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REPRODUCTIVE BIOLOGY, SYSTEMATICS, AND EVOLUTION IN THE POLYCHAETE FAMILY ALCIOPIDAE

Stanley A. Rice

Abstract.—Fourteen species of alciopid polychaetes were collected from the western Atlantic Ocean near Grand Bahama Island. Specimens were collected using a submersible equipped with a special zooplankton-capturing device. Eight of the nine known alciopid genera were represented in the collections along with a new species in the genus *Krohnia*. This new species is described and the relationships among alciopid genera are reexamined in light of new information from field observations and reproductive biology.

Six families within the Class Polychaeta are considered to be holopelagic spending their entire life cycle in the water column. These six families include: Alciopidae, Iospilidae, Lopadorhynchidae, Pontodoridae, Tomopteridae, and Typhloscolecidae. A number of other polychaete families contain one or more species that may be truly pelagic, such as some species within the Polynoidae (Dales and Peter 1972) while many species of other families spend part of their life cycle in the water column either as larvae or adults but at some point return to a benthic habitat and thus are not truly pelagic.

Each of the holopelagic polychaete families shows special morphological and reproductive adaptations to life in the water column. A transparent body that renders individuals nearly invisible in the natural habitat has evolved in the Alciopidae, Tomopteridae, and Typhloscolecidae. Swimming aids have evolved such as flattened, composite setae in the Lopadorhynchidae, and parapodial paddles without setae in the Tomopteridae. The Alciopidae have developed enlarged, complex eyes, grasping eversible proboscides and sperm storage organs in females as pelagic adaptations.

Most pelagic polychaetes are fragile and do not stand up well to physical abuse. As a result, specimens collected in plankton nets are often damaged and fragmented, making taxonomic work difficult and live observation nearly impossible.

The development and application of advanced sampling gear operated from a non-tethered submersible has resulted in the collection of undamaged living specimens of the family Alciopidae

and has provided an avenue for in situ observation of behavior.

The present paper contains an account of alciopid species collected from the western Atlantic Ocean including a description of a new species. New information is presented on the structure of alciopid sperm and their relation to sperm storage mechanisms in the females. The evolutionary relationships among genera within the Alciopidae are reexamined in light of this new information.

Materials and Methods

The specimens described and illustrated in this paper were collected from the northwest Providence Channel, Bahama Islands between September 1979 and April 1980. Collections were made using the Johnson Sea-Link submersible operated out of Harbor Branch Foundation, Inc., Fort Pierce, Florida. Most specimens were collected at depths between 90 and 250 m. All collections were made during darkness so that specimens could be attracted to the submersible by use of floodlights.

Living specimens were returned to the surface and immediately fixed for electron microscopy (EM) or for taxonomic studies. Specimens intended for EM studies were fixed for 2 hours at room temperature in a 2.5% glutaraldehyde buffered with 0.2 M sodium phosphate, followed by postfixation in 1% osmium buffered with 1.25% sodium bicarbonate. Thick and thin sections were cut on a DuPont MT2-B ultramicrotome. Scanning electron microscope (SEM) specimens were fixed and postfixed as above followed by dehy-

Table 1.—Currently recognized genera in the Family Alciopidae, following revisions of Støp-Bowitz (1948).

Fauvel (1923)	Støp-Bowitz (1948)
<i>Alciopa</i> Audouin and Milne-Edwards (1833)	* <i>Naiades</i> Delle Chiaje (1830)
<i>Vanadis</i> Claparède (1870)	<i>Vanadis</i> Claparède (1870)
<i>Greeffia</i> McIntosh (1885)	* <i>Alciopa</i> Audouin and Milne-Edwards (1833)
<i>Asterope</i> Claparède (1870)	<i>Torrea</i> Quatrefages (1850)
<i>Callizonella</i> Apstein (1891)	<i>Krohnia</i> Quatrefages (1865)
<i>Corynocephalus</i> Levinsen (1885)	<i>Alciopina</i> Claparède and Panceri (1867)
<i>Rhyncherella</i> Costa (1862)	<i>Plotohelmis</i> Chamberlin (1919)
<i>Callizona</i> Greeff (1876)	<i>Rhyncherella</i> Costa (1862)
	* <i>Watelio</i> Støp-Bowitz (1848)

* Monotypic genera (Fauchald 1977).

dration to acetone. Critical point drying was accomplished using liquid CO₂ as the transition solvent. Dried specimens were mounted and coated with gold-palladium and viewed on a Zeiss Novascan 30 scanning electron microscope.

Systematics of the Family Alciopidae

The family Alciopidae Ehlers, 1864, contains a relatively homogeneous assemblage of species that resemble, in many characteristics, the Phyllocodidae (Dales 1955). The single unifying characteristic of all alciopids is the possession of two greatly enlarged, complex eyes. The structure and function of these organs have been described by Hermans and Eakin (1974) and Wald and Rayport (1977). In general, alciopids have long, thin bodies that are semi-transparent to transparent in life. Five small antennae are present on the prostomium; four antennae on the anterior margins and one median antenna between the eyes. The first three segments bear 3–5 pairs of tentacular cirri. The proboscis is eversible with distal papillae or fleshy lateral horns for grasping. Parapodia are uniramous with conical setigerous lobes and leafy dorsal cirri. Setae may be simple or compound. Segmental glands are present laterally or dorsally on most parapodia.

Early systematic accounts of the Alciopidae are often confusing and may contain descriptions based upon incomplete and damaged specimens. Important references in the early literature include Greeff (1876), Apstein (1900) and Fauvel (1923). Støp-Bowitz (1948) revised the genera within the Alciopidae (Table 1). Recent literature on the family includes: Dales (1955); Tebble (1960, 1962); Day (1967); Dales and Peter (1972); Uschakov (1972) and Fauchald (1977).

Presently, there are nine recognized genera in the Alciopidae (Table 1) and 31 species, including the new species described herein. The principal diagnostic characteristics used to separate genera and species within the Alciopidae include: 1) the prostomial shape and appendages; 2) the proboscis morphology; 3) number and shape of tentacular cirri on the first three segments; 4) parapodial morphology and 5) type and distribution of setae.

Prostomium.—A pair of enlarged eyes are prominent on all species and often obscure other features of the head (Fig. 1A–F). The angle of the eyes may be downward, upward, forward, or slanted to the side. Dales (1957) used the angle of the eyes as a diagnostic character but this has been criticized by Tebble (1962) as being unreliable. Located anteriorly between the eyes is a small truncated extension of the prostomium bearing four short antennae. These antennae vary from inconspicuous to prominent and often have sensory tufts that are visible with the SEM (Fig. 1B). A single median antenna is present between the eyes.

Proboscis.—An eversible proboscis is present in all species but shows considerable variation in size and shape between species (Fig. 2A–F). Chitinized jaws are never present; however, some species have hardened papillae lining the inner surface of the everted proboscis (Fig. 2E–F). Fleshy marginal papillae are often present on the distal border of the proboscis and these may be accompanied by long fleshy horns in some species (Fig. 2A–B). Proboscis horns and papillae are generally equipped with mucus glands that presumably aid in prey capture. The relative length of the proboscis along with the number and shape of papillae and horns are diagnostic.



Fig. 1. Anterior view of selected alciopid polychaetes showing orientation of eyes, prostomial antennae and tentacular cirri. A, *Alciopina parasitica*; B, *Krohnia lepidoa*; C, *Vanadis crystallina*; D, *V. formosa*; E, *Alciopa reynaudii*; F, *Rhynchonerella moebii*.

Tentacular cirri.—The first three segments in all alciopids are asetigerous and apodous. These segments bear tentacular cirri that may be elongate and cylindrical, flattened, or conical. Day (1967) has developed a tentacular formula for describing the number, arrangement and shape

of the tentacular cirri on the first three segments. This formula is represented by

$$1 + \frac{1}{0 \text{ or } 1} + \frac{1}{0 \text{ or } 1 \text{ or } N}$$

where 1 = tentacular cirrus present; 0 = tenta-

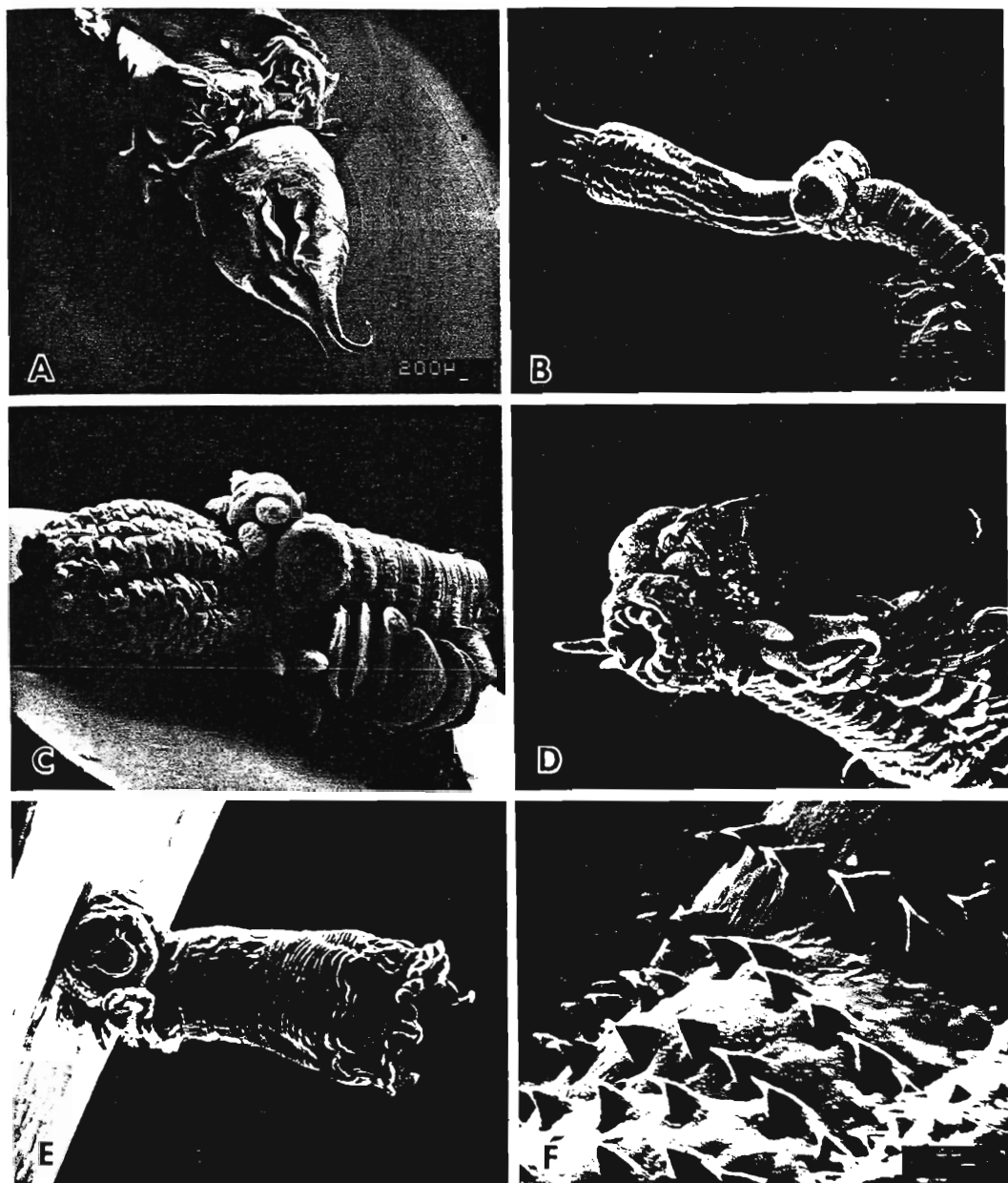


Fig. 2. Anterior views of selected alciopid polychaetes showing eversible proboscides. A, *Alciopa reynaudii*; B, *Vanadis formosa*; C, *Rhynchonerella angelini*; D, *R. petersi*; E, *Torrea candida*; F, *T. candida* close-up of chitinized papillae on inner surface of proboscis.

cular cirrus absent and N = normal lamellar cirrus present. For example, *Krohnia lepidota* has a single pair of tentacular cirri on segment 1; 2 pairs of tentacular cirri on segment 2; and a dorsal pair of tentacular cirri plus a ventral pair of

lamellar cirri on segment three. The tentacular formula is then

$$1 + \frac{1}{1} + \frac{1}{N}$$

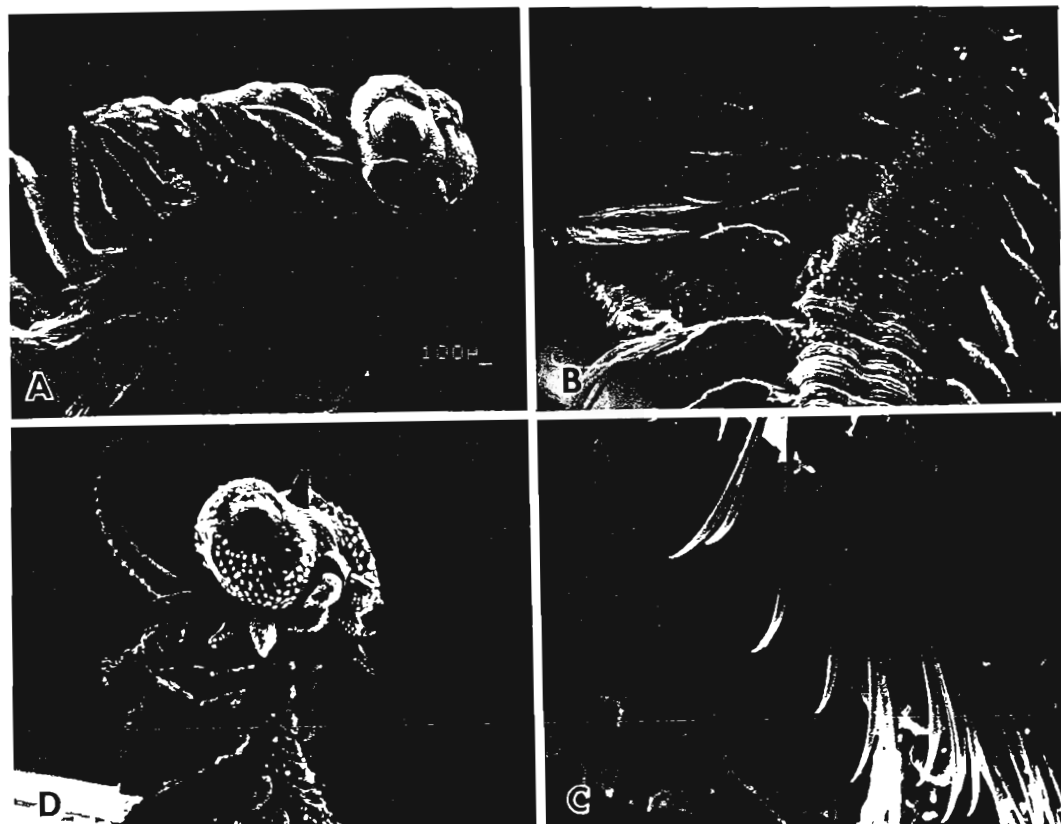


Fig. 3. *Krohnia foliocrirrata*, new species. A, anterior end, lateral view; B, anterior ventral view showing ventral cirri and transition from acicular to capillary setae at setiger 7 (60 $\times$); C, close-up of anterior fascicle of acicular setae (500 $\times$); D, *K. lepidota*, anterior end showing antennae, tentacular cirri and dorsal cirri.

For reference to a particular cirrus, the designations D2 and D3 are used to denote dorsal cirri on segments 2 and 3 respectively, while V2 and V3 denote ventral cirri on segments 2 and 3 respectively.

Parapodia.—In alciopids, the first parapodial segment is segment 4. The first few parapodial segments may be reduced in some species and may be asetigerous. All parapodia are uniramous with a single acicula that may extend beyond the end of the parapodial lobe. One or two fleshy digitiform appendages may be present in some genera. Dorsal cirri are generally large and foliaceous while ventral cirri are lamellar in most segments. In females of some species, the dorsal cirri on the first few parapodial segments are modified into seminal receptacles for sperm storages (see Discussion below).

Parapodial glands are present laterally and dorsally between parapodial lobes on most body

segments. These are referred to as "segmental glands" by many authors but are different from the nephridial organs which are known as "segmental organs." The parapodial glands range in size from small oval projections in some species to elongated, kidney-shaped structures extending from the dorsal to the ventral cirrophore. These glands appear to function as mucus-secreting organs and are often darkly pigmented.

Alciopid setae may be simple or compound. Capillary setae alone are present in some genera while other genera possess various combinations of compound spinigers, acicular setae, and capillaries.

Krohnia foliocrirrata, new species
Figs. 3A–C, 4A–B, 5G

Material examined.—BAHAMAS: Northwest Providence Channel, 26°16.5'N, 77°42'W, 20 Apr

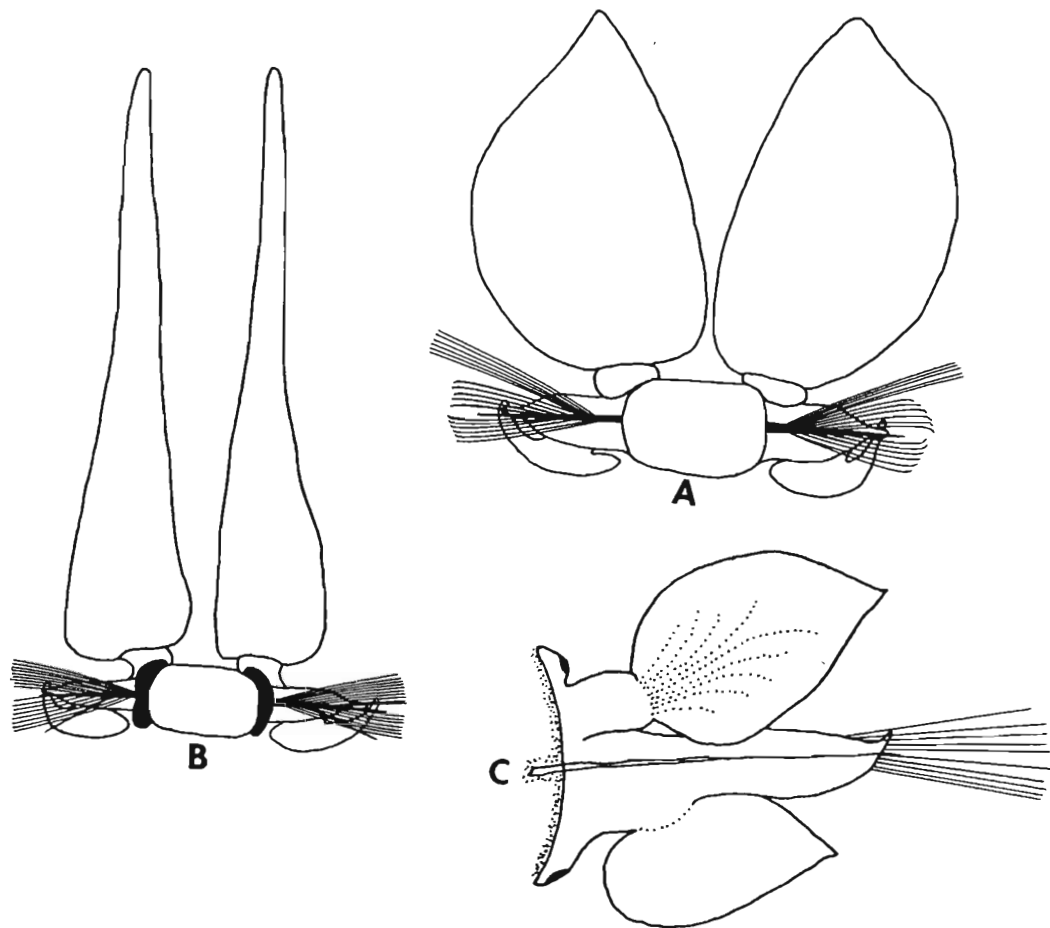


Fig. 4. *Krohnia foliicirrata*. A, anterior parapodium, posterior view; B, posterior parapodium, posterior view showing segmental glands; C, *K. lepidota*, typical mid-body parapodium (from Day 1967).

1980, submersible dive 812, 450 ft, Holotype (USNM 97376); 24°43'N, 76°17'W, 13 Jun 1981, submersible dive 598, 500 ft, coll. P. Eckelbarger, 2 paratypes (USNM 97375); 19 Apr 1980, submersible dive 810, 510 ft, 1 specimen; 14 Jun 1981, submersible dive 602, 485 ft coll. M. Youngbluth; 24°38.7'N, 76°13.5'W, 1 specimen; 14 Jun 1981, submersible dive 603, 370–425 ft, coll. C. Jacoby, 24°39'N, 76°13.1'W, 2 specimens.

Description.—Prostomium short and blunt with four short ovoid antennae, ventral pair of antennae slightly longer and more pointed than dorsal pair. One digitiform median antenna present between eyes and directed anteriorly. Eyes large and directed laterally and slightly anterior-

ly. Five pairs of tentacular cirri present; tentacular formula:

$$1 + \frac{1}{1} + \frac{1}{N}$$

First 3 pairs of tentacular cirri (1, D2, V2) pointed and similar in length. D2 slightly longer than others. D3 much longer than preceding cirri and flattened, blade-like; D3 about three times longer than adjacent parapodial lobe. V3 small and lamellar (Fig. 3A), similar in shape to subsequent ventral parapodial cirri.

Setae well developed on all parapodia. Parapodial lobe elongate with distal postsetal digitiform process. Single acicula present, extending beyond distal end of parapodial lobe just ventral

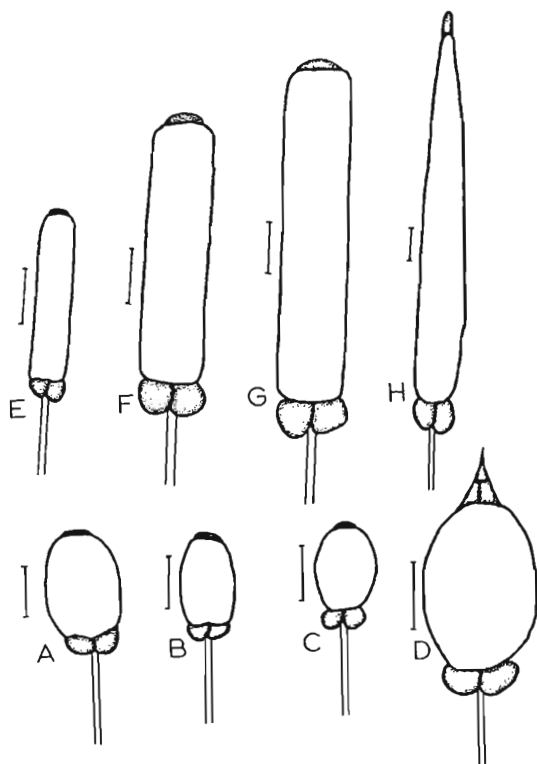


Fig. 5. Sperm morphology of selected alciopid genera. A, *Alcipoa*; B, *Rhynchonerella*; C, *Naiades*; D, *Torrea*; E, *Vanadis*; F, *Krohnia lepidota*; G, *K. foliocirrata*; H, *Plotohelmis*.

to digitiform process. First 6 parapodia with broad fascicle of distally curved acicular setae (about 30 setae each) dorsal and ventral to acicula, and few fine capillary setae dorsally. Posterior to setiger 6, capillaries more numerous with 1-4 acicular setae present ventrally (Fig. 3B-C).

Dorsal cirri well developed on all parapodia. Anterior dorsal cirri pyriform, slightly longer than wide and about three times longer than parapodial lobes. Posterior dorsal cirri lanceolate, much longer than wide and up to six times longer than corresponding parapodial lobes. Ventral cirri similar throughout body, lamellar in shape, distally pointed and extending dorsally just posterior to parapodial lobe (Fig. 4A-B).

Pigment granules present in dorsal cirri, especially posterior cirri, and along ventral margins.

Pygidial cirrus long, slender and appearing slightly beaded. Proboscis short and rounded with

12 marginal papillae. Muscular pharynx extending internally to setiger 7.

Remarks.—Living animal largely transparent, slow-swimming with serpentine motion when observed in the field. Eyes red in reflected light. Tips of tentacular cirrus D3 and dorsal parapodial cirri with opaque, light yellow pigment. Posterior dorsal cirri with increasing pigmentation. This species differs from *K. lepidota* (Krohn, 1845) and *K. excellata* (Uschakov, 1955) primarily by the presence of very long, lanceolate dorsal cirri throughout the body. Pigmentation patterns described for *K. lepidota* by Støp-Bowitz (1948) and Uschakov (1972) are absent on *K. foliocirrata*.

Krohnia lepidota collected from the same area as *K. foliocirrata* have few (1-3) acicular setae present in anterior parapodia and have a long cylindrical pair of tentacular cirri (D3) on segment 3. These cirri bear distinct marginal papillae (Fig. 3D). In contrast, *K. foliocirrata* has numerous acicular setae present in anterior parapodia and has a pair of tentacular cirri (D3) that are elongate and flattened.

The mature sperm from the coelom of males are similar in shape but different in size in the two species. *Krohnia lepidota* sperm average 11.0 μ m in length ($n = 5$) while *K. foliocirrata* sperm average 13.9 μ m in length ($n = 5$).

Etymology.—The species name is derived from the elongated, leaf-like dorsal parapodial cirri.

Distribution.—Northwest Providence Channel, Bahamas, British West Indies.

Alciopids Collected from the Bahamas

Fourteen species of alciopids were collected during four cruises near the Bahama Islands. Eight of the nine known genera are represented by one or more species (Table 2). Nearly all specimens collected were preserved and embedded in Epon for electron microscope studies. A detailed diagnosis of the species present in Bahamian waters will have to await further collections. Of the four cruises listed in Table 2, intensive sampling of alciopid polychaetes was attempted only during the latter three cruises, with only two species, *Krohnia lepidota* and *Vanadis formosa* collected on all three. Six species were collected on only one cruise. Overall, the most abundant species encountered was *V. formosa*, although on one dive, a swarm of hundreds of *Rhynchonerella*

Table 2.—Alciopid species collected from the Bahama Islands, BWI.

Species	Date collected				Depth range (M)	Sex
	June '79	Sept '79	Nov '79	Apr '80		
<i>Alciopa reynaudii</i>		X		X	60–240	M and F
<i>Alciopina parasitica</i>		X		X	90–120	M
<i>Krohnia lepidota</i>		X	X	X	120	M
<i>Krohnia foliocrirata</i>				X	112–152	M
<i>Naiades cantrainii</i>			X	X	122	F
<i>Plotohelms tenuis</i>				X	134–168	M and F
<i>Rhyncherella angelini</i>	X			X	122	M and F
<i>Rhyncherella moebii</i>		X	X		—	M
<i>Rhyncherella petersi</i>				X	—	M and F
<i>Torrea candida</i>				X	134–168	M and F
<i>Vanadis crystallina</i>		X			122	M
<i>Vanadis fuscipunctata</i>			X		—	M
<i>Vanadis minuta</i>			X		—	F
<i>Vanadis formosa</i>		X	X	X	90–182	M and F

angelini was encountered. Most alciopid species were small and transparent, making collection by sight quantitatively unreliable. In addition, many species were observed but not collected due to limited time and capacity of the collection device. Thus reliable estimates of population densities of alciopid polychaetes will have to await further study.

Sperm Morphology

Sperm morphology has been examined in all 14 species collected, using light and electron microscopy. Representative sperm morphologies are presented in Fig. 5. Alciopid sperm display a wide variety of shapes from short and oval to long and pointed. These shape-variations are due to differences in sperm nuclear morphology, since all species examined have short middle pieces with globular mitochondria. The drawings of alciopid sperm presented in Fig. 5 were made from light microscope observations and from SEM photographs (Fig. 6). Studies on sperm ultrastructure using the TEM are currently underway and will be reported elsewhere.

The sperm morphology of *Alciopa*, *Alciopina*, *Rhyncherella*, *Naiades*, and *Torrea* is of the type classified as "primitive" by Franzen (1956). Sperm of this shape are generally spawned into seawater and swim to the female or to the spawned eggs. The elongated sperm present in *Vanadis*, *Krohnia*, and *Plotohelms* are most likely asso-

ciated with some modification of the primitive mechanism of sperm release and fertilization.

The morphology of sperm stored within female seminal receptacles was examined in sectioned specimens of *Vanadis formosa*, *Torrea candida*, and *Naiades cantrainii*. In both *V. formosa* and *T. candida*, the stored sperm had various modifications not seen in mature coelomic sperm from males. These differences along with ultrastructural descriptions of seminal receptacles will be presented elsewhere.

Figure 7A–D shows two modes of sperm storage found in the Alciopidae. The simple mode of sperm storage is represented by *Rhyncherella moebii* in which sperm are embedded in the epidermis of parapodial lobes. A more complex sperm storage mechanism is represented by *Vanadis formosa* (Fig. 7D) where anterior dorsal cirri are modified to form seminal receptacles. This latter method of sperm storage was also observed in other species of *Vanadis*, *Torrea candida*, and *Naiades cantrainii* collected from the Bahamas.

Discussion

Few new species within the Alciopidae have been described during the past three decades. This is likely related to the difficulty encountered in obtaining complete, undamaged specimens suitable for taxonomic study. Many of the alciopid species are pan-tropical in distribution. Some accounts of the same species from widely

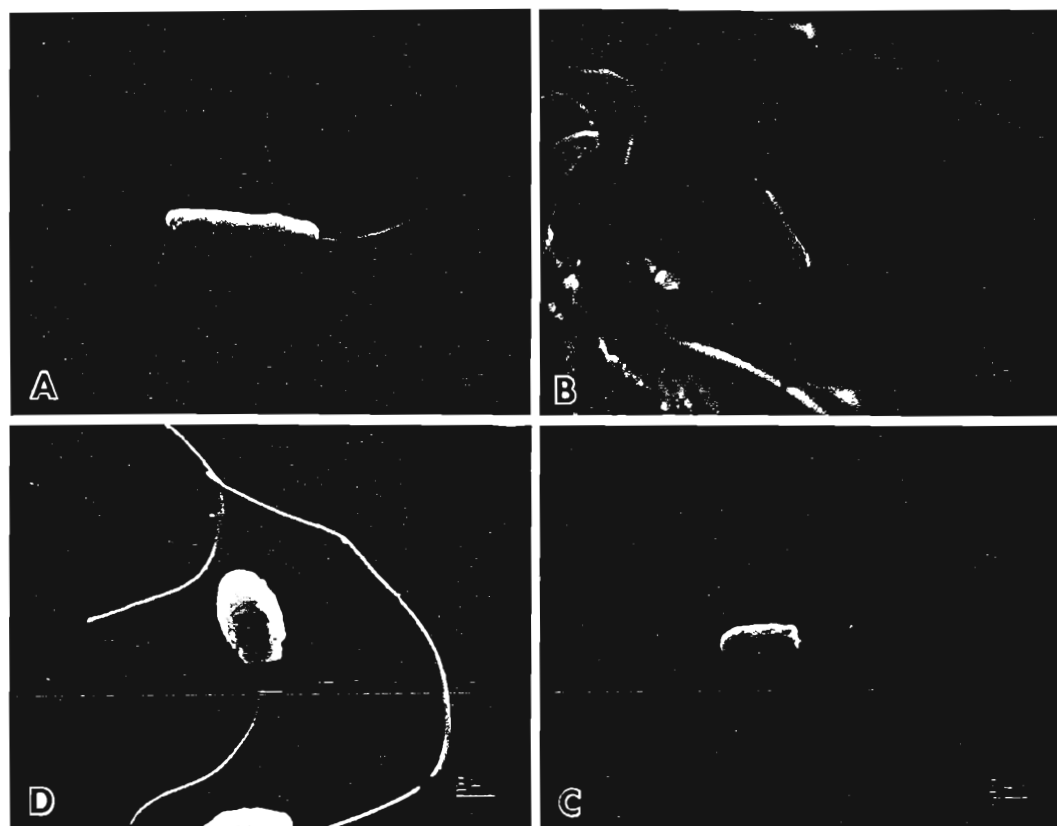


Fig. 6. SEM micrographs of selected alciopid spermatozoa. A, *Vanadis formosa*; B, *Plotohelmis tenuis*; C, *Rhynchonerella angelini*; D, *Alciopa reynaudii*.

separated populations suggest that evolutionary divergence may be occurring (see Uschakov 1972); however, studies on reproduction and development of these species are needed to confirm these suspicions. As collection techniques are improved and additional specimens become available for study, it is likely that additional new species will be discovered.

There is little doubt that *Krohnia foliocirrata* is distinct morphologically. It differs from the other two species in the genus (*K. lepidota* and *K. excellata*) by possession of greatly elongated dorsal cirri and by the presence of numerous acicular setae in the first six anterior parapodial segments. More subtle differences include the shape of the prostomial antenna and the flattened shape of the third dorsal tentacular cirri in *K. foliocirrata*. The difference in the size of the spermatozoa between *K. lepidota* and *K. foliocirrata* (Fig. 5) suggests that reproductive divergence has

occurred. The appearance of *K. lepidota* and *K. foliocirrata* when alive is sufficiently distinct to allow differentiation between the two species at a glance. Unfortunately, most alciopids lose many of their unique characteristics when preserved; thus many useful features are lost when living specimens are not available.

Generic Relationships within the Alciopidae

Dales (1955) presents a thorough treatment of the evidence supporting the evolution of the Alciopidae from a common ancestor of the Phyllocodidae and develops a scheme representing the evolutionary relationships among the genera of alciopids. These relationships are based upon standard morphological features that can be easily observed in preserved material.

The main features that suggest a common ancestry for alciopids and phyllocodids include the common possession of five prostomial antennae,



Fig. 7. Two modes of sperm storage found in the Alciopidae, A, B, C, *Rhynchonerella moebii*, showing increasing magnification of stored sperm on parapodial lobes; D, *Vanadis formosa*, showing modified dorsal cirri of the first two parapodial segments used as seminal receptacles.

leaf-like dorsal cirri, uniramous parapodia, an eversible proboscis, long, slender bodies, and good swimming ability. The special characteristics of the alciopids that indicate a divergence from the common ancestor and an adaptation to pelagic life include greatly enlarged eyes, proboscis modifications for capturing prey, transparent or semitransparent bodies, and reproductive modification (sperm storage).

Several workers have noted that the alciopid genera can be divided into two somewhat distinct groups (Støp-Bowitz 1948; Dales 1955; Uschakov 1972). Following Dales (1955), one group is characterized by having compound setae that may be acicular or capillary, while the second group has only simple setae that may be acicular or capillary (Fig. 8, after Dales 1955). The genus *Watelio* is intermediate between the two groups. Støp-Bowitz (1948) divides the alciopid genera into two groups on a slightly different basis. He

describes one group with one pair of tentacular cirri on each of the first three segments; only slender setae (either simple or compound); proboscis with long lateral horns and females with seminal receptacles. Støp-Bowitz (1948) includes the genera *Torrea*, *Naiades*, *Vanadis*, and *Alciopa* in this group, with the note that seminal receptacles had yet to be found in *Alciopa*.

The second group recognized by Støp-Bowitz (1948) is characterized by having two pairs of tentacular cirri on segments 2 and 3, two types of setae (acicular and capillary that may be simple or compound), proboscis without lateral horns and females without seminal receptacles. Included in this group are the genera *Alciopina*, *Platelmis*, *Krohnia*, *Rhynchonerella*, and *Watelio*, with the note that females of *Krohnia* and *Rhynchonerella* may carry sperm between the pedal lobe and ventral cirrus. Uschakov (1972) follows the same basic arrangement as Støp-Bowitz

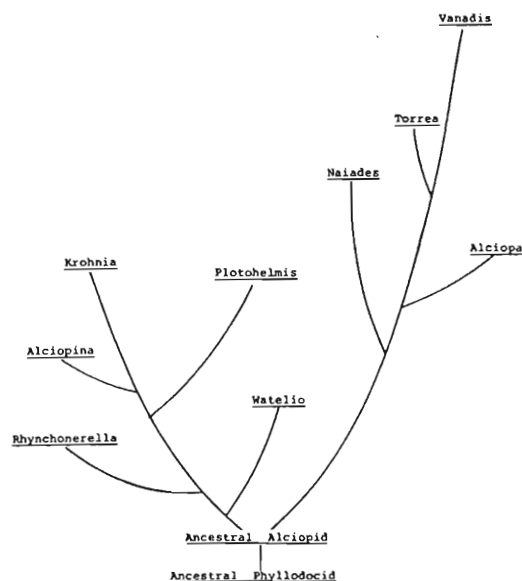


Fig. 8. Proposed scheme of evolutionary relationships among genera of the Alciopidae.

(1948) except that he places the genus *Alciopa* in the second group rather than the first based upon his specimens which have two types of setae, simple and compound. Støp-Bowitz (1948) and Day (1967) describe *Alciopa* as having only one type of setae, compound spinigers, and suggest that swollen anterior ventral cirri in females may serve as seminal receptacles. Dales and Peter (1972) consider *Alciopa* monospecific, while Uschakov (1972) lists three species in the genus. Comparative morphological and reproductive studies on species in this genus are clearly needed.

Dales (1955) and Uschakov (1972) consider the Alciopidae to have arisen from an ancestral stock similar to the present-day phyllocodid genus *Eulalia*. This ancestral stock would likely have had a benthic adult form, a swimming reproductive stage, primitive sperm that were shed into the water, a sucking rather than grasping proboscis, uniramous parapodia, and leaf-like parapodial cirri. This ancestral alciopid may have taken up a holopelagic existence through a persistent planktonic larval stage (neoteny) or through a free-swimming adult stage that remained in the water column.

The specific characteristics of the ancestral alciopid are not known; thus the best approach to understanding relationships within the Alciopidae

Table 3.—Morphological and reproductive characteristics of Alciopidae genera.

I. Proboscis length:	
1. Short	
2. Long	
II. Proboscis horns:	
1. Present—long	
2. Present—short	
3. Absent	
III. Proboscis teeth:	
1. Present	
2. Absent	
IV. Setae:	
1. Capillaries only	
2. Compound spinigers	
3. Capillaries + compound spinigers	
4. Capillaries + simple acicula	
5. Compound spinigers + simple and compound acicula	
6. Compound spinigers + simple acicula	
V. Body transparency (alive):	
1. Opaque	
2. Transparent	
VI. Anterior parapodia:	
1. Well developed	
2. Reduced or absent	
VII. Sperm type:	
1. Primitive	
2. Modified	
VIII. Sperm storage:	
1. Present—external	
2. Present—internal	
3. Absent	
IX. Distal parapodial cirrus:	
1. One present	
2. Two present	
3. Absent	
X. Tentacular cirri (pairs):	
1. 3 pairs	
2. 3–4 pairs	
3. 4 pairs	
4. 4–5 pairs	
5. 5 pairs	

is to examine differences and similarities among extant genera. Far too few characteristics are presently available for rigorous numerical analysis of alciopid genera; however, preliminary analysis using ten morphological or reproductive characteristics appear to support the generic relationships proposed by Støp-Bowitz (1948).

The characteristics used in this analysis are listed in Table 3. Most of the characteristics represent standard morphological features that are

Table 4.—Summary of generic characteristics in the Alciopidae. See Table 3 and discussion for explanation of character scoring.

	<i>Rhyncho-</i> <i>nerella</i>	<i>Alciopina</i>	<i>Krohnia</i>	<i>Poto-</i> <i>helmis</i>	<i>Alciopa</i>	<i>Naiades</i>	<i>Torrea</i>	<i>Vanadis</i>	<i>Watelio</i>
I. Proboscis length	1	1	1	1	2	1	2	2	2
II. Proboscis horns	3	3	3	3	1	2	2	1	3
III. Proboscis teeth	2	2	2	2	2	2	1	2	2
IV. Setae	5	4	4	6	3	1	2	2	3
V. Body transparency	1	1	2	2	1	2	2	2	*
VI. Anterior parapodia	1	1	1	1	1	2	2	2	1
VII. Sperm type	1	1	2	2	1	1	1	2	*
VIII. Sperm storage	1	3	1	3	2	2	2	2	3
IX. Parapodial cirrus	1	3	1	3	2	3	3	1	1
X. Tentacular cirri	5	5	5	4	2	1	1	2	3

* Unknown.

available from the literature. Dales (1955) and Day (1967) discuss these characteristics and their taxonomic importance. Two new characteristics, sperm type and body transparency, are included in Tables 3 and 4.

Sperm type.—The alciopid genera display a range of sperm morphology from the "primitive" type to the "modified" type as defined by Franzen (1956). Five genera have primitive sperm while three genera have modified sperm (Figs. 5A–H, 6A–D). The sperm of *Watelio* have not been described. None of the alciopid sperm presently described have the elongated middle piece that is characteristic of modified sperm in other polychaetes (Franzen 1974; Rice 1981). Modification of sperm structure has been found to correlate with specialized modes of reproduction in polychaetes, involving spermatophore production, copulation and/or sperm storage by females (Franzen 1956, 1982). Specialized sperm transfer mechanisms would likely be advantageous to pelagic species, especially if encounters between appropriate mates are infrequent.

The ability of female worms to store sperm represents an additional adaptation to pelagic life where sexual encounters may be rare. Sperm storage has been used previously in alciopids as generic characteristic (Støp-Bowitz 1948; Day 1967; Uschakov 1972). In the present review, sperm storage is classified as internal in species of *Vanadis*, *Torrea*, and *Naiades* where specialized seminal receptacles are present (Fig. 7D). External sperm storage is reported in *Krohnia* and *Rhynchonerella* where seminal receptacles are absent (Fig. 7A–C).

Body form.—Observation of living alciopids

in their natural habitat has revealed a divergence in appearance and swimming ability among genera. Some genera, such as *Rhynchonerella* and *Alciopa*, have muscular bodies that appear opaque to translucent when alive. These worms are strong swimmers and progress rapidly through the water. Other genera, including *Vanadis*, *Torrea*, *Plotohelmis*, *Naiades*, *Alciopina*, and *Krohnia* have transparent bodies when alive and lack extensive body musculature even though they may reach considerable size. The alciopids swim slowly in a spiralling, sinuous fashion and would appear to rely upon their invisibility rather than their swimming ability for predator avoidance.

Calculation of a Pearson product-moment correlation coefficient matrix (Sokal and Sneath 1963) using the 10 characteristics from Table 4 (admittedly a small number of characteristics) results in two groups of genera. One group of four genera shows a relatively high correlation ($r = 0.818$) and corresponds to the second group of Støp-Bowitz (1948). This group includes *Rhynchonerella*, *Alciopina*, *Plotohelmis*, and *Krohnia*. The remainder of the alciopid genera are not strongly correlated with each other nor with the above group of four genera. A proposed arrangement of the alciopid genera is presented in Fig. 8. The two branches correspond to the generic groups proposed by Støp-Bowitz (1948), which are supported by the present analysis. *Watelio* has intermediate characteristics between the two main branches although Støp-Bowitz (1948) includes it with the *Rhynchonerella* branch.

The generic arrangement proposed in Fig. 8 differs from that proposed by Dales (1955) presented in Fig. 9. Dales' (1955) scheme arranges

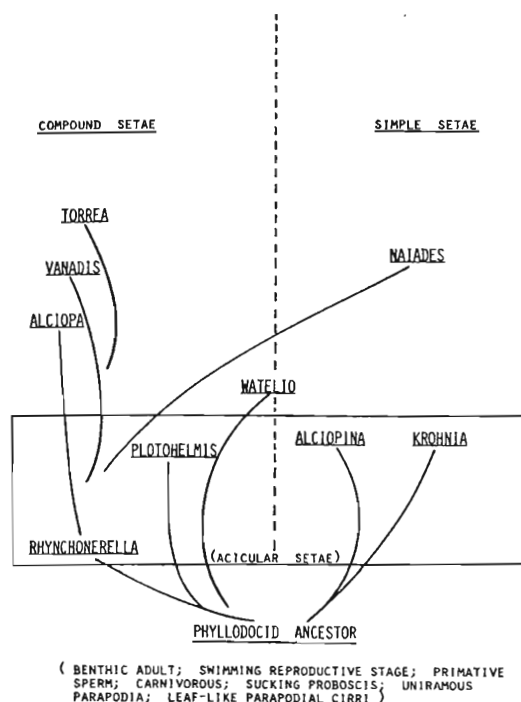


Fig. 9. Evolutionary relationships among genera of the Alciopidae (after Dales 1955).

the genera on the basis of simple or compound setae with acicula-bearing genera grouped at the base of the diagram. The arrangement in Fig. 8 has all acicula-bearing genera in the branch leading to *Krohnia* and generally with only slender setae in the opposite branch. Both branches in Fig. 8 depict an upward transition from opaque-bodied fast-swimming worms to transparent-bodied slow-swimming forms at the top. In addition, the genera with modified sperm are positioned at the top of each branch in Fig. 8. The progression of genera up each branch in Fig. 8 is thus intended to represent increasing adaptation or modification for pelagic life.

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Division of Science and Mathematics, University of Tampa, Tampa, Florida 33606.