



Short Communication

Molecular phylogeny and character evolution of the chthamaloid barnacles (Cirripedia: Thoracica)

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ABSTRACT

The Chthamaloidea (Balanomorpha) present the most plesiomorphic characters in shell plates and cirri, mouthparts, and oral cone within the acorn barnacles (Thoracica: Sessilia). Due to their importance in understanding both the origin and diversification of the Balanomorpha, the evolution of the Chthamaloidea has been debated since Darwin's seminal monographs. Theories of morphological and ontogenetic evolution suggest that the group could have evolved multiple times from pedunculated relatives and that shell plate number diminished gradually (8 → 6 → 4) from an ancestral state with eight wall plates surrounded by whorls of small imbricating plates; but this hypothesis has never been subjected to a rigorous phylogenetic test. Here we used multilocus sequence data and extensive taxon sampling to build a comprehensive phylogeny of the Chthamaloidea as a basis for understanding their morphological evolution. Our maximum likelihood and Bayesian analyses separate the Catophragmidae (eight shell plates and imbricating plates) from the Chthamalidae (8–4 shell plates and no imbricating plates), but do not support a gradual reduction in shell plates (8 → 6 → 4). This suggests that evolution at the base of the Balanomorpha involved a considerable amount of homoplasy.

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1. Introduction

Barnacles of the superfamily Chthamaloidea (Cirripedia: Thoracica: Sessilia: Balanomorpha) are an important component of most rocky intertidal systems with fewer species occurring in the shallow subtidal zone. They are widely distributed, occurring both in tropical and temperate seas and have been present in the fossil record since the upper Cretaceous (Newman et al., 1969). Chthamaloids are central to understanding the evolution of the Balanomorpha and model organisms in intertidal ecology, larval settlement, and antifouling technology.

The Chthamaloidea are currently subdivided into two families: (1) the Catophragmidae, with the subfamilies Catophragminae (*Catophragmus* and *Catolasmus*) and Catomerinae (*Catomerus*); and (2) the Chthamalidae with the subfamilies: (i) Euraphiinae (*Caudoeuraphia*, *Pseudoeuraphia*, *Microeuraphia* and *Euraphia*), (ii) Notochthamalinae (*Octomeris*, *Pseudoctomeris*, *Hexochamaesipho*, *Chamaesipho*, *Rehderella*, *Nesochthamalus* and *Notochthamalus*) and (iii) Chthamalinae (*Chthamalus*, *Jehlius*, *Chinochthamalus* and *Tetrachthamalus*) (Martin and Davis, 2001; Newman, 1996; Pitombo and Burton, 2007; Southward and Newman, 2003).

Within the suborder Balanomorpha (acorn barnacles), the Chthamaloidea are argued to exhibit the most plesiomorphic morphology (Anderson, 1983; Newman and Ross, 1976; Newman et al., 1969), because they show character states intermediate between the Balanoidea, the asymmetric Verrucomorpha and pedunculated scalpellid barnacles. These states include the presence of up to eight wall plates surrounded by whorls of small imbricating plates (see below), a membranous basis and a scalpellid-like oral cone and mouthparts with a bullate labrum, simple mandibular palps, tri or quadridentoid mandibles with well developed incisor teeth and strong setose or pectinated first and second maxillae, and with only first and second cirri modified to serve as mouth cirri (maxillipeds).

Despite their importance for understanding the diversification of the Balanomorpha, the phylogeny of the Chthamaloidea is poorly understood and character evolution has never been studied using a robust phylogenetic tree with a good representation of chthamaloid species. Molecular investigations of the chthamaloid relationships are limited to a single study by Fisher et al. (2004), which included only nine species sequenced for the 16S rRNA gene, and to phylogenetic analyses of the genus *Chthamalus* (e.g., Wares et al., 2009). At the morphological level, ontogenetic and comparative studies suggest that a condition with eight wall plates encircled by rows of imbricating plates (as in the Catophragmidae)

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represent the most plesiomorphic state in the Balanomorpha (Darwin, 1854). This condition approaches the morphology seen in both the Brachylepadomorpha (fossil taxon with one extant survivor) and in pedunculated species such as *Pollicipes* and *Capitulum*, which are arguably close extant relatives to the sessilian barnacles. The morphology found in *Chthamalus*, *Notochthamalus*, *Nesochthamalus*, *Hexochamaesipho* and the Euraphiinae is argued to have evolved by loss of the imbricating plates and reduction of wall plate number from 8 to 6. Further reduction by plate fusion is argued to have led to the four wall plates found in *Tetrachthamalus*, *Chamaesipho* and *Jehlius* (Buckeridge, 1995; Newman, 1987; Zullo, 1963). Morphological characters, if developed to their full potential, may well offer important insights into the evolution of the Chthamaloidea, but the use of many plesiomorphic states in the current classification is questionable and opens the possibility that the constituent taxa represent para- or polyphyletic assemblages.

In this study, we used multilocus sequence data to build a phylogeny of the superfamily Chthamaloidea using, for the first time, representatives from all of the five subfamilies and a total of 14 of the 18 genera. We then used this phylogeny to test systematic hypotheses of the main taxonomic subdivisions in the Chthamaloidea and to test theories concerning the evolution of plate structure.

2. Methods

2.1. Molecular analysis

We collected 32 chthamaloids (ingroup) representing all the subfamilies in the group and six verrucomorphs (outgroup) (Table 1 and Fig. 1). Molecular and morphological evidence support our outgroup choice (Pérez-Losada et al., 2008; Pérez-Losada et al., 2004). Specimens were preserved in 70% EtOH and are housed in the crustacean collections at the Monte L. Bean Life Science Museum (Brigham Young University), the Zoological Museum of the Hebrew University of Jerusalem, and the Mina and Everard Goodman Faculty of Life Sciences (Bar Ilan University). Barnacle DNA extraction, amplification, and sequencing were performed as described in Pérez-Losada et al. (2004). The 18S rRNA (1,822 bp), 28S rRNA (1,742 bp), 12S (345 bp) and 16S (527 bp) genes and the COI (670 bp) gene were sequenced using primers in Pérez-Losada et al. (2004) and Folmer et al. (1994), respectively. We generated 91 new sequences (JX083861–JX083951).

2.2. Phylogenetic analyses

Nucleotide sequences from each gene region were aligned using MAFFT v6 (Katoh, 2008) under the global (G-INS-i) algorithm and default settings. Phylogenetic congruence among gene regions was assessed using the Wiens' (1998) protocol. No areas of strongly supported incongruence were observed among gene trees. All gene regions were analyzed as separate partitions (COI was subdivided into 1st+2nd and 3rd codon positions) under the best-fit model of evolution selected by JModelTest v1.0.1 (Posada, 2009). The general time reversible model of evolution with proportion of invariable sites and gamma distribution was selected for each data partition (GTR + Γ + I). Maximum likelihood analysis of the concatenated partitions was performed in RAXML v7.2.0 (Stamatakis et al., 2008) using 1,000 searches and 100 runs. Clade support was assessed using the non-parametric bootstrap procedure with 5,000 bootstrap replicates run in the portal CIPRES Science Gateway portal (Miller et al., 2010).

We also performed a Bayesian–Markov chain Monte Carlo (BMC) analysis of the concatenated partitions in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). Three independent

Table 1

List of Chthamaloidea (ingroup) and Verrucidae (outgroup) included in this study and location of collection. GB = GenBank.

Species	Location
Chthamaloidea	
Catophragmidae	
Catomerinae	
<i>Catomerus polymerus</i>	GB
Catophragminae	
<i>Catopragmus imbricatus</i>	Bermuda
Chthamalidae	
Chthamalinae	
<i>Chthamalus anisopoma</i>	Puerto Peñasco, Gulf of California, Mexico
<i>Chthamalus antennatus</i>	Sydney, Australia
<i>Chthamalus bisinuatus</i>	GB
<i>Chthamalus challengerii</i>	GB
<i>Chthamalus dentatus</i>	South Africa
<i>Chthamalus fragilis</i>	New England, USA
<i>Chthamalus malayensis</i>	Hong Kong, Japan
<i>Chthamalus montagui</i>	GB
<i>Chthamalus proteus</i>	Hawaii, USA
<i>Chthamalus stellatus</i>	GB
<i>Jehlius cirratus</i>	GB
<i>Tetrachthamalus obliteratus</i>	Eilat, Israel
Euraphiinae	
<i>Caudoeuraphia caudata</i>	Northwestern Australia
<i>Euraphia</i> sp1	Northwestern Australia
<i>Euraphia</i> sp2	Northwestern Australia
<i>Microeuraphia</i> sp1	Northwestern Australia
<i>Microeuraphia</i> sp2	Northwestern Australia
<i>Microeuraphia depressa</i>	Michmoret, Israel
<i>Microeuraphia rizhophorae</i>	Brazil
<i>Microeuraphia withersi</i>	Townsville, Australia
Notochthamalinae	
<i>Chamaesipho brunnea</i>	Wellington, New Zealand
<i>Chamaesipho columna</i>	Devenport, New Zealand
<i>Chamaesipho</i> sp.	Tasmania, Australia
<i>Chamaesipho tasmanica</i>	Tasmania, Australia
<i>Hexochamaesipho pilsbryi</i>	Japan
<i>Nesochthamalus intertextus</i>	Japan
<i>Notochthamalus scabrosus</i>	GB
<i>Octomeris angulosa</i>	Sydney, Australia
<i>Octomeris brunnea</i>	Phuket, Thailand
<i>Pseudoctomeris sulcata</i>	Japan
Verrucidae	
<i>Altiverruca</i> sp.	GB
<i>Metaverruca recta</i>	Ogasawara Islands, Japan
<i>Rostratoverruca krugeri</i>	Nansei Islands, Japan
<i>Rostratoverruca</i> sp.	GB
<i>Verruca laevigata</i>	Chile
<i>Verruca stroemia</i>	Vigo, Spain

BMCMC analyses were run in CIPRES with each consisting of four chains. Each Markov chain was started from a random tree and run for 10^7 cycles, sampling every 1,000th generation. Model parameters were unlinked and treated as unknown variables with uniform default priors and they were estimated as part of the analysis. Convergence and mixing were monitored using Tracer v1.5 (<http://tree.bio.ed.ac.uk/software/>). All sample points prior to reaching stationarity were discarded as burn-in. The posterior probabilities for individual clades obtained from separate analyses were compared for congruence and then combined and summarized on a 50% majority-rule consensus tree. Likelihood topological tests were conducted using the Shimodaira and Hasegawa (S–H) (1999) test as implemented in RAXML.

2.3. Plate evolution

The evolutionary history of shell plate variation was assessed using the Bayesian approach implemented in BEAST v1.7 (Drummond and Rambaut, 2007). This method takes into account error associated with both the characters under study (mapping

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