

## Phylogeny of Alciopidae (pelagic polychaetes): a cladistic analysis

*Baoling WU & Lua HUA*

Department of Marine Biology, First Institute of Oceanography of SOA  
Hongdao Road 13, Qingdao 266003, P. R. China

### ABSTRACT

The phylogenetic relationships of the nine genera in the family Alciopidae are reexamined using a cladistic analysis. Three phyllodocid genera *Eulalia*, *Phyllodoce* and *Notophyllum* are used as outgroups to polarize the 13 morphological characters. The results indicate that the nine genera can be divided into two groups which agrees with the ideas of STOP-BOWITZ (1948) and RICE (1987). It is proposed that two subfamilies can be recognized in the Alciopidae: (1) Watelinae, which includes the genera *Alciopina*, *Krohnia*, *Plotohelms*, *Rhynchonerella* and *Watelio*, and (2) the Alciopinae, containing the genera *Alciopa*, *Naiades*, *Torrea* and *Vanadis*.

### RÉSUMÉ

#### Phylogénie des Alciopidae (polychètes pélagiques): une analyse cladistique

Les relations phylogénétiques de neuf genres de la famille des Alciopidae sont réexaminées à l'aide de l'analyse cladistique. Trois genres de phyllodociens *Eulalia*, *Phyllodoce* et *Notophyllum* sont utilisés comme groupes extérieurs pour polariser les 13 caractères morphologiques. Il apparaît que les neuf genres peuvent être divisés en deux groupes, ce qui est en accord avec les idées de STOP-BOWITZ (1948) et RICE (1987). On propose que les Alciopidae soient partagées en 2 sous-familles: (1) Watelinae, incluant les genres *Alciopina*, *Krohnia*, *Plotohelms*, *Rhynchonerella* et *Watelio*, et (2) Alciopinae, incluant les genres *Alciopa*, *Naiades*, *Torrea* et *Vanadis*.

### INTRODUCTION

The pelagic family Alciopidae is composed of nine genera which spend their entire life in the water column (RICE, 1987). Genera in this family include *Alciopa*, *Alciopina*, *Krohnia*, *Naiades*, *Plotohelms*, *Rhynchonerella*, *Torrea*, *Vanadis* and *Watelio*. Alciopid polychaetes form a monophyletic group as indicated by the two large telescopic eyes. This characteristic is not found in other polychaetes. Alciopids also possess five small cephalic tentacles, an eversible proboscis with soft marginal papillae or two lateral horns, 3-5 pairs of tentacular cirri in the three anterior segments, uniramous parapodia and a transparent to semitransparent body.

Two major views on the evolutionary relationships among the nine genera of Alciopidae have been proposed. The first view, represented by HERING (1892), APSTEIN (1900) and STOP-BOWITZ (1948), is that the Alciopidae can be divided into two groups: (1) in the first group the proboscis has two long lateral horns, females with one or two pairs of receptacula seminis, setae of only one type, either simple or compound. This group includes *Alciopa*, *Naiades*, *Torrea* and *Vanadis*. (2) The second group the proboscis lacks lateral horns, females lack receptacula seminis, and at least two kinds of setae are present. This group includes *Alciopina*, *Plotohelmis*, *Krohnia*, *Rhynchonerella* and *Watelio*.

DALES (1955) also places the nine genera into two groups based on setal type. The first group only has simple setae and contains *Alciopina* and *Krohnia*. The second group possesses compound setae except, for *Naiades*, which has only simple setae, and includes *Alciopa*, *Naiades*, *Plotohelmis*, *Rhynchonerella*, *Torrea* and *Vanadis*. The genus *Watelio* is intermediate between the two groups.

Recently, RICE (1987) has utilized morphological and reproductive characters in his study of generic relationship in the Alciopidae. His results fully with those of STOP-BOWITZ (1948). The purpose of this study is to use cladistic methods to reevaluate the phylogenetic relationships of alciopid genera.

## MATERIAL AND METHODS

Thirteen morphological characters were used in the present analysis, all of which have been used in traditional alciopid taxonomy (STOP-BOWITZ, 1948; FAUVEL, 1953; DALES, 1957; TEBBLE, 1960; DAY, 1967; USCHAKOV, 1972; WU, 1978; RICE, 1987). The character states of the alciopid genera and of the outgroups are listed in Tables 1 and 2. All character states are consistent among a genus except for the proboscis of *Vanadis longissima* which has small marginal papillae but no lateral horns. The other 12 species of *Vanadis* have lateral horns, and we treat the proboscis of all *Vanadis* as having lateral horns.

Prostomium and Eyes (I-II): Alciopidae are characterized by two large eyes with red lenses which may be directed anteriorly, laterally, upward or downward. This character is chosen to distinguish the nine alciopid taxa from the outgroup. The prostomium of some genera extends in front of the eyes, but in others the eyes project forward, with the small prostomium between them.

Proboscis (III-V): The eversible proboscis of Alciopidae is either long or relatively short, some with soft marginal papillae or two lateral horns which are provided with mucus secreting cells (DALES, 1955).

Tentacular cirri (VI): There are 3-5 pairs of tentacular cirri in the first three segments, the formula is (USCHAKOV, 1972): 1+1/0 or 1+1/0 or 1 or N, in which 1 = tentacular cirrus, 0 = tentacular cirrus absent, N = normal podial cirrus.

Parapodia and receptacula seminis (VII-VIII): Several anterior parapodia are reduced in some alciopid genera but fully developed in the others. All normal parapodia are uniramous. Mature females of some genera, such as *Vanadis*, often bear 1-2 pairs of dorsal cirri (from segment 4-5) modified into receptacula seminis for reproduction.

Setae (IX-XI): Four types of setae occur in alciopids, they are capillaries, simple aciculae, compound aciculae and compound spinigers. Some genera have either capillaries or spinigers; others may possess two or three kinds of setae.

Distal paraodial cirrus (XII): one or two cirriform terminal appendages often exist at the distal end of the podial lobe of some alciopid genera.

Body transparency (XIII): Some genera such as *Alciopa*, *Alciopina* and *Rhynchonerella* have strong muscular bodies and are semitransparent to opaque when alive. The other six genera lack such a developed muscular system and have transparent bodies.

The alciopids clearly arose from benthic phyllodocids somewhat like the present day phyllodocid genus *Eulalia* (DALES, 1955; USCHAKOV, 1972). PLEIJEL (1991) used cladistic analysis to divide the family Phyllodocidae into three subfamilies in which the genera *Eulalia*, *Phyllodoce* and *Notophyllum* occupied the central position. These three genera were selected as outgroups to polarize the 13 characters.

The BRANCH AND BOUND algorithm from the phylogenetic computer package PAUP (version 2.4.1, David L. Swofford, Ill. State Nat. Hist. Surv., Urbana 61820) was used to find out the most parsimonious trees. All of the multistate characters are treated as ordered. All characters were given equal weight. The IBM computer at the First Institute of Oceanography was also used in this work.

## RESULTS AND DISCUSSION

Thirty-three cladograms obtained, all with a consistency index of 0.60 and a length of 25 steps. But there is only one cladogram (Fig. 1) with the lowest F value of 0.201, So only this cladogram has been chosen to do the analysis work. The analysis indicates:

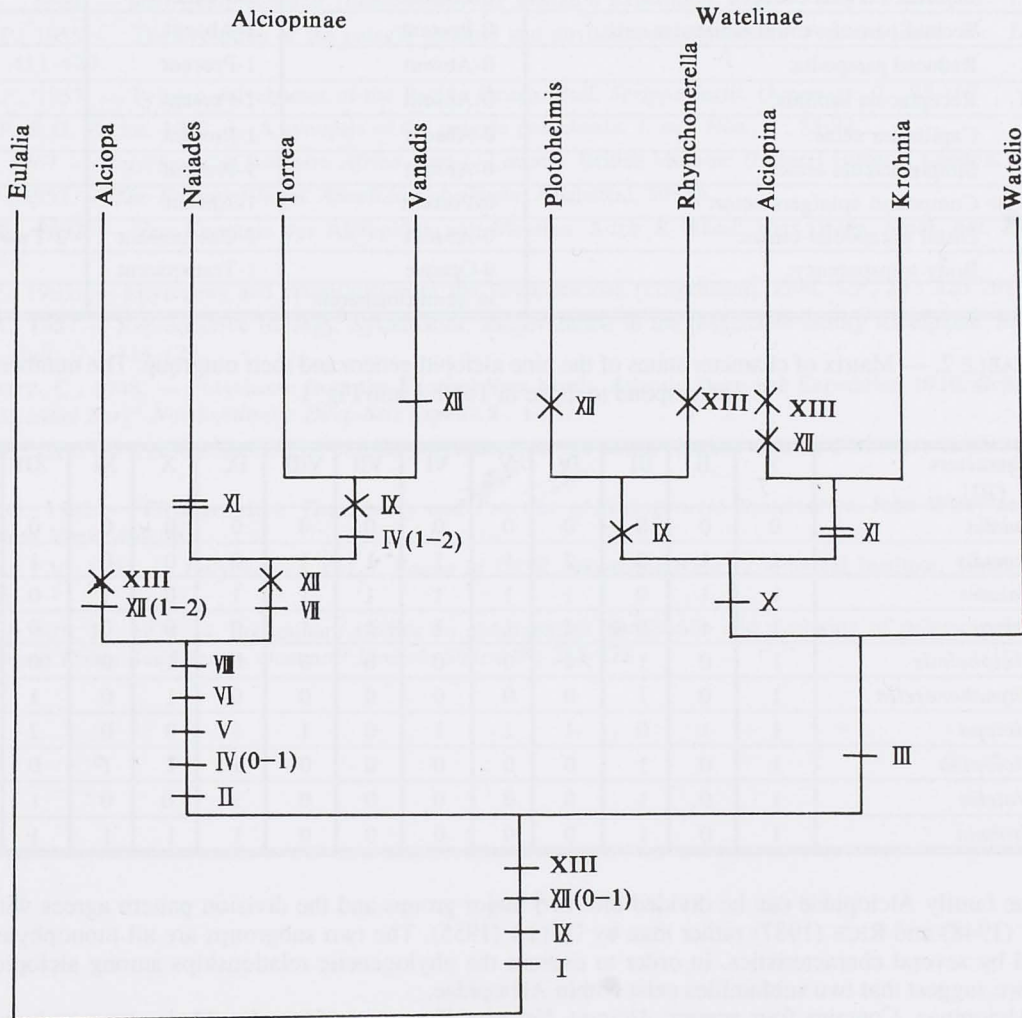


FIG. 1. — Cladogram of the Alciopidae, with phyllocoid genus *Eulalia* as outgroup. Consistency index is 0.600, F value is 0.201. Progression = "—", regression = "X", Parallelism = "=". Numbers in parentheses indicate character-state changes in multistate characters, e.g., IV (1-2) indicates that character IV goes from state 2 to state 3.

1. The plesiomorphic character states for the common hypothetical ancestor of the nine alciopid genera are: The prostomium project in front of the eyes; the eyes are enlarged; the sucking proboscis with soft papillae but no lateral horns; the second ventral cirri present; the parapodia uniramous and all fully developed; both capillaries and compound spinigers setae present; one distal parapodia cirrus present; with transparent body. It is very clear that this hypothetical alciopid ancestor lived a pelagic life, but it still leaves some primitive features similar to its ancestral benthic form.

TABLE 1. — Coding of morphological characters for the alciopid genera. The numbers correspond to those in the data matrix in Table 2 and the cladogram in Fig. 1.

I.	Enlarged eyes:	0:Absent	1-Present	
II.	Prostomium projecting in front of the eyes:	0-Yes	1-No	
III.	Proboscis length:	0-Long	1-Short	
IV.	Lateral horns on proboscis:	0-Absent	1-Short;	2-long
V.	Papillae on proboscis:	0-Present	1-Absent	
VI.	Second pair of ventral tentacular cirri:	0-Present	1-Absent	
VII.	Reduced parapodia:	0-Absent	1-Present	
VIII.	Receptacula seminis:	0-Absent	1-Present	
IX.	Capillaries setae:	0-Absent	1-Present	
X.	Simple acicula setae:	0-Absent	1-Present	
XI.	Compound spinigers setae:	0-Present	1-Absent	
XII.	Distal parapodial cirrus:	0-Absent	1-One present	2-Two present
XIII.	Body transparency:	0-Opaque	1-Transparent	
		to semitransparent		

TABLE 2. — Matrix of character states of the nine alciopid genera and their outgroup. The numbers correspond to those in Table 1 and Fig. 1.

Characters OIU	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
<i>Eulalia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vanadis</i>	1	1	0	2	1	1	1	1	0	0	0	1	1
<i>Naiades</i>	1	1	0	1	1	1	1	1	1	0	1	0	1
<i>Torrea</i>	1	1	0	2	1	1	1	1	0	0	0	0	1
<i>Plotohalmis</i>	1	0	1	0	0	0	0	0	0	1	0	0	1
<i>Rhynchonerella</i>	1	0	1	0	0	0	0	0	0	1	0	1	0
<i>Alciopa</i>	1	1	0	1	1	1	0	1	1	0	0	2	0
<i>Alciopina</i>	1	0	1	0	0	0	0	0	1	1	1	0	0
<i>Watelio</i>	1	0	1	0	0	0	0	0	1	0	0	1	1
<i>Krohnia</i>	1	0	1	0	0	0	0	0	1	1	1	1	1

2. The family Alciopidae can be divided into two major groups and the division pattern agrees with STOP-BOWITZ (1948) and RICE (1987) rather than by DALES (1955). The two subgroups are all monophyletic ones specified by several characteristics. In order to express the phylogenetic relationships among alciopid genera clearly, we suggest that two subfamilies exist within Alciopidae.

(1) Alciopinae. Contains four genera: *Alciopa*, *Naiades*, *Torrea* and *Vanadis*. Their common hypothetical ancestor is as follows: prostomium does not extend anterior to the eyes; the eversible proboscis with lateral horns but lacks soft papillae; second pair of ventral tentacular cirri absent; females with one or two pairs of receptacula seminis, parapodia with capillaries and compound spinigers setae, and one podial cirrus.

(2) Watelinae. Contains five genera: *Alciopina*, *Krohnia*, *Plotohalmis*, *Rhynchonerella* and *Watelio*. Their common hypothetical ancestor is similar to the genus *Watelio* and has the following characteristics: proboscis relatively short; no lateral horns; females lacking special receptacula seminis; parapodia with capillaries and compound spinigers setae and one podial cirrus; body transparent.

3. Alciopidae can not be divided into subgroups based on setae type. However, in the evolution of the family into subfamilies, this character changes greatly which gives it an important status in genus classification. Finally it should be emphasized that the above views need testing when more information on alciopids are available, which will make it possible to do a cladistic analysis at the species level.

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