

Evolutionary relationships among squids of the family Gonatidae (Mollusca: Cephalopoda) inferred from three mitochondrial loci

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Abstract

The oceanic squid family Gonatidae (Mollusca: Cephalopoda) is widely distributed in subpolar and temperate waters, exhibiting behavioral and physiological specializations associated with reproduction. Females of several species undergo muscular degeneration upon maturation; origins of this complex morphogenic change are unknown, hindering our understanding of ecological and morpho-physiological adaptations within the family. To provide further information regarding the evolutionary relationships within Gonatidae, three mitochondrial loci (12S rRNA, 16S rRNA, and cytochrome *c* oxidase subunit I) were analyzed for 39 individuals representing fourteen gonatid and six outgroup cephalopod species. In addition to elucidating relationships among gonatids, molecular data provided more information than morphological data for problematic specimens. Although some data sets are incongruent or have low nodal support values, combined molecular analysis confirms the presence of gonatid groups previously established by morphological characteristics (i.e., possessing radular teeth in seven longitudinal rows and muscular mantle tissue). These characteristics are basal to taxa possessing radular teeth in five longitudinal rows and less muscular mantle tissue, indicating that the derived forms are those species exhibiting physiological adaptation such as tissue degeneration upon maturation and egg brooding.

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1. Introduction

Gonatidae (Mollusca: Cephalopoda) is a family of oegopsid oceanic squid characterized by quadriserial armature on the arms, with most species possessing hooks on arms I–III (in two central rows) and a rhomboidal or heart-shaped fin (Nesis, 1973, 1987). The family is composed of 17–19 species (Nesis, 1982, 1985; Sweeney and Roper, 1998) with three recognized genera: *Gonatus*, *Gonatopsis*, and *Berryteuthis*, which are distinguished

from each other by tentacle and radular morphology (Nesis, 1973). *Gonatus* possesses complex tentacle fixing apparatus, and a radula consisting of five longitudinal rows of teeth. *Gonatopsis* is distinguished by the absence of tentacles in adults, and presence of either seven or five longitudinal rows of teeth in the radula. Members of *Berryteuthis* have no hooks on the tentacle club, weakly differentiated fixing apparatus on tentacles, and a radula with seven longitudinal rows of teeth. Nesis (1971, 1973) suggested that the ancestral gonatid was an oceanic shallow water squid, with a powerful and muscular mantle, rhomboid or oval fin, radula with seven rows of longitudinal teeth, arms and tentacles equipped with only suckers, and a poorly developed tentacular fixing apparatus. Thus, more derived forms were species that migrated to deeper waters, exhibiting less muscular mantle and arm

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crown tissues, and possessing five longitudinal rows of radular teeth.

Several species of gonatid exhibit a characteristic previously identified only with octopods: post-spawning egg care or brooding, where the female cares for the eggs until hatching (Hunt and Seibel, 2000; Katugin, 2003; Okutani et al., 1995; Seibel et al., 2000). All other extant decabrachian cephalopods freely spawn with or without egg-masses, or lay their eggs on substratum, but none are known to exhibit parental care. During brooding, gonatid females do not feed; instead, they utilize the digestive gland weight and lipid energy conserved during maturation. Gonatid females known to brood also exhibit morphological change upon maturation, which is believed to be related to post-spawning egg-care (e.g., Hunt and Seibel, 2000; Katugin, 2003; Katugin and Merzlyakov, 2002; Seibel et al., 2000). During brooding, muscle tissue degrades, tentacles are autotomized, and mantle and arms become water logged (Katugin, 2003; Katugin and Merzlyakov, 2002). To date, seven gonatid species have been recorded to exhibit this change upon maturation, which include *Gonatus berryi*, *Gonatus madokai*, *Gonatus onyx*, *Gonatus pyros*, *Gonatus tinro*, *Gonatus fabricii*, and *Gonatopsis octopedatus* (Arkhipkin and Bjorke, 1999; Katugin, 2003; Katugin and Merzlyakov, 2002; Nesis, 1993; Seibel et al., 2000; Young, 1973).

Although the reproductive strategies of all gonatid species have yet to be determined, brooding appears to occur in more derived forms, those that already exhibit fragile arm and mantle tissue and are usually found at greater depths (Nesis, 1973). Although brooding is present in Octopoda, gonatids are distantly related (e.g., Carlini and Graves, 1999; Lindgren et al., 2004) and exhibit different physiology and behavior during brooding (Boletzky, 1992), indicating that brooding has evolved independently in Gonatidae. Brooding octopods glue their eggs together into “long straight or branched strings” (Norman, 2000), which are either attached to substrate or carried within their arm webs, keeping them oxygenated and free of debris (Boletzky, 1992; Cosgrove, 1993; Norman, 2000). In gonatids, females that brood their eggs hold them between their arms, floating midwater until hatching (Katugin and Merzlyakov, 2002; Okutani et al., 1995; Seibel et al., 2000), and evidently do not exhibit such invested care as octopuses. Male and immature female members of brooding species have been recorded as having delicate arm and mantle tissue, implying that at least in some species, such as in *Gonatus madokai* and *Gonatus tinro* (Katugin, 2003), morphogenic change in tissue precedes or coincides with maturation. Therefore, it is possible that muscular degeneration may be a species character influenced by physiology and environment. Whether or not tissue degeneration and associated egg brooding is a synapomorphy of Gonatidae can be tested using an independent non-morphological approach, such as a molecular phylogenetic analysis.

No combined sequence-based phylogenetic hypothesis exists for Gonatidae, although an allozyme-based phylogeny has been recently generated (Katugin, 2004). Previous molecular work has been completed using the cytochrome *c* oxidase subunit I locus (COI; Seibel et al., 2000) to identify juvenile gonatids from southern California waters as well as incorporating two species of *Gonatus* in a COI based, higher-level phylogeny to investigate relationships between coleoid cephalopods (Carlini and Graves, 1999). In the present study comparisons between brooding strategies, morphology, and physiology were made to the molecular phylogeny of three mitochondrial loci for 14 gonatid species and analyzed to determine whether these life history characteristics were important in the radiation of this family of squids.

2. Methods

2.1. PCR amplification and sequencing analysis

DNA was extracted from gill or mantle tissues of 39 individuals representing 14 gonatid species (13 nominal species and one undescribed species) as well as six out-group species (Table 1) using Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA). PCR amplification was carried out in 50 μ L reactions using Promega *Taq* Polymerase (see Nishiguchi et al., 2004 for further descriptions of PCR methods) for fragments of three mitochondrial loci: 12S rRNA (404 bp), 16S rRNA (528 bp), and cytochrome *c* oxidase subunit I, COI (658 bp) (see Nishiguchi et al., 2004 for primer information and annealing temperatures). Although nuclear data has proven useful in higher-level analyses (e.g., Lindgren et al., 2004), nuclear loci have been determined to be too conserved for discerning species-level relationships among cephalopods (e.g., Nishiguchi et al., 2004). Sequences were obtained using an ABI PRISM 3100 Genetic Analyzer (Foster City, CA). External primers were excluded from resulting forward and reverse chromatograms which were assembled and edited using either Sequencher v. 4.1 or v. 4.2 (Gene Codes, Ann Arbor, MI). Resulting sequences were compiled and partitioned in Genetic Data Environment (GDE, Smith et al., 1994). For non-coding genes (12S and 16S), sequences were partitioned in GDE using secondary structure models and unambiguous regions; 12S was partitioned into five fragments and 16S was partitioned into eight. The protein-coding gene COI was tested as one entire fragment for the analysis.

2.2. Phylogenetic analysis

Individual and combined sets of molecular data were analyzed using the direct optimization program POY (Wheeler et al., 2002), with parsimony as the optimality

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