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MOLECULAR SYSTEMATICS OF THE COLEOIDEA

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ADVANTAGES AND DISADVANTAGES OF A MOLECULAR APPROACH TO COLEOID PHYLOGENY

Recent higher-level classifications of extant coleoids were derived from subjective interpretation of similarities among taxa in morphological and anatomical characters (VOSS, 1977; CLARKE, 1988; SWEENEY & ROPER, 1998). While these classifications have been useful to cephalopod biologists, they were constructed under the implicit assumption that overall similarity is the criterion for grouping taxa. This is an invalid assumption, if the aim of a scheme of classification is to reflect the evolutionary history of the group. Furthermore, the measure of similarity used in these classifications was subjective, not algorithmic, so that they cannot be validated or falsified, or compared with results obtained through phylogenetic studies. VOSS (1977, p. 575) wrote that "the systematics of the class is still far from the stage when the broad evolutionary picture can be seen." Morphological phylogenetic studies that used an explicit method of constructing relationships (e.g., parsimony) have largely focused on lower-level relationships, such as those among genera within a family (VOSS & VOSS, 1983; ROELEVELD, 1988; VOIGHT, 1993; ANDERSON, 1996). Only recently have such studies attempted to determine relationships above the family level using rigorous and repeatable cladistic methodologies (YOUNG & VECCHIONE, 1996; VOIGHT, 1997; YOUNG & HARMAN, 1998). Recent paleontological studies have also invoked parsimony (BERTHOLD & ENGESER, 1987; DOYLE, DONOVAN, & NIXON, 1994), but they only included the apomorphic characters that support the phylogeny without reference to apomorphic characters that could potentially support an alternative hypothesis.

The few phylogenetic studies published to date using molecular sequence data have employed explicitly defined methods of phylogenetic reconstruction and have focused on higher-level relationships within the group (BONNAUD, BOUCHER-RODONI, & MONNEROT, 1994, 1997; CARLINI & GRAVES, 1999; CARLINI, REECE, & GRAVES, 2000; CARLINI, YOUNG, & VECCHIONE, 2001), with the notable exception of ANDERSON (2000), who examined loliginid relationships using molecular sequence data. The definition of an objective method to estimate phylogenetic relationships using molecular characters is, of course, a necessary consequence of factors particular to molecular data. These include the greater number of characters used in molecular analyses, the unclear relationships among the four possible character states (nucleotides), and the greater potential for homoplasy in unordered multistate characters.

The change in systematic focus from descriptive accounts of species, genera, or families toward an increased interest in understanding relationships among coleoid families, suborders, and orders may reflect a growing trend in cephalopod systematics. Undoubtedly, this change in phylogenetic focus is also related to the nature of the molecular data, where an understanding of the relationships between alternate character states is perceived to be unnecessary. The only assumption about character evolution required for molecular studies is that all the terminal taxa included in the study possess the gene of interest (i.e., that the set of molecular characters used in the analysis are homologous). To the extent that this is the only assumption required to obtain meaningful results from molecular studies, it is

an easy assumption to meet. For a rigorous phylogenetic analysis of morphological characters, however, the requirements are much stiffer: a thorough knowledge of the ancestral states of all characters and an understanding of the relationships between alternate character states are also compulsory. For example, Young and Vecchione (1996) eliminated half of the morphological characters they surveyed, due to lack of sufficient knowledge about character evolution. Therefore, when undertaking an objective phylogenetic study that seeks to determine relationships among many morphologically disparate families, it is far easier to satisfy the perceived requirements of molecular character data.

However, an emerging paradigm in the molecular phylogenetic literature is the increased recognition of the problems associated with analyzing molecular data without regard to the patterns and processes of molecular evolution (Swofford & others, 1996; Yang, 1996; Huelsenbeck & Crandall, 1997). Several attributes of molecular data render questionable the conclusions drawn from molecular studies that do not account for the peculiarities of nucleotide sequence evolution. These include, but are not limited to, superimposed substitutions (i.e., saturation), rate heterogeneity among lineages, rate heterogeneity among characters, bias in base frequencies, bias in codon usage, and non-independence of substitutions across characters. Reconstruction methodologies, such as unweighted parsimony and neighbor-joining on uncorrected distance data, can provide incorrect estimates of phylogeny under such circumstances (Felsenstein, 1978). In these cases, more sophisticated methods of phylogenetic reconstruction, which employ realistic models of molecular evolution more in keeping with the observed patterns, such as weighted parsimony and maximum likelihood, are required to produce reliable estimates of phylogeny (Huelsenbeck, 1995). It is important to bear in mind that these asymmetric patterns of molecular evolution

among characters and among taxa are the norm and not the exception, and that phylogenetic hypotheses derived from analyses that have not considered or corrected for these patterns should be interpreted with caution.
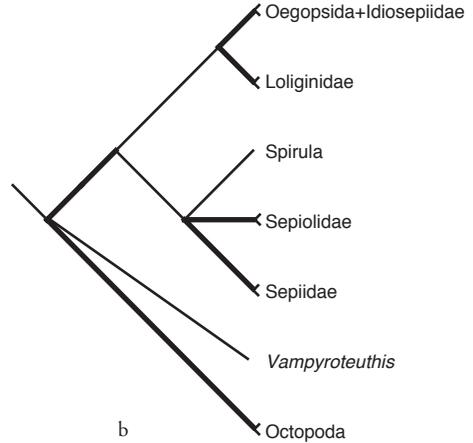
MOLECULAR PHYLOGENETIC STUDIES OF THE COLEOIDEA

Most molecular phylogenetic studies of cephalopods have focused on mitochondrial genes. Bonnaud, Boucher-Rodoni, and Monnerot (1994) examined decapod relationships using unweighted parsimony (Fig. 1*a*) and neighbor-joining analysis of a ~500 bp portion of the 16S rRNA gene. The outgroup taxon in the study was *Octopus*; the ingroup included representatives from 7 oegopsid families (13 taxa), myopsid squids (3 taxa), and 3 sepioid families (11 taxa). The monophyly of the Decapodiformes was supported by the parsimony analysis but was not supported by the results from neighbor-joining analysis. The monophyly of the order Sepioidea *sensu* Voss (1977), as including the 5 families Idiosepiidae, Sepiadariidae, Sepiidae, Sepiolidae, and Spirulidae, was not supported by either analysis. The Sepiolidae grouped outside of the remaining decapods, reinforcing the recommendation that their taxonomic status be raised to ordinal rank (Fioroni, 1981; Clarke, 1988). *Spirula* did not cluster with any of the sepioids included in their study; instead it nested within oegopsid clades. The 5 sepiid taxa represented formed a monophyletic group in the neighbor-joining distance tree but not in the parsimony analysis. To explain the failure of the 16S data to unequivocally support the monophyly of the Sepiidae, a morphologically well-defined family, Bonnaud, Boucher-Rodoni, and Monnerot (1994) proposed two hypotheses: (1) either the evolutionary rate of the 16S rRNA is more rapid in the Sepiidae than in other coleoid groups, or (2) a Mesozoic emergence of
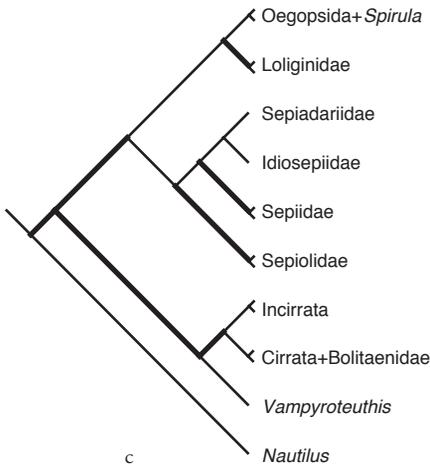
16S: Bonnaud, Boucher-Rodoni, & Monnerot, 1994
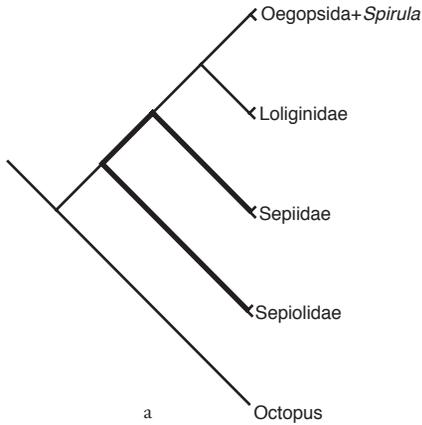
COIII: Bonnaud, Boucher-Rodoni, & Monnerot, 1997

COI: Carlini and Graves, 1999

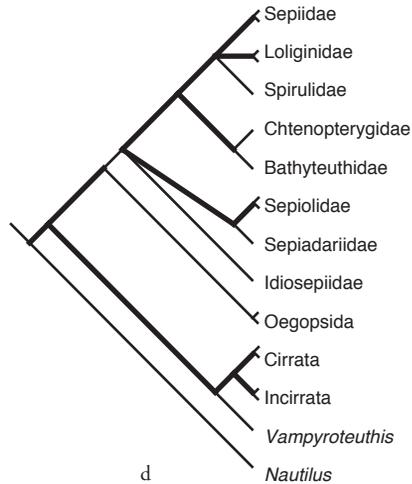Actin Genes: Carlini, Reece, and Graves, 2000

Fɪɢ. 1. Summary of phylogenetic hypotheses from four studies that have examined higher-level relationships within the Coleoidea based on molecular sequence data; *dark lines* designate strongly supported groups, as determined either through bootstrap analysis or through concordance in results from different reconstruction methodologies; *unforked branch tips* represent taxonomic groups represented by only a single specimen; the monophyly of such groups was not tested in the phylogenetic analyses; *a,* results obtained in unweighted parsimony analysis of a ~500 bp portion of mitochondrial 16S rRNA gene (Bonnaud, Boucher-Rodoni, & Monnerot, 1994); *b,* results from neighbor-joining analysis of a 500 bp portion of mitochondrially encoded cytochrome *c* oxidase III gene (Bonnaud, Boucher-Rodoni, & Monnerot, 1997); *c,* results derived from unweighted parsimony, weighted parsimony, and maximum likelihood analyses of a 657 bp portion of mitochondrial cytochrome *c* oxidase I gene (Carlini, 1998; Carlini & Graves, 1999); *d,* summary of results obtained in analysis of a 784 bp fragment of two unlinked nuclear genes, Actin I and Actin II, using unweighted parsimony, weighted parsimony, and maximum likelihood methodologies (Carlini, Reece, & Graves, 2000).

the sepiids, rather than a Cenozoic emergence, as was suggested previously by paleontological evidence (TEICHERT, 1988). They considered the second hypothesis more likely. The 16S study also did not support the monophyly of the Teuthoidea, Myopsida, nor Oegopsida. The conclusions of BONNAUD, BOUCHER-RODONI, and MONNEROT (1994) must be tempered with a consideration of the taxonomic sampling. Pertinent to the conclusions about sepioid relationships, representatives of 2 of the 5 families of the sepioids (Idiosepiidae, Sepiadariidae) were not included. This is important because KHROMOV (1990) has suggested a close relationship between the sepiadariids and sepiolids. He considered the Sepiolidae, Sepiadariidae, and Idiosepiidae to be more closely related to each other than to the Sepiidae and Spirulidae. NAEF (1923) also proposed a close relationship between the sepiadariids and the sepiolids. Relationships among the few oegopsid families included in the study were highly unstable across the two methods of analysis employed. Bootstrap analysis of the neighbor-joining distance tree did not support any of the oegopsid interfamily relationships. One of the main conclusions BONNAUD, BOUCHER-RODONI, and MONNEROT (1994) drew from the 16S study was that a gene with a slower evolutionary rate was necessary to investigate the higher-level phylogeny of the decapods.

The second molecular study conducted by BONNAUD, BOUCHER-RODONI, and MONNEROT (1997) used neighbor-joining analysis of a 500 bp fragment of the cytochrome *c* oxidase III (COIII) gene to examine coleoid relationships (Fig. 1*b*). Similar to the 16S study, taxonomic sampling was proportionately greater for the loliginidae, sepiidae, and sepiolidae than for other decapod groups. The taxa represented in the COIII study included two octopods, *Vampyroteuthis*, two oegopsid families (three taxa), myopsid squids (three taxa), and four sepioid families (seven taxa). The monophyly of the Decapodiformes was well supported in all analyses. The position

of *Vampyroteuthis* was equivocal. Only one of the neighbor-joining distance trees presented supported placement of *Vampyroteuthis* with the Octopoda, although this particular analysis did not include the Sepiolidae (see fig. 6 in BONNAUD, BOUCHER-RODONI, & MONNEROT, 1997). The additional sepioid family included in the COIII study was the Idiosepiidae, which consistently placed with one of the two oegopsid families. However, the sepiadariids were not included in the COIII study, so the placement of *Idiosepius* within the Oegopsida rather than with other sepioids could be due to the omission of the Sepiadariidae. Quite different from the results from the 16S study, the Sepiolidae did not emerge basal to the remaining decapods. The difference in the placement of the sepiolids between the two studies may be due to the differences in the substitution patterns of the two genes, although an alternative explanation for this difference was the inclusion of an additional octopod and of *Vampyroteuthis* in the COIII study. The position of *Spirula* was highly unstable across the four trees presented. The monophyly of the myopsid squids was strongly supported, although their position within the decapods was also unstable. The COIII study also concluded that a more conserved gene was necessary to allow a more accurate assessment of deeper-level decapod relationships.

The results of BONNAUD, BOUCHER-RODONI, and MONNEROT (1994, 1997), although enlightening, indicated a need for additional molecular studies of the Coleoidea. Taxonomic sampling of the Oegopsida and Octopoda was limited, so relationships within these groups were not examined. Neither study conducted a rigorous test of the monophyly of the Sepioidea; such a test would require representatives from all five of the constituent families. The authors concluded that 16S and COIII data were saturated, due to some anomalous relationships obtained from the analyses of the two genes, although evidence for saturation (i.e., plots of pairwise sequence divergences versus total sequence divergence) was not presented

in either study. If the 16S and COIII data were saturated, a gene with a slower evolutionary rate might provide more insight into the evolutionary relationships of decapods.

A third molecular study (CARLINI & GRAVES, 1999) examined relationships of coleoid cephalopods using unweighted and weighted parsimony analysis of a 657 bp fragment of the cytochrome *c* oxidase I (COI) gene (Fig. 1*c*). The COI gene is the most conserved protein-coding gene in the mitochondrial genome, and it exhibits a slower evolutionary rate than the 16S gene in vertebrates (BROWN, 1985; CUMMINGS, OTTO, & WAKELEY, 1995; ZARDOYA & MEYER, 1996). The taxonomic sampling of the COI study included representatives from the following taxa: *Vampyroteuthis*, 4 families of incirrate octopods (8 taxa), 2 families of cirrate octopods (2 taxa), 20 families of oegopsid squids (25 taxa), 2 genera of myopsid squids (3 taxa), 5 families of the Sepioidea (8 taxa), and a nautiloid as an outgroup. Phylogenetic relationships were constructed using the parsimony criterion, either unweighted or weighted, and clade stability was assessed by parsimony bootstrap analysis. The monophyly of the Decapodiformes was well supported in all of the analyses. The Octopodiformes were split into two adjacent clades in the unweighted parsimony analysis but were found to be monophyletic in the weighted parsimony analysis. The monophyly of the Sepioidea was not supported by the COI results, as *Spirula* consistently placed within an oegopsid clade. In the unweighted parsimony analysis, the sepiolids emerged basal to the remaining decapods, followed by the remaining sepioids, and then the teuthoids+*Spirula*. Weighted parsimony analysis supported the monophyly of the sepioids, exclusive of *Spirula*. Within the Teuthoidea, phylogenetic relationships were unstable, exhibiting low levels of bootstrap support and inconsistencies between the unweighted and weighted analyses. The monophyly of each of the families containing more than a single representative

(Cranchiidae, Cycloteuthidae, Enoploteuthidae, Gonatidae, Loliginidae, Ommastrephidae) was well supported, although relationships between most oegopsid families were inconsistent.

Subsequent to the publication of the COI study, representatives from 3 previously unrepresented oegopsid families (4 taxa), and an additional cirrate family (2 taxa) were obtained (CARLINI, 1998). In the analysis of the more comprehensive COI data set, maximum likelihood methodologies, as well as unweighted and weighted parsimony techniques, were used to construct phylogenetic relationships. With respect to the conclusions drawn for higher-level relationships, the results obtained from analyses of the comprehensive data set were in agreement with CARLINI and GRAVES (1999). The monophyly of the Octopodiformes was supported by the parsimony and maximum likelihood analyses. Sepioid monophyly was not supported, as *Spirula* placed with the oegopsids and the sepiolids and remaining sepioids were split, although the sepiolids no longer emerged basal to the remaining decapods. Interestingly, in the weighted parsimony and maximum likelihood analyses, the Sepiidae and Loliginidae were found to be sister taxa. As with the unweighted and weighted parsimony analyses of the smaller data set, analyses of the larger data set (including maximum likelihood) yielded unstable relationships among most oeogopsid families. Finally, neither study used a nuclear gene to examine phylogenetic relationships among coleoid cephalopods. As nuclear and mitochondrial genes possess unique evolutionary histories, the results obtained from phylogenetic analysis of nuclear genes frequently differ from the results obtained through the analysis of mitochondrial genes (AVISE, 1994). In addition, nuclear genes often prove informative at different levels of phylogeny than mitochondrial genes.

Molecular sequence data was obtained for two related nuclear genes, Actin I and Actin II. These sequences, 784 bp in length, were

analyzed using unweighted and weighted parsimony and maximum likelihood methodologies to examine coleoid phylogenetic relationships (CARLINI, REECE, & GRAVES, 2000). The two genes produce different gene products: Actin I codes for a muscular type of actin, and Actin II codes for a cytoplasmic type of actin. These two unlinked genes exhibited differing evolutionary rates and were therefore informative at different levels of phylogeny. As in the COI study, a nautiloid was used as an outgroup, and the ingroup taxa included *Vampyroteuthis*, 3 incirrate families (6 taxa), 1 cirrate family (2 taxa), 5 sepioid families (8 taxa), the Loliginidae (2 taxa), and 19 oegopsid families. Relative to the COI gene, the Actin I gene was highly conserved, while the Actin II gene was informative at a broader range of divergences than the Actin I gene; the Actin II gene was also less variable than the COI gene. Therefore, both actin genes were more informative at deeper levels of divergence than were any of the mitochondrial genes. Perhaps as a result, the actin genes both revealed a different pattern of basal divergence than did the mitochondrial genes. The 16S, COIII, and COI genes supported an early divergence of the sepioid (*Spirula* excluded) and teuthoid groups, while both nuclear genes supported a more recent divergence of the sepioid and myopsid lines from ancestral oegopsids (Fig. 1*d*). The monophyly of the Octopodiformes, Cirrata, Incirrata, and Decapodiformes were well-supported in all analyses of the actin data sets. Support for a sister-group relationship between the Sepiadariidae and Sepiolidae was also obtained. The Chtenopterygidae and Bathyteuthidae were closely related to one another, and these two oegopsid families were also related to a well-supported clade consisting of the myopsids, *Spirula*, and the Sepiidae. Relationships among the oegopsid families remained unclear, and the monophyly of the Oegopsida was not supported. Results from the Actin I and Actin II genes were not concordant with each other, with respect to the relationships among many

oegopsid families, nor with respect to the relationships between the Loliginidae, Sepiidae, and *Spirula*. In congruence with the COI results, neither gene supported the monophyly of the Sepioidea. Results from analysis of simulated data sets indicate that the lack of support for the monophyly of the Sepioidea is due to phylogenetic structure rather than noise in the molecular data. As the actin genes are highly conserved in comparison to the 16S, COIII, and COI genes, fewer characters supported relationships among more recently diverged taxa.

FUTURE MOLECULAR PHYLOGENETIC RESEARCH

Other molecular phylogenetic studies have examined lower-level relationships within the Coleoidea, including relationships within the Loliginidae (ANDERSON, 2000), Sepiidae (BONNAUD, BOUCHER-RODONI, & MONNEROT, 1997), Onychoteuthidae (BONNAUD & BOUCHER-RODONI, 1998), Octopoda (CARLINI, YOUNG, & VECCHIONE, 2001), and Octopodidae (DE LOS ANGELES BARRIGA SOSA & others, 1995). As with morphological studies, it is much easier to satisfy the assumptions required in the analyses of molecular data sets when considering more closely related taxa, as taxon-specific biases are less likely among more recently diverged taxa. Furthermore, there are many more molecular markers available for addressing questions of more recent evolutionary phenomena (<50 myr) than are available for intermediate radiations (50 myr–200 myr) (FRIEDLANDER, REGIER, & MITTER, 1992). Therefore, in the future, the application of molecular techniques to examine intrafamilial relationships is likely to be an important source of information about the more recent evolutionary history of coleoids.

However, our knowledge of deeper-level relationships within the Coleoidea remains limited, and there is a great need for research directed toward resolving relationships within the group, particularly among the oegopsid families. The oegopsid

families, however, pose a special problem for molecular and morphological studies. All of the molecular analyses conducted to date suggest a rapid radiation of oegopsid families and have demonstrated that the group is polyphyletic. As a consequence, an analysis specific to the oegopsid families would not make logical sense. Furthermore, the choice of an appropriate outgroup(s) is also problematic. Results from the analysis of mitochondrial genes suggest that members of the Sepiolidae, Sepiidae, or Loliginidae might be informative outgroups. In contrast, results from the analysis of nuclear genes suggest that using members of any of these families as an outgroup would violate the assumption of ingroup monophyly, as each represents a more derived lineage within the decapod clade. However, using an outgroup that is clearly distant from the oegopsids, such as *Vampyroteuthis* or an octopod, would also confound the analysis, because the use of distantly related outgroups is not informative for constructing ingroup relationships (WHEELER, 1990). In order to accurately determine relationships among oegopsid families, a top-down approach is still required to identify the major oegopsid clades and their sister groups. Each of these clades could then be considered in more detail in a lower-level phylogenetic study, which would include more representatives from each nonmonotypic family. If the major oegopsid clades contained non-oegopsid taxa such as *Idiosepius* or *Spirula*, representatives from these taxa would obviously have to be included in the sampling scheme of the lower-level study, along with sister-group representatives for outgroup comparisons. In the same way that a single suite of morphological characters cannot be expected to provide information at all levels of phylogeny, a single suite of molecular characters (i.e., a gene) is unlikely to be universally informative. Clarification of coleoid relationships will probably occur gradually through a piecemeal approach, building on information obtained in previous studies.

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