Crassostrea* Genus as a Model for Evolutionary Analysis

5.1 Phylogenomic insights into *Crassostrea* evolution

Sometimes, classification is not just a matter of “looking at it roughly”. The evolution of the oyster genus is an example. At first, many species were grouped together, such as Magallana, which was originally part of the oyster genus *Crassostrea*. But when the genetic data was later presented, the differences suddenly became apparent. Especially the comparison of mitochondrial and nuclear DNA-not only is there a genetic boundary, but there are also some details in appearance that can match. Of course, not all species are so different. For example, the angulata and the giant oyster (*C. gigas*) look very similar at first glance. But when you go deep into the chromosome-level genome, the results are a bit unexpected: their genetic structure remains quite consistent, and many positions are one-to-one (Figure 3) (Qi et al., 2022). But then again, there are differences between the two. Some gene regions still have unique variations, which may be the places that determine their respective adaptation methods and even the potential direction of species differentiation. Another interesting discovery is that some Asian oyster species have almost the same gene order in their mitochondria. From this point of view, it is likely that these species have been separated for a short time and can be considered as “relatives” who have just separated (Ren et al., 2010).

5.2 Fossil evidence supporting *Crassostrea* lineage history

Genetic data alone is not enough, the dimension of time must be supplemented by fossils. There are actually quite a few oyster fossils, and they are widely distributed, which is quite unexpected. In other words, they have already traveled to many corners of the world. These fossils are not just "similar", many of them can also be seen from the shape of the shell, the size of the ligament and other characteristics. For example, the Hong Kong oyster (*Crassostrea hongkongensis*) is a typical combination. Its shell shows a unique morphology in fossils, and it can also be genetically separated from other species (Lam and Morton, 2003). And these fossils not only let us know what someone looks like, they also help a lot - they are used to calibrate the "molecular clock". In other words, they can tell us when these species began to differentiate and spread. Without these reference points, the timing of many evolutionary events is actually "uncertain".

5.3 Synthesis of molecular and fossil data in *Crassostrea*

When we look at genetic data and fossil evidence together, we have a more complete understanding of the evolution of oysters. The results of molecular phylogeny are roughly consistent with the fossil timeline. This also supports the claim that Asian oyster species have recently diversified, and it also shows the overall evolutionary history of the oyster genus (Salvi and Mariottini, 2016). Putting genetic and morphological data together can not only help us distinguish some species that are originally difficult to classify, but also find hidden species that have not been discovered before. For example, research on Hong Kong oysters shows that its distribution range may have expanded northward (Liu et al., 2022). Combining genomic research with fossil data is a good way to understand the evolution and adaptive diversity of oysters. It allows us to see farther and see more clearly.

6 Future Directions and Methodological Advances

6.1 Advances in sequencing and analytical tools

In recent years, sequencing technology and analytical tools used in oyster research have advanced rapidly. We now have high-quality reference genomes, such as the genomes of the American oyster (*Crassostrea virginica*) and the ball oyster (*Saccostrea glomerata*). These data allow us to carefully study their genetic structure, which gene families have become more abundant, and which genes are related to environmental adaptation (Powell et al., 2018). In addition, transcriptome and proteome analysis also allows us to better understand how oysters cope with stress, how they grow shells, and how they determine sex. Whole-genome studies have found that the genetic structure has changed in many places, and even the number of genes has changed. These changes may be the reason for the different appearances and differences in adaptability (Modak et al., 2021). These new technologies can not only be used to compare different types of oysters, but also provide a lot of useful tools for evolution, living environment research and aquaculture (Zhang et al., 2012).

6.2 Challenges in data integration

It's easier said than done. Although gene sequencing and analysis technology are becoming more and more advanced, once these data are put together with fossil data, problems begin to emerge. Especially in some oyster genera (such as Ostrea), which have many changes, the situation is even more complicated. Sometimes, genetic analysis gives a relationship map, but when you look at the fossil classification, it doesn't match at all (Li et al., 2021a). At this time, you will find that the existing classification system may not be enough, and there are far from enough new fossil samples. Let's talk about morphology. The appearance of oysters is very "changeable". The shape of the shell is greatly affected by the environment. Sometimes even the same species can look different in different places. Therefore, it is often easy to misjudge based on appearance alone. Moreover, unfortunately, the fossil record we have is not complete, and there are many gaps, which has a great impact on the use of molecular clocks to push time (Anzai et al., 2024). Of course, it doesn't mean that these problems cannot be solved. It's just that to connect genes, environment and evolutionary trends in series, we need to rely on more solid experimental design and analysis methods. Which ones are caused by the genes themselves? Which ones are forced by the external environment? These need to be separated step by step (Sirovy et al., 2021).

6.3 Opportunities for multidisciplinary research

Now, more and more studies are combining genetics, paleontology, ecology and environmental science (Jin, 2024). This approach gives us the opportunity to gain a deeper understanding of the origin, distribution changes and adaptability of oysters. For example, some studies have used the Mg/Ca ratio in oyster shells to estimate ancient seawater temperatures. This can link past climate change with the evolution of oyster populations (Bougeois et al., 2016). Genome sequencing and data analysis tools continue to improve, which can drive us to discover more new things. Collaboration between different disciplines will also help us more fully understand how oysters adapt to the environment and whether they have the ability to recover in the face of environmental changes (Zhang et al., 2016).

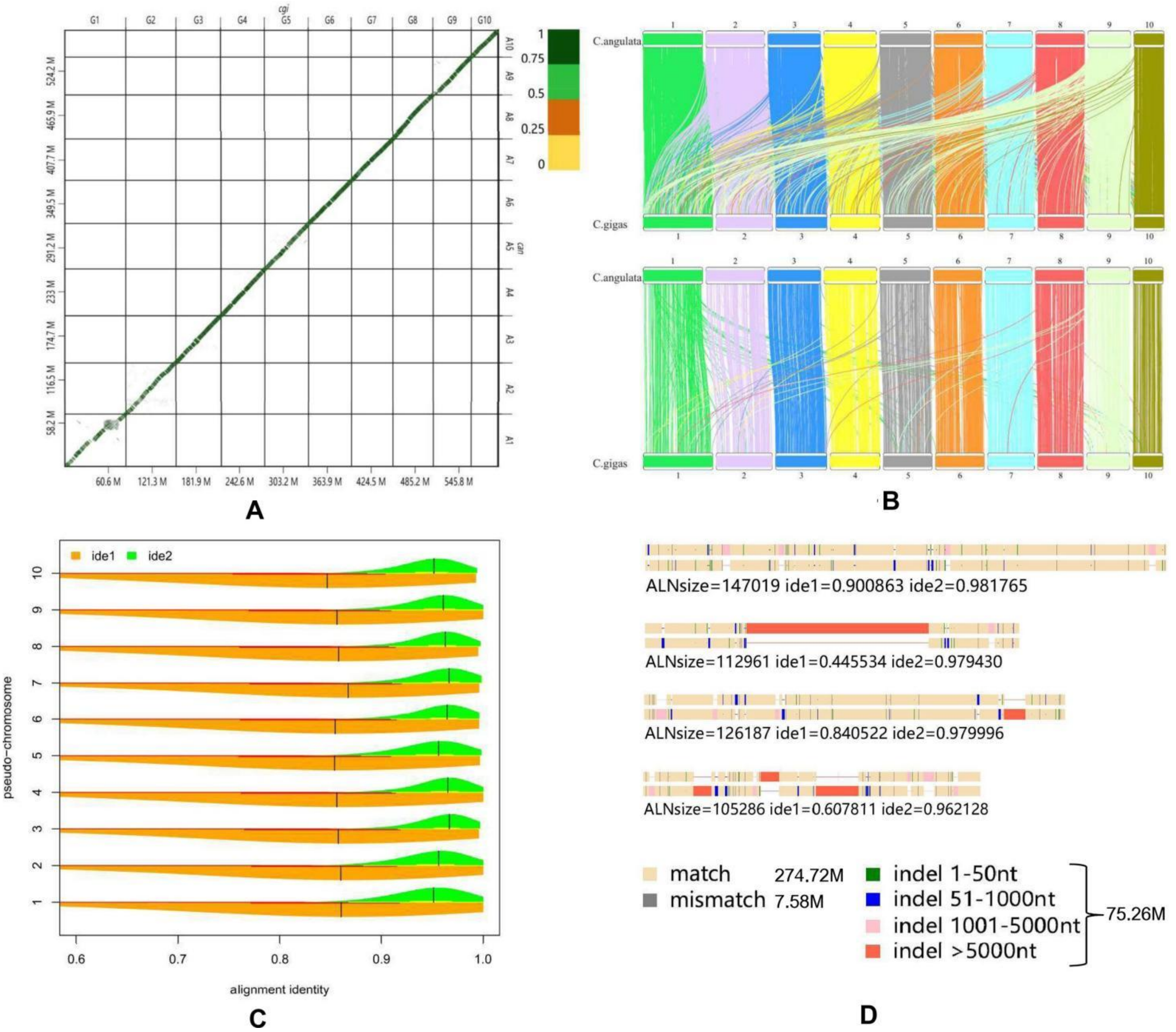


Figure 3 The direct DNA sequence comparison between *C. angulata* and *C. gigas* genomes. (A) The dot plot for the comparison of the 10 pairs of pseudo-chromosome sequences. Top x-axis: G1-G10, the pseudo-chromosomes (10 largest scaffolds: cgiscf1-cgiscf10) in the *C. gigas* genome. Right y-axis: A1-A10, the pseudo-chromosomes (10 largest scaffolds: canscf1-canscf10) in the *C. angulata* genome. Bottom x-axis: the length of G1-G10. Left y-axis: the length of A1-A10. The sequence identities were represented by the upper right colors. (B) The synteny of conserved DNA blocks between the two genomes. The two images were drawn from DNA blocks with a size of ≥1 000 bp and ≥10 000 bp (max=226 631 bp), respectively. (C) The distribution of alignment identities of the conserved DNA blocks in the 10 pairs of pseudo-chromosomes. x-axis: sequence alignment identity. y-axis: the 10 pseudo-chromosome pairs. The black vertical lines in the bean plot denote the median values. ide1: the alignment identity measured by the gap-uncompressed method. ide2: the alignment identity measured by the gap-compressed method. (D) A sketch map for the large indels in the alignments of conserved DNA segments. The four DNA alignments are from A3:13,369,498-13,506,783 vs G3:12,755,799-12,900,025, A5:4,508,362-4,563,006 vs G5:5,295,108-5,404,622, A6:20,475,358-20,598,634 vs G6:21,302,015-21,412,762, and A7:6,838,813-6,932,940 vs G7:7,304,889-7,382,157, respectively (Adopted from Qi et al., 2022)

7 Conclusion

Not all species have their origins as clear as in books, but in the case of oysters, at least now there is a much clearer picture than before. Judging from current genetic data and fossil records, they probably appeared near the Arctic in the early Jurassic period. Later, with the opening of the Atlantic Ocean and the changes in the Tethys Ocean, the species and number gradually increased. But things are not that simple. What you see is a group of shells that look similar, but what the genes tell us is a very clear lineage. That's how those hidden species that "can't be seen but are really different" were discovered. In addition, they are particularly sensitive to environmental changes and their appearance often changes, which made it difficult to tell which one is which. Fortunately, fossils have also added a few key points, especially some early shell shapes and attachment methods, which can reveal a lot of clues-their evolution is obviously the result of the combined effects of both the environment and genes.

Putting these data together gives us the opportunity to piece together the evolutionary map of oysters. When did it diversify, how did it spread, and who its ancestors were? These questions were originally difficult to answer, but now we have a clue. Moreover, more importantly, it allows us to deal with some "stuck" places, such as how to distinguish between similar morphologies, and which reproduction method appeared first and which characteristics came later. Another point to remember is that fossils are not only to see "what they looked like in the past", they are also a key tool for adjusting the "molecular clock". With these references, we can match the rhythm of genetic variation with the timeline and construct a more convincing evolutionary time frame.

To gain a deeper understanding of the evolution and adaptability of oysters, we still have to rely on the cooperation of multiple disciplines such as genomics, paleontology and ecology. Future research should collect more genetic data of oysters, improve the classification methods of fossils, and further study how environmental changes affect the evolution of oysters. Such comprehensive research can not only help us figure out the history of oysters, but also provide scientific references and management suggestions for the protection of these ecologically and economically important shellfish.

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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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