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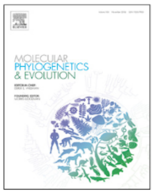

Molecular phylogeny of the Pectinoidea (Bivalvia) indicates Propeamussiidae to be a non-monophyletic family with one clade sister to the scallops (Pectinidae)

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ABSTRACT

Scallops (Pectinidae) are one of the most diverse families of bivalves and have been a model system in evolutionary biology. However, in order to understand phenotypic evolution, the Pectinidae needs to be placed in a deeper phylogenetic framework within the superfamily Pectinoidea. We reconstructed a molecular phylogeny for 60 species from four of the five extant families within the Pectinoidea using a five gene dataset (12S, 16S, 18S, 28S rRNAs and histone H3). Our analyses give consistent support for the non-monophyly of the Propeamussiidae, with a subset of species as the sister group to the Pectinidae, the Propeamussiidae type species as sister to the Spondylidae, and the majority of propeamussiid taxa sister to the Spondylidae + *Pr. dalli*. This topology represents a previously undescribed relationship of pectinoidean families. Our results suggest a single origin for eyes within the superfamily and likely multiple instances of loss for these characters. However, it is now evident that reconstructing the evolutionary relationships of Pectinoidea will require a more comprehensive taxonomic sampling of the Propeamussiidae *sensu lato*.

1. Introduction

Scallops Pectinidae Rafinesque, 1815 are one of the most ecologically and morphologically diverse families in the class Bivalvia. With over 250 extant species currently considered valid, they are distributed across polar, temperate, and tropical marine ecosystems of shallow sublittoral reefs, sandy bays, sea grass beds and coarse substrates of the continental shelves, with a smaller number of species restricted to deeper water (Serb, 2016). Pectinidae is an ideal model to study the evolution of complex traits due to the number and biological diversity of extant species, the link between shell morphology and habitat use (Stanley, 1970), and their high preservability in the paleontological record (Valentine et al., 2006). Researchers have investigated the evolution of traits such as shell shape (Serb et al., 2011, 2017; Sherratt et al., 2016; Stanley, 1970), behavior (Alejandrino et al., 2011), swimming mechanics (Guderley and Tremblay, 2013; Hayami, 1991; Millward and Whyte, 1992; Tremblay et al., 2015), and phototransduction (Faggionato and Serb, 2017; Gomez et al., 2011; Kingston et al., 2015; Porath-Krause et al., 2016; Serb et al., 2013). One compelling set of phenotypes is the complex sensory systems, including eyes, found in this family (Audino et al., 2015a, 2015b, 2015c; Land, 1965; Speiser et al., 2011, 2016; Speiser and Johnsen, 2008). Most

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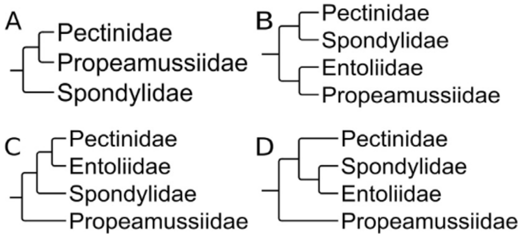

Fig. 1. Existing hypotheses of relationships among pectinoidean families: (A) molecular data (Bieler et al., 2014; Matsumoto and Hayami, 2000); (B) paleontological and morphological data (Waller, 2006); (C) paleontological and morphological data (Waller, 1991); (D) morphological data (Waller, 1978).

work has concentrated on the eyes of scallops, which were first described in 1791 (Poli, 1791). Subsequent research focused on the anatomy and optics of these eyes to understand how the eyes capture light and focus images (Land, 1965; Palmer et al., 2017; Speiser et al., 2016; Speiser and Wilkens, 2016). Recent molecular approaches have provided insights into the evolution of gene families involved in scallop photoreception (Gomez et al., 2011; Kojima et al., 1997; Pairett and Serb, 2013; Piatigorsky et al., 2000; Porath-Krause et al., 2016; Serb et al., 2013). However, in order to understand the origin and evolution of these and other traits, the family Pectinidae needs to be placed in a deeper phylogenetic framework within the superfamily Pectinoidea.

The relationship of the Pectinidae to the other families in the Pectinoidea has been highly contentious due to high levels of homoplasy in shell characters (Dijkstra and Maestrati, 2012; Hertlein, 1969) and alternative interpretations of the fossil record (Waller, 2006, 1991, 1978) (Fig. 1). As a result, three families (Propeamussiidae, Spondylidae, Entoliidae) singly or in combination have been proposed to be the sister taxon to the Pectinidae by different authors at different times. The prevailing view has been that the Propeamussiidae Abbott, 1954, or glass scallops (~200 species), represent the closest relatives of the Pectinidae. Propeamussiids possess very thin, often translucent shells and inhabit the marine epipelagic (80 m) to the abyssal (4000 m) zones. They appear to be a lineage of relict species that survived severe environmental changes at the end of the Cretaceous by inhabiting deep and/or cold-water refugia (Waller, 1991) where most modern propeamussiids and the oldest extant lineage of Pectinidae (Camptonectinae: *Delectopecten*) are still found. Additionally, propeamussiids and some pectinid lineages have a similar shell shape. These data suggest a possible sister relationship between the two families, which has been supported by other studies which include molecular data for their phylogenetic analyses (Bieler et al., 2014, Fig. 30; Matsumoto and Hayami, 2000) (Fig. 1A). Recently, one lineage of micro glass scallops (1.5–6 mm as adults) was elevated to its own family, the Cyclochlamydidae Dijkstra and Maestrati, 2012; however its phylogenetic relationship to the Pectinidae is unknown. There remains two other pectinoidean families: the Entoliidae Teppner, 1922, a mostly extinct family with only two extant monotypic genera (*Entolium*, *Pectinella*) (Waller, 2006), and the Spondylidae Gray, 1826 or thorny oysters (68 species), a cementing family with finger-like protrusions on the shell. These less-studied families have been hypothesized to be the sister group to the Pectinidae, either separately (Waller, 2006, 1991) (Fig. 1B vs C) or together as the sister clade (Waller, 1978) (Fig. 1D). New data on the age of first known fossil occurrences in conjunction with morphological characteristics are the basis of a revised phylogenetic hypothesis supporting the Spondylidae as the sister group to the Pectinidae, with Entoliidae + Propeamussiidae forming a second clade (Waller, 2006) (Fig. 1B). A molecular phylogeny based on a single mitochondrial gene also supports the Pectinidae + Spondylidae relationship. However, multigene datasets of mitochondrial and nuclear markers have recovered Spondylidae + Propeamussiidae as the sister group to the Pectinidae (Alejandrino et al., 2011; Puslednik and Serb, 2008). To date, no molecular phylogenetic analysis has included more than three pectinoidean families (Plazzi et al., 2011; Plazzi and Passamonti, 2010; Sharma et al., 2012; Sun and Gao, 2017), which has prevented more definitive resolution.

We generated a 18S rDNA dataset for 60 pectinoidean species and five species of Limidae to complement an existing multigene dataset (Sherratt et al., 2016) and broadened the taxonomic representation to include four of the five extant families of Pectinoidea. We then calibrated the multi-locus phylogenetic hypothesis using fossil data from three families. Using this framework, our goal was clarify the phylogenetic relationships between Pectinidae and other families within Pectinoidea.

2. Materials and methods

2.1. Specimens and samples

We assembled 60 taxa from four of the five extant families in the superfamily Pectinoidea plus five species of Limidae to serve as the outgroup. We sampled 18 species from the Propeamussiidae, 37 species of Pectinidae, four species of Spondylidae, and a single extant species of Entoliidae (supplementary Table S1). Due to the challenges of acquiring samples, we were unable to include taxa from the newly described family Cyclochlamydidae. Samples used in this study were obtained from colleagues and museum collections (see supplementary Table S1 and Acknowledgments). The majority of Indo-Pacific specimens included in this study were obtained during expeditions organized by the MNHN and Pro-Natura International as part of the *Our Planet Reviewed* program, and by the MNHN and the Institut de Recherche pour le Développement as part of the *Tropical Deep-Sea Benthos* program. Species identifications of the Indo-Pacific specimens were determined by Henk H. Dijkstra at the Naturalis Biodiversity Center (Netherlands). All tissues were preserved in ethanol and shell voucher specimens are available from museum collections listed in supplementary Table S1.

2.2. Molecular laboratory methods

Total genomic DNA (gDNA) was extracted from either mantle or adductor tissues following the manufacturer's protocol of the Qiagen DNeasy Blood and Tissue kit. A portion of the nuclear gene 18S ribosomal RNA (~700 bp) was amplified using the 18S a2.0 forward (5′-ATGGTTGCAAAGCTGAAAC-3′) and 18S 9R reverse (5′-GATCCTTC CGCAGGTTCACCTAC-3′) primers (Giribet et al., 1996; Whiting et al., 1997). PCR reactions were carried out in 25 µl total volume reactions containing 12.5 µl 2x MyTaq Red Mix (Bioline), 1 µl of 10 µM 18S rRNA forward and reverse primers (18 s a2.0 and 18 s 9R, respectively), 9.5 µl double distilled water, and 1 µl of template. Reactions underwent one round of PCR consisting of an initial denaturation step (2 min at 95 °C) followed by 30 cycles of chain denaturation (15 s at 95 °C), primer annealing (15 s at 50 °C), and elongation (10 to 60 s at 72 °C). Roughly 5 µl of the amplification products were visualized on a 2% agarose gel using a 1 kb size standard. Samples with the expected band size (~700 bp) were sent to Iowa State University DNA Facility for Sanger sequencing using Applied Biosystems 3730 × l. In total, 18S rRNA sequences for 60 taxa (16 Propeamussiidae species, 35 Pectinidae species, three Spondylidae species, one Entoliidae species, and five Limidae species) were successfully generated.

The 18S rRNA sequences were added to a multigene dataset consisting of two mitochondrial genes (12S and 16S rRNAs) and two nu-

Alejandrino et al. (2011).

2.3. Phylogenetic analyses

DNA sequences for each gene portion were aligned separately in MAFFT v7.222 (Katoh and Standley, 2013) using the automatic algorithm to select the best alignment method and remaining settings/options set as default. Ambiguously aligned nucleotides due to large insertion-deletions (indels) in 12S, 16S, and 28S rRNA genes were removed using settings for a less stringent selection on the Gblock 0.91b server (Castresana, 2000; Dereeper et al., 2008; Talavera and Castresana, 2007). Individual gene alignments were concatenated in Geneious v4.7.6 (Kearse et al., 2012) to produce a final dataset of five gene regions: 12S rRNA (1–315 bp), 16S rRNA (316–674 bp), 18S rRNA (675–1161 bp), 28S rRNA (1162–1937 bp), and histone H3 (1938–2276 bp). Mitochondrial-only (12S and 16S rRNAs) and nuclear-only (18S rRNA, 28S rRNA and histone H3) datasets were also produced.

Phylogenetic analyses were carried out under maximum likelihood (ML: (Felsenstein, 1981)) and Bayesian inference (BI: (Mau et al., 1999)). Nucleotide substitution model was determined using PartitionFinder2 (Lanfear et al., 2016). For this analysis, the datablock was defined by gene, as above, with branch lengths unlinked. All evolution models and schemes were investigated using Akaike Information Criterion with sample size correction (AICc) metric. ML analyses were conducted using RAxML-HPC v8.2.9 on XSEDE (Stamatakis, 2014) as implemented on the CIPRES Scientific Gateway v3.3 (Miller et al., 2010). Branch support was determined with 500 bootstrap iterations for best-scoring ML tree. All other parameters were set at the program's default. BI analyses were conducted using MrBayes v3.2.6 (Ronquist et al., 2012) as implemented on the CIPRES Scientific Gateway v3.3. We ran three independent analyses, each with eight Markov chain Monte Carlo (MCMC) chains sampling every 100 generations and the temperature for heated chains set at 0.15. The MCMC analysis was set to run for 50 million generations or until a standard deviation of split frequency value of 0.01 was reached signifying convergence following the stoprule after 4.2 million generations. The post-run analyses were set with a 50% burn-in and all other parameters not mentioned above were left at the program's default. We then visually inspected the combined trace files to confirm acceptable mixing and high ESS (effective sampling size) across all parameters (> 300) in Tracer v1.6 (Rambaut et al., 2018). Post-burn-in trees were used to construct the 50% majority rule consensus tree and to estimate posterior probabilities.

We used the Approximately Unbiased (AU) test (Shimodaira, 2002) to compare our results to six alternative phylogenetic hypotheses. These alternative topologies were generated via ML in RAxML to constrain either (1) a monophyletic Propeamussiidae or (2) a clade of Propeamussiidae that excluded *Parvamussium ina*. In addition, four hypotheses from previous studies (Fig. 1) were compared. Site-wise likelihoods were calculated in RAxML for the unconstrained and constrained ML topologies and analyzed in CONSEL (Shimodaira and Hasegawa, 2001) using default parameters for *p*-values.

Divergence time estimation was conducted using RevBayes version 1.0.9 under the Fossilized Birth-Death model (Hohna et al., 2016). A relaxed molecular clock model was defined assuming an uncorrelated exponential model on branch rates. Posterior probabilities were sampled by Markov Chain Monte Carlo process (MCMC) for 500,000 iterations. Maximum clade credibility tree, with a burn-in of 10%, was generated after pruning the five fossil taxa used to calibrate internal nodes. Fossil ages were incorporated based on available data in Waller (2006) and in the Paleobiology Database (https://paleobiodb.org/). considering the fossil record of *Argopecten* spp. (15.99–2.61 MYA), an extant genera. The Spondylidae was constrained around 171.6–168.3 while Entoliidae was calibrated based on the fossil of *Pectinella spp*. (251.3–247.2 MYA). Finally, the Limidae was also constrained between 330.9 and 323.2 MYA, based on *Paleolima spp*.

3. Results

A total of 111 sequences were generated in this study and 196 sequences were obtained from previous work (Sherratt et al., 2016) for 60 species across four families of Pectinoidea with five species of Limidae serving as the outgroup. The lengths of each gene region after alignment were: 12S rRNA: 315 bp; 16S rRNA: 359 bp; 18S rRNA: 487 bp; 28S rRNA: 776 bp; histone H3: 339 bp. DNA sequences were deposited in GenBank (NCBI accession numbers MH MH463998- MH464109; Table S1). Our concatenated five-gene dataset had a total aligned length of 2276 bp. The molecular dataset was complete for 54 of the 65 taxa, while the remaining 11 taxa lacked at least one gene. Incomplete gene sets occurred in some species from all four families of Pectinoidea, but there was no pattern based on taxonomic membership (supplementary Table 1). PartitionFinder 2 suggested a four partition scheme. A GTR + G evolution model was suggested for 12S and 16S partitions and a GTR + I + G evolution model for 28S and 18S + H3 partitions. However, after 200 million generations, the MrBayes analyses still had not reached convergence suggesting the PartitionFinder scheme too complicated given the dataset, requiring us to use a less complicated substitution model. A general time reversible (GTR) model with gamma-distributed rates across nucleotide sites was applied to ML and both BI analyses using the gene partitions described above.

ML and BI analyses of the concatenated five gene dataset reconstructed the same five lineages of pectinoidean taxa and produced similar topologies (Fig. 2 for ML; Fig S1 for BI phylogram). The only difference between the two topologies was that the Bayesian analysis was unable to resolve the relationships among the five pectinoidean clades. Interestingly, the relationships among these clades in the ML topology did not match any of the proposed phylogenetic hypotheses for Pectinoidea (Fig. 1). The single representative of Entoliidae (*Pectinella aequoris*) was recovered as sister to the remaining pectinoideans in the ML tree with high support (100% BS). The Propeamussiidae is not monophyletic, with the majority of the species (n = 13) forming a clade with low support (64% BS, 78 PP). The type species, *Propeamussium dalli* was not a member of this clade, but rather the sister group (55% BS, 72 PP) to a well-supported monophyletic Spondylidae (100% BS; 100 PP). A third propeamussiid lineage of three species was a moderately supported clade that was the sister group to the Pectinidae (64% BS, 86 PP), and a fourth was represented by *Parvamussium ina* nested within the Pectinidae (66% BS, 89 PP). Thus, the Pectinidae as currently conceived is paraphyletic in our analyses, and the Propeamussiidae polyphyletic. Non-monophyly of the Propeamussiidae was also supported in ML and BI analyses of the mitochondrial-only and nuclear-only datasets (Figs. S2–S5).

Using the best tree from each ML analysis, AU tests were performed to statistically compare our results against competing hypotheses that constrain the Propeamussiidae as monophyletic and that constrain the Propeamussiidae as monophyletic to the exclusion of *Parvamussium ina*. Additionally, we compared our results with four alternative sister groups for the Pectinidae described in previous studies (Fig. 1). The AU test significantly rejected (*p*-values < 0.01) the hypotheses with a monophyletic Propeamussiidae + Pectinidae (Fig. 1A), Spondylidae + Pectinidae (Fig. 1B), and Entoliidae + Pectinidae (Fig. 1C) (Table 1).

We estimated divergence dates among extant taxa using five fossil

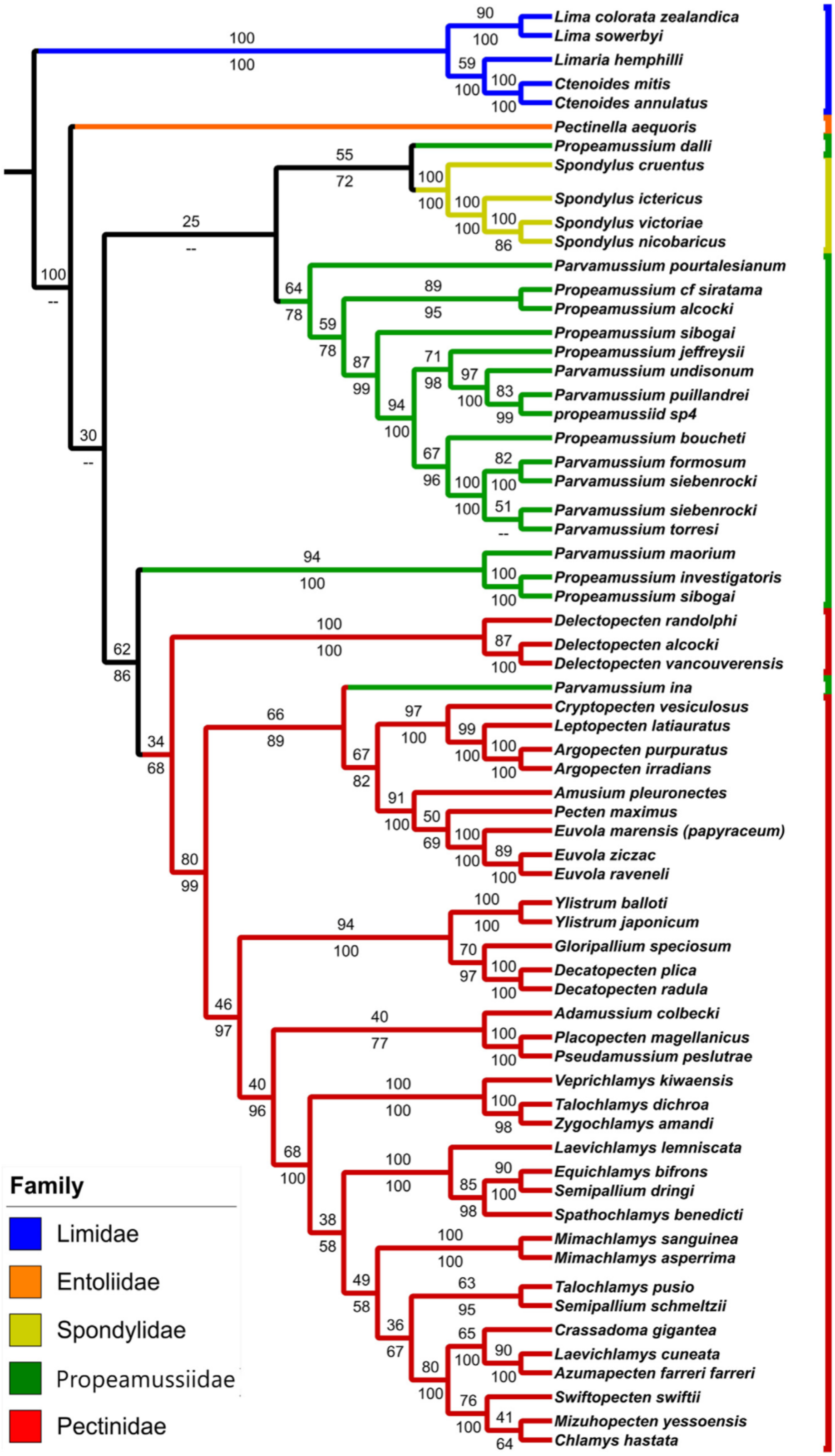

Fig. 2. Maximum likelihood phylogeny of pectinoidean families (lnL = −25647.23) based on combined 12S, 16S, 18S, 28S and histone H3 sequences. Taxa are color coded by family. Numbers above the branches indicate bootstrap support; numbers below branches are Bayesian posterior probabilities. A dash (–) indicates no support for that node.

Table 1
Summary of AU tests of alternative pectinoidean topologies.

Topology	AU test *p*-value*
Unconstrained ML	0.599
Monophyletic Propeamussiidae	0.323
Monophyletic Propeamussiidae, excluding *Pa. ina*	0.574
Fig. 1**A Hypothesis**	**0.011**
Fig. 1**B Hypothesis**	**0.014**
Fig. 1**C Hypothesis**	**0.005**
Fig. 1D Hypothesis	0.069

* RAxML constraint analyses and corresponding *p*-values of AU tests implemented in CONSEL. Siginficantly different topologies are in bold.

First, the time-calibrated phylogeny recovered the Entoliidae taxon as sister to largest Propeamussiidae clade with an inferred divergence time of approximately 300.3 MYA (Late Carboniferous). Second, the Pectinidae is monophyletic in the time-calibrated phylogeny as *Parvamussium ina* was the sister lineage to the family. Divergence times place the origin of the Pectinidae in the Permian (284.25 MYA) and the Spondylidae in the Late Jurassic (154.33 MYA). The divergence time of the superfamily Pectinoidea was estimated to be approximately 395 MYA (Devonian).

4. Discussion

Four different sister group relationships to the scallops have been hypothesized based on morphological evidence spanning the paleo- and neontological record or from molecular data. A traditional interpretation of shell similarity between the Propeamussiidae and some scallop

Fig. 3. Divergence time estimation analysis of Pectinoidea inferred via Bayesian Inference under the Fossilized Birth-Death model. Bottom axis represents millions of

taxa led some to conclude a sister group relationship between the two families (Fig. 1A). However, morphological comparison of fossil and Recent taxa and re-interpretation of first occurances in the fossil record have been the basis of three other possible topologies. Waller (1978) proposed Spondylidae + Entoliidae (= Syncyclonemidae) to be the sister taxon of the Pectinidae based on a single synapomorphy of lip morphology, but noted that these taxa have many primitive features and resemble the fossil precursors to the Pectinidae more than the extant members (Fig. 1D). Subsequently, Waller (1991) presented a revised hypothesis with the Entoliidae alone as the sister to the Pectinidae (Fig. 1C). Most recently, fossil evidence from the Mesozoic appears to bridge morphological gaps among pectinoidean lineages (Waller, 2006). This and recognition of a "pectiniform" in an early stage of spondyliid growth led Waller (2006) to propose the Spondylidae as the sister lineage to the Pectinidae (Fig. 1B). Two of these hypotheses (Fig. 1C, D) place the Propeamussiidae as sister to all other Pectinoidea. Interestingly, molecular phylogenetics has largely supported a fifth relationship, with the Propeamussiidae + Spondylidae as the sister group to the Pectinidae. Our estimated phylogenies show both a propeamussiid clade sister to the Pectinidae as well as a second propeamussiid lineage that shares a common ancestor with a monophyletic Spondylidae (Figs. 2 and 3). Thus, our data support the traditional hypothesis, in part, but highlights two important future directions. First, the non-monophyly of the Propeamussiidae suggests that the characteristics that have been used as synapomorphies for the family should be re-examined. Second, if the relationship between Spondylidae and *Propeamussium dalli* (the type species) holds, a taxonomic revision of the Propeamussiidae will be necessary.

Few published time-calibrated phylogenies have included the Pectinoidea, and those that do have been inferred from a small subset of pectinoidean taxa (e.g., Bieler et al. 2014). In constrast, our estimation of divergence times for the Pectinoidea is based on a larger taxonomic sampling that includes four of the five families and fossil taxa from three of these families (Entoliidae, Pectinidae, and Spondylidae). Through this sampling strategy, we were able to independently estimate age of the superfamily. Interestingly, our time-calibrated phylogeny supports a somewhat earlier origin of the Pectinoidea (Late Devonian, 395 MYA) than currently accepted date of the Early Carboniferous period (358.9 MYA) when †Pernopectinidae is regarded as the stem group of the superfamily (see Waller 2006). Future inclusion of fossil taxa in phylogenetically informed macroevoutionary analyses will be critical for interpreting patterns of diversification and extinction for the group.

Understanding relationships among the families of Pectinoidea could give an interesting context to the evolution of eyes within the superfamily. Eyes occur ventrally and often serially repeated on both left and right mantle lobes, located at the end of short stalks on the middle fold (Dakin, 1910). Scallops possess many single chambered eyes with a mirror-like reflector lining the back of the eye which focuses light back onto a double-retina system in the middle of the eye (Land, 1965; Palmer et al., 2017). Pectinidae and Spondylidae are known to have this unique eye structure, while Propeamussiidae were thought to lack eyes (Waller, 1972); however, the absence of eyes in propeamussiids may reflect their distribution in dysphotic (200–1000 m) or aphotic (> 1000 m) depths (Waller, 2006, but see Morton and Thurston, 1989). There has been some debate regarding the presence or absence of eyes in extinct entoliids. Eyes may be present in the extant genus *Pectinella* [(Waller, 2006) images of the eyes were not illustrated], but with only two extant species, fluid-preserved specimens are rare (e.g., no specimens in the largest US collection USNM, co-author EE Strong) and we have been unable to secure a specimen for examination. If eyes are present in the Entoliidae (Waller, 2006) and be examined from both historical and habitat perspectives.

5. Conclusion

The results of these current analyses suggest a novel topology for relationships within the superfamily Pectinoidea. Our results tentatively indicate the Propeamussiidae may be polyphyletic, but the AU test results do not reject all alternative hypotheses in which the family is constrained to be monophyletic. The inclusion of molecular data for a species of Entoliidae for the first time provides the first test of its phylogenetic placement as the sister to all other Pectinoidea. Our phylogenetic hypothesis also impacts the interpretation of trait histories in the superfamily with implications to phenotypic evolution. For instance, our data tentatively supports the hypothesis for a single origin of eyes in the superfamily. Future work should focus on bolstering support for this scenario through the examination of a more comprehensive molecular dataset. However, if the relationships recovered here hold, a taxonomic revision of the Propeamussiidae is warranted.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2019.05.006.

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