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Article

Phylogenetic insights into the evolution of sound production in spiny lobsters (Palinuridae)

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Abstract

This study investigates theevolutionary lineage and sound production mechanisms of spiny lobsters (Palinuridae), distinguishing between Stridentes, those capable of producing a rasping sound, and Silentes, those that do not. Utilizing comprehensive gene analyses (including COI, 12S, 16S, 18S, 28S, H3, NaK, PEPCK, SSR), this research seeks to resolve the phylogenetic relationships within the Palinuridae family. The methodology encompassed cataloguing all available gene information, alignment, and concatenation into a single dataset for a rigorous maximum likelihood analysis. The results challenge previous understandings, revealing Stridentes as a paraphyletic group from which Silentes emerged. This study proposes a novel phylogeny for the Palinuridae to the genus level, highlighting the need for further sampling and advances in gene sequencing to refine these findings. This comprehensive approach offers a clearer picture of the evolutionary history of sound production in spiny lobsters and their phylogenetic relationships, contributing to a better understanding of arthropod evolution and the intricate mechanisms of sound production.These results complement recent mitogenomic studies that reveal cryptic lineages within widespread species, underscoring the need for ongoing taxonomic revision within Palinuridae and for deeper study of the evolutionary role of sound production.

Keywords spiny lobsters; sound production; phylogenetic analysis; Palinuridae; Stridentes; Silentes

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1 Introduction

Spiny lobsters are a group of reptantian, decapods belonging to the family Palinuridae (Booth and Philips 1994; Briones-Fourzan, 2014; Scholtz, 1995). They are characterized by the absence of chelae, or claws, having spiny antennae, the presence of a phyllosomal larval stage, and are very robust (Scholtz, 1995). Despite the similarities in appearance, they are not closely related to members of the Nephropidae family and are not true lobsters (Patek & Oakley, 2003). They are found in most of the world's oceans and are typically a warm water species although there are several cold-water species including the California spiny lobster (*Panulirus interruptus*) (Briones-Fourzan, 2014). Palinuridae have 54 extant species in 12 genera and constitute one of the most important fisheries in the world (Briones-Fourzan, 2014). They are also being explored for aquaculture,with recruitment of *Panulirus argus* into submerged sea cages demonstrating their cultivation potential (Davis, 2006). As ecosystem engineers, spiny lobsters also contribute to the stability and resilience of reef and kelp forest ecosystems, highlighting their ecological importance beyond fisheries (Steneck, 2002).

Palinuridae can be broken up into two groups, those that produce a rasping sound, Stridentes, and those that do not, Silentes (Patek & Oakley, 2003). This study will attempt to determine whether Stridentes and *Silentes* are monophyletic groups or if one of these groups is paraphyletic. Also, it will attempt to confirm the topology of the Palinuridae family tree to the level of genus.

Most Lobster species use their chelae as a form of protection to ward off potential predators. Spiny lobsters on the other hand lack chelae but use their very robust spine covered antennae bases to pinch potential predators. This is referred to as force production. This form of predator response is commonly a second line of defense for many spiny lobsters as most can produce a rasping sound to ward off potential predators.

1.1 Sound production

The mechanisms for sound production in spiny lobsters are as of yet unique in the animal kingdom. While other arthropods are capable of producing sounds through frictional forces via a mechanism that is analogous to a stick rubbing on a washboard and relies on the hardness of both surfaces to produce the sound, spiny lobsters have been shown to produce their rasping sounds through a stick-slip mechanism akin to a bow being drawn across the strings of an instrument (Patek, 2001). A soft plectrum is rubbed against a microscopically shingled file directly below the eyes (Fig. 1). The production of these rasping sounds is, therefore, not dependent on the hardness of the plectrum and file, which allows the spiny lobster to produce rasping sounds even directly after molting. This advantageous ability permits them to ward off predators even while in their most vulnerable state (Patek, 2001; Patek & Oakley, 2003).

Fig. 1 Depicts the unique stick-slip mechanism of sound production utilized by Stridentes spiny lobsters, highlighting how a soft plectrum is drawn across a microscopically shingled file to produce rasping sounds (Adapted from Patek, 2001).

Recent microscopy studies of the stridulating file have revealed fine-scale sensory structures, including mechanosensory setae, that may provide feedback to help lobsters control and modulate their rasping sounds, suggesting a more complex mechanism than previously understood (Hamilton, 2019). Stridentes spiny lobsters have also been known to attract mates by using their rasps as a mating call (George, 2005). In addition to their role in communication, acoustic fieldwork has shown that these rasp signals can propagate over hundreds of meters and, under quiet conditions, may even travel kilometers, highlighting their potential importance in predator deterrence and long-distance signaling (Jézéquel, 2020).

1.2 Previous studies

Most recent studies, including those by Pollock (1995), L.M. Tsang et al. (2008; 2009), and F. Palero et al. (2009), have posited that Stridentes and Silentes are both monophyletic groups within the Palinuridae family (Figs 2-4). These analyses have provided significant contributions to our understanding of the family's evolutionary relationships, utilizing a variety of genetic markers. Palero et al. (2009) focused on mitogenomic and nuclear genes Cytochrome Oxidase subunit I (COI), 16S ribosomal RNA (16S), 18S ribosomal RNA (18S), 28S ribosomal RNA (28S), and Histone 3 (H3) to construct their phylogenetic tree (Fig. 2). Tsang et al. (2008) used the sodium-potassium ATPase alpha subunit (NaK) and Phosphoenolpyruvate Carboxykinase (PEPCK) genes to delve into the broader MacruraReptantia infraorder, which includes diverse crustaceans like lobsters and crayfish (Fig. 3) and expanded their analysis in 2009 to incorporate the Histone 3 gene, further delineating the distinctions between Stridentes and Silentes (Fig. 4).

Earlier, Patek and Oakley in 2003 employed both morphological and molecular dataanalyzing the 16S, 18S, and 28S genesto reveal varying tree topologies, thus contributing to the ongoing discussion regarding the classification of Stridentes and Silentes (Fig. 5). However, to ascertain whether Stridentes is genuinely a monophyletic group with Silentes nested within, a unified analysis that synthesizes all available data is essential.

While earlier studies debated whether Stridentes and Silentes were monophyletic or paraphyletic groups (Patek & Oakley, 2003; Tsang et al., 2009; Palero et al., 2009), more recent phylogenomic and review-based work has emphasized both the progress and the remaining uncertainties in Palinuridae phylogeny. Wolfe (2019) used large-scale genomic data across Decapoda to recover Palinuridae as monophyletic in their preferred topology but also noted alternative topologies that challenge the stability of Silentes as a distinct clade. Likewise, Farhadi (2024) synthesized the latest time-calibrated phylogenies and biogeographic data for all spiny lobster species, underscoring that the relationships among genera, and the evolutionary origin of sound production, remain unresolved. This study builds on that foundation by integrating a broader set of nuclear and mitochondrial genes to test the evolutionary history of sound production in spiny lobsters at the genus level. This comprehensive approach mitigates the piecemeal limitations of previous studies and is critical for establishing a more accurate phylogenetic framework, better capturing the true evolutionary narrative of the Palinuridae.

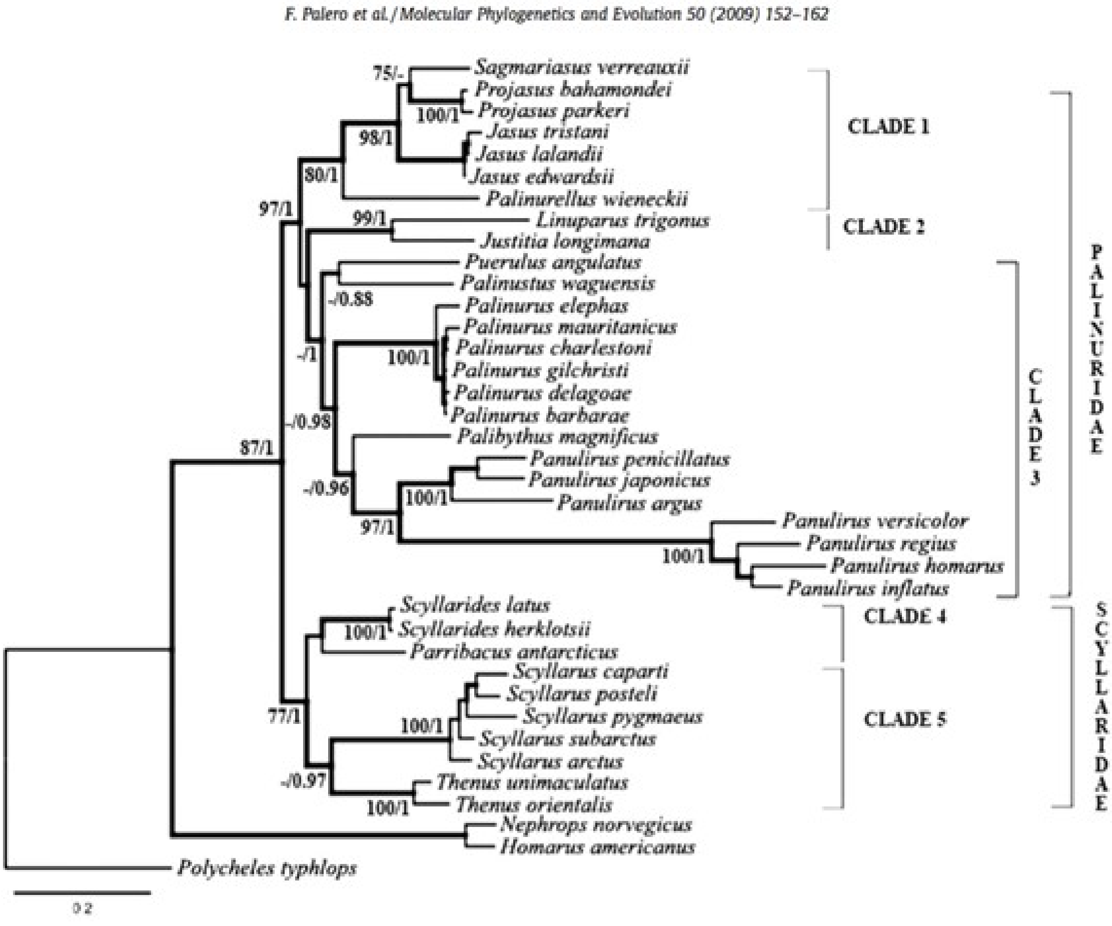

Fig. 2 Phylogenetic tree from the study by F. Palero et al., as published in 2009 in 'Molecular Phylogenetics and Evolution'. It demonstrates the evolutionary relationships within the Palinuridae and Scyllaridae families of marine crustaceans. This phylogeny is constructed using data derived from five genetic markers: cytochrome oxidase I (COI), 16S ribosomal RNA, 18S ribosomal RNA, 28S ribosomal RNA, and Histone 3 (H3) genes. The tree elucidates three distinct clades within the Palinuridae. The bootstrap support values, listed at the nodes, reflect the statistical confidence in the branching patterns shown. Notably, the outgroup taxa include *Polycheles typhlops*, *Nephrops norvegicus*, and *Homarus americanus*.

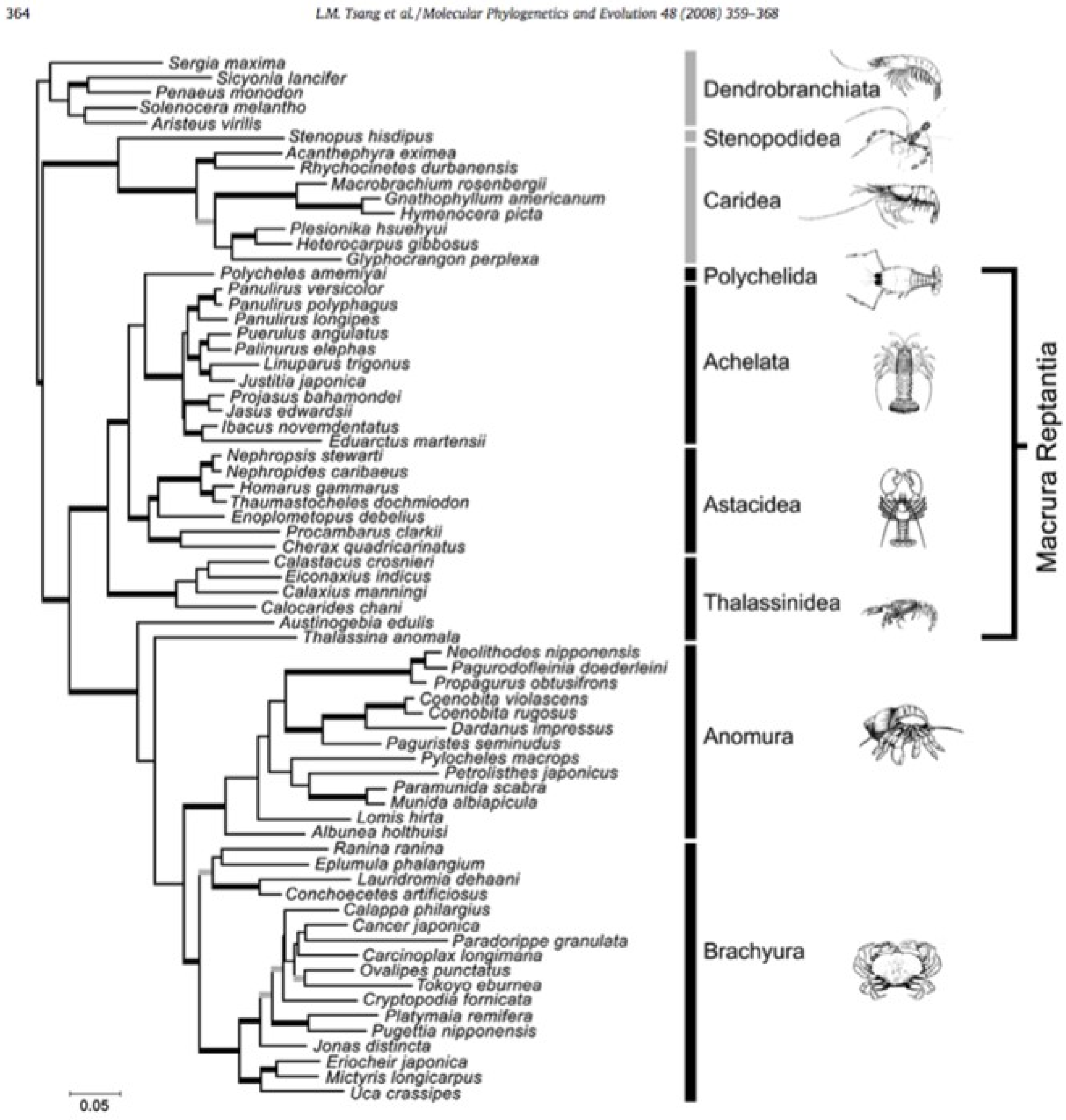

Fig. 3 Depicts a phylogenetic tree from L.M. Tsang et al.'s 2008 'Molecular Phylogenetics and Evolution' study, examining decapod crustaceans of the infraorder Macrura Reptantia, which includes lobsters and crayfish. Derived from the NaK and PEPCK genes, this this tree traces evolutionary connections across various decapod taxa, such as Caridea, Achelata, and Brachyura. Bootstrap values indicate the statistical support for the clades. Illustrated decapod representatives for each infraorder highlight the correlation between genetic ancestry and physical form, presenting an evolutionary framework for this diverse group

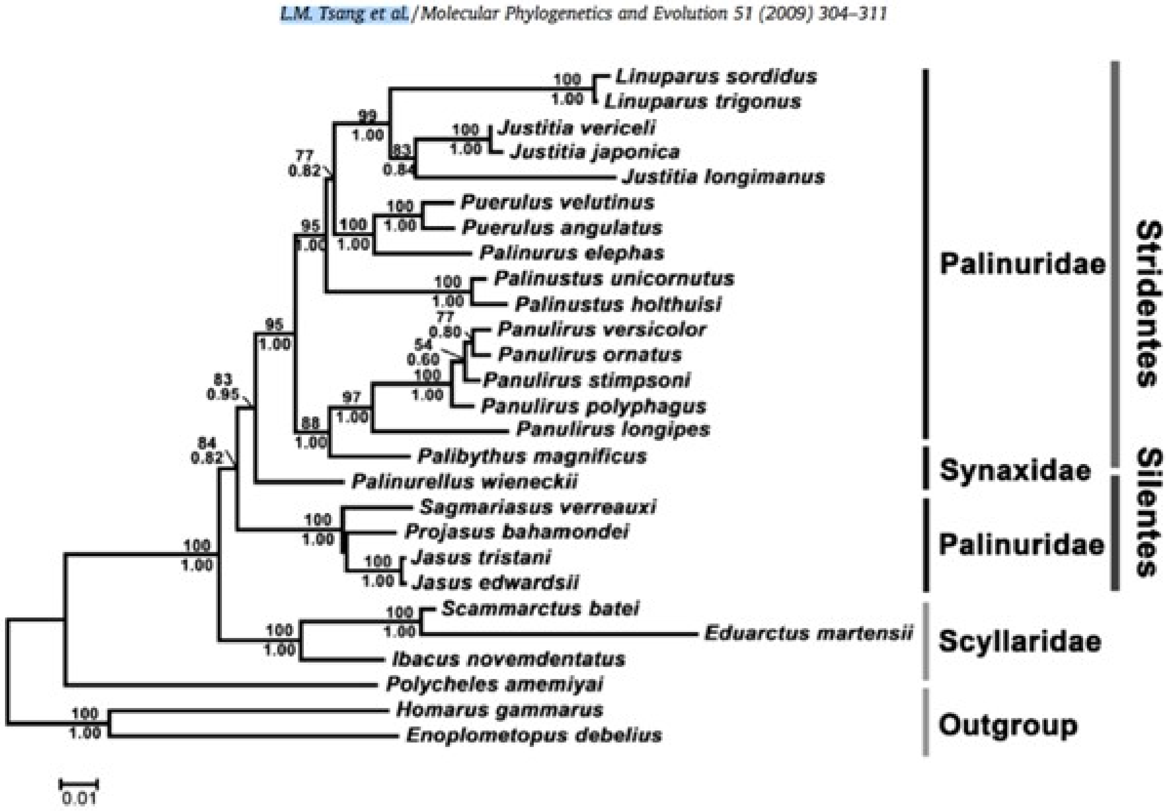

Fig. 4 Phylogenetic tree from L.M. Tsang et al., featured in Molecular Phylogenetics and Evolution (2009), illustrates the genetic relationships within the Stridentes and Silentes groups of the Palinuridae family. The tree is exclusively derived from sequencesthe NaK, PEPCK, and H3 genes, key markers that provide insights into evolutionary linkages. The vertical bars to the right categorize the family into Stridentes, known for their sound-producing abilities, and Silentes, which lack this feature, alongside the closely related Synaxidae and outlying Scyllaridae as the outgroup. Bootstrap support values at the nodes indicate the reliability of the inferred relationships, with the scale bar representing genetic distance.

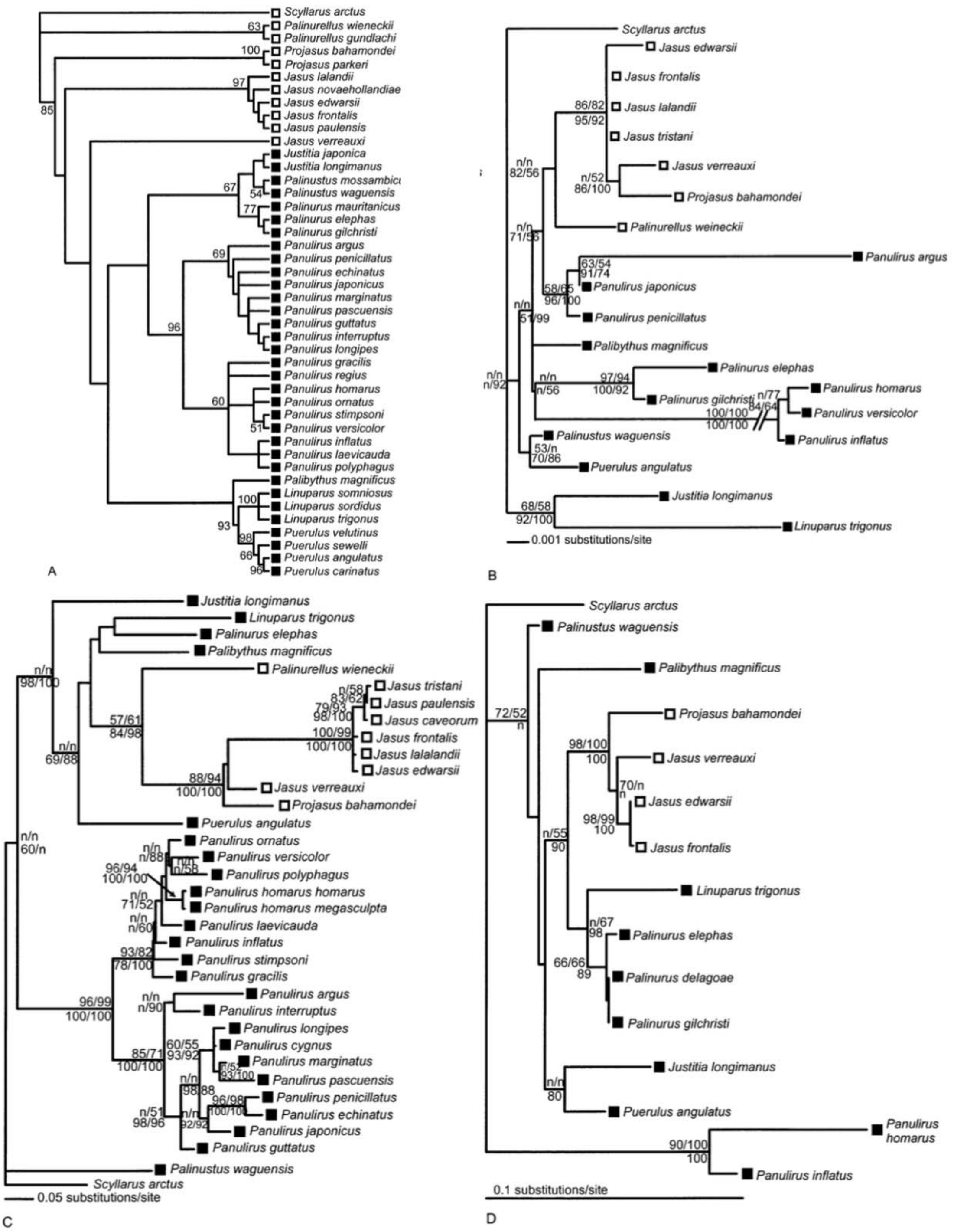

Fig. 5 These trees, published by Patek and Oakley in 2003, display the diverse methodologies used to elucidate the phylogenetic relationships within the Palinuridae family. Panel A presents a tree based on morphological features, showcasing the traditionalapproach to understanding species' relationships through physical characteristics. Panels B, C, and D illustrate trees constructed from molecular data, specifically the 16S, 18S, and 28S ribosomal RNA genes, respectively. White squares represent Silentes and Black squares represent Stridentes. Each tree provides a different perspective on the evolutionary pathways of Palinuridae species, reflecting the variations that can arise from different data types.

More recently, large scale phylogenetic research has slowed and more targeted reserche is being conducted at the species level. Singh et al. (2017) utilized multilocus genetic data, including mitochondrial (COI and hypervariable control region) and nuclear (ITS-1 intron and β-tubulin) markers, to reveal *P. homarus* rubellus as a genetically distinct species, separated from *P. homarus homarus* during the Oligocene. Their molecular approach underscores the influence of larval dispersal and ocean currents on speciation, emphasizing the need for taxonomic revision within this lineage to enhance conservation and management efforts.

Jeena et al. (2015) investigated the molecular phylogeny of 11 key lobster species from the Indian coast using mitogenomic and nuclear DNA sequences. Their work established precise genetic identities for these lobsters, notably identifying Thenus unimaculatus and confirming Panulirus homarus subspecies as *P. homarus homarus*. The study underscored the independent evolutionary paths of the Scyllaridae and Stridentes within the Palinuridae, offering crucial insights for species identification and conservation efforts.

2 Materials and Methods

All available gene information for the family Palinuridae along with the chosen out-group of Ibacusperonii were cataloged and one representative from each species for each available gene was used. The dataset combined both mitogenomic and nuclear markers, including cytochrome oxidase subunit I (COI), 12s, 16s, 18s, 28s, Histone 3(H3), sodium-potassium ATPase alpha subunit (NaK), phosphoenolpyruvate carboxykinase (PEPCK), and small subunit ribosomal (SSR). The gene sequences were organized in mesquite, aligned with muscle, and then concatenated into a single NEX file. A phylip file was then exported from mesquite and ran through RAxML to assess maximum likelihood with rapid bootstrapping for 100 replicates using the GTRGAMMA model. A maximum likelihood tree with bootstrap support was produced.

A new NEX file was created in Mesquite and the original out-group, *Palibythus magnificus*, and *Puerulus velutinus* were then added to the matrix. To determine the pair wise distance between the taxa *P. magnificus* and *P. velutinus*this new NEX file was then ran through PAUP and the Jukes-Cantor (JC) model corrected distance and the uncorrected distance was calculated.

3 Results

The resulting maximum likelihood tree confirmed that Stridentes is a paraphyletic group with Silentes emerging from within Stridentes (Fig. 6). Bootstrap values above the value of 50 were given for the major nodes of the tree (Fig. 7). The uncorrected pair wise distance between *P. magnificus* and *P. velutinus*is. 04005 and the JC modeled distance is .03900. Similar mitogenome-based analyses have confirmed species-level placements within Panulirus, such as the assignment of *P. pascuensis* to its proper clade, underscoring the value of complete mitochondrial datasets in refining phylogenetic resolution (Barrios, 2024).

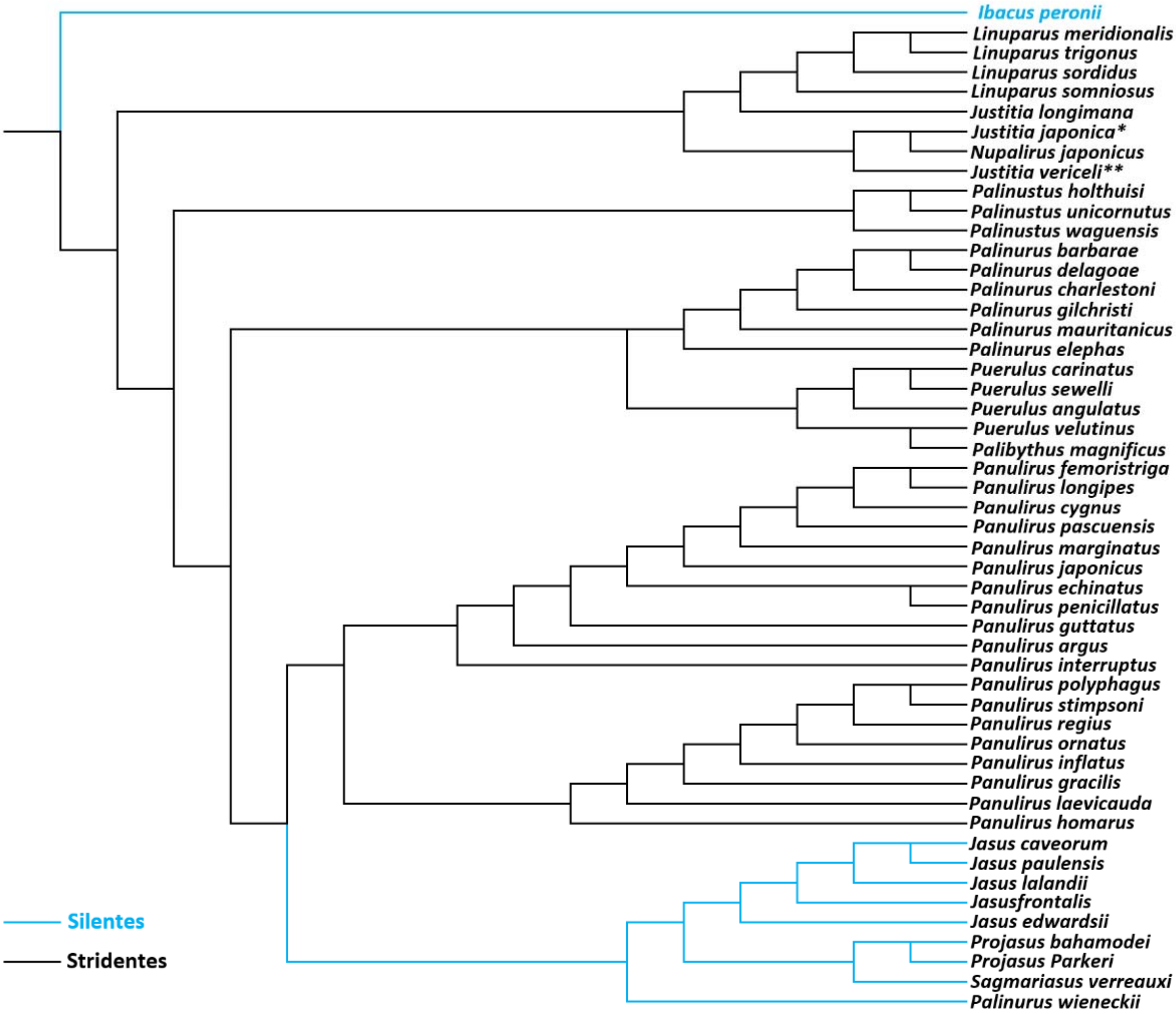

Fig. 6 This phylogenetic tree, generated using RAxML, portrays the latest findings on the genetic relationships within the Palinuridae family, distinguishing between the sound-producing Stridentes (black branches) and the non-sound-producing Silentes (blue branches). Taxonomic clarifications are noted with asterisks, indicating that *Justitia japonica** is a synonymm for *Nupilurus japonicus* and *Justitia vericeli*** is a synonym for *Nupilurus vericeli*.

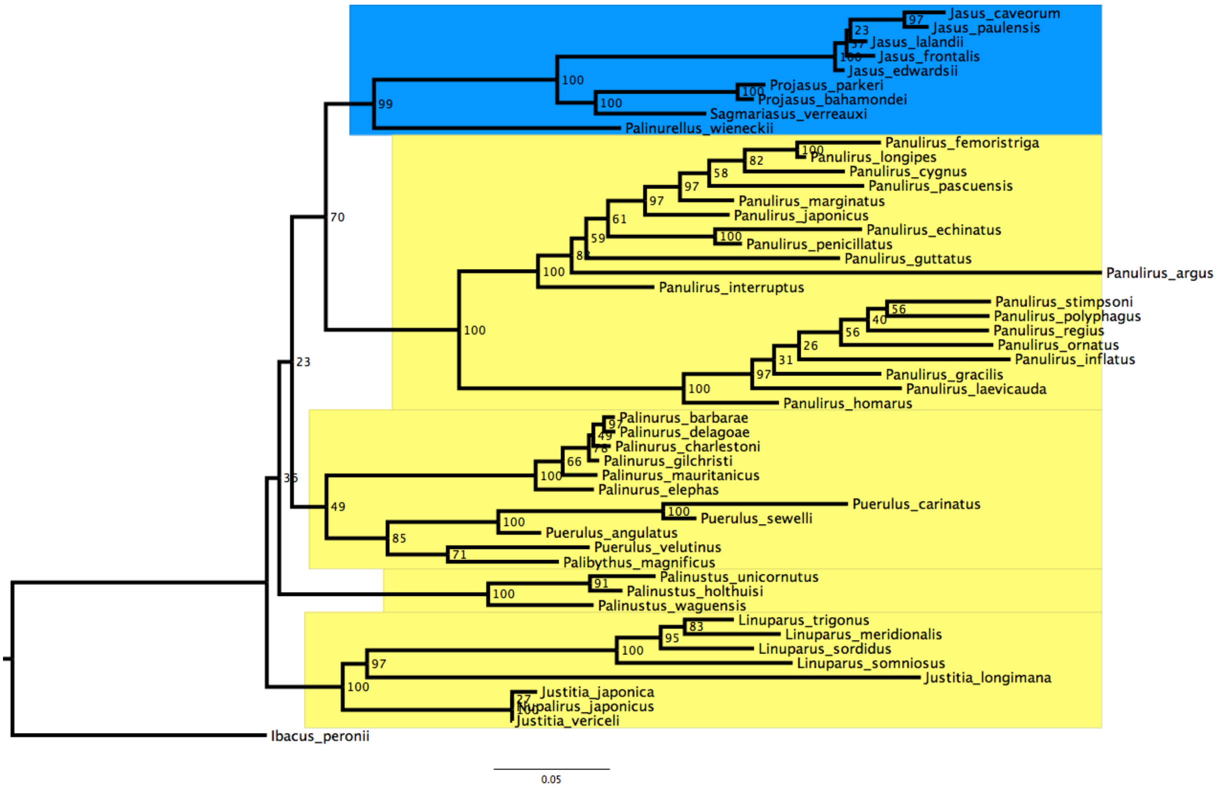

Fig. 7 displays a Maximum Likelihood phylogenetic tree with bootstrap values indicated at each node, generated through RAxML analysis. The tree stratifies a range of lobster species within the families Palinuridae and Scyllaridae, revealing the evolutionary relationships and genetic distances between them. Highlighted in blue are members of the Silentes group, characterized by their lack of sound production, while the Stridentes group, capable of producing sound, is marked in yellow. The bootstrap support values, denoting the level of confidence in the tree's branches, are prominently displayed, showing high support for most clades.

4 Discussion

Previous studies attempted to make conclusions about the structure of the phylogenetic tree for the Palinuridae family tree with only a limited dataset. With the addition of more sample data, this study has elucidated a more comprehensive and nuanced picture of the phylogenetic relationships within the Palinuridae family. Unlike earlier works that relied on smaller, more fragmented datasets, often limited to partial mitochondrial or nuclear sequences,the present research employed a holistic approachthat parallels more recent mitogenomic analyses, incorporating a wide array of genetic markers to construct a robust phylogenetic tree.

The findings of this research not only challenge the conventional classification of Stridentes and Silentes as distinct monophyletic groups but also shed light on the evolutionary dynamics within the Palinuridae family. The data compiled here implies that Stridentes is not a monophyletic group.

Recent phylogenomic analyses have also examined the placement of Stridentes and Silentes within the Palinuridae. Wolfe (2019) recovered Palinuridae as monophyletic in their preferred topology, with Stridentes and Silentes forming distinct clades, but noted that alternative topologies occasionally placed Silentes near the slipper lobsters (Scyllaridae), leaving the evolutionary origin of silence unresolved. Similarly, Farhadi (2024) highlighted that, despite advances in molecular datasets, questions remain about the precise phylogenetic relationships within Palinuridae, particularly at the genus level. Complementary mitogenomic work has also refined within-genus relationships, placing *Paneliruspascuensis* as sister to *Panulirus cygnus* and *Panulirus* *longipes* and reinforcing the monophyly of *Palinuridae* and *Panulirus* (Barrios, 2024). The results presented here contribute to this ongoing debate by providing a comprehensive analysis that integrates multiple nuclear and mitochondrial markers, supporting the interpretation that Stridentes is paraphyletic and that Silentes emerged from within this group. This revelation underscores the complex evolutionary history of sound production among spiny lobsters and suggests a more intricate relationship between sound production capabilities and phylogenetic development than previously understood.

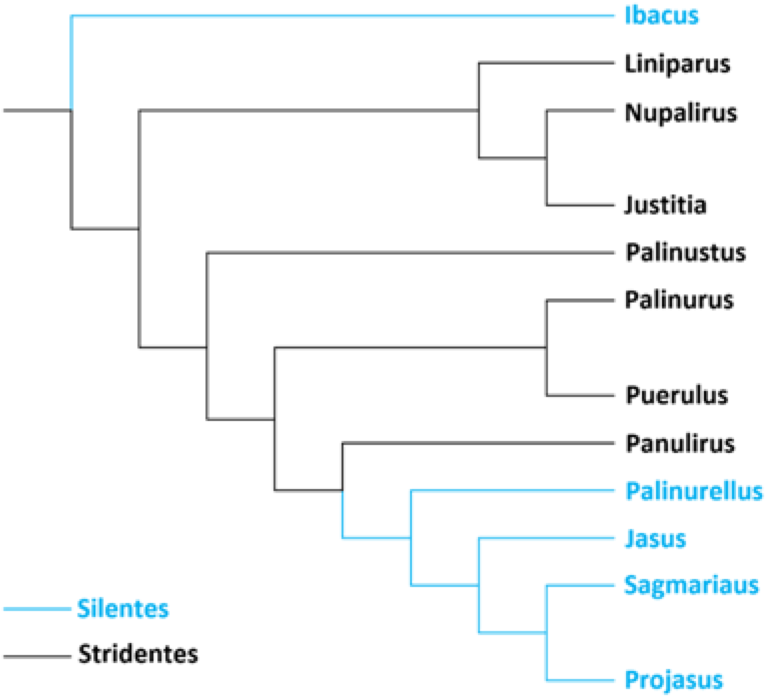

Fig. 8 Presents a revised phylogenetic tree where Stridentes are shown as a paraphyletic group, lacking a unique common ancestor due to the inclusion of Silentes. This tree also proposes the reclassification of Palibythus into the Puerulus genus, suggesting a closer genetic relationship.

More sampling is needed to strengthen the support for this tree. Even with this massive dataset, there are still some ambiguities in the tree, namely the nesting of *Palibythus magnificus* within the genus *Puerulus*. The close genetic similarity between *P. magnificus* and *P. velutinus*, as indicated by the JC distance of just 0.03900, suggests that current taxonomic classifications may need revisiting. With *P. magnificus* and *P. velutinus* having a JC distance of just 0.03900, it is likely that they should be in the same genus, and the genus *Palibythus*, with its one member, should be absorbed by *Puerulus*. Beyond genus-level ambiguity, recent mitogenomic work has uncovered deep cryptic lineages within widespread species such as *Panulirus polyphagus* (Jeenaetal., 2024). Their study identified multiple divergent conspecific lineages across the Indian Ocean, suggesting that hidden genetic structuring may be more common within Palinuridae than currently recognized. This complements the present study by highlighting that phylogenetic complexity occurs not only at the genus level, as demonstrated here with Palibythus and Puerulus, but also within species, underscoring the need for finer-scale genomic resolution in future phylogenetic and taxonomic assessments.Comparable findings of hidden genetic structure have been reported in other spiny lobsters, where mitogenomic evidence revealed deeply divergent lineages within the widespread species *Panulirus polyphagus*, further demonstrating the need for ongoing taxonomic revision in the family (Jeena, 2024).

This study's comprehensive genetic analysis not only challenges previous phylogenetic models but also paves the way for future research to explore the genetic underpinnings of sound production and its evolutionary significance in spiny lobsters. I am proposing this new phylogeny to the level of genus based on the above results (Fig. 8). Furthermore, the findings highlight the critical role of sound production in the survival and reproductive strategies of spiny lobsters, indicating a potential area for deeper ecological and behavioral investigations.

In conclusion, the expanded dataset and methodological rigor of this study have provided valuable insights into the phylogenetic relationships and evolutionary history of the Palinuridae family. More sampling and innovations in gene sequencing will only better tune this phylogeny even more in the future. The implications of this research extend beyond the confines of taxonomy and evolutionary biology, offering glimpses into the adaptive innovations that have enabled spiny lobsters to thrive in diverse marine environments.

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